Application of quantitative vegetation reconstruction techniques to Late Holocene records at Inshriach Forest Claire L. Twiddle Submitted by Claire Twiddle to the University of Exeter as a thesis for the degree of Doctor of Philosophy, March 2010 This thesis is available for library use on the understanding that it is copyright material and that no quotation from the thesis may be published without proper acknowledgement. I certify that all material in this thesis which is not my own work has been identified and that no material has previously been submitted and approved for the award of a degree by

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Signed.....

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Abstract:

This thesis considers some of the main issues surrounding the quantitative models that have been developed to reconstruct vegetation from pollen assemblages. Conducted within a pine dominated woodland, a palynologically difficult landscape, to determine vegetation changes over the late Holocene the results highlight the complexities of undertaking such studies in these contexts.

Pollen productivity estimates were calculated from moss samples over the woodland using complete sets and derived subsets to detect influences of sampling design on resultant model output. Differences in the PPE sets were compared using reconstructions from simulation models in comparison to observed vegetation patterns. The results indicate that both parameter calculation and model reconstructions were influenced by the landscape form and composition. Sensitivity of the models to such small variations in parameter values heightens the need for robust data generation and increased investigation to controlling factors on pollen productivity.

Performance of the reconstruction models experienced variation with respect to deposition basin size and site specific characteristics. Overall, the regional reconstructions proved to generate more confident estimates of vegetation cover whilst local scale reconstructions were subject to greater variability. Comparison of the quantitative modelling to standard interpretation and the modern analogue approach shows contrasts between the results obtained with respect to limitations associated with each method and the time frames, recent (*ca.* 100 years) and longer (*ca.* 3000 years), over which they were applied. Consequently, no one quantitative approach could be identified as being superior as site specific variations were recognised in relation to the most suitable approach. In response, a hierarchical technique is proposed to utilise the benefits of each technique and to obtain detailed information to strengthen interpretations. However, it is stressed study specific constrains that determine the available resources will influence the ability to fully apply this composite approach.

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Chapter 1: Introduction and background

1.1 Introduction

Since the pioneering works by von Post (1916) approaches to understanding vegetation change using pollen analysis have progressed significantly. Over the last 30 years focus has shifted to synthesis of the processes underlying production, dispersal and deposition in contrast to the more descriptive stance of some of the earlier studies (Fagerlind, 1952; Davis, 1963; Tauber, 1965; Janssen, 1972; Andersen, 1974; Parsons and Prentice, 1981; Sugita, 1994). The rationale behind this is to strengthen knowledge of the system in contrast to the end product alone. Such studies have supported the development of quantitative reconstruction techniques with the aim of providing an alternative and more 'user-friendly' output to the standard qualitative interpretations (Overpeck *et al.*, 1985; Sugita, 2007c; Sugita, 2007b; Broström *et al.*, 2008; Gaillard *et al.*, 2008).

Currently, there are two approaches that can be applied to obtain quantitative information: modern analogue and reconstruction models. The former uses correlation between fossil pollen assemblages and analogous modern sites to infer landscape characteristics for the past. However, a shortcoming of this approach is the representation of past landscapes by those that are prevailing at present often involving non-analogue situations (Jackson and Williams, 2004). An alternative is the reconstruction model which incorporates algorithms based upon process observations to create mechanistic models (Gaillard *et al.*, 2008). In essence, a correction factor is applied to the pollen data to account for differential landscape and species specific properties that influence the pollen representation of prevailing vegetation patterns in a depositional context. Both of the above quantitative approaches have the advantage of objectivity in the output and provide a stronger representation of the spatio-temporal characteristics of the landscape than that previously available.

Palaeoecological applications are primarily concentrated in two areas:

- To provide a reflection of landscapes in the past: recent publication of Vera's (2000) work for instance questioned the degree of openness in past landscapes and ultimately the ability of pollen analysis to determine this characteristic. Debate surrounding this issue has increased but the questions still remain and without addressing key methodological aspects definitive conclusions are elusive (Bradshaw and Mitchell, 1999; Bradshaw et al., 2003; Mitchell, 2005).
- Aid management of future change via conservation strategies: increased impetus is towards management of systems to create 'natural' landscapes (Anon, 1994). However, there is increasing debate over the characteristics of structure of these landscapes that are

the aim of the management criteria (Willis *et al.*, 2005; Willis and Birks, 2006). This is of increased importance in relation to enhancing and conserving habitats for a number of native flora and fauna which have been identified in the Red Data Book.

Within these areas palaeoecology has had a vital role and will continue, especially within conservation, with a consensus towards increasing the use of long term records to formulate policy and action plans (Froyd and Willis, 2008). Use of quantitative techniques will aid this by having a defined spatial representation and absolute data presentation which can provide information that is not generated by the qualitative approach. The implications of this are that more focused questions can be addressed in relation to vegetation openness, anthropogenic activity and ecosystem structure. However, these techniques, primarily the reconstruction models, are developmental and do not fully replicate the complexity of the systems they aim to model. Validation studies are therefore required to test the influence of parameter variation on the model output and the potential to use these models in different environmental contexts. The aim of this thesis is to address some of these issues to investigate the benefit of applying the quantitative techniques in pine woodland contexts in contrast to standard interpretive approaches and to assess the use of the information obtained to continued management of the landscape

1.2 Factors influencing the use of pollen as a palaeoenvironmental tool

As identified by von Post (1916) there is a relationship between pollen occurring within a sedimentary profile and the vegetation occurring around it; however, this relationship is not a simple one and there are still unknown aspects relating to how vegetation manifests itself in the pollen assemblage. These specifically relate to pollen productivity, dispersal and preservation of the pollen within the depositional environment. When combined it is these factors which result in the over- and under-representation of species and create complexity in unravelling the pollen-vegetation relationship.

1.2.1 Pollen productivity

Pollen is produced by the plant to be dispersed in order for the species to reproduce. Species can be classified based upon their dispersal mechanism; anemophilous plants, such as *Pinus* spp., which disperse through the use of wind and have high pollen productivity; zoophilous whereby pollen is predominantly dispersed through insects, and have lower pollen productivity relative to wind pollinated plants; autogamous which are pollinated by both wind and insects (Jackson, 1994); and self pollinating taxa. Such differences have to be taken into account, as the greater quantities produced by anemophilous species are more likely to be incorporated into the sediments and better represented within the pollen record.

Empirical studies have been conducted in order to derive estimates of pollen productivities for a number of taxa predominantly within Scandinavia and Europe. Tree taxa values have been obtained from Europe by Andersen (1970), Prentice *et al.* (1987), Sugita *et al.*, (1999), Soepboer *et al.*, (2007), and von Stedingk *et al.* (2008). Calcote (1995) has done similar work in northern America. Herb and some tree taxa pollen productivities have been estimated from studies within Denmark, Norway, Sweden, the Swiss Jura and the UK (Hjelle, 1998; Sugita *et al.*, 1999; Bunting, 2003; Broström *et al.*, 2004; Nielsen, 2004; Räsänen *et al.*, 2007; Mazier *et al.*, 2008). However there are errors associated with these. Estimates derived from Gaillard (1992; 1994) are only comparable with other open areas as these do not represent forested or semi-open landscapes, hence the pollen productivity estimates (PPEs) can only be used in equivalent contexts due to the range of landscape and environmental conditions which affect the calculation of these i.e. vegetation composition, wind speed and direction.

Comparison of these initial datasets has highlighted the potential for physical and biological influences on the values obtained. The former includes variations within yields occurring due to habitat stresses placed upon the plant, such as when a species reaches the limit of its geographical range; survival becomes the primary aim of the plant thus it decreases or ceases pollen production (Hicks, 2006). Hjelle (1998) found differences between the PPEs calculated for *Plantago lanceolata*, Apiaceae, and *Potentilla*-type which were dependent upon whether the vegetation was at coastal sites or inland. Parshall and Calcote (2001) also suggested that this is a reason for the dissimilarity of pollen records obtained from similar vegetation composition in differing regions.

Biological factors controlling production include age and species variation. For example, pollen production does not commence until the plant reaches maturity, which is dependent upon the species as to when this occurs (Hicks, 2006). Consequently, caution has to be taken when estimates of productivities are obtained from modern data as overestimation of the pollen-producing vegetation can lead to erroneous estimates. Further variation occurs within species which are related to management of the landscape and, more importantly, the type of species present at the site. In relation to the latter a number of studies have found that the estimates for pollen productivity can vary according to the species present from specific genera (Randall *et al.*, 1986; Caseldine, 1989; van der Knapp, 1990; Hjelle, 1998; Nielsen, 2004; Nielsen and Odgaard, 2005).

1.2.2 Dispersal

Dispersal distance of pollen grains is dependant upon a number of factors including; productivity and dispersal mechanism of the plant in question contributing to sources of pollen; fall speeds of the pollen grains being released; and the atmospheric conditions prevailing at the time of spore release.

1.2.2.1 Sources of pollen

Tauber (1965) suggested a number of transportation methods by which pollen reaches the deposition site: trunk space, rainout and canopy components. Trunk space is the component that is carried through the interstitial spaces of the woodland and is subjected to low wind speeds and impaction onto foliage, which can increase with density of the woodland. The rainout component is derived from pollen held within the atmosphere being deposited during precipitation as the pollen forms the nuclei of raindrops or is captured during rainfall. This has a much greater influence upon the pollen assemblage as studies have shown that precipitation will clear the atmosphere of pollen after only a few minutes and include a very long distance component (Hirst, 1953; Gregory, 1973). It has been argued that the latter components, trunk space and rainout, are minor within the pollen assemblage (Faegri and Iversen, 1989).

Arguably, the most important source of pollen transportation is the canopy component, defined by Tauber (1965) as pollen which is entrained and transported above the woodland canopy via air flows. Anemophilious taxa comprise the majority of this element but most taxa can be represented as pollen is designed for dispersal with the size, shape and weight of most grains facilitating this mechanism. Pollen composition of the airflow constantly changes throughout transportation in response to the turbulent nature of airflow i.e. eddies. Consequently, pollen is frequently being deposited and entrained reflecting regional vegetation patterns within the load (Tauber, 1965; Gregory, 1973). The load is then deposited due to dissipation of the source or reduction in speed or type of air flow i.e. when a basin within the woodland or the edge of the woodland is met.

1.2.2.2 Atmospheric conditions

Particles are primarily transported within the lower levels of the troposphere via convection currents and eddies which vary according to temperature, humidity and wind variations (Gregory, 1973). A number of studies have been conducted into modelling the dispersal of pollen grains and other small particles into the atmosphere under different conditions (Sutton, 1947; 1953; Chamberlain, 1975). That of Sutton (1953) is generally accepted as the most theoretically sound equation produced from these investigations; principally derived from the eddy diffusion theory and with equations available for both elevated and ground point source models, as shown in equation (1).

$$g_i(z) = b_i \gamma z^{\gamma-1} e^{-biz\gamma}$$
 (1)

where:
$$b_i = \frac{4v_g}{u\sqrt{\pi} C_z}$$

when: z = distance

 $\gamma = 0.125$ (Prentice, 1985)

 v_g = Fall velocity

 C_z = Vertical diffusion coefficient (m^{1/8})

u = wind speed

In order to account for the influence of atmospheric conditions upon pollen dispersal the above equation (1), obtained through experiments carried out by Sutton (1953) relating to particles released from a ground source, has been adopted to describe mathematically pollen release and deposition. The study also derived models for elevated sources, which in theory should relate to pollen release from arboreal sources, but these have been shown by empirical tests to be inapplicable due to the leptokurtic nature of pollen release and lack of an initial 'skip-distance', a lag between the source of release and the maximum particle concentration (Turner, 1964; Kabaleine, 1969; Tinsley and Smith, 1974; Raynor *et al.*, 1975; Caseldine, 1981). Janssen (1972) suggests that the influence of multiple point sources would mute the 'skip-distance' of the theoretical model which was based upon individuals. However, work carried out into the method of pollen release, plume or puff by Aylor (1978) and Gifford (1968), show that the latter deposits a greater amount closer to the site of release and is less susceptible to wind speed variation which Jackson and Lyford (1999) suggest should be investigated further and may be more applicable than Sutton's plume model.

Further studies are still required in order to elucidate the complicated processes that occur within a woodland environment with respect to pollen dispersal and deposition. A number of sources of differing elevation are often present thus the ground source model is potentially unrealistic for either for these situations. In addition, the works carried out by Raynor *et al.* (1974) and Raynor *et al.* (1975) show that the atmospheric conditions prevailing both spatially and temporally within a woodland are drastically simplified within this model and consequently influence the results of those using it. Additional measurements of wind speed within a woodland show that there are significant decreases within those speeds above the canopy and those below it (Rempe, 1937; Geiger, 1950). The importance of these factors are scale dependent but if local changes within vegetation patterns are to be explored then this requires further attention.

1.2.2.3 Fall speed

This parameter is defined as the speed at which particles fall through still air after equilibrium is reached and acceleration has ceased, analogous to the terminal velocity of particles (Gregory, 1973; Chamberlain, 1975). These can be calculated using Stoke's Law, equation (2), which is an equation

derived through input parameters such as grain size and the volume and viscosity of the medium through which the grains are travelling.

$$v_s = \frac{^2}{_9} \frac{\sigma - \rho}{\sigma} gr^2 \tag{2}$$

where: v_s = fall velocity in cm s⁻¹

 σ = density of sphere in g cm⁻³

 ρ = density of medium

g = acceleration of gravity (981 cm s⁻²)

 μ = viscosity of medium

r = radius of sphere in cm

This equation was formulated for spherical grains but observations show that it is not applicable for all grains. In response Falck (1927) conducted experiments with elliptical particles and produced an equation (3), for the expected fall velocity with respect to the volume of a spherical particle of the same volume (Gregory, 1973).

$$v_e = v_s^{3} \sqrt{(^a/b)}$$

where: v_s = fall velocity of a spherical particle of the same volume a and b = axes of the ellipsoid

Measurements of the fall speeds for the most commonly occurring taxa have also been conducted using a number of methods including direct observation, the use of a fall tower, inertial separation and stirred settling. Results from these accords well with theoretically derived estimates from Stoke's Law, although it was noted that there was variation between *Pinus* species (Durham, 1946; Eisenhut, 1961). It was also noted from the study by Buller (1909) when carrying out measurements that temperature and humidity affects fall speeds as a consequence of changing hydration levels. Payne (1981) found similar results when the volume of the grains were reduced by an average of 46% with changing hydration levels, with similar results reported in Heslop-Harrision (1979) and Blackmore and Barnes (1986). Whether these variations are significant enough to affect representation of species within the pollen assemblage remains to be investigated.

1.2.3 Deposition and Preservation

Deposition of pollen occurs onto most surfaces including foliage of other plants, however in a number of environments the grains are subjected to reworking and mixing before being entrained into the sedimentary profile. For example, a grain deposited upon the surface of a peat bog can be subjected to some post-depositional movement although this is expected to be minimal the limits of this have yet to be fully defined (e.g. Clymo and Mackay, 1987), whereas grains deposited upon a lake surface will be mixed with the sample homogenised prior to deposition on the surface sediments. Further post-depositional processes such as sediment focusing, scavenging and within-lake processes can distort the assemblage (Davis, 1968; Davis, 1973; Davis *et al.*, 1984).

Taphonomic issues are further exacerbated by preservation differences that are site dependant. Sporopollenin, the substance from which pollen grains are composed, is susceptible to biological and chemical breakdown; inter- and intra-species variation within this component within the pollen wall leads to differential preservation (Cushing, 1967; Birks and Birks, 1980; Havinga, 1984). As these issues are most prevalent in aerobic locations and can influence the relative proportions and composition of the sample anaerobic environments are preferred where the probability of degradation is low, such as peat bogs. However, further work is necessary in order to elucidate the processes taking place and quantify the effects of these.

1.2.4 Data representation

The most effective form of data presentation in pollen analysis is still under debate; which is more reliable in reflecting compositional changes, proportion or absolute data? The primary form of data representation is in the form of percentages due to the assumed noise incorporated within absolute data e.g. inter-annual variability. However, with percentages the individual components are interrelated, therefore as taxon 1 varies taxon 2 mirrors the change regardless of whether these are occurring within the vegetation itself, hence, interpretation of the data is affected (Prentice, 1985; Jackson and Smith, 1994; Hicks, 2001; 2006), but percentages do not give any representation of density or spatial patterning. Thus high percentage values can correspond to low density close to the site of deposition or high density but at an increasing distance from the site.

Absolute values or Pollen Deposition Rates (PDRs), defined from (Davis, 1969) as 'the net number of grains accumulated per unit area of sediment surface per unit time', have been used within pollen analysis since the work of Davis and Deevey (1964) and Davis (1969) championed the technique. Data are derived through establishing pollen accumulation over the surface sediments (cm⁻² yr⁻¹), applying this to the core by calculating the rate of sedimentation or peat accumulation. As with most methods there are some limitations associated with these that have to be addressed (Bennett,

1994). Critically, the chronological constraints have to be robust in order for accurate application of the yearly sedimentation rates. Without these the inevitable errors within the chronology are too great to obtain any reliable information from the fossil assemblage. Further errors occur due to a range of factors: the loss of pollen grains from the sediment due to poor preservation; differential production of species in response to habitat or climatic changes, sediment focusing and changing sedimentation rates associated with limnological and catchment processes (Davis *et al.*, 1973; 1984).

Despite a general preference for percentage data, increasing emphasis is being placed upon the use of PDRs or PARs (Pollen Accumulation Rates) due to advances within chronological constraints for the recent past and to improve ecological information. A number of studies demonstrate variations within data when percentages and PDRs are compared and that patterns inherent within the percentage data become artefacts of the method (Davis *et al.*, 1984; Hicks, 2001). An area where this has been invaluable is the study of tree lines and the threshold values that can relate to the presence/absence of a species at a site (Ritchie, 1969; Hyvärinen, 1975; Hicks, 2001; Seppa and Hicks, 2006). Use of such data enhances the understanding of pollen production of individual taxa and the interrelationship between taxa. For example, annual monitoring of pollen provides good representation of production. Expression of these data in absolute terms facilitates comparison with a number of external forcing factors. A number of studies have shown mean July temperature to be a major influence on pollen production providing more detail of the underlying factors than would be available from percentage data (Hicks, 2001; 2006; McCarroll *et al.*, 2003; Barnekow *et al.*, 2007).

1.3 Quantitative vegetation reconstruction models

Modelling as an approach to vegetation reconstruction is becoming more widespread as knowledge of the vegetation systems increases as does computational power. A number of models are available at present e.g. Pollscape (Sugita *et al.*, 1999), HumPol (Middleton and Bunting, 2004), REVEALS (Sugita, 2007b), and LOVE (Sugita, 2007c), which use both vegetation and pollen data to numerically or graphically reconstruct plausible landscape scenarios. The most recent development of these models involves construction of viable vegetation maps from the pollen data which can also be based upon geology, topography and edaphic factors of the landscape in question, although representative definitive landscapes cannot be reconstructed due to the assumptions and unknown factors involved within the process (Bunting and Middleton, 2009). The results, however, provide an important insight into pollen-vegetation dynamics and provide a different perspective upon reconstructed landscapes.

Simulation programs that are available at present are derived from a number of pilot studies which have advanced the field of pollen-vegetation studies. Introductions into the major developments are given below.

1.3.1 Development of the R-Value

Studies conducted since the pioneering works have been primarily concerned with the application of pollen analysis for qualitative representation of the vegetation record. However, during the 1950s and early 1960s a greater emphasis was placed upon the method being used to quantitatively reconstruct vegetation. A major development towards this was a proposal by Davis (1963) for the calculation of what she termed the R-value, a factor that corrects for the production and dispersal characteristics of individual species and reduces the subjectivity of using percentages as suggested by Fagerlind (1952). It is derived from the ratio between the percentage of a taxon in the vegetation, obtained through mapping, and its pollen percentage within a sample taken at the site. When calculated in relation to a single taxon this provides an objective basis for comparison between different species. In support of this Davis (1963) used the *Pinus* horizon of North America, a marker horizon characterised by rapid increases in *Pinus* pollen, within all pollen diagrams of the region. She suggested that this rise was not related to vegetation change but was an artefact of interpretations associated with differential dispersal and productivity of the taxon.

Although the use of the R-value as a correction factor aids interpretation in one sense, a number of authors suggest that the same conclusions can be achieved without the need for considering this factor (Faegri, 1966; Janssen, 1970). In addition there are a number of assumptions that underlie the model which in most cases cannot be met (Comanor, 1968; Livingstone, 1968). These include the even distribution of vegetation within the landscape, all plants within landscape are pollen producing and there is no variation within sedimentation rates, productivity or preservation through time. Livingstone (1968) repeated the work of Davis (1963) upon which her model was based, and concluded that the *Pinus* maximum is a feature of the landscape and it was the vegetation mapping strategy employed by Davis which led to the erroneous conclusions. Consequently, the sampling radius to be employed has to be considered when undertaking similar studies to incorporate the full pollen rain contributing to the sample site, which was not sufficient in Davis' (1963) case.

Alternative methods have been suggested to reduce the errors inherent when R-values are derived. Livingstone (1968) calculated the R-value ratio by using the mean of all taxa as the standardising term instead of the value for a single taxon which he suggested would remove errors as using a single taxon value would multiply the errors by the error of that taxon. Parsons and Prentice (1981) dispute this implying that it was statistically unreliable and, in fact, would be perturbed by extreme

values. They proposed the use of Maximum Likelihood functions to obtain the R-value, which can be applied to both absolute and proportion data. Thus, if the distribution of the observed values is known, a statistically valid estimate for the unknown value can be gained which reduces the errors incorporated into other methods. Moreover, the use of one site for the calculation of this value is not statistically valid, therefore a range of sites is required in order to obtain robust and applicable estimates of this value; something that was not done in Davis' study (Parsons and Prentice, 1981; Parsons *et al.*, 1983).

1.3.2 Linear regression and the pollen-vegetation relationship

Despite the problems inherent within the calculation of the R-value model it did stimulate the need for further studies within the subject area to understand the complex relationship between pollen and vegetation in order to fully appreciate the archive available.

Andersen (1970) was the first to propose the use of a linear model, equation (4), in order to relate absolute pollen values to the absolute abundance of vegetation within the landscape assuming that this relationship is proportional. Developing the model of Davis (1963) this included a correction factor for the vegetation which was calculated in similar way to the R-value estimate, or through the slope of the regression line, although as absolute values were used this was classed as a productivity estimate. Inclusion of the intercept of the regression line onto the y-axis represents the pollen originating from outside the vegetation sampling radius. Accepting the point that the vegetation sampling radius cannot be large enough to incorporate all of the pollen being produced, due to long distance transport, there will always be a component from outside this radius.

$$P_{ik} = \alpha_i \, V_{ik} + b_i \tag{4}$$

where: P_{ik} = Pollen proportion of taxon i at site k

 α_i = Index of pollen representation (RPP)

 v_{ik} = Abundance of taxon i within the vegetation around sampling site k

 b_i = Background pollen influx from outside the sampling radius

Andersen (1970) uses the term 'exotic' pollen for this component although it is now termed the background pollen component. Andersen (1970) compared his P_{rel} (relative pollen productivity or RPP) values to that of R_{rel} values (relative R-values) for trees in Europe which showed consistent results supporting the application of the linear regression model. Empirical testing of the model by Bradshaw (1981) and Webb *et al.* (1981) generated a non-linear relationship when pollen and vegetation percentages were used as the results were subject to the 'Fagerlind Effect' (Fagerlind,

1952) which causes over representation of some taxa and under representation of others creating curvature of the graph. Webb *et al.* (1981) found that this was primarily a function of the species pollen production and dispersal with *Betula* and *Pinus* being overrepresented and *Ulmus* and *Picea* being under-represented (Figure 1.1). Further testing of this relationship concluded that the pollen and vegetation could not be related using a linear function if percentages were used unless the values for the predominant taxa were below 30%.

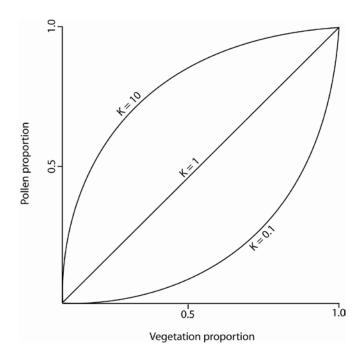


Figure 1.1: The relationship between two taxa when one has a greater productivity than the other resulting in the Fagerlind Effect. Reproduced from Prentice (1988).

1.3.3 Extended R-Value model

Essentially, the model proposed by Andersen (1970) provided a method by which the pollen and vegetation could be related but absolute values are rarely used with proportions being preferred within most studies as these reduce the 'noise' within the data (Davis *et al.*, 1984). Consequently, Prentice and Parsons (1983) developed a model to correct for the Fagerlind Effect and allow use of the linear model with percentage data, hence, the Extended R-value model (ERV).

Firstly, Parsons and Prentice (1981) identified that the α_i component of Andersen's linear model could be calculated using the maximum likelihood method (using the distribution from

observations) if it was assumed that the background pollen loading was equal to zero, as this is similar to the R-value, thus;

$$Y_{ik} = \alpha_i \, x_{ik} \tag{5}$$

Where; Y_{ik} = Pollen deposition rate

 α_i = Relative pollen productivity

 x_{ik} = Absolute vegetation abundance

In order to calculate the background component within the area Parsons and Prentice (1981) and Prentice and Parsons (1983) produced two models, both with inverse forms available, within the Extended R-Value, which deal with differing data sets;

Model 1: Assumes that the background pollen component is constant and that
 it is a proportion of the total pollen loading at the site; thus, the pollen value is
 subjected to a correction factor.

$$E(n_{ik}/n_{.k}) = \underline{\alpha_i \nu_{ik}} \quad (1 - \sum_{j=1}^t z_j) + z_i$$

$$\underline{\Sigma}^t_{j=1} \alpha_j \nu_{jk}$$
(6)

 Model 2: Assumes that the ratio of the background pollen input to the taxon specific vegetation abundance is constant.

$$E(n_{ik}/n_{.k}) = \underline{\alpha_i v_{ik} + z_i}$$

$$\Sigma^{t}_{j=1} (\alpha_j v_{jk} + z_i)$$
(7)

Where: α_i = relative pollen productivity

 v_{ik} = vegetation percentage

 z_i = background component

As these models differ slightly both models are usually applied to data sets and the most suitable form chosen. Due to the nature of the data and the questions to be answered this decision cannot be made prior to the calculations being carried out (Prentice and Parsons, 1983). Prentice and Webb III (1986) applied the ERV models to data obtained from Wisconsin and Upper Michigan which

had previously reflected non-linearity due to the Fagerlind effect. Results showed a reduction in the scatter of the points and increased linearity supporting the application of the ERV model to percentage pollen-vegetation data.

Subsequent development of this model by Sugita (1994) has added another equation to the Extended R-value (8):

 Model 3: Assumes that pollen loading is constant and as such a correction factor is applied to the pollen loadings to adjust for the inaccuracies in calculating the pollen productivities.

$$P_{ik} \cdot Y_{ik} = \alpha_i \cdot \psi_{ik} + z_i \tag{8}$$

Where: α_i = relative pollen productivity

 ψ_i = distance weighted plant abundance

 w_i = background component

In addition to this Sugita (1994) suggested using distance weighted plant abundance. Empirical studies show that pollen deposition takes the form of a leptokurtic curve (Jackson, 1994; Jackson and Lyford, 1999). Therefore greater deposition of pollen occurs closer to the source of distribution, which Sugita (1994) argued would make vegetation closer to the site of deposition more important with respect to sources of pollen. A number of different weighting methods can be applied to the vegetation data and these are discussed in section 1.3.5.

There are a number of assumptions which underline the basis of the ERV dependant upon which model is used for analysis. The models assume:

- 1. There is a linear relationship between pollen and vegetation in absolute terms
- 2. Pollen productivity is constant for all taxon at the site
- 3. The background component is constant between sites
- 4. The z_i/y_{ik} term of model 1 is constant among site k
- 5. The z_i/x_k term of model 2 is constant among site k

1.3.4 Prentice-Sugita model of pollen loading

The ERV models described above have been combined and developed for use with absolute pollen and vegetation data in order for the pollen loading at a specific point to be calculated (Prentice, 1985; Sugita, 1993; 1994). Differences between the two models relate to the sites to which it is applicable. Prentice's model is for use within bog or moss environments where reworking is minimal; Sugita's model is primarily for use within lakes where there is a larger surface area over which the pollen is deposited before it is subjected to mixing creating a homogenised assemblage to be deposited within the lake sediments.

Andersen's (1970) equation forms the basis of the Prentice-Sugita model (9) although the vegetation term is replaced by a distance weighted function which is applicable to the limits of the sampling radius. Prentice (1985) applied the use of Sutton's (1953) equation for particle dispersal at a ground source with parameters representing stable conditions an average wind speed of 3m s⁻¹. This uses the dispersal properties of pollen within the atmosphere in order to weight each species accordingly.

$$Y_{ik} = \alpha_i \cdot \psi_{ik} + \omega_i \tag{9}$$

Terms included within the Prentice model for deposition at the centre of a basin are thus;

$$\psi_{i,k} \equiv \int_{R}^{Z} X_{i,k}(z) \cdot g_{i}(z) dz$$
 (10)

$$\omega_{i,k} \equiv \alpha_{i,k} \int_{z_c}^{\infty} X_{i,k}(z) \cdot g_i(z) dz$$
(11)

The terms included within Sugita's model for deposition of pollen over the lake surface are;

$$\psi_{i,k} \equiv (1/2 R) \cdot \int_{R}^{Z} X_{i,k}(z) \left[\int_{z-R}^{z+R} g_{i}(x) dx \right] dz$$
 (12)

$$\omega_{i,k} \equiv (\alpha_i/2R) \cdot \int_{Z_c}^{\infty} X_{i,k}(z) \left[\int_{z-R}^{z+R} g_i(x) dx \right] dz$$
(13)

Where:

 $g_i(x) = a$ function to describe the amount of pollen remaining airborne at distance x from the source

R = radius of the lake or bog in metres

x =distance from pollen source in metres

 X_i = mean abundance of species i at distance z from the centre of lake or sample point

z = distance from centre of lake or bog

Z_c = distance from the centre of the lake or bog within which the pollen is compared to plant abundance

 α_i = pollen productivity of species *i*

 ψ_i = distance weighted plant abundance of species *i* within distance Z_c

 ω_i = proportion of pollen of species i coming from a distance greater than Z_c

As with the ERV model there are a number of underlying assumptions within the models taken from Sugita (1994):

- 1. Wind is the primary transportation mechanism of the pollen to be deposited at the site.
- 2. The weighting terms use Sutton's (1953) equation for a ground source model thus $g(x) = -d\phi_i(x)/dx$
- 3. The basin is a circular opening within a canopy
- 4. There is an even wind direction

Jackson and Lyford (1999) also suggest that the model should use a range of parameters for inclusion within the Sutton weighting term as pollen is rarely released under stable conditions and therefore the values applied to the Prentice-Sugita model would only provide a lower estimate for pollen deposition. As mentioned, the Sutton equation is a simplification of the processes occurring, and thus only provides an estimate for dispersion. Further work is required to understand the complexities of the processes taking place.

1.3.5 Defining the source area of pollen

Empirical studies show that pollen dispersal takes the form of a negative exponential curve; therefore vegetation closer to a sample point will contribute a greater proportion of pollen which is split into local, extra-local and regional components (Figure 1.2). Davis' (2000) proposed analogy of this is a witch's hat: the centre, or cone, relates to the increasing proportion of pollen that is contributed from plants that are closest to the sample point reflecting site to site variations whereas the brim reflects the background pollen. It is important to define these distances within a study, for

if the vegetation sampling radius is too small, results will not be representative of the environment; in addition, it allows for local and regional vegetation changes to be distinguished from each other.

Two formal definitions of this area are available. The first, defined by Prentice (1985) is the 'characteristic source area' which is the area from within which ~70% of the pollen in a sample is derived for homogenous landscapes. However, empirical and simulation studies conducted by Sugita (1993; 1994) emphasised that a large proportion of pollen was derived from the wider landscape, or background pollen input. Consequently, Sugita (1994) defined the 'Relevant Source Area of Pollen' or RSAP as the distance beyond which the goodness of fit between pollen and vegetation does not improve. In contrast to earlier assumptions Sugita suggested that between 35% and 50% of the pollen at a specific point would be derived from within this area. These two definitions are now applied to situations relating to the deposition site used as with the Prentice-Sugita model; thus, the characteristic source area relates to deposition upon the surface of a bog or point source, where the local pollen input is of greater importance, whereas Sugita's definition is applicable to lakes. These are interchangeable terms and a full definition of terminology should be sought in all studies when used.

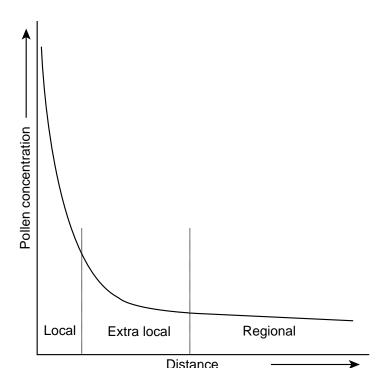


Figure 1.2: The leptokurtic nature of pollen dispersal. The shape of the curve varies depending upon the productivity of the species and its fall speed. The graph can be split into fractions which relate to differing vegetation composition with increasing distance from the sampling point.

RSAP can be obtained from using the ERV models of Prentice and Parsons (1983) and Sugita (1994) by defining distance using concentric circles weightings can be applied and used to calculate vegetation abundance surrounding the deposition site. ERV models can then be run for contiguous circles to obtain a maximum likelihood estimate of correlation with the corresponding sample site. Consequently, the RSAP can be defined when maximum likelihood values reach the lowest value and subsequently reach an asymptote. To undertake this, vegetation is weighted with multiple methods available including;

- No weighting: It is assumed that there is an even wind strength in all directions. Some studies where this has been applied have shown that this can produce good correlation where the vegetation is homogenous. However, within a heterogeneous landscape the results show poor correlation (Jackson, 1990; Jackson and Kearsley, 1998).
- Inverse distance: Weighting is applied to all species equally within the concentric rings giving more weighting to plants closer to the site of pollen deposition (Prentice and Webb III, 1986).
- Inverse squared distance: Again, this weights all species equally using ¹/d² to give an increased weighting to those species close to the site of deposition and is based upon the leptokurtic nature of pollen dispersal. This has been used in studies by Webb *et al.*, (1981), Prentice and Webb III (1986) and Schwartz (1989).
- Prentice-Sugita: Devised by Prentice (1985) and Sugita (1994) this is a taxon specific weighting based upon the species specific dispersal and fall speed characteristics from Sutton's (1953) dispersal equation.

Calcote (1995) compared the outputs when different weighting factors were applied to the data. When no weighting term was applied an RSAP could not be defined due to fluctuating values and hence no asymptote being reached. On the contrary, \(^1/d^2\) and Prentice-Sugita weightings produced a good correlation between the estimated RSAP for the sites used. Similar results were found by Nielsen and Sugita (2005) when comparisons of distance weighting functions were carried out using a simulation program for sites in Denmark. However, Nielsen and Odgaard (2005) not only found \(^1/d\) weighting to have the lowest Maximum Likelihood scores but when multivariate analysis was conducted on the pollen and vegetation a greater amount of variation was explained when this weighting was used. Consequently, although the Prentice-Sugita model may be the most theoretically sound variations within fall speed and atmospheric parameters remain that can affect the performance of this.

1.3.5.1 Variations affecting RSAP

Studies carried out to define RSAP for a number of vegetation environments have shown that this not only varies with the species present but also with physical factors. One of the variations within the RSAP, identified during the early studies, showed a positive relationship between lake size and source area of pollen derived from empirical and theoretical studies (Andersen, 1970; Jacobson and Bradshaw, 1981; Prentice, 1985; Jackson, 1990; Sugita, 1994; Calcote, 1995). This is a response to a decreased importance of plants around the edge of the basin as the ratio of margin to surface area is reduced. On the contrary, the proportion of background pollen is heightened as a greater the surface area allows for increased deposition upon it and subsequent incorporation within the sample (Davis, 2000). Hence, larger lakes record regional vegetation whereas smaller lakes and moss samples more local changes within vegetation structure.

Additional variation occurs from the patch size and distribution of species within the matrix. Sugita *et al.* (1999) noted that rare species within the landscape increased the RSAP as the regional vegetation percentages were reached at a much greater distance than those abundant within the landscape, although simulation studies by Bunting *et al.*, (2004) do not seem to show a similar pattern. In addition, those species which have habitats that place them closer to a lake at a specific site have lower RSAP as values are reached at a shorter distance (Jackson, 1990; Sugita *et al.*, 1999). Further simulations conducted by Bunting *et al.* (2004) indicate that when patch size of the vegetation and cell size of the simulation grid were increased there was a concomitant increase in the RSAP of the taxa used. Interestingly these were of the same magnitude, thus a cell size or patch size of 50m was reflected in a RSAP of 300m; when increased to 400m RSAP increased to 1600m in both scenarios. Consequently, further studies are required to elucidate the major sources of variation in obtaining accurate representation of landscapes such as patch-matrix relationships. What is the significance of the size of different communities within the vegetation and how can these be represented in the past? In addition, does the spatial patterning of these consistently produce different results?

1.3.6 Simulation programs

At present, there are two suites of programs available to model pollen deposition and RSAP based upon the mathematical equations and assumptions of the Prentice-Sugita and ERV models. Figure 1.3 shows the components of the Pollscape (Sugita, 1994; Eklöf *et al.*, 2004) and Humpol (Bunting and Middleton, 2005) suites.

Pollscape initially allowed for theoretical or empirical landscapes to be constructed within a one dimensional grid and uses the ring-source model of Sugita (1994). Essentially, a community of one

species is defined as the matrix within which patches of different species are placed. Parameter values necessary for the distance-weighting of Sutton's equation include pollen productivities, individual taxon fall speeds and wind speeds. An additional value for the background pollen component not calculated within the model also has to be defined. Calculation of the pollen loading for a specific point within the landscape can then be compared with actual data.

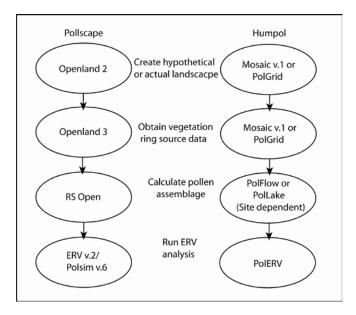


Figure 1.3: Components of the Pollscape and Humpol simulation packages (Sugita, 1999; Bunting and Middleton, 2005).

Validation studies of the Pollscape programme via comparison of simulated and actual pollen and landscape data were undertaken by Calcote (1995) within a closed woodland environment in Michigan, Sugita *et al.*, (1999) assessing landscape openness upon pollen deposition within Swedish landscapes and Nielson (2004) within an open and semi-open landscape in Scandinavia.

Despite the applicability of the Pollscape models to landscape scenarios, Bunting and Middleton (2005) produced the Humpol suite of programs. A number of aspects of the modelling process are developed in these although the main principles of the Prentice-Sugita and ERV models in calculating the pollen loading and RSAP remain the same. These are:

1. The model uses a 2D cell-based grid which allows for the cells to be used in quantifying vegetation data rather than the ring source model. It also allows for vegetation matrices to be included within the model which are composed of a number of species rather than the uniform communities of the Pollscape model which, it is argued, are unrealistic for the

- complex cultural landscapes seen within Europe (Bunting, 2002; 2003; Middleton and Bunting, 2004).
- 2. Nesting of a number of grids allows for a number of scales to be used, which removes the background component that had to be input into the Pollscape model as this can be calculated within the program itself.
- 3. As values correspond to individual cells further parameters can be added. The authors use wind data allowing for a wind rose to be used within the simulation, therefore it removes the assumption that wind direction is even around the site of deposition.
- 4. Due to the cellular approach the site of deposition is defined as the centre of the grid. In order for a whole lake surface to be considered these values can be averaged and thus different depositional environments explored

The suite of Humpol programs have been validated through simulation of hypothetical landscapes by Bunting and Middleton (2005), but also through 'real' landscapes by use of DEMs constructed within GIS. Fyfe (2006) and Caseldine and Fyfe (2006) used this approach to test the effects of agricultural expansion on Exmoor and an elm decline-landnam phase in Ireland, respectively. Use of this method aids interpretation allowing for construction of plausible vegetation structures and rejection of those that do not correspond to the pollen assemblage (Caseldine *et al.*, 2007).

1.3.6.1 Landscape Reconstruction Algorithm

Recent developments of pollen reconstruction processes have proposed the use of the Landscape Reconstruction Algorithm method built upon principles described in this chapter. The model utilises differences in the representation of vegetation at multiple sites, which reflect differing dispersal characteristics and sources allowing generalisations to be made. A number of steps are incorporated in order to: determine the vegetation around a pollen sampling point, distinguish the regional vegetation and thus background pollen component and to reconstruct local vegetation patterns from small lakes or bogs. Essentially the model divides the pollen assemblage by removing the influence of the regional pollen so that the remaining assemblage can be considered a reflection of the local vegetation (Sugita and Walker, 2000; Anderson *et al.*, 2006). In order to use this method two simulation models are required: REVEALS (equation 14) in order to reconstruct the regional vegetation and determine the background pollen component present at smaller sites (Sugita, 2007b) and LOVE (equation 15) for use with small lakes/bogs to reconstruct local vegetation from small sites (Sugita, 2007c).

$$\hat{V_i} = \frac{n_{i,k} / \hat{\alpha}_i K_i}{\sum_{j=1}^m \left(n_{j,k} / \hat{\alpha}_j K_j\right)}$$
(14)

$$v_{i,k} = \frac{n_{i,k} / \hat{\alpha}_{i}}{\sum_{j=1}^{t} \frac{n_{j,k}}{\hat{\alpha}_{j}}} \bullet \left(1.0 + \sum_{j=1}^{t} \hat{S}_{j}\right) - \hat{S}_{j} \qquad where \quad \hat{S}_{i} \equiv \frac{\hat{V}_{i} \bullet \int_{Z_{RSAP}}^{Z_{max}} g_{i}(z) \cdot dz}{\sum_{j=1}^{t} \left(\hat{V}_{i} \bullet \int_{R}^{Z_{RSAP}} g_{i}(z) \cdot dz\right)}$$

$$(15)$$

Where:

 V_i = estimate of regional vegetation

 $v_{i,k}$ = estimate of local vegetation

 $n_{i,k}$ = pollen counts for taxon i at site k

 α_i = relative pollen productivity estimate

 K_i and $g_i(z)$ = pollen dispersal and deposition function analogous to Sutton's model

Assumptions underlying the models are the same as those underlying the ring-source model presented in section 1.3.4. The two conditions are that the REVEALS model requires large lakes which are defined by Sugita (2007b) as those greater than 47 hectares (radius>400m) whilst those for the LOVE model are aimed at determining the local pollen rain and therefore should be smaller sites. This distinction is required to be certain that the regional pollen rain is accurately detected within the REVEALS model to ensure robust results when the LOVE model is used.

1.4 Thesis aims and structure

The ability to quantitatively reconstruct past vegetation patterns is appealing to many palaeoecologists but involves uncertainty. Although the techniques outlined above provide a greater understanding of the formation processes behind pollen assemblages, the development of the mechanistic models simulating these are still to fully incorporate all aspects of the system. These models are still in an early developmental stage and their simplicity at present is an essential stage in the process to increased complexity.

In order to further understand and develop the models, studies are required to undertake two approaches: validation and application. The former represents the comparison of model output with known systems to ensure that the characteristics of the algorithms are accurately representing the

processes. More detailed studies are required to increase the complexity of the models by assessing the influences of external (to the model) factors on the model output. Primarily, this thesis aims to combine these two approaches by obtaining quantitative vegetation reconstructions from pollen data using the Landscape Reconstruction Algorithm (Sugita, 2007b; 2007c) and comparing this with known vegetation patterns from management data at Inshriach Forest, the field location for this study. In addition, investigations into changes in patch-matrix structure of the vegetation and their influence on the pollen assemblages and model output will be conducted. Determining the influence of this on past vegetation reconstruction is a critical aspect to the application of the LRA which derives the RSAP distance from pollen quantities and dispersal alone.

The site of Inshriach was chosen as the focus of the study as records of all planting, felling and management undertaken are kept by the Forestry Commission and there is therefore a comprehensive data set relating to vegetation change in the woodland since the 1940s. Accessing this data will enable the pollen record to be compared to actual vegetation patterns. In addition, a project is currently underway to increase Capercaillie (*Tetrao urogallus*) populations within the forest. In order to breed, the species requires leks, or large open areas within the woodland environment. Understanding the distribution and size of these prior to the extinction of the Capercaillie in the 1790s will aid management in the future and hopefully provide a suitable habitat for the birds and allow numbers to increase.

1.4.1 Aims and objectives

The overall aim of this thesis is to assess the applicability of quantitative techniques to pine woodland contexts and their benefit to improving the understanding landscape change in such environments. Within this study the specific objectives are:

- Obtain pollen productivity estimates (PPEs) for woodland and heathland around Inshriach Forest.
 - Do different data collection methods influence the PPEs for the same taxa?
 - Do samples from open and enclosed sites differ in their estimate of pollen productivity?
 - Are spatial patterns of the samples used reflected in PPEs calculated?
- How well does the Landscape Reconstruction Algorithm assess vegetation patterns?
 - Do changes in the patch-matrix relationship affect the simulation of the landscape?
 - Does the presence of juveniles within the vegetation affect the model results?
 - Can the Landscape Reconstruction Algorithm models (REVEALS and LOVE) be applied to a closed pine woodland environment?

- Use pollen assemblages from sites around Inshriach Forest to:
 - Determine the degree of vegetation change over historical and millennial time scales.
 - Assess the application of palaeoecological data to the development of future management strategies.

1.4.2 Thesis outline

Chapters 2 and 3 outline the site details and methods used within the project respectively. The subsequent chapters present and discuss the results of the study. Chapter 4 details the process required to obtain pollen productivity estimates. Comparisons of methods previously used are addressed within this chapter to generate a number of PPEs for the main taxa in Inshriach Forest. Statistical analysis is conducted to elucidate the relationship between pollen and vegetation at the site to determine the influences on the derived PPEs. The most suitable of these values are chosen through a validation process using the quantitative models to simulate data for comparison with observed data for current landscape patterns.

Chapter 5 details the vegetation changes that have occurred within Inshriach Forest over two time periods: four sites are used to assess changes over the historical time period, *ca.* 100 years, whilst one site outlines the longer vegetation history, *ca.* 3000 years. In addition to standard interpretation of the data, the semi-quantitative Modern Analogue Technique (Overpeck *et al.*, 1985) is used to compare the fossil horizons to modern samples gathered from the field site.

Information presented in Chapter 5 is used within the LRA models to simulate vegetation proportions from a number of time-slices. The results of this modelling, presented in Chapter 6, are compared to estimated vegetation proportions from management records to assess the performance of the models at Inshriach Forest.

Chapter 7 discusses the results in light of the principal issues surrounding the use of these models with their evaluation in contrast to MAT or standard interpretations. Chapter 8 provides a summary of the overall thesis findings.

Chapter 2: Site details and Holocene vegetation development

2.1 Site description

Inshriach Forest is situated in the Spey valley of the Cairngorm Nature Reserve, north-east Scotland (Figure 2.1). Currently owned by the Forestry Commission the site covers around ~2000 hectares (ha) and predominantly composed of Scots pine (*Pinus sylvestris* (L.)), Douglas Fir (*Pseudostuga menziessii* (Mirb) Franco.), Lodgepole Pine (*Pinus contorta* Douglas ex Loudon), Norway Spruce (*Picea abies* (L.) H. Karst), Sitka Spruce (*Picea sitchensis* (Bong.) Carrière), European (*Larix deciduas* Mill.) and Japanese Larch (*Larix kaempferi* (Lindle.) Carrière). Most of these species have been planted and managed by the Forestry Commission since its acquisition in 1935.

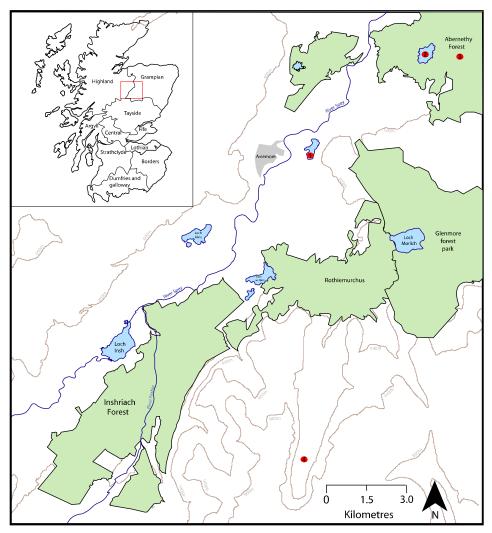


Figure 2.1: A map showing the location of Inshriach Forest (insert) in relation to other major woodlands and sites mentioned in the text within the Cairngorms Nature Reserve. 1: Loch Pityoulish; 2: Loch Garten, 3: Abernethy Forest 4: Loch Finich

Being situated within the Cairngorms the area around Inshriach Forest has a distinct topography ranging in elevation from 200 - 1000 meters above sea level (Figure 2.1). The lower elevation areas are underlain by Dalradian deformed and metamorphosed sedimentary rocks with the higher plateaus formed of granite intrusions (Gordon et al., 2006). A number of rivers dissect the lowest valleys of the area, such as the Rivers Feshie, which is a tributary of the River Spey. Dramatic differences occur in the climatic regime in response to these variations in local topography. Strong south westerly winds drive the differences in the climate experienced in this region, with the winds strongest between November and March (Roy, 1997). The main Cairngorm plateau experiences low annual temperatures, high wind speed, high rainfall with increased frequency of extremes. In contrast, the lower valley areas that dissect this have warmer temperatures in most months, have lower wind speeds and lower average rainfall (Green, 1974); for example, rainfall in the valley regions is 900mm yr. in contrast to the Cairngorm plateau which can be 2250mm yr. (Brown and Clapperton, 2002). Soil formation is supported by the climatic regime which is spatially variable and complex (Harrison, 1997). Podsols are the main soil type underlying the woodland with alluvial deposits encasing the River Spey and peats within the more waterlogged areas (Bruneau, 2006).

Native woodlands of the Rothiemurchus Estate and Abernethy Forests comprise Scots pine and some deciduous taxa such as birch, predominantly represented by *Betula pendula* but also *B. pubescens*. Pine woodland is classified by Rodwell (1991b) as H18 (*Pinus sylvestris – Hyloconium splendens*) and its sub-variants also being suggested as natural, in the sense that pine has regenerated by natural means (McVean and Ratcliffe, 1962). The ground flora of this community is dependant upon the density of the stems influencing the light availability. Birch is the main deciduous taxon which forms woodlands with either a similar ground flora to that of the H18 pine woodlands or a grass-herb dominated flora where the soils are brown earth (Gimmingham, 2002). Additional taxa are present, such as alder (*Alnus glutinosa* (L.) Garten), hazel (*Corylus avellana* L.), and willow (*Salix cinera* L.) in suitable locations such as river or loch margins, whereas others are sparse i.e. rowan (*Sorbus aucuparia* L.) and ash (*Fraxinus excelsior* L.) (Ratcliffe, 1974).

The landscape around Inshriach Forest is occupied by a diverse range of heathland and agricultural areas associated with topographical, geological and edaphic variation. Heathland, mainly *Calluna vulgaris* dominates on the acid soils which comprises the H12 community of Rodwell (1991a) with infrequent occurrences of bearberry (*Arctostaphylos uva-ursi*). Variations in the species composition of this community occur with altitude with *Calluna* dominating the lowland regions to a limit of ~600 m a.s.l. whilst montane taxa i.e. *Empetrum nigrum* ssp. *hermaphroditum* become more important constituents above this limit (Gimmingham, 2002). Ratcliffe (1974) also notes

areas of pure heather, although different age structures, interspersed in this which forms through previous management regimes i.e. burning or grazing. A second heathland type that is confined to the more alluvial, lowland areas is heather-bearberry co-dominant heath (*Calluna vulgaris-Arctostaphylos uva-ursi*) which is characteristic of the Cairngorms (Gimmingham, 2002).

The lower-lying regions support a range of vegetation communities with agriculture also a main land-use on the fertile alluvial soils. Surrounding Loch Insh are marshes which are managed by The Royal Society for the Protection of Birds (RSPB) due to the diverse range of wildlife which are supported by the wetland environment including alluvial *Alnus-Fraxinus* woodland (Joint Nature Conservation Committee, 2009).

2.2 Holocene vegetation development

As with most areas of Britain, Scotland has undergone dramatic changes in landscape and vegetation structure throughout the Holocene. This period is defined as the last 11,700 yrs BP and its start is marked by increasing temperatures associated with the demise of the Last Glacial Maximum (Walker *et al.*, 1994; Walker *et al.*, 2009; Gibbard *et al.*, 2010). Early Holocene vegetation patterns were dominated by natural changes occurring associated with local climatic gradients, topographic variation, soil development, species migration and community structure. In contrast, the majority of late Holocene vegetation changes have been anthropogenically driven; natural changes have taken place and the vegetation has responded to natural forcing factors but it is the effect of human activity that has made the most dramatic imprint on the landscape. Initial impacts were minimal, and are more difficult to detect from the palaeoecological record, due to the low population and limited needs of the communities. Increasing population pressure and material demands of the historical period caused dramatic changes in the vegetation structure reducing the woodland areas substantially and replacing it with heathland and settlements.

Outlined here is an introduction to regional landscape changes throughout the Holocene. This aims to provide a context to the local changes which are subsequently described.

2.2.1 Regional vegetation change throughout the Holocene

Although Scotland is characterised by a number of local climatically and topographically distinct areas the general trends in vegetation patterns can be ascertained. As with most processes, vegetation succession is time transgressive and therefore it is the timing of the changes that distinguishes areas. The following description outlines the development of the current vegetation patterns for Scotland with particular reference to the Highlands and eastern Scotland.

Vegetation changes occurring at the start of the Holocene resulted in a dramatic change in the landscape. Prior to this Britain experienced a stadial, marked by reduced temperatures, between *ca*.12,900 cal. years BP and 11, 500 cal. years BP, the Loch Lomond Stadial or Younger Dryas (Walker *et al.*, 2009), during which corrie glaciers and small ice caps grew and extended over a large proportion of western Scotland (Sissons, 1979; Hibbard, 1999). Vegetation in Scotland at the time was principally tundra type with low growing, alpine shrubs and herbs (Birks, 1970; Bennett, 1996). Increasing temperatures at the termination of this period around 11,700 cal. years BP marks the start of the temperate Holocene period (Walker *et al.*, 2009). Climatic amelioration allowed for the re-colonisation of many of the woodland taxa that had characterised the British Isles in previous interglacials that had found suitable refugia during unfavourable conditions. This time period is frequently represented in pollen diagrams from Scotland as a tripartite sequence of grasses, *Empetrum, Juniperus* and then pioneer arboreal species (Lowe, 1994).

As a pioneer species birch (*Betula pendula* Roth. and *B. pubescens* Ehrh.) was one of the first arboreal species to arrive into Scotland and spread from the eastern margins; dates given for the arrival range between 11,140 cal Yr BP and 10,186 cal Yr BP (Huntley, 1981; Huntley and Birks, 1983; Tipping, 1994). Variations in the timing relate to the expansion rate of the species and the site specific conditions, and whether they were conducive to the colonisation of the species. However, the rate (based on uncalibrated ¹⁴C dates) at which birch colonised the region was rapid; Huntley and Birks (1983) suggest a rate of 250 my⁻¹ taking less than 1000 years to become dominant throughout Scotland and the rest of Great Britain (Birks, 1989). Although birch presence represented ~50% TLP, other taxa at the time included willow (*Salix cinerea* L.) and juniper (*Juniperus communis* L.) which formed an open scrub vegetation structure (Birks, 1970; Gordon, 1993).

With further climatic amelioration hazel (*Corylus avellana*) began to spread into Scotland around 10,000 cal Yr BP later forming a dense woodland structure with birch and willow (Birks, 1989; Gordon, 1993; Tipping, 1994). Colonisation occurred from the west at a rapid pace with a number of dates for the rational limit summarised by Boyd and Dickson (1986); estimates of expansion rates from Huntley and Birks (1983) of 1500 my⁻¹ are high due to seed dispersal aided by fluvial sources, small mammals and human agents, but controversy surrounds the latter theory (Tallantire, 2002). Hazel was largely confined to the lowland regions of Scotland, due to the increased risk of frost at higher altitudes, which restricted its range expansion despite climatic amelioration (Birks, 1989). It is for this reason, and its aversion to infertile soils, that the occurrence of pollen from this species is limited within the pollen diagrams from the Highlands region (Birks and Mathewes, 1978).

Following the establishment of birch-hazel woodland pine began to spread into Scotland c. 8800 cal Yr BP (Bennett, 1984). Sites suggest a range of dates between 8800 cal Yr BP and 7800 cal Yr BP for the arrival and expansion of pine (O'Sullivan, 1973; O'Sullivan, 1976; Birks and Mathewes, 1978; Bennett, 1984; Tipping, 1994). Initial hypotheses suggested that pine reached Scotland via paths through England from refugia in Central Europe and Spain, however, the estimated rates needed to cover the distance between the arrival date of c. 8800 cal Yr BP for southern England and c. 8800 cal Yr BP in Scotland are incompatible with known rates of spread for the species; Bennett (1984) suggests a rate of 280m y⁻¹, and Huntley and Birks (1983) a rate of 150 my⁻¹ (based upon ¹⁴C chronologies). Consequently, there is a suggestion that a second refugia for Scots pine could have been in Ireland, which would account for the quicker expansion in Scotland and account for the two foci from which spread of the species took place; the south east Highlands and the north west (Huntley and Birks, 1983; Birks, 1989). Genetic studies have been carried out in order to elucidate the origins of Scottish pine which conclude that there are two origins for the pine species within Scotland inferring two separate initial groups (Kinloch et al., 1986; Tipping, 1994). However, limited evidence for a land bridge between Scotland and Ireland has placed doubt on this theory as the explanations for dispersal are problematic (Kinloch et al., 1986). Unfortunately, this hypothesis cannot be tested further as the native pine population that would have formed the second group became extinct c. 2000 years ago and therefore cannot provide samples to enable genetic testing (Huntley and Birks, 1983).

The ability of Pine to out compete at this time was a response to the climatic conditions prevailing being advantageous to its growth (Birks, 1970): Consequently, pine replaced a number of established species i.e. birch and hazel in the Highlands (Birks and Mathewes, 1978). However, on some better substrates it failed to compete with birch and therefore in some areas formed a pine-birch woodland structure interspersed with pure stands of each species (Bennett, 1984). However, elm (*Ulmus glabra* Huds.), oak (*Quercus petraea* (Matt.) Liebl.), and ash (*Fraxinus excelsior* L.) spread into parts of Scotland during the time of the pine expansion around 7800 cal Yr BP (Bennett, 1984). Due to their habitat preferences these were confined to the lowland areas, where the soils were more fertile and hence flourished at times of optimal climatic conditions (Tipping *et al.*, 2006). This is especially true of alder (*Alnus glutinosa* (L.) Gaertn.), which requires a ubiquitous water resource for growth and seed dispersal, and therefore colonised the valleys of eastern Scotland (Bennett, 1984). Although their effect on the established vegetation was low these species did displace pine on some areas as it was unable to compete, seeing a decline in its dominance (Birks, 1970; Huntley, 1981; Tipping, 1994). Further species present at this time but not major constituents of the woodland were ash, rowan (*Sorbus aucuparia* L.), bird cherry (*Prunus padus* L.)

and aspen (*Populus tremula* L.) forming the highly diverse woodlands as suggested by Tipping *et al.* (2006).

Complications relating to the arrival and spread of pine, and other tree species, relate to the time transgressive and erratic nature of the process. Different sites represent different ages depending upon their location relative to each other. This may not seem like a major problem but the nature of pollen dispersal complicates this further, especially when considering pine pollen. As pollen can be dispersed vast distances it is difficult to delimit local and regional components unless this is built into the initial project design (Andersen, 1974; Prentice, 1985; Sugita, 1993). It is also difficult to define values that correlate to local, regional or no presence within the landscape surrounding a sample site. Smith and Pilcher (1973) defined the terms empirical limit and rational limit to define a species curve when it becomes continuous and when the curve reaches sustained high values respectively. To reduce the subjectivity inherent within this method a more quantitative approach has been to define values for local presence of species based upon pollen percentages. Bennett (1984) assigned a value of 20% of the total pollen sum to define the presence of pine within the local vegetation. Recently however, Froyd (2002; 2005) compared fossil pine stomata (cells deposited through the decay of conifer needles indicating on site presence) with pollen profiles and suggested that the value of 20% was too high. The results of Froyd (2005) showed that stomata were being recovered even when pollen values were as low 0.4% which casts doubt over the use of pollen to define quantitative presence-absence limits.

2.2.1.1 Natural and anthropogenically driven vegetation development in the early – mid Holocene

By the mid-Holocene woodlands had reached their fullest extent within Scotland (Bennett, 1984; Tipping, 1994). Pine was the predominant woodland forming species but with deciduous and shrub species this was also a period of high diversity. However, climatic changes occurring around 4500 cal. Yr BP with increased rainfall and decreased temperatures (Roberts, 1998; Bell and Walker, 2005). Contemporaneous with this was the spread of blanket peat, predominantly within the upland areas. Mechanisms relating to the spread of the peat are unknown at present, although it is suggested that pockets would have formed within small topographic hollows, through water collection, which then spread and coalesced over the landscape (Tipping, 1994). However, the onset and duration of this is spatially variable and therefore difficult to generalise. Subsequent to the spread of peat and decline of woodland within the landscape is the expansion of heathland with species such as *Calluna vulgaris* (Heather Ling), *Erica sp.* (Heath) and *Vaccinium sp.* (Bilberry/Crowberry). As this is times transgressive the dating of this feature is associated with the

regional pattern of vegetation change, however most occurrences appear from *c*a. 3100 cal Yr BP onwards (Birks, 1970; O'Sullivan, 1974; O'Sullivan, 1976; Huntley, 1981).

Further expansion of the heathland has been associated with human activity within the landscape primarily through deforestation of the remaining woodland and concomitant suppression of the treeline (Gimmingham, 2002); however, the nature of the pollen dispersal of pine makes effects of early human communities hard to distinguish within the palaeoecological record and there has been some debate over the inferences that can be made from these records with respect to early human activities (Barclay, 1997; Finnlayson and Edwards, 1997). Environmental evidence in conjunction with archaeological artefacts provides details as to the communities inhabiting the landscape in the past and their impact upon it can be elucidated.

The earliest records of human activity within Scotland date back to the Mesolithic, with the earliest artefacts dated to *ca.* 9000 cal Yr. BP (Finnlayson and Edwards, 1997). During this period impacts upon the landscape, and the woodland, were at a minimum due to the low population and the hunter-gatherer nature of these groups. A large proportion of the information available suggests that these communities were focused around the coastal regions with provision of shelter and food with limited impact upon the inland landscape (Finnlayson and Edwards, 1997). Similar patterns are seen throughout the Neolithic although there is increasing dependence upon the landscape and the resources it provides with land clearance associated with the adoption of agriculture. This was primarily confined to the lowland regions of the country where the soils were fertile and thus supported deciduous woodland (Steven and Carlisle, 1959). Limited influences are detected in the palaeoecological record due to the small pockets of communities and low intensity of activity.

Increasing population and technological advancement into the Bronze Age intensified human activity, and saw expansion of land utilisation into the uplands (Henshall, 1963; Burgess, 1985). However, arable activity was still centred upon the lowland regions with evidence to suggest that there was delineation between the controlled and 'wild' landscapes with the uplands primarily used for pasture (Cowie and Shepherd, 1997; Davies and Tipping, 2004; Tipping and Tisdall, 2004). Potentially, these were some of the most intensive periods of land clearance that took place but climatic deterioration into the Iron Age (2600 – 1700 cal Yr BP; Hingley, 1992) forced a decline in some areas (e.g. Davies, 2007). But there is continuing evidence to suggest this was not ubiquitous with visibility of agricultural activity in the pollen record an explanation for this difference (Edwards and Whittington, 2001; Dark, 2006; Tipping *et al.*, 2008)

2.2.1.2 Pine decline

Early Mesolithic and Neolithic impact on the woodlands was predominantly small scale human induced variation but by the Bronze Age increasing demand was associated with population expansion and clearance was expanded. At this time, *ca.* 4000 cal. Yr BP, a major decline in the pine pollen proportions dominates diagrams from most Scottish sites. Further evidence is associated with the occurrence of *in situ* pine stumps within peat deposits at a number of sites in the Highlands (Birks, 1975; Bridge *et al.*, 1990). A significant amount of work has been undertaken in order to explain this decline (Bridge *et al.*, 1990). Presently, a number of factors have been suggested to have influenced the decline of pine, these include: climate change and associated peat spread; anthropogenic activity, volcanic eruption, edaphic deterioration, and pathogen attack and support for most of these hypotheses is available (O'Sullivan, 1975; Gordon, 1993; Tipping, 1994; Tipping *et al.*, 2006). However, there are no definitive associations between pollen records and causative factors and it is likely that a range of factors were responsible.

The most convincing hypotheses proposed to explain the pine decline are climate change, peat expansion and anthropogenic activity. Many authors have suggested coeval climate change and peat expansion as the trigger to change as the increased wetness increases plaudification which reduces the available habitats for the woodland species and its ability to reproduce (Lamb, 1964; Pennington *et al.*, 1972; Birks, 1977; Bennett, 1984). However, there are a number of studies that suggest that this cannot be the only cause to the decline as the perturbations are too short to cause such a dramatic decline, and there is no direct relationship between the pollen and climatic record (O'Sullivan, 1975; Lowe, 1994; Anderson, 1998; Tipping *et al.*, 2006). A development of this hypothesis is that increasing fire events could have aided the spread of peat by reducing the permeability of the soil, which due to increasing rainfall, aided peat expansion (Bradshaw, 1994; Anderson, 1998). In Ireland in a comparable situation Bradshaw (1994) found a close correspondence between the charcoal record and pine pollen curve. However, more recent studies have not replicated this relationship (Froyd and Bennett, 2006; Pratt, 2007).

A second major hypothesis is related to the effects of the Hekla 4 volcanic eruption which was one of the most explosive Holocene eruptions releasing 9 km³ of material with associated effects such as acid precipitation and a dust veil (Blackford *et al.*, 1992). These authors found a correspondence between the Hekla 4 tephra layer and the decline in pine pollen for a number of sites in Northern Scotland and suggested that the decline, coincidental with the tephra, could have been in response to the effects of the volcanic eruption; especially with the marginality of the woodland increasing susceptibility. Although volcanic eruptions can have an effect on vegetation structure it is probably unlikely the eruption could have been the cause of such a dramatic change (Birks, 1994). Further

evidence from Ireland also suggests that the dating of the work by Blackford *et al* (1992) is incorrect and when calibrated the tephra layer follows the pine decline with the most recent age at *ca.* 4300 cal. Yr BP (Pilcher and Hall, 1992; Pilcher *et al.*, 1996; Pilcher and Hall, 1996).

Despite human activity being attributed to the decline in pine it also remains unlikely (Rackham, 1980; Bennett, 1984). The nature of anthropogenic activity is usually on a small, local scale which contradicts with the rapid, wide spread nature of the pine decline. As mentioned, the nature of pollen analytical studies and especially dating of the events is site specific. Correlation of features is increasingly difficult due to multiple, inter-connected factors. Understanding how the pollen record is influenced by the presence of pine will be an invaluable insight and aid the understanding of the potential cause and details of the event further. It is likely that the true cause of this feature is a combination of the proposed hypotheses but further work is required until which point the true explanation will remain elusive.

2.2.1.3 Influences of anthropogenic activity in the Late Holocene

By the Roman period the Scottish landscape was under considerable management and extensive clearance had occurred with the population reaching 5 million (Smout, 1997b). Roman control of the country was at a minimum in the north, beyond Hadrian's Wall and the Antonine Wall, but there is evidence of a number of marching forts and hoards ranging from a number of periods from the first century to fourth century A.D. (Hanson, 2004; Maxwell, 2004). With respect to the hoards it is expected that these were gifts from occupying Roman legions to encourage allegiance from the native tribes and infer linkages between the groups (Hanson, 2004). Despite the large marching legions occupying numerous forts scripts from Roman writers and commanders at the time suggest that there was a vast forest which has come to be known as the Great Caledonian Forest. However, recent studies imply that this 'romantic' view of a vast woodland area could be a mis-interpretation, with a number of doubts as to the size and location of the woodland being raised (Breeze, 1997). As Smout (2006) suggests although there was considerable deforestation within the historical period it would not have been enough to remove the quantities suggested by the Romans and later writers. Furthermore, a number of studies from the eastern Highlands and southern Scotland show active pastoral activity prior to Roman arrival, with a cessation of this and increased woodland regeneration during the Romano-British period (Whittington and Edwards, 1993; Dumayne-Peaty, 1999). However, the degree of spatial variability displayed in some records requires site specific data to be gathered to elucidate true patterns (Dumayne-Peaty, 1998).

Immediately following the Roman period landscape change was characterised by a reduction in the amount of agricultural activity and woodland utilisation until the arrival of the Norse communities

around 1100 cal Yr BP or *ca.* A.D. 800 (Crone and Watson, 2003). Dependence on timber for construction of longhouses and ships during the 9th century, in addition to the everyday needs of the community, impacted on the structure and extent of the woodlands (Crone and Watson, 2003). Timber was predominantly oak at this time as this would have been the dominant species within the lowlands; archaeological artefacts, including a Norse long boat, also support this theory (Crone and Watson, 2003). Crannogs, a form of lake dwelling, were also a major local drain for woodland resources at this time. Alder and birch were the main sources of wood for construction of walls and floor boards with a strong oak frame to support this (Crone and Watson, 2003). Although there is little evidence remaining in the landscape today it is suggested that coppicing would have been a management method used in order to provide the necessary resources for this type of structure reducing the amount of clearance required and maintaining sufficient materials (Rackham, 1990).

By the 11th century A.D. (900 Yr BP) foremost activity was focused around the lowlands where the greater populations were found. To support these communities a large proportion of the land was cleared and prepared for agriculture, the low regions being fertile and suitable for this process; remaining woodlands were used as Crown hunting grounds, timber sources and grazing lands (Peterken, 1981; Smout, 1993; Mason et al., 2004). The grazing lands were predominantly based in the upland zone, which were utilised as shielings to form wood pasture landscapes. The latter became of increasing importance during the 14th century (ca. 600 Yr BP) due to high wool prices and associated stock increases placing heightened demand on grazing land (Smout, 1993). Under normal circumstances this would be seen as detrimental to the landscape as woodland would be reverted to open land due to lack of regeneration; however, the profit that could be generated from the export of wool ensured that these lands were managed and retained in order to sustain the stocks (Crone and Watson, 2003). Secondly, land previously controlled by the Crown for hunting Forest was released to private owners and monasteries allowing them to undertake any form of management which in most cases involved clearance or grazing (Steven and Carlisle, 1959). Despite a large proportion of the landscape being under management demand for timber was still high and therefore shortages of the resource ensued in response to a lack of management within timber woodlands on overexploitation. This prompted legislation to be imposed by James I which aimed to reduce grazing and increase plantation; failure to implement this correctly lead to tougher demands and penalties during the early 1500s (Steven and Carlisle, 1959).

By the 17th and 18th centuries (300 – 200 Yr BP), woodlands were under increasing pressure from commercial and non-commercial sources, more so within the lowlands and it was frequently stated that the resources were 'exhausted'. Here deciduous species formed the majority of the woodland which responded well to coppicing and other forms of management in addition to being valuable

sources of timber. Oak was the most valuable commodity not only due to its timber properties but also as its bark was required for tanning. It is the latter use that inflated the prices of this resource during the late 1700s and secured its place in the landscape. However, once a chemical alternative was found prices plummeted and most land set aside for this purpose was returned to grazing (Lindsay, 1977; Stewart, 2002). A second detrimental impact on the lowland woodlands was the establishment of ironworks which required large volumes of charcoal to fuel the furnaces. One of the largest companies, based in Argyll, was sustained for over 100 years with a large proportion of the woodland around the site being exploited (Stewart, 2002). The industry suffered from an increasing scarcity of woodland and the inability to support such industry within the Highlands, due to transportation and cost difficulties. In A.D. 1609 James VI prohibited the use of wood to fuel the sites as it was deemed to valuable a resources and refused permission for other sites to be constructed (Mason *et al.*, 2004).

Collapse of the timber prices in the mid-1800s (150 Yr BP) was primarily the result of legitimate trade routes opening with the Baltic and America in A.D. 1866 (Mason *et al.*, 2004; Smout, 2006). Better quality timber and cheaper transportation costs reduced the market for British timber. Although this seriously affected some areas the eastern Highlands were buffered for some time with railway and transport route construction requiring large volumes of timber (Dunlop, 1997). However, most landowners found an alternative to timber sales and with increasing transport networks and English tourists this was in the form of sporting parks (Dunlop, 1997; Mason *et al.*, 2004). A number of areas were enclosed to form these parks to preserve the vegetation for deer rather than cattle, which, although under some management regimes in order to preserve the woodland, did have some detrimental effect due to lack of regeneration.

2.2.1.3.1 Signs of management

Although the events described outline woodland destruction throughout the historic period, primarily for financial gain during the 1700s, planting and management of the woodlands was undertaken in some areas. During the 17th and 18th centuries (300 – 200 Yr BP) it was the estate owners that began the planting regime although this was initially for aesthetics and landscaping of the estate grounds. Increases in timber prices saw land unsuitable for other purposes, such as agriculture, planted at first with Scots pine and other native trees such as ash, oak and alder (House and Dingwell, 2002). As timber was a valuable resource, in some instances, stocks were managed by foresters employed by land owners to preserve the resource and make good profits. Any contracts agreed for timber utilisation at this time, predominantly in the lowlands, stated types of woodland which could be taken and those to remain untouched in order to preserve the resource and

enhance profit (Smout and Watson, 1997). Restrictions were even placed on grazing cattle within these areas in case it damaged the timber (Smout, 2006).

Throughout the 18th and 19th century (200 – 100 Yr BP) it became fashionable to have exotic tree species and woodland surrounding estates. Naturalists on voyages to new countries were paid by landowners to bring back seeds of trees which could be grown on the large estates, initially from countries in Europe but increasingly from further afield (House and Dingwell, 2002). Included within these were species that flourished under the British climate and are major constituents of the planted woodlands of today, for example Sitka spruce (*Picea sitchensis*), Norway spruce (*Picea abies*), Douglas fir (*Pseudostuga douglasii*), Lodgepole pine (*Pinus contorta ssp. Latifolia*), European larch (*Larix decidua*) and Western hemlock (*Tsuga heterophylla*). Species that grew well and provided good timber were progressively utilised to replace native species and plantations were almost purely composed of exotic species; some areas even cleared the native woodland to replace them with the new found species (House and Dingwell, 2002). These species have been exploited by the Forest Commission to provide fast growing timber stocks throughout the 20th century. Although a reversion to more native individuals is being implemented large tracks of these taxa still dominate some woodland.

2.2.1.4 Summary

Although pine has been an important component of the landscape it is unlikely to have formed the vast and dense woodland that is given to romantic description of the Caledonian forest. Since prehistory pine has been an important resource for timber and other materials and thus have been utilised in a number of ways. It is because of this exploitation that there is very little remaining of the native woodlands today. A large proportion of the woodlands are the remnants of former management regimes that took place in the 18th and 19th centuries. What little remains is usually found in the higher more remote locations where the machinery associated with the intensive felling of the 17th and 18th centuries could not reach.

2.2.2 Local vegetation patterns at Inshriach Forest in relation to the regional changes

2.2.2.1 Woodland establishment

Although a number of palaeoecological investigations have taken place within Scotland itself there are a limited number of these sites within the Cairngorms. Of these the greatest amount of information has been obtained from the forest of Abernethy to the northeast of Aviemore (Figure 2.1). Data from these records show that the majority of the vegetational patterns and changes within this region are similar to those affecting Scotland as a whole; however, some variations

associated with local human communities, predominantly from the historical period, that distinguish changes from the main regional influences.

Results from palaeoecological investigations from sites within the Spey region indicate that the tripartite early Holocene sequence shown in pollen diagrams from other regions of Scotland also occurred around Inshriach. Succession from herbs to shrubs, becoming increasingly closed woodland, is consistently represented through a sequence of dominance of *Empetrum sp.* followed by juniper and eventually birch (O'Sullivan, 1974). Once colonised it was birch-hazel woodland that predominated in the landscape at the start of the Holocene until around 9500 cal Yr BP. Pine began to encroach into the woodlands around this time and became one of the canopy components to form birch-pine woodland comprising one of the most dominant vegetation types within the region displacing hazel. Sites covered by O'Sullivan (1974; 1976) and Birks (1970), although within the Speyside region, show slight differentiation in the commencement of this zone. For example the pine expansion is dated to 8831±69 cal Yr BP at Loch Pityoulish (O'Sullivan, 1976); at Abernethy it is at ca. 8000 cal Yr BP (Birks and Mathewes, 1978); at Loch Garten this was c. 8300 cal Yr BP (O'Sullivan, 1974); Loch Enich and Alt na Feithe is later, around 7800 cal Yr BP (Birks, 1970). Inconsistency cannot be attributed to differences between the material dated in the studies as most were conducted upon bulk material with only the latter two sites on pine stumps; however, in situ sedimentary process and contamination can also make bulk dates highly error prone (Björck and Wohlfarth, 2001). Spatial variation also affects the dating of arrival and expansion of alder with differentiation between the empirical limit, defined as the point at which a species pollen curve become continuous (Smith and Pilcher, 1973), being reached at Loch Pityoulish in contrast to Loch Garten and Loch a 'Chnuic. Availability of suitable waterlogged environments at these sites controls the presence of alder; the former saw alder become a major component of the woodland whereas around Loch Garten and Loch a 'Chnuic this was limited to the wetter river margins (O'Sullivan, 1974; 1976). Further components of the birch-pine woodland were aspen and oak, with the quantity of these differing depending upon the local conditions. For example O'Sullivan (1976) found values for oak of up to 10% AP following alder establishment showing greater diversity within this locality than in other areas within the Highlands.

As represented in most regions of Scotland the pine decline is also visible within the Highland region, albeit more distinctive in some areas than others. For example around Loch Garten the decline is minimal and the dominance of birch-pine woodland remains. However, at around 4200 cal Yr BP at Loch Pityoulish there is a distinct decline in pine proportions with a corresponding increase in birch. Although this represents a statistical change to some degree the increase in birch

is also related to range expansion with opening of suitable habitat areas devoid of pine (O'Sullivan, 1976).

Whilst natural processes have been the main forcing factors throughout the early Holocene, continuing perhaps later than most areas within the Highlands, there is archaeological evidence for human activity within the Spey valley region from 6200 cal Yr BP (O'Sullivan, 1974). Anthropogenic influence on the landscape has been detected within the pollen record for a number of sites with variety and intensity differing between sites. A number of archaeological artefacts have been discovered within the region relating from the Neolithic period through to the Iron Age (Armit and Ralston, 1997; Cowie and Shepherd, 1997). Palaeoecological evidence of this is detected in the pollen assemblages as heathland expansion and presence of pastoral and arable anthropogenic indicators. For example, woodland clearance associated with heathland formation around 3981±542 cal Yr BP at Loch Garten which the author associated with Neolithic or Early Bronze Age clearance but cannot be taken as conclusive (O'Sullivan, 1974).

2.2.2.2 Historical utilisation and dominance of the landscape

Palaeoecological evidence for the impact of early human communities within the Speyside region is limited. This may be a consequence of low activity or low site resolution. O'Sullivan (1974, 1976) suggests that prehistoric communities existed within the Abernethy area around 3500 cal Yr BP and it is likely that utilisation of the landscape was not limited to this area alone. Population expansion and technological advancement intensified land use and increased presence within the archaeological record. Utilisation of both the landscape and its resources gradually increased and by the Middle Ages had attained their highest levels. From around 800 Yr BP (A.D. 1100) onwards the landscape around Inshriach was an important focus for shielings or transhumance, involving herding of cattle to higher ground within the summer months for pasture (Holl and Smith, 2007). Ross (2004) estimates that this region supported ~700 individual cattle per year (between A.D. 1750 - 1753) from a number of communities surrounding Glen More. Land-use of this kind creates an open structure with grazing land punctuated by individual ageing trees, or 'veteran' trees, which forms wood pasture (Quelch, 2001). The degree of grazing limits regeneration of woodland and maintains the open structure and in some cases, the trees are pollarded as they provide important resources and shelter within the landscape (Holl and Smith, 2007). These areas were maintained by the farming communities of the lowlands during the summer months and were a highly important aspect of their lifestyle. Although such systems were formed within the lowland areas these are not visible in the landscape today due to the subsequent land management modifying these. In contrast, a number of the remote upland areas which typically support these areas still prevail today and are targets for management (Holl and Smith, 2002).

By the 15th – 16th centuries (500 – 400 Yr BP) the woodlands provided a major resource for wood and timber, to support construction and domestic needs such as fire (Smout and Watson, 1997); however, this was changing. Scarcity of woodland within the lowlands and increased wood pasture exacerbated pressure on the woodlands of Speyside to provide materials for an increasing number of non-local groups. Low intensity timber extraction commenced in Speyside in A.D. 1539 (*ca.* 400 Yr BP), which subsequently increased within the 1600s, for example the first timber sales from Rothiemurchus and Glenmore were made in A.D. 1658 (Mason *et al.*, 2004). Trees that were targeted at this time were mature, selected for the needs of the buyer and spread across the woodland enabling the woodland to adapt and recover from this activity. A survey of the woodlands taken at this time describe Rothiemurchus forest as 'great fir wood two miles in length but very broad' (where fir relates to coniferous trees) and Abernethy as 'great fir wood 24 miles in compass' (Mason *et al.*, 2004). These suggest that although there was exploitation of these areas it remained limited at this period with the woodlands prominent features.

Speculative timber contracts and fellings began in the mid 18th century with gradual intensification of activity. Initially, clearance concentrated on the best trees which gave the woodland time to recover but the opening of the Napoleonic War increased demand for timber to strengthen the ship building industry and the country's needs during this time due to a lack of imported timber (Carlisle, 1977; Smout, 2006). Dramatic fellings began to take place with large areas being stripped of woodland, in a method known as clear-felling, to leave devastating effects on the landscape (Stewart, 2002). Lindsay (1977) presents details of a woodland survey from A.D. 1750 (200 Yr BP) which estimates that only 5% of the land area in the Highlands was under woodland cover. However, this may not be the case as in some areas the clearance aided the regeneration of woodlands, for example in Rothiemurchus. Pine requires large open spaces to enable seedlings to establish and develop therefore the large areas of disturbed land provided the perfect seed beds and led for prolific regeneration of some woodlands (House and Dingwell, 2002).

During the late 18^{th} century and throughout most of the 19^{th} century it was the Highlands that experienced the greatest degree of landscape change. Forced eviction of farming communities marked the start of the so-called Highland Clearances which dominated between A.D. 1790 and A.D. 1855. Financial stresses due to the collapse of raw material prices required landlords to readdress income and expenditure (Richards, 2002). The solution was to actively 'relocate' tenant farmers or remove them from the estate to enable the land to be utilised for sheep farming and, later c.A.D. 1820, also for deer forest. These removals affected a wide area of the Scottish Highlands and Islands with evidence of this from the Rothiemurchus estate. It was not until the later part of

this period, in A.D. 1827, their tenants were eventually removed by the Grants of Rothiemurchus to introduce sheep farming and later converted to deer forest in A.D. 1843 (Richards, 2002).

2.2.2.3 Commercial exploitation

Large scale commercial exploitation for timber has been taking place within Scottish woodlands since at least the 18th century. Rackham (1990) defines timber as trees of greater than 2 foot in girth whereas the smaller diameter branches were termed wood and was predominantly used for construction, in this case ship building. Initially the more accessible areas were utilised which spared the woodlands of Speyside, which Steven and Carlisle (1959) define as Rothiemurchus, Inshriach, Glen Feshie, Glen More, Abernethy and Dulan Valley, however a number of improvements within the transportation routes changed this and the forests subjected to similar exploitive activities seen throughout Scotland. Although fellings on a commercial basis had begun within the Speyside region around A.D. 1650 one of the first large scale exploitations within Rothiemurchus was in A.D. 1726 when a York trading company bought and removed 60,000 trees (Smout and Watson, 1997; Mason *et al.*, 2004). Richards (2002) suggests that this was associated with financial difficulties of the Grants which later encouraged the clearance of tenants from the estate. A similar deal was struck in the 18th century between the Abernethy estate owners and a Hull company and marked the start of the commercial fellings (Steven and Carlisle, 1959).

Use of rivers to transport timber to the major ports, for exportation or shipbuilding had, for some time, been on a small scale. However, once commercial practice had been adopted larger quantities of timber were being produced and therefore modification of the river networks took place to accommodate the large log booms, of up to 50 logs, being produced (Smout, 1997). Within the Speyside region this also included the construction of sluices on the lochs in order for sufficient flow to be produced to transport the goods even if the river flow was low (Steven and Carlisle, 1959; Carlisle, 1977; Whyte and Whyte, 1991; Dunlop, 1997). For example, Loch Morlich was adapted with a sluice, that is still visible at present, so that wood felled from the Rothiemurchus woodland could be transported via Inverdruie and out to Garmouth (Mason *et al.*, 2004).

Although woodland utilisation was not a new concept, as can be seen from the total loss of woodland in the lowlands, the impact on the Highlands at this time was much more intensive than it had previously suffered. Earlier exploitation had been on a much smaller scale with only the mature trees being affected which allowed the system to recover but the large scale commercial clearances were much more detrimental (Mason *et al.*, 2004). Demand for timber heightened during the Napoleonic Wars, not only for the needs of the military but also the country due to reduced imports from Scandinavia and the resources of Speyside bore the greatest impact from this

adding to that of the commercial industry. The high value placed on the timber inflated prices resulting in more timber being sold by landowners in order to gain maximum profit, for example 10,000 trees were sold from Inshriach and Glenfeshie in A.D. 1819 (Dunlop, 1997; Smout, 2006). Efforts were made by some of the landowners to counteract the destruction Rothiemurchus used a clear felling technique (totally felling areas before moving onto the next area) which allowed areas to regenerate, yet the volume of timber being removed was of such a size that it was difficult to buffer the impacts (Mason *et al.*, 2004).

During the mid-1800s a reduction in duty saw the recommencement of timber imports from Scandinavia (Dunlop, 1997). Associated price reductions led to a shift in the focus of the woodlands from sources of timber to recreation. Improved infrastructure, construction of the railways system and, more specifically, the Highlands Railway, gave the English tourists increased freedom for recreational activities such as hunting, shooting and fishing (Dunlop, 1997). Consequently, the woodlands of the Speyside region such as Rothiemurchus were transformed to deer forests in order to cater for the new source of income (Smout, 2006). Additional emphasis was also placed on management to encourage regeneration and preserve the remainder of the woodlands as a sustainable resource. This was initially in the form of planting although these were 'exotic' species (those that are not native to Britain and have subsequently been introduced i.e. Douglas Fir, Spruce, Larch) that could, if required, provide good quality timber in the future (Smout, 2006).

Repetition of the detrimental effects of the Napoleonic War occurred with the declaration of World War I. Again, due to reduced foreign imports the demands for timber to fuel both military and domestic needs were met by the Scottish woodlands, and again it was the woods of Speyside that felt the brunt of this action with Inshriach, Rothiemurchus and Abernethy all being severely affected exploiting the recovered timber stocks and some 'natural' areas (Steven and Carlisle, 1959; Carlisle, 1977; Smout, 1993; Dunlop, 1997; Smout and Watson, 1997). A structure to the felling was produced, unlike during the Napoleonic Wars, whereby the oldest, most suitable trees were exploited initially in order to let the younger trees grow and mature (Dunlop, 1997). In addition, a special Canadian regiment was brought in to improve access by construction of roads to the more inaccessible areas, some of which remain today, and to undertake the felling, due to lack of local manpower. The remnants of these effects can still be seen in some of the roads in the area and the shape of some of the woodlands such as Inshriach (Dunlop, 1997). In total ~ 1,200 hectares of land were felled during this time leaving a large mark on the landscape.

Following the end of WWI the Forestry Commission was formed to manage woodlands and timber resources it was realised that should a similar situation occur again, then the remaining resources

would not be sufficient to support the needs of the country (Dunlop, 1997). Glenmore was one of the first woods to be purchased in A.D. 1923, with Inshriach bought in A.D. 1935 (Mason *et al.*, 2004). With the start of WWII the implementation of the Commission's management proved beneficial.

2.3 Importance and nature of management at Inshriach Forest

2.3.1 The history and policy of the Forest Commission

Initially, a body of commissioners and MPs were tasked with improving forestry practice with the aim of providing social and economic benefits to deprived areas. However, with the events of WWI, greater emphasis was placed on the need for timber reserves and the Forestry Commission was formed (Pringle, 1994; Foot, 2002). The Forestry Act of 1919 laid out the primary objectives of the commission as 'the general duty of promoting the interests of forestry, the development of afforestation, and the production and supply of timber in the United Kingdom' (Pringle, 1994). Consequently, a planting regime was undertaken with state and private funding supporting its work. Within the following 10 years the commission managed over 150,000 hectares of woodland throughout the United Kingdom (Pringle, 1994). By the end of the 1940s a woodland inventory was conducted which indicated that around 3.64 million acres of land were under woodland within the UK with a large contribution from the Forestry Commission planting regimes (Pringle, 1994).

For the first 30 years of the Commission its main concern had been with providing domestic timber reserves for industry, however during the 1950s the focus of the Commission began to change. This new direction was expressed in the Zuckerman report within the late 1960s and later in the Forestry Act of 1967. It was suggested that the Commission's role was not purely economic and that social benefits should also be central to its policy. Consequently, planting regimes were undertaken within the upland regions of both Scotland and Wales which were undergoing depopulation due to lack of job opportunities and social depravation with the aim of increasing social benefits and provide economic regeneration (Pringle, 1994).

By the end of the 1960s further development of the Forestry Commission's policy had occurred and a greater emphasis was placed upon the recreational and aesthetic nature of the woodlands. Implementation of the Wildlife Act of 1981 ensured that conservation of the landscape was high on the agenda and forced a further change in policy. In response, it was realized that greater diversification of species should be used within the planting schemes with more importance placed upon the native species of the local area reducing the 'traditional' method of block planting of a single species. Therefore in the 1990s increased diversification within the species used and

preservation of the 'native' woodlands, which would have been replaced with plantations under the initial Forestry Commission policy, commenced (Foot, 2002).

2.3.2 Landscape change and management under the Forestry Commission

Acquisition of woodlands presently owned by the Forestry Commission took place over a number of years and is ongoing. Initially, the purchase of woodlands was in order to meet the demand for timber. Planting regimes were already in place over many of the owned sites. However exotic species were preferred over 'native' species as they were fast growing with good timber quality and yields (Pringle, 1994). In this context the term 'exotic' is used to mean those species that are not native to the British Isles and were brought in by other means and have since been planted and established, including Sitka spruce, Lodgepole pine, Douglas fir, Japanese and European larch. In some cases native and established stands of Scots pine were removed to be replanted with exotic conifers (Foot, 2002). Although the growth of broadleaves is naturally limited within the Highlands of Scotland at present it is a component of the woodland over lower land areas, however little planting of these species was undertaken. During the first 10 years of the Forestry Commission over 37,000 hectares of land had been planted with conifers as against only 1,800 hectares of broadleaved woodland (Pringle, 1994).

Woodlands were created by planting large blocks of uniform species in compartments of known size using rows of trees with predefined spacing of 1.7m-2m between each row. These are managed by division into smaller compartments in order to record management to individual sections of the woodland. Management at these smaller scales is undertaken to create the largest yields and the best timber. These include:

- Thinning: A large proportion of seedlings are initially planted within a compartment. Once established the trees are removed through felling, on a 6 to 10 year cycle depending upon the growth rate of the species being thinned, to give the remaining stock greater access to light and nutrients and thus better growing conditions and production of better timber at maturity (Hibberd, 1991). This can be done using two methods, selective or row removal. In the former the poorer individuals are chosen for removal whereas the latter is based upon rows therefore not all flawed trees are removed (Hibbard, 1986). This is dependent upon the production and financial objectives.
- Beating up: Between one and two years after planting seedlings that have not become established or have died are removed from the site and replaced (Hibberd, 1991). This gives the greatest possible chance to create a suitable stock from the compartment.

Clear felling: During the earliest years of the Commission, especially during World War II
the removal of all trees at a site would be carried out and subsequently replanted. As all
individuals were planted at the same time with weaker trees removed, maturity was
achieved at the same time.

During the early years of the Forestry Commission a large proportion of the felling and other management activities were carried out by hand. Machinery was often too large and expensive to take to some of the more remote areas, the Highlands especially, therefore horse logging was used to remove the timber from the site in addition to floating techniques, but they all had a low impact upon the landscape. During the 1950s the development of the Cutherbertson plough revolutionised management. This small mechanised plough could reach inaccessible areas and prepared ground for planting that was previously too difficult to undertake. Consequently, large areas of unproductive land could be planted, mainly with Sitka spruce as this could grow in adverse conditions, which significantly increased the land under management by the Forestry Commission (Foot, 2002). Introduction of machinery such as the Harvester and Forwarder have further allowed for the intensification of the practice with areas cleared rapidly but at the expense of greater environmental impact.

Although technology allows greater extraction new policies have controlled this during the course of the 20th Century. Emphasis has been placed on the woodlands being aesthetically pleasing and natural rather than just as a timber resource. Consequently, there has been diversification of the species used with deciduous-lined roads and trackways to hide the coniferous blocks (Foot, 2002). Increasing attention was given to native species and the creation of nature reserves for old growth woodlands within the landscape, although a large emphasis was still centred upon timber production.

2.3.3 Future of the woodlands and the landscape structure – management strategies

Increasingly, the future of forestry and the landscape linked with it is becoming associated with the idea of sustainable management. This is defined by the World Commission on Environment and Development (Brundtland, 1987) as:

"sustainable development meets the needs of the present without compromising the ability of future generations to meet their own needs".

Consequently, future plans of the Forestry Commission for woodland, specifically within Scotland, are to provide a sustainable resource providing economic and social benefits to all who use it. Development of the Scottish Forestry Strategy (Forestry Commission, 2006a) and subsequent

associated implementation plans (Forestry Commission, 2006b) state the objectives for the Forestry Commission Scotland and the methods to achieve these.

The Forestry Commission has been increasing the amount of native woodland within Scotland since the 1990s to attain one of the main objectives of the Scottish Forestry Strategy (Forestry Commission, 2006a; 2006b). At present only around 10% of the woodlands within Scotland are 'natural' and the aim is to increase this through regeneration and planting of native species, including Scots pine and a number of broadleaf species (Forestry Commission, 2002). Felling of 'exotic' taxa is currently underway to increase habitats, resources and to encourage recolonisation by native fauna i.e. Capercaillie and red squirrel (Forestry Commission, 2003). During the initial years of the Forestry Commission planting of exotic conifers was done on a block basis, with single species being planted over wide areas, as described above. The consensus is to reduce this by creating diverse woodland areas with a number of species, thus reducing patch size and providing habitats for a wide range of ground flora and fauna (Peterken and Stevenson, 2004). Once the 'exotic' species have been removed both natural regeneration and planting will be used in order to regenerate the woodland, with seeds and seedlings sourced locally in order to retain a native woodland structure.

The fauna of the woodlands are also to benefit from the future directive of the Forestry Commission. Generation of native woodlands and the associated vegetation increases habitat space for new and existing species. For example, the increase in deadwood and ground species will encourage insects and small mammals to colonise the woodlands. In addition, creation of corridors and 'island' (small fragments of woodland within open landscapes) linkages will enable expansion of ranges and population growth (The Woodland Trust, 2000). In response, work is underway to encourage species that currently inhabit some of the old growth woodland such as deer, Capercaillie and red squirrel. By creating vegetation structures and habitats that are suitable for these species that population expansion will promote a natural ecosystem. For example, the Capercaillie (Tetrao urogallus) requires an open pine woodland structure to promote the growth of Vaccinium myrtillus, Juniperus and Calluna and provide leks for mating (Dennis, 2002). Projects are currently underway in a number of areas to promote population growth within six populations (EU Life Project, 2007) but providing the optimal habitat conditions are crucial and require an understanding of natural pine woodland dynamics. Undertaking projects to fulfil the directives the form of the woodland in relation to the patch-matrix structure will develop due to the interactions between the evolving species composition. Currently, landscape metrics are being implemented to elucidate the structural and spatial form of natural woodlands to aid conservation strategies (Watts et al., 2005).

Removal of exotic species, exclusion of some mammals and use of native taxa are methods implemented to remove the uniform structure of current managed woodlands with a more natural system. The Forestry Commission proposes two routes for future management schemes for the woodland; fully natural and intervention (Peterken and Stevenson, 2004). The former is a nonintervention technique whereby there is limited management and the woodland is left to develop. Initially this would form an even-aged structure, a similar response to current management practices, but with time this would form an uneven structure with diverse species and habitats (Peterken and Stevenson, 2004). In contrast, some intervention will be undertaken to allow for timber production, increased diversity and control of mammals. Sitka spruce is one of Scotland's most valuable timber exports and consequently its contribution to the economy is vital (Forestry Commission, 2006a). Peterken and Stevenson (2004) suggest that with restricted management of the woodlands addition of Sitka spruce, in limited numbers, would allow for revenue to be created for future costs incurred in management of the landscape. At present it is the latter method that is favoured as this helps return a large proportion of woodlands into stands with a more natural structure yet still enables forestry to be undertaken which does not compromise the economic benefits of the industry, thus, providing a sustainable timber resource with limited impacts upon the Reduction in the size of machinery, patch size of individual species stands and abandonment of the clear felling technique will go some way towards creating more natural woodlands such as those during the latter part of the Holocene where they were utilised under low intensity.

The difficulty with the lower intervention schemes is defining the 'natural state'. Historical land use has to be considered as the result of a range of anthropogenic influences at different spatial scales and intensities. Interconnections between the two forcing factors cannot be assessed on an individual basis which creates complexity in defining natural systems. Inventories outlining natural woodland presence employ a number of time periods to define such systems in the UK. For Scotland this marker is a woodland parcel indicated as natural on Roy's Military maps of A.D. 1750. Although a defined threshold this provides a baseline for current strategies but should longer perspectives be considered? Manning *et al.* (2009) introduced a concept of landscape fluidity and that the dynamic processes involved in the perpetuation of woodland cannot be defined in a single point. Quantification of past changes in formation and composition of these woodlands has the potential to provide a more informed and less-structured approach to management.

2.4 Conclusion

Natural and anthropogenic processes have interacted within the Scottish landscape to create range of unique systems. The scale and intensity of these create a diverse mix of ecosystems and increase

the complexity of implementing regimes to mange the influences of future environmental and social changes. A decision over which landscapes require intervention, and to what level, is an area where palaeoenvironmental information has the potential to a valid contributor.

Correspondence between the information provided by the palaeoenvironmental record and that obtained from analysis of the contemporary landscape facilitates the incorporation of this information. Further emphasis, therefore, is placed on the elucidation of the patch-matrix interaction and influence on the representation of this within pollen assemblages.

Chapter 3: Methods

This chapter outlines the methods employed to obtain the information to achieve the objectives of this thesis. As data was collected for contemporary and palaeoenvironmental analysis these methods are described separately. The initial sections deal with the collection of data for the calculation of pollen productivity estimates. The later sections describe the palaeoenvironmental methods used in relation to both the historical and longer time periods simultaneously.

3.1. Modern surface pollen sample collection for pollen productivity estimation

The aim of the analysis was to obtain productivity estimates for the dominant taxa within Inshriach Forest. These were chosen based upon the most dominant species within the woodland at the present, mainly 'exotic' arboreal species but also those that occurred within fossil samples obtained from sites within the woodland.

3.1.1 Field data

3.1.1.1 Sample location and collection

It has been suggested that to obtain robust estimates of pollen productivity for species the number of sites being used should at least double the number taxa being examined (Broström *et al.*, 2008); consequently, for this study an initial target 34 was defined. However due to poor pollen preservation of some samples this was reduced to 29 for the final analysis.

Although lake sediments can be used for this analysis moss samples are more readily available, have shown to provide good records of pollen deposition and have been widely applied to similar pollen-vegetation studies (Broström *et al.*, 1998; Hjelle, 1998; Jackson and Kearsley, 1998; Sugita *et al.*, 1999b; Bunting, 2003; Räsänen *et al.*, 2004; Bunting *et al.*, 2005; Mazier *et al.*, 2006; von Stedingk *et al.*, 2008). Given the lack of suitable lake sites for such sampling in the study area it was decided that moss samples would provide a better representation of the vegetation within the landscape and therefore a more robust base for PPEs. This also reduced the relevant source area of pollen and therefore was better suited to PPE sample sites and especially Inshriach due to its small area.

Samples were collected throughout a number of areas within Inshriach Forest in September 2007 using a random-stratified technique. Individual or groups of compartments in the forest were selected on the basis of their main components, to ensure that difference in age, density, structure and species would be accounted for within the samples. Sample sites were then chosen at random

within these sectors. A number of managed and natural sites from outside Inshriach, chosen at random, were included in the analysis to ensure that different community variations were accounted for. It has been suggested that a minimum distance be left between the sites used for pollen samples, von Stedingk and Fyfe (2008) use 500m and Broström *et al.* (2004) suggests 400m, to remove the influence of spatial autocorrelation on the independent nature of the samples. Due to the size of Inshriach it was not possible to ensure that this was the case with all samples taken and although every effort was made to reduce this, some of the vegetation sampling areas of some sites overlap slightly but it is not envisaged that the RSAP overlap significantly as forests hollows in closed woodland was estimated by Calcote (1995) at 50m.

Samples were obtained by placing a tube onto the moss bed to provide an area of moss of standard size as suggested by Räsänen *et al.* (2004). Although it has been shown that amalgamating a number of samples gives an improved representation of taxa this does not facilitate the calculation of pollen accumulation rates (Broström *et al.*, 2004). Moss was removed from the hummock using scissors incorporating all moss down to the older brown sections. Where possible mat forming species such as *Sphagnum* were used to be confident that post-depositional loss of pollen was minimised. However, this was not always achievable and the available species had to be used as an alternative. It is envisaged that due to the growth forms of the species sampled at the majority of sites this difference in species will not severely impact upon the amount of pollen collected or bias between species (Cundill, 1991; Räsänen *et al.*, 2004).

Pollen samples were counted to 300 non-*Pinus* grains to encourage greater diversity within the samples to allow correlation with the vegetation data, which resulted in counts in excess of 2500 grains in some instances. High counts were also chosen to reduce the influence of *Pinus* for the modelling process. If standard counts had been used the dominance of *Pinus* would have been such that little variation would have occurred between the sites removing the potential for confident productivity estimates. Sugita (2007a) has suggested that for the modelling and PPE methodology that higher counts are desirable to reduce the errors associated with the data consequently, this should benefit the method by also reducing errors.

3.1.1.2 Vegetation mapping

Vegetation surrounding the site was mapped for analysis to obtain the RSAP and PPEs. Methods described by Broström *et al.* (2004), of mapping vegetation by walking in circles whilst gradually increasing distance from the sampling point, gives a comprehensive data set relating to vegetation cover. However, these methods were primarily constructed for use within open landscapes and within woodlands these are too challenging and time-consuming. In woodlands that are particularly

densely stocked, such as Inshriach, these methods become unsuitable, consequently, the methods undertaken were a slight modification of those of von Stedingk *et al.* (2008):

- O 10m Ground vegetation was recorded in 1m quadrats at the cardinal points around the moss sample site (N, S, E, W). The remaining herbaceous vegetation within a 10m radius of the sample site was mapped and recorded using randomly placed quadrats within the different vegetation communities. The location, species and DBH (Diameter at Breast Height) of trees within this area was also recorded along with canopy coverage.
- 10 100m Transects were run out from the moss sample site in the direction of the cardinal points (N, S, E, W). Along a 100m transect and 2m wide all trees were recoded and DBH taken. Along the same transect estimates of canopy cover were taken every 5m by taking a digital photograph from head height in order that the area was standardised. Distinct changes in ground flora were noted but accurate mapping was not carried out between 50 100 metres as Bunting (2003) showed a ~5m source area for non-arboreal moorland taxa such as those comprising the ground flora.

3.1.2 Remote sensing data

Vegetation data within the field was collected out to a radius of 100m from the sample point. To extend this distance to 1000m management data, in the form of a Forestry Commission stock map, and classification of aerial photographs was used to estimate the areas containing the main species to be used within the analysis.

3.1.2.1 Management data set

This comprised a stock map of Inshriach Forest, in polygon format, obtained from the Forestry Commission encompassing all data relating to the present vegetation structure of the forest including species, density, planting age, and area. This was composed of vegetation data from April 2007 and therefore equivalent to the collection of moss samples from the woodland during September 2007. Using ArcGIS data from this map was extracted in 10m wide concentric rings around the sample points. Correction of these values was made by using information relating to the percentage coverage of the taxa known for each compartment from the records to ensure that presence was not over-estimated (discussed in section 3.1.2.3).

3.1.2.2 Classification of aerial photographs

As the 1000m radius at some sample points extends further than the Forestry Commission data set it was necessary to undertake additional analysis to increase the coverage of the vegetation map. Previous studies have used aerial photographs and digitised the different vegetation communities from these and added community composition data at a later stage (Broström *et al.*, 2004; Nielsen,

2004; Soepboer et al., 2007). Here it was decided to implement classification techniques to produce the vegetation map given the large area to be analysed and the roughly homogenous form. Classification of images is an established technique within remote sensing and can be implemented for use with land cover including woodland (Cochrane, 2000; Ozesmi and Bauer, 2002; Coppin et al., 2004; McLauchlan et al., 2007; Wolter et al., 2009). The method uses the spectral properties of the pixels within an image based as a representative of the parcel or area of land which can then be grouped based upon these properties in supervised or unsupervised techniques (Lillesand and Kiefer, 1994). The former uses predefined 'training sets' to relate information about the image to actual properties, which is then used to classify the remainder based upon the spectral signature (Campbell, 2002); unsupervised classification does not involve any learning by the software and the spectral signatures of the pixels are considered without any definition from the user (Campbell, 2002). As with most methods there are errors and limitations dependant upon the resolution and type of data being used for the classification, but also with the method itself. Misclassification of pixels can arise from the poor selection of training areas as they supply the knowledge to the program as the classes to be defined and the spectral information of these (Campbell, 2002). Program errors occur when the spectral properties are difficult to distinguish despite a good training Robinove (1981) suggests that this occurs where there is a continuum of groups to be distinguished rather than distinct boundaries limiting the use of the method in some areas or forcing combined groups of characteristics. If such a situation emerges, then combining the groups into larger sets is advisable or application of different classification methods (Robinove, 1981).

Image classification for this project was undertaken on aerial photographs. Due to the availability of data and the flight paths two sets of images were used; a larger set taken in 2000 which covered the majority of Inshriach Forest and the areas to the south, east and west with a resolution of 40cms and a smaller set taken in 2005 for the sites to the north of Inshriach on the Rothiemurchus estate around Loch an Eilein with a higher resolution of 25cm. Both sets of aerial images were obtained during the spring of their representative year, a time when land use types and species can be easily distinguished (Lillesand and Kiefer, 1994). Images of Inshriach Forest were obtained in hard copy as these were not available in digital format and therefore were scanned at 900 dpi to gain as high a resolution as possible to reduce errors associated with having to undertake this; the Loch an Eilein images were acquired in digital format so no pre-processing was necessary. Due to the difference in resolution, quality and area covered by the images both sets were analysed separately to increase the performance of the classification method; however, the procedure followed was the same for both data sets.

Initially, the images were georeferenced within ArcMap and transformed using first order polynomials with a cell size of 40cm to provide accurate representation. MultiSpec (@Perdue Research Foundation; available for download at http://cobweb.ecn.purdue.edu/~biehl/MultiSpec/) was then used to classify the images based upon spectral properties of the characteristics. Both images were classified using four groups, woodland, grassland, heathland, and felled/non-pollen producing with a further group, birch, included within the Loch an Eilein dataset. A number of training sets were defined for each group, the quantity of which were dependent upon the area of the known portions of the groups and accuracy of these to define test sites. Within the Inshriach set management data was used to help identify composition of the different groups along with ground truthing (visiting the area to gain knowledge of the species composition). Field data and user knowledge of the vegetation patterns around Loch an Eilein were used to aid the selection of training sites for the Rothiemurchus map. Training sets were added and subtracted in order to gain the best reference and reliability accuracy for the class and overall accuracy for the whole data set using the error matrix computed by the software. Once an accuracy of over 85% was obtained the dataset was accepted for full classification (Table 3.1). This has been identified as the minimum accuracy requirement for the test sites to ensure that a good classification is carried out (Robinove, 1981; Campbell, 2002). This accuracy figure is identified from the performance of test sites, areas of known land-use and predefined during selection of training sites, which are used to assess the value of the training sites in classification of the image. Omission and commission of pixels between different groups can be assessed by comparing those pixels assigned to the correct groups from these test parcels. Further identification of accuracy is achieved from calculation of the KHAT statistic used to represent the amount of information gained from the supervised classification which could not be the result of chance (Lillesand and Kiefer, 1994). The higher the KHAT value the lower the chance that this pattern was produced by chance alone.

Maximum Likelihood Classification (MLC) was conducted to classify the remainder of the image based upon the initial training data. Unlike other methods this uses the full range of the spectral and brightness properties of the different training pixels to classify each unknown pixel (Campbell, 2002). Consequently, the method accounts for any variability that is seen within the data which gives a better representation of the image rather then the variability introduced from different sources i.e. shadows. Due to the similarities in spectral properties on the Inshriach image between woodland and water these areas were combined within the classification. This developed from shadows within the woodland appearing black and therefore being classed as water, also black on the images. Consequently, to raise the accuracy of the area being falsely classified as woodland the decision was taken not to include a water category within the training set. Once the full MLC analysis had been undertaken, and an image gained, a mask of the water bodies from the image was

Inshriach

Class	Woodland	Grassland	Heathland	Felled/ Non- pollen	Sum	Reference accuracy (%)	Reliability Accuracy (%)
Coniferous woodland	3850615	178354	185018	38000	4251987	92.3	98.7
Grassland	72228	555889	70695	41872	740684	81.6	85.6
Heathland	40427	19685	356833	143476	560421	77.0	43.6
Felled/Non -pollen	206	25117	90375	566113	681811	85.0	74.6
	3963476	779045	702921	789461	6234903		

Overall accuracy - 88.5%

KAPPA Statistic - 79.1%

Loch an Eilein

Class	Coniferous woodland	Deciduous woodland	Grassland	Heathland	Non- pollen	Sum	Reference accuracy (%)	Reliability Accuracy (%)
Water	303309	5165	0	1082	3	309559	98.6	94.3
Coniferous woodland	5199	53472	2185	13770	41	74667	76.9	57.6
Deciduous woodland	9	211	36930	1115	7	38272	62.3	32.3
Grassland	0	2058	2627	5	32	4722	63.9	50.7
Heathland	2390	4118	38206	102942	65	147721	55.2	91.8
Non-pollen	0	0	0	0	487	487	97.6	94.4
Sum	310907	65024	79948	118914	635	575428		

Overall Accuracy - 87.3%

KAPPA Statistic - 81.6%

Table 3.1: Details of test class performance for the classification of aerial images at Inshriach Forest and Loch an Eilein. The overall statistic represents the classification accuracy of the whole image whilst the reference and reliability accuracy refer to individual classes.

overlaid within ArcMap. This gave the lochs and River Spey in the area a no-data value for the later data extraction ensuring that these areas would not be included as woodland. A similar process was taken for major roads and urban areas. It is envisaged that this will not impact upon the calculation of vegetation data for the PPE analysis as the areas where this situation occurred had data available from the Forestry Commission data set and therefore the classification data was not

required. The overall aim of this classification process was to define the heathland areas and small stands of birch and pine.

3.1.2.3 Extracting data from the vegetation maps

Data were extracted from the classification maps in ArcMap using concentric circles around each moss sample point. Rings of 10m radius were constructed around the point from 100m to 1000m radius. Although some studies have previously increased this resolution to 1m radius rings due to the high-resolution nature of the vegetation data this would have been too computationally demanding to produce for the full 30 sites.

Forestry Commission data

Extraction of data from the Forestry Commission stock data involved some manipulation prior to being used. As the coverage of species within each compartment was based upon the total area of the compartment this had to be adjusted to represent the actual stocking of the area. When planting takes place there is predetermined spacing of the rows of seedlings in addition to some mixing between species and genera. Consequently, all the areas for the compartments were corrected by the mixture of species within the area. For example, if the area for a compartment of Scots pine was stated as 4000 m² yet only 50% of this was stocked the actual area used to represent the compartment of this would be 2000m². Although this does not fully accounted for the difference in the canopy cover for the trees it is a more accurate representation of the actual coverage than using the whole area of the compartment and therefore was used in preference, as not doing so could distort the vegetation data and impact on the estimates of productivity. As data were available to sub-compartment level so the heterogeneous nature of the compartments was accounted for, however, at the sub-compartment level it was assumed that the coverage was homogenous. Where non-pollen producing areas were encountered i.e. urban areas or roads, the total area of the sectors were corrected to account for this non-vegetated area.

Classification map

Calculation of the species composition of the communities was based on collected data from Inshriach and information relating to the NVC classification of the communities. For example, the composition of heathland was based upon quadrat data obtained from sample points surrounding the Rothiemurchus estate. This was the area within which the majority of the survey distances encroached and therefore was deemed to be representative of the community. Grassland was taken as such and not split into its various agricultural components as the spectral properties were too similar to create distinctions.

Woodland was split into two classes where possible; coniferous and deciduous. The predominant natural component of the coniferous woodland is pine and used to represent this class. Deciduous communities were classified as birch only. Although this is likely to under-represented the subordinate species within the vegetation surrounding Inshriach there are two reasons for using this methodology. Primarily, the landscape around Inshriach and Rothiemurchus is dominated by 'natural' woodland of which the main species are Scots pine and birch. It is therefore reasonable to assume that these would be the predominant components within any survey undertaken. Secondly, if there are other species present within the woodlands these would be in very low density and therefore not significantly alter the results obtained. Although alder and ash are found at the Insh Marshes this area was not included in any of the survey distances.

3.1.3 Calculation of pollen productivity estimates

3.1.3.1 Data collation

As is shown above a number of data sets were created containing information about the vegetation patterns around the sample sites in addition to the woodland and the surrounding area. Ensuring accurate representation of this data for inclusion in the modelling process is fundamental to gaining robust productivity estimates. Consequently, data gathered within the field were used for the first 100m at all sites as this was seen as the most accurate dataset available. Estimates of percentage and absolute coverage extracted from the classification and stock maps were combined where necessary and applied from 110m to 1000m. For some sites the 1000m radius of the vegetation survey area was confined within the stock map data and therefore did not require additional information. Some of these areas were uneven joins for which ArcView GIS was used to clip the appropriate dataset to ensure no overlap between values.

Because data within the immediate 100 metres of the sampling point were collected in two formats; basal area and canopy cover, both of these formats were expressed as a percentage of the total sector area with initial absolute coverage obtained by averaging the raw data from the four transects within each distance class. In most cases this was the full sector when close to the site but with increasing distance non-pollen producing areas were encountered such as rivers, lochs and urban areas which were excluded from the total area. For the canopy cover a similar method was chosen but reversed as the data were originally collected in percentage cover format; however, the areas used were still corrected for the presence of non-pollen producing areas. Proportions are used within the ERV models 1 and 2 but for use within model 3 data was converted into area proportions (m^2/m^2) .

3.1.3.2 ERV Analysis

Extended R-Value or ERV analysis was used to correlate the vegetation values at increasing distances from the sample site to the pollen obtained from the sample. By distance weighting the vegetation, using a number of techniques, and calculating the Maximum Likelihood score (ML score) at each of these points decreasing values should occur until an asymptote is reached, the relevant source area of pollen or the point at which the statistical correlation between the pollen and vegetation does not improve (Sugita, 1994).

At present there are three versions of the ERV model available (see section 1.3.3) which have variants associated with how the background proportion is represented but also the format of the data that is included in the model. All three versions of the model are applied here to the data set and that which shows the lowest ML Scores taken as the most reliable model for the data and assumed to give the best PPEs (Prentice and Parsons, 1983).

In addition to the variants with the models themselves the user also has numerous weighting techniques available and again all are included within initial model runs to gain the best model output. The three weightings available are: \(^{1}/\d\), inverse distance (m) of the ring; \(^{1}/\d^{2}\), inverse distance (m) squared; Prentice-Sugita weighting, a taxon-specific weighting based upon Sutton's dispersal equation. Further details of these weighting functions are available in section 1.3.5.

Software used for the calculation of pollen productivities within this project were written by Sugita (*pers. comm.*). Two versions of the ERV software were used; ERV v.6.4 and ERV v.1.2.3. The most recent model, ERV v.1.2.3, was used for the initial calculations of the data set when taxon-specific weighting was applied to the dataset. Unless stated all runs had a wind speed of 3m s⁻¹ and diffusion coefficients to replicate stable atmospheric conditions.

Estimates of RSAP were obtained visually and using moving window linear regression via software constructed for this purpose (S.Sugita, *pers. comm.*). The latter method uses statistical analysis to compare the gradient of a linear model to zero, if there proves to be no statistical difference then the RSAP is estimated as the centre of the window used (Gaillard *et al.* 2008). The window is selected by the investigator in relation to the full transect length to optimise the results of the analysis.

3.1.4 Validation of PPEs

The Humpol software (Middleton and Bunting, 2004) was used as an objective comparison of the suitability of the PPEs obtained from the ERV analysis for use within the context of Inshriach. Using this software pollen deposition at four sites throughout Inshriach was simulated from

construction of modern vegetation maps within ArcMap. Subsequent, comparison with the actual deposition recorded in surface samples from the identified points was used to identify the best PPE datasets using statistical analysis.

A map of the regional landscape (60km x 60km) surrounding Inshriach Forest was obtained from LCM 2000. This dataset was produced by the Centre of Ecology and Hydrology by classification of remote sensing images from 1997/98 and covers the whole of the UK (Fuller *et al.*, 2002; Fuller *et al.*, 2005) The map is constructed of vectors each representing a different vegetation class which are shown in Table 3.2. Each class was chosen to highlight the variation within the vegetation patterns within the spectral properties of the images but also ensure that diversity within the actual land use classes was also identified. Classification of the images was also supported by field data collected from a number of areas within the UK to verify the results (Fuller *et al.*, 2002).

As each class within the LCM 2000 data represents a community as opposed to actual taxa the composition of the communities was established. Accuracy of these can impact on the results of the verification process affecting the outcome and therefore is a critical part of the analysis. Consequently, a number of resources were consulted to establish suitable arrangement of taxa, such as field data, literature and previous field study reports, and proportions for the identified land-use classes as listed in Table 3.2. Due to the area covered by the data a number of communities not used in the classification map were encountered. It is these areas where the literature was heavily relied upon i.e. mixed broadleaved woodland and montane communities.

Error is induced within the process as there are a number of combinations that can be used to define the land-use classes. However, it was decided to choose compositions for the groups before any analysis was undertaken as circularity would be inherent if the species proportions were subsequently adjusted whilst using an initial set of PPEs generated during the analysis influencing the results of later statistical analysis. Once results of statistical analysis had been obtained the proportions of the different taxa were varied within the land-use classes with all values used to assess the effect of any error from the vegetation patterns used within the results obtained.

		PPE			
Community	Composition	Value	Source		
Bare	100% NPP	_	_		
Water	100% NPP	_	_		
Montane	41% Calluna	Various	Inshriach		
	27% Ericaceous	0.025	von Stedingk et al. (2008)		
	61% Calluna	Various	Inshriach		
Open dwarf shrub heath	15% Vaccinium	0.025	von Stedingk et al. (2008)		
	7% Ericaceae	0.025	von Stedingk et al. (2008)		
	61% Calluna	Various	Inshriach		
Dense dwarf shrub heath	15% Vaccinium	0.025	von Stedingk et al. (2008)		
	7% Ericaceae	0.025	von Stedingk et al. (2008)		
Arable	100% Cerealia type	1.78	Broström et al. (2004)		
Grass	100% Poaceae	0.55	Broström et al. (2004)		
Calcareous grass	100% Poaceae	0.55	Broström et al. (2004)		
	41% Calluna	Various	Inshriach		
Bog shrub	24% Ericaceae	0.025	von Stedingk et al. (2008)		
	23% Poaceae	0.55	Broström et al. (2004)		
	93% Pinus	Various	Inshriach		
Coniferous	2% Larix	Various	Inshriach		
Connerous	3% Picea	Various	Inshriach		
	2% Betula	Various	Inshriach		
	20% Betula	Various	Inshriach		
Mixed broadleaves	20% Alnus	2.33	Sugita et al. (1999)		
wiixed broadleaves	20% Corylus	0.78	Sugita et al. (1999)		
	20% Fraxinus	0.39	Sugita et al. (1999)		
Deciduous	50% Betula	Various	Inshriach		

Table 3.2: Vegetation community structure details for maps used to simulate pollen deposition around Inshriach Forest. Pollen productivity estimates (relative to *Picea*) and sources are given for those not obtained from Inshriach.

As PPEs for only 5 taxa were available for testing from Inshriach the remaining taxa required substitute values from previously published work for some analyses. These were obtained from Broström *et al.*, (2004), von Stedingk *et al.*, (2008) and Sugita *et al.*, (1999) as, at present, these provide the most robust data set and a suitable range of taxa for use at Inshriach. Although the difference in climate, site conditions and methodological techniques may induce some error into the applicability of these values their continued use within the project can standardise these. Other values are available for the taxa in question from other regions (Nielsen, 2004; Bunting *et al.*, 2005; Räsänen *et al.*, 2007; von Stedingk *et al.*, 2008) but the number and range of taxa within those studies are not as comprehensive as those from Broström *et al.* (2004). Furthermore, available estimates are limited to those studies which have values for *Picea*, as this is the reference taxon for the Inshriach dataset so this reduces the number of studies which is further reduced by the values required for the taxa within Inshriach. For *Corylus* and *Alnus* the number of estimates is limited to the study by Broström *et al.*, (2004) which further support the use of these values within the modelling.

As with the ERV model wind speed was set to 3m s⁻¹ with stable atmospheric conditions. These are the standard parameters that have been used in a number of studies and therefore allow comparison of the results with previously published work.

3.2 Statistical analysis

Analysis of the datasets was initially used to determine patterns and correlation between the pollen and vegetation data collected for PPEs. This was conducted using multivariate techniques and geostatistical analysis. Multivariate techniques were also used to explore correlation between contemporary and fossil samples as a modern analogue approach.

3.2.1. Multivariate statistics

Analysis of the data is performed in a multi-dimensional space allowing for description of singular or multiple datasets. Multiple linear regressions are performed on the sample and species data with the aim of consolidating these into as few axes as possible to explain the greatest amount of variation whilst retaining the information provided (Pielou, 1984). Two formats are available, constrained and unconstrained. The former, also known as indirect analysis, is used where environmental variables are not available and therefore the axes are formulated in the direction of greatest variability between samples and species (Leps and Smilauer, 2003). In constrained analysis (direct analysis), the axes are placed in the direction where the greatest variability in the samples can be explained by the environmental variables (explanatory factors). When it is expected

that environmental variables have an overriding influence on the data these can be classed as covariables; partial analyses can remove the influence of these prior to the analysis to ensure that patterns are expressed purely in relation to the explanatory variables (Leps and Smilauer, 2003).

A number of techniques are included under the term multivariate statistics, unimodel and linear ordination. Preliminary data analysis (Detrended Correspondence Analysis) is conducted to determine the most suitable approach for the dataset which is dependant upon the heterogeneity of the data i.e. linear methods are suitable for relatively homogenous datasets, therefore the full ecological range of the species is not fully represented by the data (Leps and Smilauer, 2003). Data transformations are subsequently applied to modify the data to obtain the greatest amount of information from the ordination to fulfil the objectives of the analysis. ter Braak and Šmilauer (2002) outline these processes which include:

- scaling of data to determine the criteria for placement of the samples in the ordination i.e.
 sample scaling enables distance to represent dissimilarity between the samples
- transformation of the data by division of the individual scores by the species standard deviation removes the influence of the dominant taxa
- centering each species/sample (dependent upon the focus for this) is weighted by the variance
- standardising is required if the data is provided in different units

The primary objectives of the multivariate analysis in this study were to: (1) assess the relationship between samples in a single dataset (modern and fossil); (2) analyse the relationships between vegetation proportion and composition in the pollen samples; (3) determine similarities between fossil and modern sites from the four basins used. Initially a DCA was conducted to determine the length of gradient. As species response is assumed to be unimodal the range of this accounted for the sample dataset has to be determined to define the most appropriate techniques to explain variation. Linear methods are adopted when the fully range is not available with the unimodel when sufficient data explains the full range (Leps and Smilauer, 2003). There are two thresholds for determining this; Leps and Smilauer (2003) used 4 S.D (standard deviation units) whilst ter Braak and Prentice (1988) suggest 2 S.D. The justification for the latter is that the rise and fall of the unimodal model is over 4 S.D. This study will employ the threshold of Leps and Smilauer (2003) as this has been employed within a large proportion of pollen analytical studies published. To achieve these, the main method used was Principle Components Analysis (PCA) as most of the datasets were represented by linear gradients. When explanatory variables were available the constrained form of this, Redundancy Analysis (RDA), was most suitable. Decisions over the data

transformation techniques were adopted on an individual basis and details of these are given when the results are presented in Chapter 4. Where RDA was applied Monte Carlo permutation tests were run to test the significance of the correlation between the vegetation data and pollen data (ter Braak and Šmilauer, 2002).

3.2.2 Geostatistical analysis

Spatial patterning is present to greater or lesser extents in most variables measured for scientific investigation. Autocorrelation is the degree to which samples are related within a given distance allowing the prediction of variables at unknown points. Legendre (1993 p.1615) defines this well:

"Spatial autocorrelation may be loosely defined as the property of random variables taking values, at pairs of locations a certain distance apart, that are more similar (positive autocorrelation) or less similar (negative autocorrelation) than expected from randomly associated pairs of observations".

However, this property removes the independent nature of the samples which invalidate a number of statistical methods. Presence of spatial autocorrelation can be identified through the use of geostatistical analysis which encompasses a number of techniques to derive information relating to spatial patterning. One such method is semi-variogram analysis which uses the variance between two points at differing lag classes (distance separation) to assess spatial correlation using the algorithm shown (16).

$$\gamma(d) = \left[\left[1/2n_d \right] \sum_{i=1}^{n} \left[y_{(i+d)} - \left(y_{(i)} \right)^2 \right] \right]$$
(16)

Where: n_d = the number of sample points within the distance class.

 y_i = the measured parameter at site i

The basis of this approach is the underlying notion that sample points closer together have heightened similarity as they are influence by similar underlying processes (Legendre and Fortin, 1989). The principle of stationarity is also encompassed by the method which assumes unit mean and variance within the data with only lag (distance between points) influencing variance (Webster and Oliver, 2000). Once plotted against lag distance the form of the semi-variogram can be used to describe features of the physical property modelled (Figure 3.1): the range, identifying the lag distance at which independence is attained; the sill which marks the sample semi-variance.

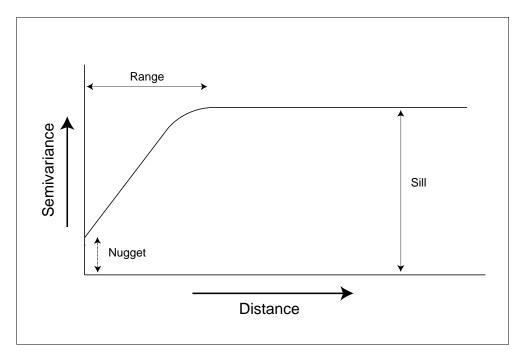


Figure 3.1: Features of the experimental variogram; see text for details.

Geostatistical analysis has been applied to a number of areas such as remote sensing, soil properties (Ettema and Wardle, 2002), palaeoclimatology (Telford and Birks, 2005) and more recently ecology (Legendre and Fortin, 1989; Rossi *et al.*, 1992). Elucidating the complexity in ecosystem patterning is an area that has received significant interest. These studies have shown that features within semi-variograms can be used to identify patch sizes and the scale of variability within the process or feature modelled (Legendre and Fortin, 1989); however, little attention has been paid to applying these techniques to both pollen and vegetation patterns from a contemporary landscape despite being used for temporal pollen variations (Oliver *et al.*, 1997). The ERV analysis applied to this study aims to identify the spatial scale at which pollen reflects the vegetation surrounding it, which parallels the principles of geostatistical techniques. Consequently, use of semi-variograms with both pollen and vegetation data here aims to identify the spatial scale at which these samples incorporate variation and whether they fulfil one of the underlying assumptions of most statistical analysis; independence.

The pollen set contained the counts of 29 modern moss samples as used within the ERV analysis with coordinates for these locations. A similar set was constructed from the transect data used within the ERV analysis for the vegetation. Combined samples taken from the field comprising the 100 metre transect (40 samples per site) and estimated vegetation data using the Forestry

Commission data to 1000 metres. At each of these points the vegetation was estimated within a 2m x 10m area with the Cartesian co-ordinates of the centre of this area used as the identifier.

Geostatistical analysis was undertaken within the Gstat package (Pebesma and Wesseling, 1999; Pebesma, 2004) available for use in R (The R Development Core Team, 2009). Experimental semi-variograms were constructed using the standard formula shown in equation (16) with a lag of 50 metres used within the vegetation analysis and 500 metres for the pollen data to incorporate sufficient samples within each distance class. Theoretical models were fitted by eye as although automatic methods are available i.e. ordinary least squares, to undertake this process a number of studies have shown that these increase computational time and remove any investigator knowledge that can benefit the placement of the models (Gething *et al.*, 2007).

3.3 Palaeoenvironmental analysis

Collection and extraction of data to elucidate landscape changes occurring over a time frame of ca. 100 - 3000 years were carried out at the four sites (Table 3.3). At each location a number of palaeoenvironmental analyses were conducted to provide information upon the vegetation change but also catchment processes. Details of the time scales at each site were provides by a radiometric chronology, 210 Pb or 14 C which was dependant upon the time frame being assessed.

Sample site location	Lake area (hectares)	Latitude	Longitude	Core length (cm)	Water depth (m)	Dating method
Lochan Geal (Short - B)	4.5	57" 7' 46.5	3" 53' 55.7	27	9.5	²¹⁰ Pb
Lochan Geal (Long - TAP)	4.5	57" 7' 48.2	3" 53' 52.6	120	14	¹⁴ C
Loch Alvie	53	57" 9' 44.3	3" 53' 0.9	30	14	²¹⁰ Pb
Loch an Eilein	36 Forest	57" 9' 0.2	3" 49' 17.7	31	10	SCP
Inshriach Forest	hollow (78.5m ² area)	57" 6' 12.8	3" 51' 37.7	80	N/A	²¹⁰ Pb

Table 3.3: Coring site locations and details of sediment cores extracted from the basins.

3.3.1. Core acquisition

A single core of 0.80 metres was obtained from the Inshriach Hollow by extracting the peat using two monolith tins by firstly digging a small trench and cleaning the sampling face. This method was used to ensure that enough sediment would be available for all analysis yet also allow for a

high resolution sampling technique. The two monoliths were frozen on return to the laboratory to ensure that a high resolution sampling could be obtained by thinly slicing the cores at 0.5 cm intervals.

Short cores were obtained from the lochs (Loch Alvie, Loch an Eilein, and Lochan Geal) using a gravity coring device as these would provide enough sediment volumetrically for the analyses required but also temporally to ensure that the timeframe of interest for the project is obtained. Furthermore, an undisturbed sediment-water interface was necessary to obtain an accurate representation of the prevailing vegetation patterns. The deepest portions of the lochs were identified through measurement with an electronic bathymetric reader and these areas used for the coring. These are areas that have been suggested as providing the most suitable locations for coring by reducing the sedimentary processes that may be influenced by lake level fluctuations and bioturbation (Lehman, 1975; Davis *et al.*, 1984). It has also been suggested that the centre of the basin is a suitable location and in most cases this was also the deepest portion of the loch. In Lochan Geal this was also the centre of the basin and Loch Alvie this was just off centre. Loch an Eilein was the only exception to this with the core being collected away from the centre of the basin. Cores were subsequently sampled in the laboratory at varying resolution, the regional lochs at contiguous 1 cm samples and Lochan Geal at contiguous 0.25cm samples.

An additional long core was obtained from Lochan Geal to provide a long-term representation of changes at Inshriach Forest. This was extruded from the deepest portion of the loch, close to the sampling location of the shorter core, using a Tapper corer. The core taken measured 1.20 metres in length and was sampled at 1cm resolution on return to the laboratory.

3.3.2 Radiometric dating

3.3.2.1 ²¹⁰Pb

For the majority of recent sedimentary profiles ²¹⁰Pb is the standard method for dating as this has a half-life of 22 years and therefore a range of 100 – 150 years and is thus most suited to work within the recent past (Appleby, 2001). As with most radiometric techniques the method is related to the decay of the ²¹⁰Pb isotope within the sediments. It occurs naturally within the environment from the decay of the radioactive isotope ²²⁶Rn. Age determination is calculated from the relationship of the two different portions found within the sedimentary profile with the point at which these reach equilibrium marking the limit of the dating method. The two portions are identified as:

Supported: Naturally occurring ²²⁶Rn within the sediments and thus decays *in situ*. Used as
the baseline value in most calculations.

Unsupported: ²¹⁰Pb isotope decays prior to being incorporated into the sedimentary profile. Atmospheric, direct rainfall onto the lake, deposition is the main route by which this component reaches the lake. However, it can also be deposited by rivers and overground flow through rainfall within the catchment.

Once the raw data has been obtained through counting there are a number of methods with which to obtain the dating profile. Three models are available in order to calculate the age profile from the ²¹⁰Pb values:

- Regression: If the relationship between depth and ²¹⁰Pb is linear then regression analysis can be used to determine the age of the profile.
- CRS: Constant Rate of Supply. There are a number of assumptions that underlie the model which include: atmospheric supply of ²¹⁰Pb is the primary form of unsupported deposition, the atmospheric supply of ²¹⁰Pb is constant, and there are no post-depositional processes. Basically, as the sedimentation is not necessarily constant the chronology of the profile is derived from the distribution of the ²¹⁰Pb values throughout the sedimentary profile. Thus, if the sedimentation rate varies there is not a constant unsupported component.
- CIC: Constant Initial Concentration. There is a constant initial ²¹⁰Pb (supported) element to the sediment; there is no variation from a change in the sedimentation rate in the deposition site; the supply of ²¹⁰Pb must change with a change in the sedimentation rate for the application of this method to be successful; Consequently, the technique is only valid where there is a constant sedimentation rate.

Although debate still surrounds the use of the CRS or CIC model Appleby (2001) suggests that both should be constructed for a profile and additional information about the site and the sediments being dated used to determine the correct profile and thus the dates.

At Inshriach indirect determination of the ²¹⁰Pb profile was achieved using alpha counting for Loch an Eilein and gamma counting for Loch Alvie and Lochan Geal. For the former preparation methods known ²⁰⁹Po concentrations was added to the sample prior to digestion in Nitric Acid and Hydrochloric Acid. Silver planchets were placed into the solution for 24 hours to allow the plating to occur. After drying the planchets were placed into an alpha spectrometer for 2 days until suitable concretions of ²⁰⁹Po and ²¹⁰Pb were detected to facilitate age determination from the isotope ratio.

For all other sites gamma assay was conducted on dry samples to measure ²¹⁰Pb, ²²⁶Ra, and ¹³⁷Cs at the Liverpool University Environmental Radioactivity Laboratory using Ortec HPGe GWL series

well-type coaxial low background intrinsic germanium detectors (Appleby *et al.*, 1986). ²¹⁰Pb was determined via its gamma emissions at emitted by its daughter radionuclide ²¹⁴Pb following 3 weeks storage in sealed containers to allow radioactive equilibration. Corrections were made for the effect of self absorption of low energy γ -rays within the sample (Appleby *et al.*, 1992). Subsequent measurement of ¹³⁷Cs was undertaken on the same samples also using gamma detection. This isotope occurs naturally in sediments and marks the Chernobyl fall out and earlier testing of nuclear weapons within the 1960s providing an additional independent marker.

3.3.2.2 Radiocarbon

A chronology for the long-term vegetation changes at Lochan Geal was obtained from radiocarbon dating of macrofossils. This is a well established technique for many Holocene studies as it is applicable to timescales of 10² - 10⁴ years. Accelerator Mass Spectrometer (AMS) dates were obtained for this study as this reduced the amount of material necessary for dating to allow for additional analyses on the remaining sediment. The benefits of AMS dates are evident in the low quantities of material that is required but caution has been advocated by a number of studies due to the potential for errors within this approach (Lowe and Walker, 1997). Firstly, in some cases the use of such small samples for dating can adversely influence the dating processes by increasing the risk of contamination as minute amounts can cause substantial changes in age. Secondly, although some studies have shown consistently younger ages between dates derived from macrofossils in comparison with the sediment matrix (Törnqvist et al., 1992) some macrofossils from the same horizons can give conflicting results (Gavin et al., 2003; Oswald et al., 2005). Age differences can occur between the different fractions of both limnic sediments and peat i.e. bulk humic and humin when compared to the macrofossils (Lowe et al., 1988; Shore et al., 1995; Nilsson et al., 2001). Furthermore, ages acquired from terrestrial and aquatic macrofossils can exhibit contradictions due to the source of the carbon which also differ in relation to the part of the plant selected in response to growth rate and redeposition potential (Björck et al., 1998; Turney et al., 2000; Walker et al., 2001; Oswald et al., 2005). Consequently, caution still has to be exercised when material is being selected for such purposes.

Within this study a number of macrofossils were selected for analysis with the aim of consistency for the material selected at each horizon to minimise some of the issues discussed above. Extraction of the samples from the sediment followed methods explained by Björck and Wohlfarth (2001) which involved digestion in 10% Sodium Hydroxide for 20 minutes prior to coarse sieving at 150µm using distilled water. Material was picked using a low powered binocular microscope until a sufficient amount had been retained. This was predominantly birch fruit which should

provide a reasonable age estimate given the rapid growth and dispersal of material. Floatation for a period can incorporate a lag but it is envisaged that this will not be significant enough to greatly influence the age of the material. Redeposition of the macrofossils is not expected to have occurred due to the well-preserved state of the fruits. A number of studies have investigated the amount of carbon required to provide a reliable age estimate with values ranging from 0.05mg – 1.4 mg (Björck *et al.*, 1998; Turney *et al.*, 2000; Oswald *et al.*, 2005); therefore enough material was selected to provide a mass closer to the upper estimates of this range. Material was wrapped in foil and dried at 105°C prior to being stored in glass vials. Although samples can be stored wet Wohlfarth *et al.* (1998) noted that samples stored for a long period in a cold store were more likely to provide an estimate that was younger than the actual age of the sample. Given the low carbon content of the samples the decision was made to dry the samples to ensure this risk was minimised. Samples were sent for analysis at the Beta Analytic Laboratory where the material was pre-treated (acid/alkali/acid washes) prior to measurement.

3.3.2.3 Spheriodal carbonaceous particles

During fossil fuel combustion such as coal and oil a range of particulate matter is released into the atmosphere. Included in this are spheriodal carbonaceous particles which appear as solid spheres or sponge-like particles depending upon the fuel source (Renberg and Wik, 1985; Rose, 2001; Rose, 2008). The size, morphology and weight of these particles facilitate their dispersion over large areas and therefore are found within most deposition basins. As these particles are only produced via anthropogenic burning of fossil fuels since the Industrial Revolution analysis of temporal deposition changes identify specific historical periods. A number of European based records of these particles have been published from different depositional contexts (Wik and Natkanski, 1990; Wik and Renberg, 1991; Rose *et al.*, 1995; Rose *et al.*, 1999; Yang *et al.*, 2001). Similarities in the morphology of the profiles demonstrate intensification of industrial activity during the 1800s and following WWII, with equally prominent features associated with the introduction of the Clean Air Act in the 1970s. Since Rose and Appleby (2005) used ²¹⁰Pb to provide a dating mechanism for these profiles their application as chronological marker has been encouraged.

Methods for the extraction of the SCPs followed those of Rose (1990; 1994) which included digestion of a known weight of sediment in concentrated Nitric acid, 40% Hydrofluoric acid, 6M Hydrochloric acid prior to being stored in distilled water. Contiguous samples were used to ensure that the profile could be accurately identified and compared with additional records (Rose *et al.*, 1995). A known amount of solution was checked for SCPs using a high powered binocular microscope (GXM 180M) with identification supported by Rose (2008). Identifications were conducted at x400 magnification with counting over the whole slide.

3.3.3 Sedimentological techniques

Analysis of the sedimentological properties of cores can highlight both autochthonous and allocthonous processes. Such influences can affect the accurate representation of the landscape contained in the proxy records. For example, correspondence with the management records for some sites will enable the impacts of clearance and other forestry techniques to be evaluated. This is invaluable for studying the environment as a whole and gaining an insight into the cause-effect relationships operating. At the sites around Inshriach a number of techniques were applied to the sites: Loss-on-ignition, magnetic susceptibility, particle size and charcoal. All methods are described here but use of this was site specific and therefore results are not available at all sites and distinctions are made in Chapter 5 when the results are presented.

3.3.3.1 Loss – On - Ignition

Assessment of the amount of organic matter constituent within sedimentary profiles is a widely adopted technique within palaeoenvironmental studies. Data obtained from this analysis can be used to determine variations within the sediment input to the basin and its influence on environmental proxy records.

Standard techniques, developed upon lake sediments, were used within this study, taken from Heiri *et al.* (2001). This involved combustions of sediments at a high temperature (550°C for 4 hours to determine organic content 950°C for 2 hours for carbonates) to quantify the proportion of organic material and carbonates. On a whole this method has produced good approximations for most environmental contexts and is an established technique (Shuman, 2003).

3.3.3.2 Magnetic Susceptibility

Magnetic properties are determined by application of a magnetic field to the sediments, removing it and measuring the magnetism retained by the sediment. Variations within the magnetic susceptibility are determined by mineral composition, grain size and grain shape which can be used to characterise the grains (Dearing, 1999). Such variations occur within lake sediments from allogenic sources, such as input from inflow streams, overland flow from the catchment and erosion of the catchment through anthropogenic influence, and autogenic sources, including bacterial activity (Dearing, 1999; Sandgren and Snowball, 2001). Changes in sediment input can be related to activities, natural and human induced, within the catchment and when considered with other proxies provide valuable environmental information. As the sites being studied in this project have been subjected to felling and planting cycles there have been a number of changes within the catchment. Furthermore, as these events are at known points in time they have the potential to provide a dating tool should the events be visible within the stratigraphy.

Samples were extracted at 2 cm resolution and freeze dried prior to analysis. Samples are packed into pots of known volume (10cm³), and then placed within a Bartington MS2 reader. A low frequency pulse was used with resultant magnetic properties calculated in relation to the volume of sediment used.

3.3.3.3 Particle size analysis

Changes in the proportions and type of sediment comprising the profile provide an insight into changing sediment sources through time. Such changes can be related to environmental conditions or processes occurring in the landscape at different periods.

This analysis was used at Lochan Geal to determine periods of sediment inwash into the basin. A large area of the lake margin is surrounded by steep gradients onto a ridge. This is currently owned by the Forestry Commission and supports part of a Scots pine plantation prevailing since the 1950s.

3.3.3.4 Charcoal

Fire is an important aspect of ecosystems providing a regenerative tool to the vegetation with a number of studies having examined the effects of fire within the landscape and the properties of charcoal within the palaeoenvironmental record (Patterson *et al.*, 1987; Clark, 1988; Whitlock and Larsen, 2001). Charcoal is produced from the incomplete combustion of plant matter and is dependent upon the duration and intensity of the fire in addition to the nature of the material being burnt (Whitlock and Larsen, 2001). Consequently, different quantities and size of fragments are produced from the combustion of the material. A number of studies have used this proxy to correlate pollen, sedimentological, plant macrofossil and other data to assess human and natural induced changes within the landscape (MacDonald *et al.*, 1991; Edwards and Whittington, 2000; Innes and Simmons, 2000; Moore, 2000; Froyd, 2006; Froyd and Bennett, 2006).

Despite the amount of information available relating to the nature of charcoal and widespread use of the proxy there remains a large number of limitations to the interpretations that can be made. Clark (1988) describes the taphonomy of charcoal as 'erratic' which inhibits full understanding. These predominantly arise though breakage of fragments and ease of transportation of shards which reduces ability to determine the source of the fire.

Charcoal analysis was applied to the long-term record obtained from Lochan Geal in order to determine the potential for local anthropogenic influences. Pollen slide counting of charcoal was used (x400 magnification on a high powered binocular microscope) at ~4cm intervals (higher resolution at critical areas) with a single size threshold for the long axis of 50µm. In total, charcoal

fragments were counted until 20 *Lycopodium* spores had been identified, which provided total charcoal counts of 50 – 150 fragments; the upper limit of this spectrum is close to the statistically significant limit of 200 (Finsinger and Tinner, 2005) with a ratio of ~1.0 between charcoal fragments and markers. Identification was aided by Whitlock and Larsen (2001). There are a number of counting procedures available including area, size and count (Whitlock and Larsen, 2001). Although area has been frequently used in order to gain information relating to the size distribution of the fragments (Birks and Birks, 1980) recent comparisons of the methods suggests that counts are sufficient to provide information relating to the distribution of fragments and showed a strong relationship between changes in area values and count values (Tinner and Hu, 2003; Ali *et. al*, 2009).

3.3.4 Biological analysis

3.3.4.1 Pollen

Standard methods of pollen preparation of Moore *et al.* (1991) were used for the fossil samples, which included digestion in 10% Sodium Hydroxide prior to sieving at 106µm and 10µm with further digestion in acetolysis mixture (1 part Sulphuric Acid : 9 parts Acetic Anhydride) and Hydrofluoric acid. Similar treatment was undertaken for the modern moss samples with only the exclusion of the Hydrofluoric acid treatment. Prior to preparation a known concentration of *Lycopodium* spores were added to each sample to allow for concentrations to be calculated.

Samples were counted using a high powered light binocular microscope at x400 magnification with x1000 for critical identifications: Type material at the University of Exeter and pollen identification keys (Faegri and Iversen, 1989; Moore *et al.*, 1991; Beug, 2004) were used for these and nomenclature for pollen follows that of Bennett (2005). For modern moss samples counts totalled 300 non-*Pinus* grains for the modern moss samples with fossil samples 1000 grains (inclusive of *Pinus*) excluding all spores, aquatics and exotic markers. Diagrams were drawn using Tilia (Grimm, 1991) with CONISS (Grimm, 1987) used to split the sequences into horizons.

3.3.4.2 Conifer stomata

Stomata are cells from needles of coniferous taxa which are resistant to decomposition as the needle breaks down around them; therefore detection is highly indicative of local presence of the taxa around the sampling site (MacDonald, 2001). At present, this approach supports work on tree line fluctuations as local vegetation characteristics can be identified (Ammann and Wick, 1993; Hansen *et al*, 1996; Parshall, 1999). Sweeney (2004) has published a key, and morphological information for the main taxa based upon modern data to aid the application of this method and increase data

collation. At Inshriach Forest this analysis was used to compare presence data with pollen percentages and accumulation rates at known age structures throughout the woodland history.

Conifer stomata were obtained from undertaking the standard pollen preparations described above. Samples were counted at x400 on a high-powered binocular microscope with identifications using Sweeney (2004) with counts ceased when 20 *Lycopodium* spores had been counted.

3.4 Vegetation reconstruction techniques

3.4.1. Landscape Reconstruction Algorithm

The LRA is composed of two separate programs which require analogous input data. In this study two versions of the model were used: for the short time scales REVEALS v.3.9 and LOVE v.2.2.7 were used; for the long-term modelling REVEALS v.4.2.2 and LOVE v.3.1.7 (S. Sugita, *unpublished*). This difference is to ensure that the current models were used at each stage and only differ in the form of the program and not the algorithms used. For example, the models used for the long-term reconstructions enable time periods to be used for data inclusion whereas the previous models required single horizons to be defined.

Input data to the models was in counts and therefore no manipulation of the data was done prior to being run. Parameters required include:

- Fall speeds: obtained from published data (Sugita *et al.*, 1999; Broström *et al.*, 2004; Soepboer and Lotter, 2009) of which some have been calculated from Stoke's Law.
- Pollen productivity: estimates used in most analyses were those calculated for this study from Inshriach Forest. Where this is not the case data from published sources are used to facilitate greater taxon diversity. Details of the taxa used and sources for their PPEs are given in the relevant results sections.
- Atmospheric parameters: when modelling has been undertaken using the LRA or Humpol a wind speed of 3 m s⁻¹ was used in all cases with stable atmospheric conditions. These are the standard parameters for the modelling studies and enable comparison of results between studies.

In order that the model calculates the values and error margins for the RSAP area an iterative process is used. Therefore, output from the model required correction of proportions (calculated as a proportion of the taxa included in the model run) as some values can be calculated as being negative due to the iteration process involved. The total was derived from only the positive values and thus presented results are a proportion of these with any negative values converted to zero.

3.4.2 Modern Analogue

Two methods were used for this analysis; multivariate statistics and Analogue (Simpson, 2007), a script for the R program (The R Development Team 2009). Similarities are evident between the two methods as both measure the dissimilarity between the data set components. In the former the relationship between all samples (fossil and modern) are expressed using a compilation of multiple regression analyses (described in section 3.2.1). In contrast, the analogue approach uses a distance metric (square chord distance) from the regression to relate each fossil sample to the modern data points. Although other metrics are available a recent study by Wahl (2004) highlighted this as a robust method supporting its use here. A threshold for the distance metric for selection of data is defined prior to analysis which was 0.15 as suggested by Overpeck et al. (1985) and has been used in other studies using this technique.

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Chapter 4: Pollen productivity estimate generation at Inshriach Forest

4.1 Introduction

Requirements of the quantitative models are estimates of pollen productivity for use as correction factors. This chapter outlines the process in obtaining these values from contemporary pollen and vegetation data collected from Inshriach Forest. Comparisons between the methodological aspects are used to produce numerous sample groups to highlight the degree of variability that can be incorporated into the resultant values. Subsequent validation using current models in the contemporary landscape aims to determine the most suitable PPE data for Inshriach and provide suggestions for future studies.

4.2 Modern pollen vegetation patterns in Inshriach forest

Contemporary pollen and vegetation data is necessary to calculate PPEs. This section outlines the collection criteria and properties of the sample datasets from Inshriach Forest.

4.2.1 Sample location and analysis

As discussed in Chapter 3 sample sites were chosen using a stratified random strategy with moss species used dependant on availability. Figure 4.1 relates this information in graphical format. Points represent both the moss species used at each location with size conveying the total concentration of pollen within each sample. Hyloconium and Sphagnum spp. were the main bryophytes used providing 10 and 11 samples respectively. These taxa differ in their form with Sphagnum a mat forming and Hyloconium a branching species (Smith, 1978). Concentration varies between samples; however a lack of relationship between the mosses used and the total concentration is evident. Interestingly, both the highest and lowest concentrations are obtained from Sphagnum samples at sites 15 (12976 grains g⁻¹ wet weight) and site 21 (371159 grains g⁻¹ wet weight). The mean concentration is 117478 grains g⁻¹ with the median at 71338 grains g⁻¹ wet weight. Comparison between location and concentration show a greater concordance with sites in the centre of Inshriach, and some within the Rothiemurchus estate, possessing lower concentrations than those around the margins of the woodland. For example a cluster of four samples (13, 15, 25, 26) have concentrations between 17000 and 49000 grains g⁻¹ wet weight whereas samples occurring on the margins of the woodland have concentrations of 100000 grains g⁻¹ wet weight or greater. There are some exceptions to this pattern, such as samples 30, 21 and 31 but these are limited in occurrence.

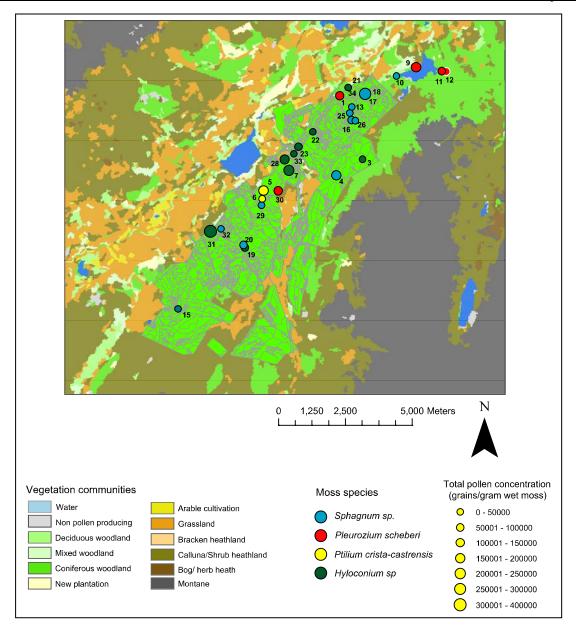


Figure 4.1: Location of modern pollen samples in Inshriach forest. Colours of the points represent moss species and the size the total pollen concentration of the samples.

Vegetation community data obtained from LCM 2000.

4.2.2 Modern pollen deposition around Inshriach

Of the 34 samples collected two had very poor pollen concentrations and were therefore excluded from the analysis. No species identifications were included as confidence could not be placed on all correct species distinctions. Therefore, the decision to combine pollen and vegetation data from the same genus for the analysis was made. This also corresponds to the standard method for presenting pollen data. As expected the remaining 32 samples were dominated by *Pinus*, as shown in the pollen diagram in Figure 4.2, with this taxon providing between 50% and 90% of Total Land Pollen

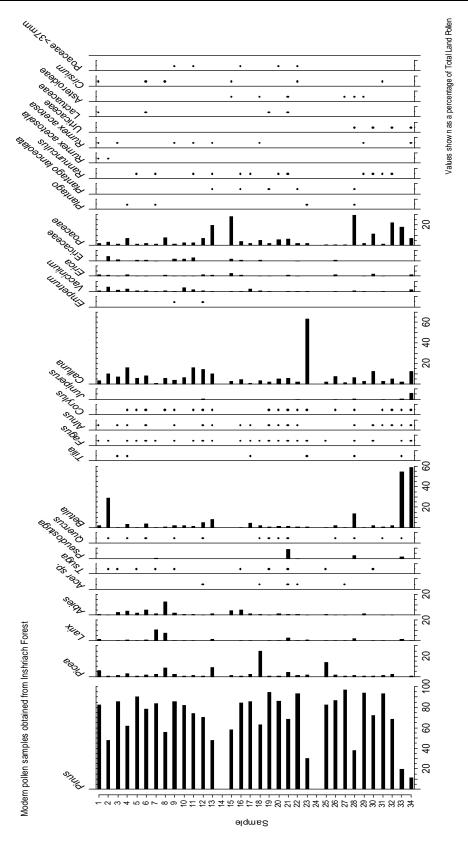


Figure 4.2: Pollen composition of the modern moss samples from Inshriach Forest. The values are percentages of total land pollen including *Pinus*. Samples 14 and 24 had too little pollen in good condition to provide a confident representation of the landscape and are not shown in the plot.

(TLP) in the majority of samples. Where this is not the case samples were derived from open heathland areas or birch woodland (samples 33 and 34). Identified within Figure 4.2 is the lack of variation between the proportions of the other taxa included within the samples. This is especially true of *Betula* and *Calluna* that have fluctuating values around 5% and 15% respectively, with limited exceptional cases where values reach ~60%. When percentages are calculated from Total Land Pollen excluding *Pinus* the variability in occurrence of the other taxa is more apparent where *Calluna* and Poaceae are the major taxa within the assemblage. *Larix* shows little change between the two diagrams indicating its low presence overall.

Diversity of non-arboreal taxa in the pollen assemblages is low in most samples as a large proportion of samples were obtained within a woodland context. Where the dominant species were Japanese larch, Norway spruce or Sitka spruce the ground flora was minimal due to the closed canopy with the main component being bryophytes. Scots and Lodgepole pine woodlands provided an array of openness which also gave a diverse ground flora. Where stems were young stocking density was high giving rise to a bryophyte-dominated ground flora, whereas the older stands that had undergone both thinning and brashing had a greater amount of light with a flourishing *Vaccinium* and *Calluna* dominated flora. Increased diversity is also seen within the heathland situations (site 23) and more open woodland, such as *Betula* in samples 33 and 34.

Multivariate analysis was conducted on the vegetation (within 100 metres of the sampling point) and pollen percentages from the 32 moss samples for the main seven taxa present within these samples i.e. pollen percentages greater than 5%. This was to determine correspondence between the two datasets and sample sites. An initial detrended correspondence analysis (DCA) was carried out and as data were in percentages this was log-transformed with centring by both samples and species. This analysis identified a gradient of less than 4 which suggests that the relationship is linear and corresponding methods should be used (Leps and Smilauer, 2003). As both the sample data and contemporaneous environmental data were available redundancy analysis was conducted (RDA). Figure 4.3 shows an RDA biplot of the vegetation data (red arrows) and the pollen data (blue arrows) from the 32 sites. High correlation between the pollen and vegetation values is demonstrated in the low angle and common directionality between the two vectors and the significance of all axes at p = 0.01 level determined from Monte Carlo permutations. As the axes are formed through correlations in the environmental variables this indicates a strong relationship between the pollen and vegetation. Larix and Picea show the greatest degree of agreement between the pollen and vegetation. The least is shown by Poaceae and *Pinus* which have the largest angle between the pollen and vegetation vectors. The location of the vectors can be used to identify relationships between the different taxa: for example, the opposite direction of Calluna to Larix and

Picea infers that these species are negatively correlated and rarely occur together. In contrast, the lower angles between Pinus, Vaccinium and Calluna imply that these taxa are related, albeit weakly. Figure 4.4 shows an additional biplot of the samples (points) and environmental variables (arrows) from the analysis. The large degree of clustering around the Pinus vector emphasizes the dominance of this taxon in controlling the variation between the pollen samples. Samples 34 and 17 have been placed beyond the Betula vector indicating higher than average pollen values for this taxon. Although this is the case for sample 34, taken from birch woodland, sample 17 was taken from pine woodland and does not contain high levels of Betula pollen within the sample questioning its placement. Sites 25, 7 and 18 were obtained from areas dominated by spruce vegetation supporting its placement along the Picea vector and proximity. Sites 7 and 18 are also located in an area of larch woodland which explains its location close to the Larix vector. The location of sample 23 reinforces the high amounts of Calluna pollen within the sample and the vegetation data.

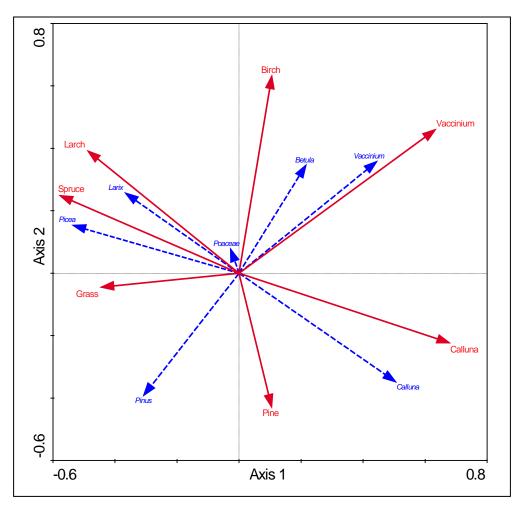


Figure 4.3: A redundancy analysis biplot showing the pollen (blue arrows, italic script) and vegetation (red arrows, bold script) data from the modern pollen samples from Inshriach Forest. Eigenvalues for axis 1: 0.14; axis 2: 0.087

The remaining 32 samples were further reduced to 29 for the ERV analysis due to insufficient pollen and vegetation data within the samples. In addition two taxa were removed, *Vaccinium* and Poaceae. Poaceae is consistently used as a reference taxon in PPE studies and its removal from this analysis necessitated the selection of a replacement. *Picea* was therefore used for this task as it represented a range of pollen and vegetation values at a number of sites. Previous studies that have included *Picea* show a variable relationship between the two taxa with environmental and methodological differences contributing to this dissimilarity. From published results the lowest value for *Picea* when relative to Poaceae obtained was 0.57 from the Swiss plateau (Soepboer *et al.*, 2007) but the highest was 7.80 (von Stedingk *et al.*, 2008). However, the Swiss plateau figure was obtained from lake analyse whereas the lowest value from moss samples is 1.80 (Broström *et al.*, 2004). To test the suitability of *Picea* as a reference taxon, trials were conducted to determine the effect of varying reference taxa upon the pollen productivity estimates (Table 4.1). The results suggested that this had very little impact within the Inshriach data set with relationships between taxa being static even though absolute values varied.

	Pollen Productivity Estimates (PPEs)				
Reference Taxon	Pinus	Picea	Larix	Betula	Calluna
Pinus	1.00	0.16	0.38	0.52	0.17
Picea	6.38	1.00	2.39	3.31	1.06
Larix	2.67	0.42	1.00	1.38	0.44
Betula	1.93	0.30	0.72	1.00	0.32
Calluna	6.03	0.95	2.26	3.13	1.00

	Ratio between PPEs				
Reference Taxon	Pinus: Picea	Larix:Picea	Betula:Picea	Calluna:Picea	
Pinus	6.38	2.39	3.31	1.06	
Picea	6.38	2.39	3.31	1.06	
Larix	6.38	2.39	3.31	1.06	
Betula	6.38	2.39	3.31	1.06	
Calluna	6.38	2.39	3.31	1.06	

Table 4.1: *Above:* A table showing PPEs when calculated using differing reference taxa. *Below:* Ratios between taxa named. The ERV 3 model was used with taxon-specific weighting and 29 sites.

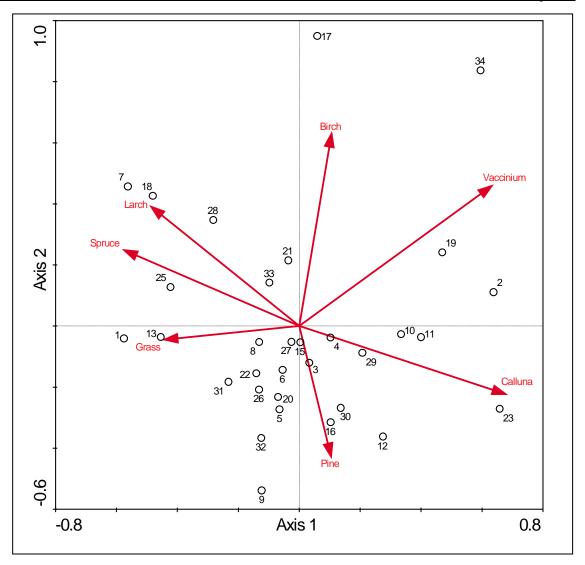


Figure 4.4: A redundancy analysis biplot showing pollen samples (open circles) and vegetation components (red arrows, bold script) from the present landscape of Inshriach Forest. Eigenvalues axis 1: 0.14; axis 2: 0.08

4.3 Generation of PPEs from the pollen and vegetation data

For the analysis the vegetation percentages and absolute values (m²/m²) used were dependant upon the model applied. The absolute values were calculated to represent values relative to the unit of measurement to enable use within the modelling software (S. Sugita, *pers. comm.*). Incremental 10m segments out to 1000m at each site were compared with the pollen deposition at the central point. Initially the 29 sites (full dataset) were used to estimate productivity but tests were also undertaken with different combinations of sites including:

• Open – composed of 11 sites around which arboreal vegetation was minimal

(within 500 m of the sample site)

- Enclosed 18 sites within natural or managed woodland locations
- Wind variation of wind speed between the range of speeds experienced in Inshriach
- Spatial patterning variations in nearest neighbour distance

4.3.1 Full dataset ERV model selection

4.3.1.1 Basal area vegetation values

Figure 4.5 shows the Maximum Likelihood (ML) scores from the three models using taxon specific weighting on the vegetation estimates. Estimates of basal area were used to represent vegetation within the first 100 metres from the sampling point.

All models show a decreasing pattern to an asymptote with increasing distance from the sampling point. ERV 1 shows a sharp reduction in values over the initial 120 m following which the curve increases slighting to form a steady asymptote. Although a similar magnitude of decrease is seen in ERV 2 model the initial decline is more gradual occurring over 320 m. Similarly, ERV model 3 also shows a gradual decline albeit succeeding an initial plateau with values decreasing 120 points over 370 m. Asymptotes, defined by eye, are reached by all models at different distances corresponding to the RSAP. However, it is ERV 3 that exhibits the lowest ML score overall and therefore should theoretically produce the best PPEs.

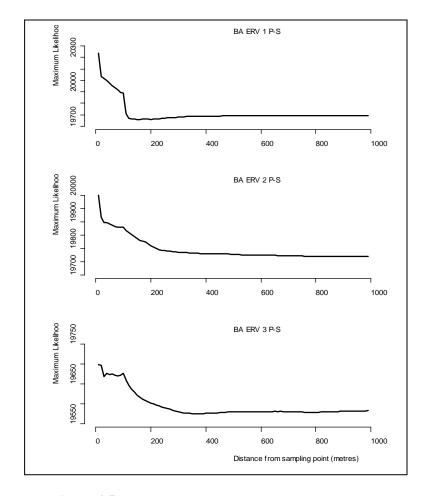


Figure 4.5: Maximum likelihood scores with increasing distance from the sample point generated from the basal area dataset

4.3.1.2 Full dataset with canopy cover vegetation estimates

Figure 4.6 shows the results from the ERV models when taxon-specific weighting is applied to the data sets with canopy cover generating the initial vegetation representation. Both ERV 1 and ERV 2 produce curves that decrease to an asymptote with increasing distance from the sampling point. Differences between these two models are represented in the gradient of this initial decline with ERV 1 showing a steep yet smooth curve whereas ERV 2 has a high degree of fluctuation. Although ERV 3 shows a gradual decrease in the initial 230 m an increase in the ML score occurs subsequent to this minimum being reached.

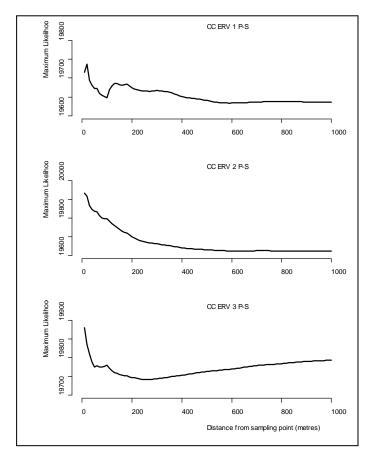


Figure 4.6: Maximum likelihood scores with increasing distance from the sample point generated from the canopy cover dataset

The lowest ML scores achieved with each model vary with ERV 1 and 2 occurring at a similar distance of 569.9 m and 609.9 m respectively. For ERV model 3 this distance is reached by 249.9 m but subsequently increases therefore placing doubt on this estimation. Based upon these low scores it is, theoretically, ERV model 2 that produces the best PPEs as the lowest maximum likelihood score denotes the best fit between the two datasets. Similar ML scores are obtained when these results are compared with the BA group indicating similarities with the relationships encountered.

4.3.2 Distance weighting functions

Whilst ERV 3 and ERV 2 produced the lowest maximum likelihood scores significant variation occurred with the application of various distance weighting functions, comprising $^{1}/d$, $^{1}/d^{2}$ and taxon-specific functions.

4.3.2.1 Basal area estimates - ERV 1

Both the taxon specific and ¹/d weightings exhibit a strong decreasing curve to an asymptote, values from the output agree and therefore show strong correlation with the lowest values reaching 19750 at 200 m in both models. An asymptote is reached shortly after this point at 510 m for ¹/d and 580 m for the taxon specific weighting. The ¹/d² weighting shows a similar decrease yet this pattern is not as strong and values not as low. The minimum values reached (20041.8) at the end of the sample distance 1000 m; although this is the end of a slightly decreasing asymptote commencing at 610 m.

ERV 2

Again, ¹/d and the taxon specific weightings show similar patterns both decreasing to an asymptote. The transition is not as sharp as that for ERV 1 with the overall decrease being much less (~200 m) over a much longer distance. The lowest values are shown by the taxon-specific weighting and therefore represent the strongest correlation between the pollen and vegetation. However, both graphs reach their lowest value at the limit of the survey distance, 990 m. The ¹/d² weighting for ERV 2 shows a weak correlation between the data; an almost straight line is produced. Values decrease from 20009.3 at 10 m to 19993.0 by the limit of the vegetation survey.

ERV 3

Shown in Figure 4.7, the taxon specific and ¹/d weightings replicate the same pattern with decreasing values to an asymptote; it is the latter that exhibits the lowest values overall and therefore the strongest correlation. The lowest value on the ¹/d curve is at 390 m with the taxon-specific weighting reaching this at a similar point, 380 m. As with ERV 2 the ¹/d² weighting reproduces a straight line with little correlation between the data sets experienced.

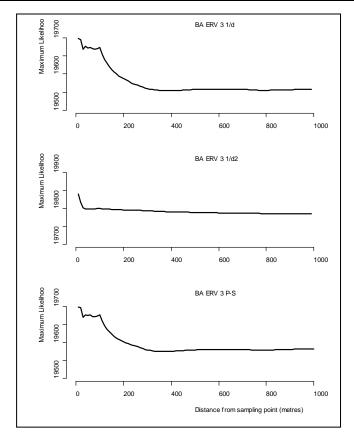


Figure 4.7: Maximum likelihood scores with distance from the sampling point for the ERV 3 model Basal Area dataset. *Top:* inverse distance weighting; *middle:* inverse-distance square weighting; *bottom:* Taxon-specific weighting.

4.3.2.2 Canopy Cover dataset - ERV 1

Correspondence occurs between the curves of the ¹/d and taxon-specific weighting functions. Both show a rapid decline in values over the first 120 m of the survey distance after which values increase slightly before decreasing again but at a shallower gradient. The lowest value along the taxon-specific curve (19633.4) occurs at 590 m. At the same point on the ¹/d curve the value is 19641.1 which shows the relationship between the two curves. Poor results are shown from the ¹/d² weighting which is represented by stable values with variation across the length of the survey area no larger than 0.3 between any points.

ERV 2

¹/d and taxon-specific weightings provide similar curves with both showing a gradual decrease in maximum likelihood scores with increasing distance from the sample point. ¹/d reaches an asymptote at 680m although values continue to decrease slightly after this point. The taxon-

specific curve shows a more defined asymptote as after 610 m (19524.6) the curve remains stable. In contrast to ERV 1 it is the taxon-specific weighting that calculates the lowest maximum likelihood scores with the ¹/d curve at 610m having a value of 19693.3. The ¹/d² function is striking by showing no variation in the maximum likelihood scores with increasing distance.

ERV 3

Again, the results from the taxon-specific and 1 /d weighting functions provide the greatest correlation, shown in Figure 4.8. However, it is the latter that shows the lowest values overall. The initial 130 m show some fluctuations in the values obtained from both models after which there is a gradual decline to the lowest point at 280 m with 1 /d having a value of 19734.5 and the taxon-specific 19742.2 after which there is a slight increase. Little change occurs overall in the values obtained from the 1 /d 2 weighting with only a slight decrease in the maximum likelihood score over the initial 160 m.

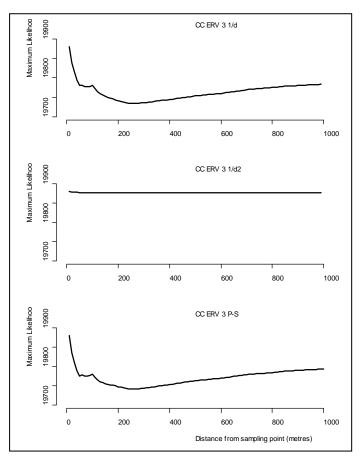


Figure 4.8: Maximum likelihood scores with distance from the sampling point for the ERV 3 model Basal Area dataset. *Top:* inverse distance weighting; *middle:* inverse-distance square weighting; *bottom:* Taxon-specific weighting.

4.3.3 Relevant source area of pollen

Estimates for the relevant source area of pollen are similar between models. This is based upon both defining the asymptote by eye (subjective) and employment of the moving-window linear regression (objective); the former is based on estimation of the distance at which the maximum likelihood curve flattens. In such cases where the score falls to a minimum and rises slightly following this the distance at which the minimum is reached is taken as the RSAP. Details of the moving window linear regression are given in Chapter 3; however, limitations within the modelling software only allow these to be calculated where the taxon-specific weighting is applied to the model. As the $^1/d^2$ weightings for all ERV models did not reach an asymptote they will not be considered here as a RSAP cannot be estimated for these models.

		Canopy cov	Canopy cover data set		Basal area data set	
		Estimated (metres)	Moving window linear regression	Estimated (metres)	Moving window linear regression	
ERV1	¹ /d	580	-	309	-	
	$^{1}/\mathrm{d}^{2}$	Not reached	-	519	-	
	Taxon- Specific	590	120	370	650	
ERV 2	¹ /d	850	-	880	-	
	Taxon- Specific	580	640	600	840	
ERV 3	¹ /d	280	-	390	-	
	Taxon- Specific	260	260	380	630	

Table 4.2: Estimates of relevant source area of pollen for the basal and canopy cover datasets of Extended R-Value models 1, 2 and 3.

Table 4.2 shows the results of the estimated RSAP and the moving-window linear regression where applicable. The distances estimated from the maximum likelihood curves show a great amount of variability associated with the model applied and the data set used within the analysis. Estimates obtained from the canopy cover data set are high for both the ERV 1 and 2 models doubling the estimates obtained from ERV 3. In contrast, the estimates from the basal area results show less consistency both within and between the models; results from ERV 1 highlight this with estimates of 309 m, 519 m and 370 m. Interestingly, when ERV 3 is considered there is a good relationship between the estimates of the two weighting functions and results are similar to those obtained from the canopy cover data set.

Consistency shown within the estimates of RSAP is not replicated within the moving-window linear regression estimates. The lowest values are continually provided by the canopy cover data set. The lowest value is obtained from ERV 1 of 120 m which is approximated as 650 m within the basal area results. Interestingly, comparable results were achieved for the estimated values from the output of ERV 3 when the moving-window results are assessed this is lost with just under 400 m difference between the estimates of the two data sets. The most consistent model between basal area in terms of relevant source area of pollen distance is model ERV 2.

4.3.4 Pollen productivity estimates

Each taxon will be considered in turn with the values from all ERV models and weighing functions. As *Picea* was chosen to be the reference taxon during the analysis this value was set to unity and therefore is not described below. All values shown are an average of the estimates obtained from the RSAP to the maximum survey distance to smooth any small amount of variation. Where this was not possible, such as an increase in ML score following the minimum, the value from the lowest maximum likelihood score was taken as the representative PPE dataset with no averaging over the survey distance.

4.3.4.1. Basal area estimates

Pinus

There is substantial variation between the values obtained for this taxon which predominantly relates to the ERV model used, Figure 4.9. The highest values were obtained from ERV 3; the most robust values from which were obtained from the taxon-specific and ¹/d weightings, 6.31 and 6.77 respectively, due to their low ML scores and correlation between the values when one standard deviation is considered. ERV 2 estimates are similar to those of the ERV 3 with less variation exhibited between the distance weighting models used. ERV 1 recorded the lowest values for *Pinus* with 2.19 when the ¹/d² weighting was used with the other functions predicting slightly higher values.

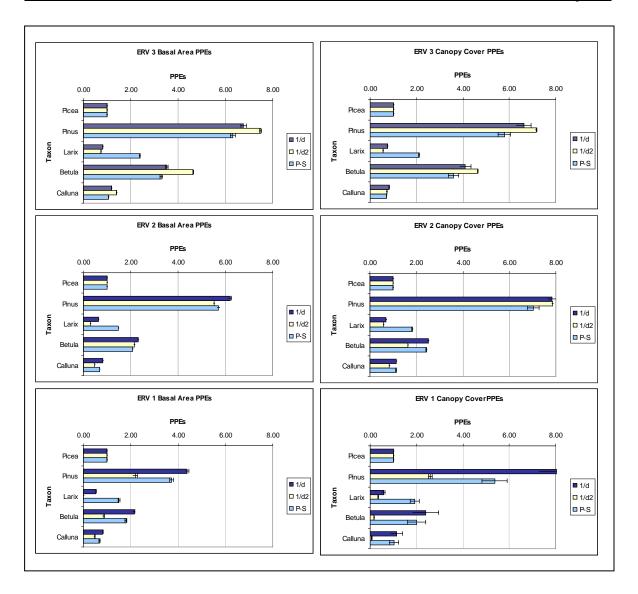


Figure 4.9: PPEs generated from the three ERV models. Values are averaged from the RSAP to the 1000 metre limit with the error bars representing 1 S.D. ¹/d: inverse distance; ¹/d²: inverse distance squared; P-S: taxon-specific weighting of Prentice and Sugita.

Figure 4.10 shows a scatter plot (adjusted pollen and vegetation data) from the RSAP distance for ERV model 3 as this produces the most linear model, especially for *Pinus*, which emphasises the strength of relationship between the two datasets. This is seen in the comparison of Figure 4.10 (a), the original vegetation and pollen data, and Figure 4.10(b) the ERV adjusted pollen and original vegetation data. ERV 2 produces a similar linear relationship although the correlation is much lower; ERV 1 produces the weakest relationship for pine with an r² value of 0.379 when adjust vegetation and pollen proportions are assessed.

The intercept of the models is placed at the origin for most taxa but for *Pinus* this is greater at 0.4 (40%) accounting for the dominance of this taxon within the background rain. When the background values for *Pinus* are calculated as a proportion of total pollen loading for each distance these show a decreasing pattern representing an increasing amount of vegetation being included within the sampling distance. However, once all of the vegetation within the 1000 m was included within the dataset the regional pollen component for *Pinus* was significant. Although this value differs between each model, dependent upon its calculation methods, they remain high with 31% for ERV 3; 38% for ERV 2 and 54% for ERV 1; these are all when the taxon-specific weighting is used for the vegetation correction factor.

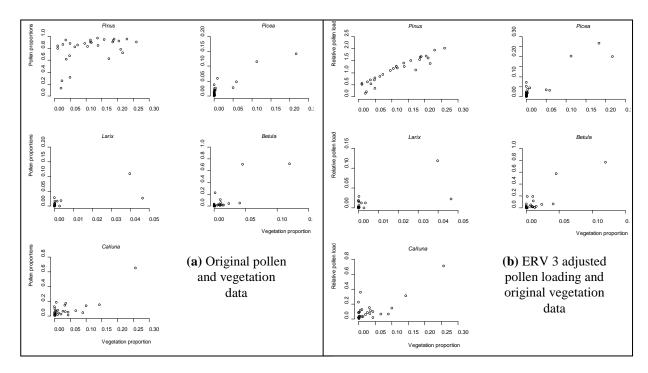


Figure 4.10: Scatter plots of pollen and vegetation data using the basal area data from (a) the original dataset used to feed the model (b) adjusted pollen loading and original vegetation parentages from ERV model 3.

Larix

Productivity estimates are consistently low when the distance functions are used for the weightings with values all below zero; however, when the taxon-specific weighting is applied these values at least double. The lowest prediction for *Larix* is ERV 1 0.004 with $^{1}/d^{2}$ weighting but this rises to 1.5 when the same model is used but the taxon specific weighing is applied. The highest value is obtained from ERV 3 with the taxon-specific weighting when it is predicted to be 2.39.

The two outlying points (sample 7 and 8) allow for calculation of a linear model for the plots but potentially force the placement of the model (Figure 4.10). Similarly, background values for this taxon are both consistent and low between the models when the taxon-specific weighting is applied with values showing no variation from 0.2 (20%) of the total pollen loading.

Betula

Estimates obtained from ERV models 1 and 2 are similar with values falling between 1.80 and 2.31 (Figure 4.9). A low value, 0.86, from ERV 1 is evident when $^1/d^2$ weighting is applied and is the lowest value obtained for this taxon. ERV 3 shows the highest values with the $^1/d$ and taxon-specific weighting 3.52 and 3.29, respectively. Although a higher estimate is provided with the $^1/d^2$ weighting, 4.64, due to the high maximum likelihood scores from this function results have to be discarded.

Scatter plots from the respective models (Figure 4.10) show these patterns identified with both ERV 1 and 2 have a low value, site 17, which pulls down the regression model affecting the productivity estimate relating to the similarity in the results obtained. This value within the ERV 3 graph (Figure 4.10) is closer to the origin, where there are a cluster of values on all graphs shown, and therefore the influence of this point is curtailed increasing the steepness of the linear regression. Background values for this taxon are low when the taxon-specific weighting is applied to the three ERV models. Values fluctuate between 0.95, 1.14 and 0.7 for ERV 1, 2 and 3 respectively, corresponding to the line intercepting the origin.

Calluna

Comparable estimates are given from ERV models 1 and 2 with most values below 1; the exception to this is from ERV 2 when the taxon-specific weighting is applied with a value of 1.19 generated. Minimal variation in output is encountered when the different weighing functions are applied. Again, ERV 3 returns the largest values for this taxon although the magnitude of this difference is not as large as seen with other taxa.

Scatter plots of these results show a better range of pollen-vegetation values than for some species; although there is a cluster of values around the origin there are more sites representing high pollen and vegetation values. The strongest linear relationship is exhibited from ERV 3 with the weakest ERV 1 contributing the strength of the relationships for all taxa. *Calluna* shows high background values relative to the other major woodland taxa within the vegetation survey distance. Values range from 3.52, 4.76 and 3.27 for ERV 1, 2, and 3 respectively when the taxon-specific weighting is applied.

4.3.4.2 Canopy cover dataset

Pinus

PPEs for *Pinus* (Figure 4.9) are consistently high regardless of model of weighting function and are greater than those seen within the basal area group. The only model to show low estimates for this taxon is ERV 1 with $^{1}/d^{2}$ weighting at 2.57 with the highest at 8.67 for the same model but $^{1}/d$ weighting. Differences within the ML scores do not appear to be a large control over the magnitude of the PPEs.

Figure 4.11 shows scatter plots of the original and adjusted pollen and vegetation for ERV 3 with taxon-specific weighting. Immediately apparent are the high vegetation and pollen values for *Pinus* within the original dataset creating an almost horizontal line. When adjusted by the ERV 3 model the *Pinus* data has the greatest change to a strong liner model whilst the other taxa show little movement from the original plot.

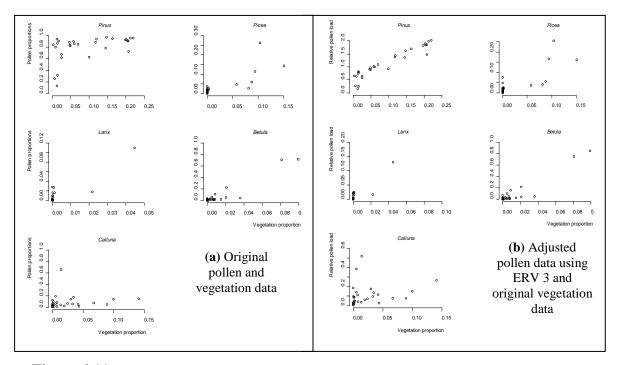


Figure 4.11: Scatter plots of pollen and vegetation data using the canopy cover data from (a) the original dataset used to feed the model (b) adjusted pollen loading and original vegetation parentages from ERV model 3.

Larix

Low values are produced for this taxon by the ¹/d and ¹/d² weighting functions with the taxon-specific consistently generating higher estimates, shown in Figure 4.9; however, there is no relationship between the model used and the values obtained. There is a large difference between

the highest and lowest values with ERV3 P-S model generated the highest value at 2.11 and 0.34 for ERV $1^{-1}/d^{2}$.

The original data scatter plot for *Larix* (Figure 4.11 (a)) is distinctive in the two outlying points that are more accentuated than in the basal area dataset, especially with the remaining sites clustered around the origin. Little change is made after the application of ERV 3 P-S. Background values for this taxon are low as previously seen.

Betula

This taxon shows a relationship to the model used rather than the weighting applied. ERV 3 provides the highest estimates for this taxon although there is not a large difference between the lowest ERV 3 value of 3.6 and the highest remaining value of 2.5. Models ERV 1 and ERV 2 give similar estimates for the productivity with most between 2 - 2.5.

The pollen and vegetation data (Figure 4.11 (a)) highlights two high values of both vegetation and pollen within the dataset, sites 33 and 34. As with *Larix* application of the model changes the plot slightly but this only affects the two higher value points.

Calluna

Estimates are low for this taxon with the lower values generally calculated from ERV 3 ranging from 0.70 - 0.82. The remaining models provide concomitant results with lower values generated when the inverse-distance squared weighting is applied. The lowest value of 0.07 is generated from ERV 1 1 /d 2 but this seems unrealistically low.

The scatter plot in Figure 4.11 has a large number of points with high vegetation proportions related to low pollen proportions creating an almost horizontal line. Although increases in the gradient of this are undertaken on the application of the ERV 3 P-S model the changes are slight. Noticeable, however, is the higher intercept of the model indicating the larger background proportion than some of the other taxa discussed.

4.3.5 *Summary*

Similarities and differences are evident in the results of the ERV analysis which are dependant upon the dataset used, canopy or basal. For example the model that produced the lowest ML scores varies between the two datasets with notable differences in the form of the graphs. On the contrary, analogous patterns are exhibited when different weighting mechanisms are used to manipulate the data. Estimates of RSAP also differ between the two groups with the canopy cover consistently

providing larger values. However, difficulties arise in assessing the accuracy and precision for determination of the RSAP. Consequently, it was decided that the largest values, moving-window estimates, would be used to represent the RSAP. As the point at which the RSAP is reached also marks stability within the productivity estimates should this be larger than the actual value little difference would be incorporated. If the distance of the RSAP was underestimated this could contain some erroneous values and significantly impact on the final estimates of productivity.

Despite differences in the ML scores there is surprising agreement in the PPEs produced between the canopy cover and basal area dataset. In the majority of cases the canopy cover produces larger estimates than the basal area, which is a likely response to the higher values feeding the models. ERV 1 produces the lowest values with some near zero estimates for the subordinate taxa. Patterns within the PPEs from weighting functions are replicated between the two groups for ERV 2 and 3, but it is the latter where there is also agreement between the magnitudes of the estimates with only a small difference occurring. If the most appropriate models are chosen upon the lowest maximum likelihood scores it would be ERV 2 for the canopy cover dataset and ERV 3 for the basal area group. On this basis estimates for most taxa show agreement but there is a large difference in the values for *Betula* where the basal area dataset produces the larger values. Overall, BA ERV 3 P-S provide the best PPEs for Inshriach as this model provides one of the lowest ML scores but also is more theoretically robust in terms of weighing mechanisms as it is based upon taxon-specific dispersal properties. By applying the weighting to each taxon individually considerations over size and shape of the grain can be made in contrast to applying a universal weight which may not be suitable to all taxa being investigated.

Dominance of *Pinus* as the background component is unsurprising but the results for *Calluna* contributing a large amount to the regional pollen rain is interesting. Low proportions of *Larix* and *Picea* support their limited presence within the managed woodlands. Similar levels of background pollen are contributed by *Betula* despite its prominence within both the natural and managed woodlands.

4.3.6 PPE generation using open and enclosed sites subset

Results presented below show PPEs derived from 'open' and 'enclosed' sites. The former represents those from non-woodland situations with the latter from forest hollows. The aim of this analysis was to test the significance of site characteristics in estimating productivity. As the previous section showed model ERV 3 with the basal area dataset to provide the lowest ML scores this was also applied here.

4.3.6.1. Open

Figure 4.12 highlights the amount of variability in both the magnitude and amount of fluctuation. The initial 40 m also returned ML values of 0 (did not record a score) that is subsequently followed by an increase to the maximum value at 100 m before declining. Associated with this is a difficulty to identify the RSAP. If measured by eye an estimate would fail to be reached yet the moving window analysis provides an estimate of 360m.

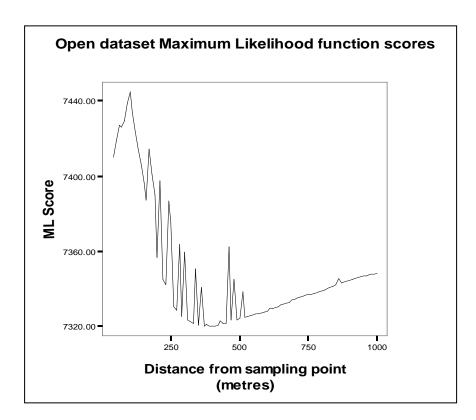


Figure 4.12: Maximum likelihood score curves for ERV analysis of samples sites within open areas.

Values obtained are shown in Figure 4.13. The dataset suggests that all of the taxa have low productivities; this is especially true for *Calluna* with a value of 0.28. *Pinus* has a similarly low value of 1.61 twice that of the value achieved for *Betula*.

Analysis of the scatter plots relating vegetation abundance to the relative pollen loading for these taxa at the RSAP suggest that both *Pinus* and *Calluna* have a strong linear relationship and should ensure that robust estimates are achieved from this analysis. Similarly, *Picea* has a strong relationship supporting its use as a reference taxon. In contrast, there are scarce points within the

upper portions of the scatter plots for both *Betula* and *Larix*, more significantly so within the latter, which may induce some error into the results.

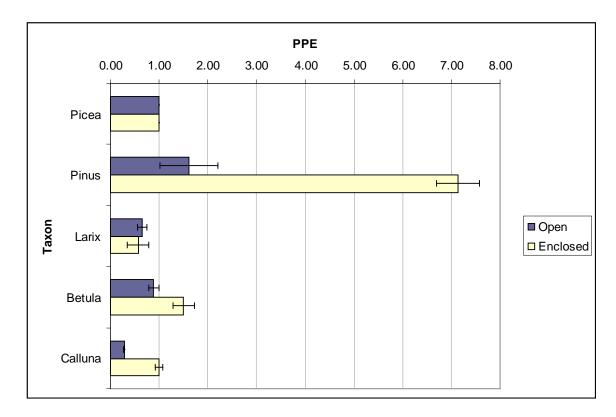


Figure 4.13: Pollen productivity estimates from the open and enclosed sites within Inshriach Forest as an average from the RSAP to the maximum sampling distance. Error bars represent 1 S.D.

4.3.6.2 Enclosed

The maximum likelihood scores show little change in overall value over the survey distance by showing only a 30 point reduction, represented in Figure 4.14. However, the patterns produced within this decrease show large fluctuations with a minima being reached twice, firstly at 100 m then subsequently at 1000 m. Although the moving-window linear regression model suggests that the RSAP is placed at 140 m there is an increase in value subsequently. Had the measurement been estimated by eye the RSAP would not be reached as the graph does not reach an asymptote as the definition necessitates.

Values obtained from the analysis are shown in Figure 4.13. *Pinus* has a high estimate comparable to the full dataset with the other taxa being much lower. *Betula* and *Calluna* express similar values with *Larix* lower still at 0.57.

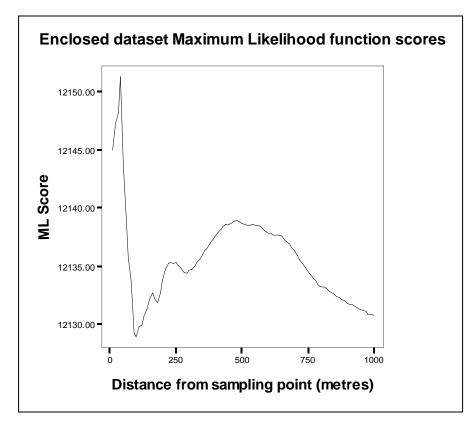


Figure 4.14: Maximum likelihood scores from the ERV analysis of sampling sites from enclosed locations within Inshriach Forest.

Scatter plots produced from the pollen and vegetation data used within the ERV analysis show that the data used within the analysis of *Pinus*, *Picea* and *Betula* have a good range of points ensuring that a robust result is achieved. *Larix* and *Calluna*, however, show a low number of points and these are concentrated around the lower vegetation-pollen portions of the graphs which will impact on the ability to fit a strong linear model to the dataset and consequently the PPEs generated

4.3.6.3 Summary

Theoretically, the lowest maximum likelihood scores represent the best fit between the pollen and vegetation data and therefore produce the best estimates of pollen productivity; consequently, the values for the open woodland sites should be more robust for Inshriach with scores 5000 points lower that the enclosed sites. However, the difference in the number and composition of sites used will have an impact on the output and there is a large difference in the number and of sites used between the two datasets, therefore a direct comparison of ML scores cannot be made. Furthermore, the amount of fluctuation in both graphs questions the representativeness of the output. With respect to the open dataset the changes are of greater magnitude yet the enclosed set shows more pronounced and sustained changes. As mentioned, determination of the RSAP is

problematical which is necessary to calculate the PPEs. Consequently, although the estimates of RSAP imply that there is a larger RSAP within the open areas than enclosed, supporting previous studies, this cannot be regarded as conclusive. On the contrary, little difference will be incorporated into the PPEs as both have low standard deviations thus variation of this distance would not significantly alter the estimates which can be taken as representative.

Dissimilarity in PPEs from the two environments is immediately evident in the *Pinus* values. Differences do occur in the other taxa but much less pronounced with *Larix* values are in agreement. Interestingly, the highest *Calluna* value occurs within the woodland context suggesting that the taxon is more productive within this situation or that the vegetation component was underestimated in the woodland. Contradiction between the *Pinus* PPEs of the two environments could relate to a number of factors within the dataset: for example differences between the number of sites in each group, pollen deposition at each site within the group, or it could ultimately suggest a difference between open and managed woodland productivities.

Further assessment of the data to examine this point suggests that the linear relationships between the pollen and vegetation differ on a group- and species-specific manner. Within the open dataset it is *Calluna* and *Pinus* that exhibit the strongest linear relationships with a good range of values. In the enclosed it is the main arboreal taxa that show this pattern for *Pinus*, *Picea* and *Betula*. Ultimately, this is a response to the occurrence of the different taxa within the environments; greater presence at sites enables more values to be plotted giving a better relationship. An interesting point is the presence of extreme values which are mainly seen within the *Larix* and *Betula* sets. These were initially identified within the pollen data discussed in section 4.2 however the reduction of sites included within the two sets accentuates this further. Therefore the *Larix* estimates within these environments should be treated with caution as there are too few points, more so in the open group, to provide representative estimates.

4.3.7 Wind speed parameter variations

Most pollen obtained from fossil samples originates from wind-pollinated taxa as this is produced in large quantities and can be carried vast distances. When PPEs are obtained it has been standard within most studies to use a wind value of 3 m s⁻¹. However, it has been shown that the average yearly wind speed for Inshriach varies between 3 - 5 m s⁻¹ (Mackay, 1999) and therefore tests were carried out on the effects of different wind speeds on the PPEs to find the most representative values for the site. The results presented above relate to the 3m s⁻¹ wind speed whereas below the extremes of the spectrum are discussed only.

Figure 4.15 shows the maximum likelihood scores from the ERV 3 model runs with the Prentice-Sugita weighting applied. Evident from the figure is the difference in the model results with changing wind speed. Overall, there is a change in both the magnitude of the maximum likelihood scores but also the patterns produced by the graphs. Firstly, 1 m s⁻¹ shows a high ML score which significantly decreases to the 5m s⁻¹ speed. The forms of the graphs differ between these two speeds with the latter showing a slightly greater decrease to a minimum after which there is a general increase in the maximum likelihood scores.

Similar patterns are identified within the estimates of RSAP as seen in the PPE values when derived using moving window linear regression. This point is not reached if the wind speed is set to 1 m s⁻¹ and then slowly decreases to 350 m if the wind speed is 5 m s⁻¹. The decrease in the RSAP slows with increasing wind speed above 3 m s⁻¹. Similar results, decreasing RSAP with increasing wind speed, are seen if the estimates are obtained by eye with 1m s⁻¹ at 790 m and 5m s⁻¹ at 380 m.

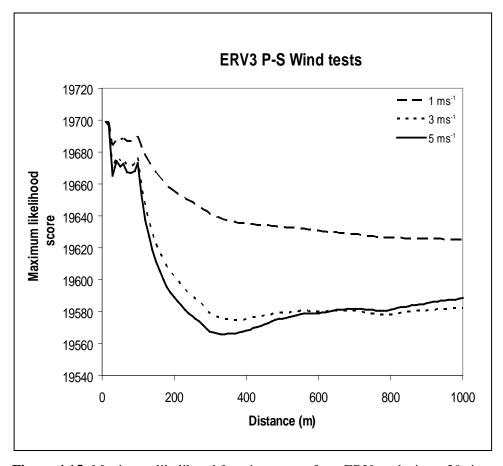


Figure 4.15: Maximum likelihood function scores from ERV analysis on 29 sites with differing wind speeds.

There is a steady increase in the proportion of total pollen loading which is accounted for by the background, or regional, component of the vegetation which is connected to the distance at which the RSAP is reached, as wind speed reduces so the RSAP falls with an increase in the regional component to the site. With a wind speed of 1 m s⁻¹ the background proportion accounts for only 11.7% of the total loading whereas at 5 m s⁻¹ this is 57% (results not shown). The main constituent of the background is *Pinus* in both cases and there is little variation in the value of this with changing wind speed with all values between 85 - 86% of the total background component. All other taxa are present within this rain but in very low abundance. *Calluna* and *Betula* are the second largest components at between 4 - 7% and ~2% respectively.

A pattern of increasing productivity estimate with increasing wind speed is shown for all taxa apart from *Larix* which mirrors this change with a decrease in values (Figure 4.16). Large error margins are clearly evident which highlights the variance within the input data. If this is taken as erroneous, *Pinus* becomes the greatest producer at 5 m s⁻¹ wind speed with a value of 7.87, which is much lower at the 1 m s⁻¹ wind speed. The same pattern is true of *Betula* and *Calluna*, with inflated values at greater wind speeds.

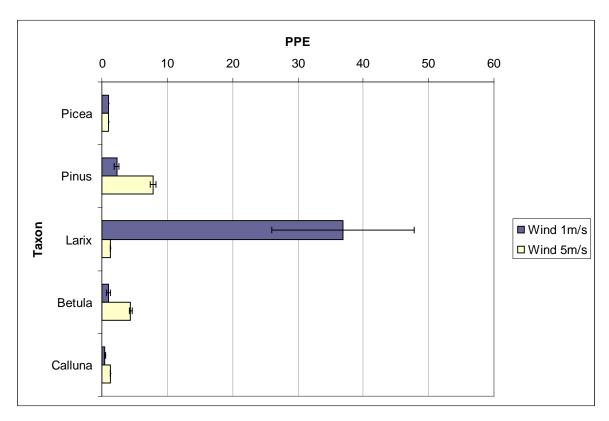


Figure 4.16: Pollen productivity estimates for wins speeds of 1 m s⁻¹ and 5 m s⁻¹. The error bars are 1 S.D. limits of the range of values from the RSAP to the maximum sampling distance.

4.4 Modelling the modern landscape of Inshriach

The aim of this analysis was to assess the similarity in modelling output when different parameters were supplemented from the PPE groups derived in analyses shown in the previous section. Simulations of pollen deposition were obtained from Humpol and vegetation estimates using the LRA. Both models were used to compare the sensitivity of different approaches to these changes and to ensure robust data selection for further analysis.

4.4.1 Humpol software suite

Pollen deposition was simulated at four sites within the region; two large lochs (Loch Alvie and Loch An Eilein) and two small sites (Lochan Geal and a small forest hollow) shown in Figure 5.1. Composition of surface samples from the sites was used to compare with the simulated pollen assemblages at the same location. This was to provide an independent validation before modelling of the cores. The grid used for the simulations was formulated from community based classification data with the composition of these communities estimated from literature and field observations (see section 3.1.4).

4.4.1.1 Full data set

For both Loch Alvie and Loch an Eilein the results obtained with the ERV 3 productivity estimates were initially identical regardless of the distance weighting mechanism applied and vegetation dataset used during the calculation of these parameters, ERV 1 and ERV 3 provide similar results as shown in Figure 4.17. ERV 2 has the best fit at both sites with ERV 3 P-S also providing confident estimates. Both large sites performed well yet it is Loch an Eilein where consistently better correspondence is identified. For example, *Pinus* at Loch an Eilein is accurately modelled in the groups with no estimate being $\pm 8\%$ of the observed value; in contrast Loch Alvie estimates are overestimated by at least 4% and as much as 25% of the actual value.

The two smaller sites, Figure 4.17, show differences between their degrees of correspondence to the actual values. The forest hollow within Inshriach (InshH1) produced very good results with the BA ERV2 P-S estimates providing the strongest correlation. Species distinctions are present with *Calluna* showing better results with the basal area groups whereas *Pinus* shows no preference. Patterns are not replicated at the Lochan Geal site where poor results are observed. Clear differences between the performance of *Pinus* and *Betula* are exhibited when the simulated and actual assemblages are compared. The dominant taxon in the simulated assemblage is the reverse of the actual patterns. Difficulty in modelling of the remaining taxa is also shown with *Calluna* being consistently overestimated in both the datasets.

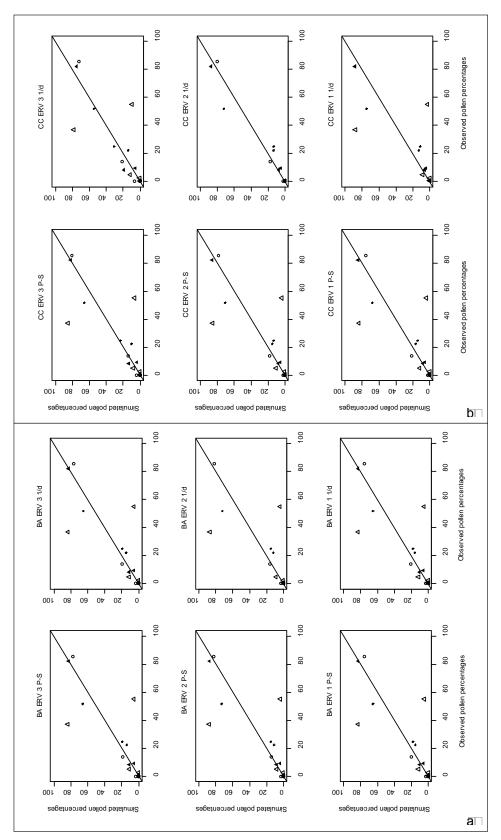


Figure 4.17: Scatter plots showing observed and simulated pollen percentages from the Humpol software. (a) Canopy cover calculated PPEs (b) Basal area calculated PPEs. Different sites are represented by symbols; ●: Loch Alvie, ▲: Loch An Eilein, ○: Insh H1 (Forest Hollow), Δ: Lochan Geal

4.4.1.2 Open and enclosed values

Differences observed between the pollen productivities for open and enclosed sites are in agreement with the simulation results from these parameters (Figure 4.18). At Loch an Eilein it is the open dataset that produces the most comparable results to the observed values. *Pinus* is simulated convincingly with this dataset whereas the enclosed dataset overestimates the occurrence of this taxon by 13%. *Calluna* is well approximated in both datasets; however *Betula* shows disparity being accurately represented within the open set but underestimated when modelled with the enclosed values. Loch Alvie shows very poor correspondence with results generated from the open dataset providing the best results between the two datasets. *Pinus* shows the poorest fit with an overestimation of 25% in the enclosed and 13% in the open dataset. *Betula* shows the best fit in both sets being simulated within the 95% confidence interval bands of the actual data from the enclosed dataset and a only a 4% underestimation in the open.

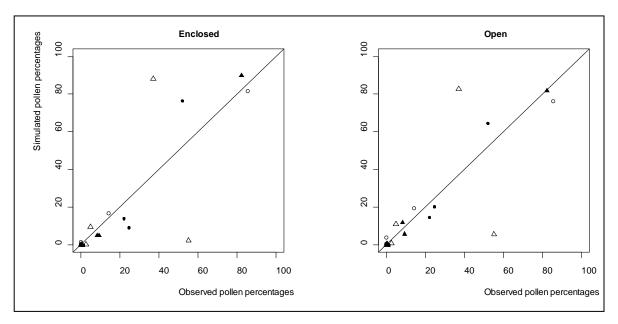


Figure 4.18: Scatter plots showing observed and simulated pollen percentages from the Humpol software. *Left:* Enclosed groups derived PPEs. *Rigt:* Open groups derived PPEs. Different sites are represented by symbols; •: Loch Alvie, Δ: Loch An Eilein, ○: Insh H1 (Forest Hollow), Δ: Lochan Geal. The line represents a perfect correlation.

At Inshriach H1 the enclosed PPEs provide an exceptional correspondence with all taxa modelled within the 95% confidence limits of the observed data. The open dataset provides a good approximation of the observed pollen percentages with *Calluna* having the largest overestimate of all taxa of 5%.

Results from Lochan Geal demonstrate the same patterns seen within the previous parameter datasets discussed in section 4.3.1.1. A severe overestimation of *Pinus* and under-estimation of *Betula* is seen in both the open and enclosed dataset. Additional over-estimates of *Calluna* in both sets suggest these PPEs are not representative of Lochan Geal.

4.4.1.3 Wind variations

Although all values were used within the software to generate the simulated assemblage profiles covering the range of potential wind speeds within the landscape of Inshriach, the two extremes of the spectrum are discussed here (1 and 5 m s⁻¹). Differences exhibited within the actual pollen productivity estimates are fed through into the simulation results for some of the taxa but this does not extend to all (Figure 4.19).

At Loch an Eilein the results of both datasets are good when considered with the actual data. *Pinus* shows only a 0.4% difference between the two PPE groups. Similarly, *Calluna* shows little difference when simulations are run with the 1m s⁻¹ or 5m s⁻¹ parameters and comparisons with the actual data show strong correspondence with the former showing marginally better results. Differences between simulated and observed data at Loch Alvie for *Pinus* are large, 13% and 14% for 1m s⁻¹ and 5m s⁻¹ respectively, demonstrating performance but also similarities between the two parameter groups. However, *Betula* values show greater disparity between the two PPE groups with the best at 5m s⁻¹, still underestimating the actual value by 4% and a 9% underestimate for 1 m s⁻¹.

Simulated results from Inshriach H1 are well approximated by both groups yet it is the 5m s^{-1} dataset that provides the best estimations. From this group *Pinus* is underestimated by 13% whereas this is 8% in 5m s^{-1} and *Calluna* is overestimated by 9% in the 1m s^{-1} group and only 4% in the 5m s^{-1} group.

As previously seen, the actual relationship between *Betula* and *Pinus* is not represented in the simulated results at Lochan Geal. Values for *Calluna* are also overestimated being ~5 - 8% greater than the actual values. However, despite not being concomitant with the observed data differences between the two PPE sets are small. Considering the differences in the PPEs themselves this is surprising.

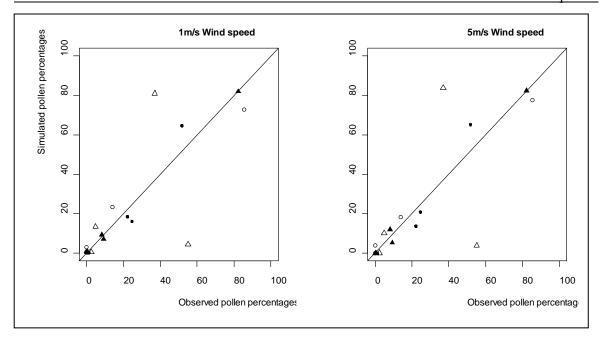


Figure 4.19: Scatter plots showing observed and simulated pollen percentages from the Humpol software. *Left::* PPEs from 1m/s⁻¹ wind category. *Right:* 5m/s⁻¹ wind speed PPE category. Different sites are represented by symbols; •: Loch Alvie, ▲: Loch An Eilein, ○: Insh H1 (Forest Hollow), Δ: Lochan Geal

4.4.1.4 Summary

Simulation of pollen assemblages with the different PPE groups indicates general stability within the output despite slight parameter changes within the Humpol software. Examination of the simulated assemblages highlights the similarity between these groups with some showing greater accordance than others. For example the open and enclosed PPEs produced distinguishable results highlighted at Loch Alvie whereas the wind test groups show constancy.

Use of statistical analysis fails to distinguish any patterns within the data. Pearson's correlation coefficient analysis was performed on all datasets to assess the strength of correlation between the observed and simulated pollen percentages. Lochan Geal was the only site that did not show a statistically significant linear relationship at the p=0.05 level and was for all PPE groups tested. This could be a manifestation of the low number of sample points within the analysis. Given the high values obtained for *Pinus* and the low presence of other taxa this could force the relationships obtained. Consequently, paired t-tests were also applied to the results to assess the significance of the groups by comparison of the means. Results suggest that all PPE groups at all sites have a statistically significant relationship at the p=0.05 level and thus there is no difference between the simulated and actual pollen percentages at the sites used within the analysis.

Determination of the 'best' PPEs is difficult, as is highlighted above. When individual taxa are considered as opposed to sites this is complicated further, as shown in Table 4.3. There is no consistency between taxa and the comparability with the actual pollen percentages both between and at sites. This suggests that it is not only the magnitude of the value for each individual but also the relationship to others that is key to the representative ability of the pollen productivity estimate groups.

	Loch An Eilein	Loch Alvie	Insh H1	Lochan Geal
Pinus	1 m s ⁻¹	CC ERV 3	BA ERV 2 PS	CC ERV 3
Picea	ERV 1 1/d	1 m/s^{-1}	BA/CC	Open
Larix	All	Open	All	1 m s^{-1}
Betula	BA ERV 2 PS	CC ERV3 PS	Enclosed	CC ERV 3
Calluna	1 m s ⁻¹	1 m s ⁻¹	CC ERV 3 PS	CC ERV 3 PS

Table 4.3: Pollen productivity estimates that produce the best comparisons with the actual pollen percentages individual taxa and sites.

4.4.2 Landscape Reconstruction Algorithm

The LRA software was used to simulate estimates of vegetation abundance surrounding the sites used within the model. The aim was to test the different PPE groups produced within this model to define the range of variation in the results and ultimately the sensitivity of the model to variations within this parameter.

The REVEALS model was used to reconstruct the regional landscape only using the two large sites. Pollen assemblages from cores within the two large sites, Loch an Eilein and Loch Alvie, and a secondary set of the 29 modern moss samples were used to feed the model to gain estimates for the regional vegetation percentages.

4.4.2.1 Full data set with lake samples

Table 4.4 presents the output of the REVEALS model for the present landscape when PPEs from different models and weightings are used. A distinction between the taxon-specific and the inverse distance weighting is evident. The latter has a strong overestimation of *Larix* while estimates for

Calluna are consistently lower in the inverse distance group than the taxon-specific by $\sim 10\%$. Pinus estimates remain relatively consistent between the groups with the largest difference being 10%. Error estimates also differentiate the two with the 1 /d group having larger margins which is most prominent in the Calluna estimates being $\sim 20\%$.

	Mean				Mean	
ERV 1	vegetation	S.E.		ERV 1	vegetation	S.E.
1/d	percentage	(%)		P-S	percentage	(%)
Pinus	23.4	20.9		Pinus	30.9	17.7
Picea	2.7	2.4		Picea	3.0	1.6
Larix	35.0	38.7		Larix	13.8	15.6
Betula	7.3	5.9		Betula	9.7	2.3
Calluna	31.6	22.9	_	Calluna	42.6	6.3
	Mean				Mean	
ERV 2	vegetation	S.E.		ERV 2	vegetation	S.E.
1/d	percentage	(%)		P-S	percentage	(%)
Pinus	19.0	24.2		Pinus	23.0	15.2
Picea	3.0	7.5		Picea	3.4	1.7
Larix	33.3	39.5		Larix	16.0	17.4
Betula	7.8	19.3		Betula	9.6	2.2
Calluna	36.8	29.1		Calluna	48.0	7.5
	Mean				Mean	
ERV 3	vegetation	S.E.		ERV 3	vegetation	S.E.
1/d	percentage	(%)		P-S	percentage	(%)
Pinus	22.7	20.7		Pinus	29.0	17.4
Picea	4.0	4.4		Picea	4.7	2.5
Larix	34.2	35.9		Larix	13.9	16.0
Betula	6.6	4.6		Betula	8.5	2.1
Calluna	32.5	20.5		Calluna	43.8	6.8

Table 4.4: Vegetation proportions and standard errors from the REVEALS model for Basal Area pollen productivity estimates. ¹/d: inverse distance weighting; P-S: taxon specific weighting of Prentice and Sugita.

Comparison of the REVEALS output with actual vegetation data signifies promising results yet at different spatial scales (Table 4.5). *Pinus* results are most comparable to the 400 km² area observed data; *Calluna* and *Picea* compare very well to the 100 km² area; *Betula* corresponds to both distances as there is little variation in either the observed or simulated data.

Species	Surrounding (centred on	Inshriach Forest	
	400 km^2	rorest	
Pinus	28.7	64.1	80.1
Picea	0.9	2.1	2.5
Larix	0.6	1.4	2.3
Betula	3.7	5.3	2.1
Calluna	66.1	27.2	13.1

Table 4.5: Vegetation coverage percentages for the area surrounding Inshriach. Inshriach Forest: Forestry Commission stocking records; surrounding vegetation data: LCM 2000 (Fuller *et al.* 2002).

Canopy cover vegetation coverage estimates are comparable to those from the basal area PPEs (Table 4.6). High *Larix* values are calculated for the inverse distance (¹/d) weighted parameters data which are ~20% greater than those from the taxon-specific weighting functions. Estimates for *Calluna* and *Betula* are both comparable to the observed data but vary in their between group consistency; the former consistently shows differences of ~10% with the taxon-specific weighting shown the higher values whereas *Betula* has comparable results between the two weighting regimes and ERV models. It is *Pinus* that shows the greatest variability and also the poorest results when compared with the observed data at the 100 km² area with results consistently underestimating the actual value, but at 400km² the comparison is strong.

ERV 1 1/d	Mean vegetation percentage S.E. (%)		ERV P-S	vegetation	S.E. (%)
Pinus	15.6	17.1	Pinus	29.7	17.8
Picea	3.5	3.0	Picea	4.1	2.1
Larix	42.3	38.3	Larix	15.0	16.6
Betula	8.6	6.2	Betula	12.1	2.6
Calluna	30.1	20.5	Callun	a 39.1	5.8
ERV 2 1/d	Mean S.E. (%)		ERV P-S	vegetation	S.E. (%)
Pinus	18.3	18.2	Pinus	25.7	17.1
Picea	3.7	4.1	Picea	4.7	2.4
Larix	37.3	38.7	Larix	17.9	18.6
Betula	8.7	11.2	Betula	11.3	2.6
Calluna	31.9	25.2	Callun	a 40.4	7.0
ERV 3 ^{1/} d	Mean vegetation percentage	S.E. (%)	ERV P-S	vegetation	S.E. (%)
Pinus	19.7	17.6	Pinus	25.1	15.3
Picea	3.4	2.2	Picea	3.8	1.9
Larix	31.8	32.9	Larix	12.4	13.8
Betula	4.8	2.5	Betula	6.1	1.4
~			~		

Table 4.6: REVEALS vegetation coverage estimates for canopy cover derived pollen productivity estimates.

Calluna

52.5

7.1

19.6

4.4.2.2 Full data set with moss samples

40.2

Calluna

Results from the moss samples (Table 4.7) reflect a different spatial scale to those of the lakes as they differ in deposition basin size. However, the between group patterns can be compared and the simulated values represent the vegetation composition of Inshriach Forest (Table 4.5). Reconstructions from both data groups, basal area and canopy cover, reflect the same patterns with the canopy cover values marginally lower. For this reason only the basal area values are presented in Table 4.7. Firstly, the estimates for *Larix* are unrealistically high as seen within the lake samples and consequently these do not reflect the proportions of this taxon win Inshriach which is only 2%. Values are inflated further when the inverse-distance weighing is used in preference of the taxon-

specific. *Calluna* values are reasonably approximated with ¹/d having a stronger correspondence to the observed values. Similarly *Betula* is accurately represented in the simulation. *Pinus* values are considerably lower than observed values with ¹/d providing the lowest estimated of ~30%, this could be in response to the inflated *Larix* and *Calluna* estimates from these groups.

ERV 1	Mean vegetation percentage	S.E. (%)	ERV 1 P-S	Mean vegetation percentage	(
Pinus	36.0	24.9	Pinus	50.2	2
Picea	8.4	15.5	Picea	9.9	
Larix	38.9	25.7	Larix	16.2	
Betula	2.0	10.3	Betula	2.8	
Calluna	14.7	17.5	Callun	a 20.9	
ERV 2	Mean vegetation percentage	S.E. (%)	ERV2 P-S	Mean vegetation percentage	,
Pinus	30.8	23.1	Pinus	39.8	2
Picea	10.2	16.8	Picea	12.1	
Larix	38.9	25.4	Larix	20.0	
Betula	2.2	10.6	Betula	2.9	
Calluna	17.9	19.1	Callun	a 25.1	
ERV 3	Mean vegetation percentage	S.E. (%)	ERV 3	Mean vegetation percentage	(
Pinus	34.1	24.7	Pinus	45.7	2
Picea	12.3	17.7	Picea	15.4	1
Larix	37.1	25.2	Larix	15.8	
Betula	1.8	9.8	Betula	2.4	
Calluna	14.7	17.9	Callun	a 20.8	

Table 4.7: REVEALS reconstructions of vegetation for Inshriach Forest using basal area derived PPEs and 29 modern moss samples from the study area.

The best results for comparison to the observed data are BA ERV 1 P-S and BA ERV 3 P-S however these still fail to fully represent the landscape. For example, the amount of *Pinus* is still underestimated by 30% and 35% respectively. In addition, estimates for *Picea* and *Larix* remain too high.

4.4.2.3 Open and enclosed REVEALS reconstructions

The reconstructed vegetation proportions from the open and enclosed pollen productivity estimates show only slight disagreement when the basal area results are considered (Table 4.8). The main difference is exhibited in the *Pinus* estimates where the open set has a value of 31% and the enclosed only 15% and the *Betula* values which had a 9% difference between the two estimates. However, estimates for *Larix* vegetation proportions concur and are a marked overestimate of the actual values.

	Enclos	sed	Op	en
Basal	Basal Mean vegetation percentage		Mean vegetation percentage	S.E. (%)
Pinus	15.9	11.8	31.2	18.6
Picea	2.9	1.4	1.3	0.7
Larix	13.7	14.1	13.7	15.7
Betula	17.2	5.5	8.6	2.2
Calluna	50.3	7.7	45.2	8.3

	Enclos	sed	Оре	en
Canopy	anopy Mean vegetation percentage S.E. (%)		Mean vegetation percentage	S.E. (%)
Pinus	0	0	40.8	39.9
Picea	0	0	2	12.5
Larix	0	0	13.2	18.9
Betula	0	0	8.3	35.4
Calluna	100	0	35.6	37.8

Table 4.8: REVEALS generated vegetation estimates from the open and enclosed PPEs using samples from two lake cores.

Canopy cover results are more varied in their correspondence with the observed data. Output from the enclosed sites are poor in response to the very low *Calluna* productivity estimate within this dominating the results estimating 100% coverage. In contrast, the open sites show correspondence with both the observed data and those generated from the basal area dataset. It is the canopy cover values that provide the best estimate of the observed data when all results are considered within Tables 4.5 and 4.8. However, the error estimates are much greater than the BA dataset, for example those for *Pinus* and *Calluna* are similar to the mean estimates whereas the remaining taxa have error estimates greater than their mean values limiting the confidence in the results.

Evaluation of the correspondence between the actual vegetation proportions and the simulated, when groups are treated as a single unit, shows that the open PPEs provide the best result. The estimates correspond to an area of between 100 km² and 400 km² around Inshriach Forest.

4.4.2.4 Wind variations

As with previous results the extremes of the wind spectrum were used within the REVEALS software (Table 4.9). Some disparity is evident between the groups although this is not as severe as the actual PPEs would suggest. Within the basal area *Larix* exhibits the greatest difference between the two wind speeds with 1ms⁻¹ group having a value of only 0.4% whereas the 5 ms⁻¹ shows a distinct increase to 27.5%. However, little difference is evident between the *Pinus* values even though the PPE of the 5 ms⁻¹ group is almost 3 times that of the 1 ms⁻¹ group. Repetition of these patterns is evident in the canopy cover dataset with almost equivalent values being generated. Slight deviation lies in the *Calluna* values where in the canopy cover dataset these are much higher in both wind speed groups being 55.8% in the 1ms⁻¹ class whereas in the basal area group this is only 45%.

Correspondence between the 1ms⁻¹ wind group and the actual vegetation data around 100 km² is strong. Although some values show some disparity this is slight and therefore is contained in the error margins. This is an improvement on the 5 ms⁻¹ which, due to the high *Larix* estimate, provides a poor correlation.

4.4.2.5 Summary

Numerous sets of pollen productivity estimates were generated from the 29 sites from Inshriach. The most significant of these variations was with *Pinus* which had values ranging from 1.61 to 7.14; however this difference was not apparent in the results of the modelling. Since this occurred in results from both the Humpol and LRA modelling this does not appear to be a manifestation of the software programs.

Estimates generated from the REVEALS model show promising results when compared to the actual data. Differences are present between the different ERV model and weightings derived PPEs which support the results of the ML score curves. The taxon-specific results consistently produce lower error margins and the least variability when different ERV models are applied. A number of groups provide strong correlations with the observed data with variations between the canopy cover and basal area groups; the former is ERV 1 P-S, the latter ERV 1 and ERV 3 with taxon-specific weighting. *Larix* is consistently overestimated in the majority of modelling results whilst the other taxa show more variability.

	Wind 1	m s ⁻¹	Wind 5m s ⁻¹	
Basal Area	Mean vegetation percentage	S.E. (%)	Mean vegetation percentage S.E. (%)	
Pinus	38.7	16.7	21.9 17.7	
Picea	2.3	1.5	5.0 3	
Larix	0.4	0.6	27.5 29.3	
Betula	13.5	6.2	5.9 2.4	
Calluna	45.0	12.5	39.7 14.5	

	Wind 1m s ⁻¹			Wind 51	5m s ⁻¹	
Canopy Cover	Mean vegetation percentage S.E. (%)			Mean vegetation percentage	S.E. (%)	
Pinus	31.9	14.7	_	21.0	16.7	
Picea	1.6	1		3.9	2.4	
Larix	0.4	0.5		25.5	26.8	
Betula	10.3	3.4		4.7	1.8	
Calluna	55.8	10.9	_	44.8	12.9	

Table 4.9: Basal and canopy cover PPE derived estimates of vegetation coverage with wind speeds of 1m s⁻¹ and 5m/s⁻¹. Values are percentages.

Comparison of the open and enclosed results is difficult as one of the enclosed sets yielded poor values. However, it appears that the open sets provide a more robust and realistic representation of the landscape especially when the BA values are used as these have consistently lower error margins. The results of the wind variations show particularly promising results with respect to the 1 ms⁻¹. Here the *Larix* values compare well to the observed vegetation proportions in both the basal area and canopy cover sets. In contrast, the same taxon is overestimated within the 5 ms⁻¹ wind group. The remaining taxa show strong correlations to the observed in both the basal area and canopy cover groups; however, it is the latter that shows slightly better results within the wind test group.

Estimation of the comparison distance was obtained from calculation of the characteristic source area of pollen (Sugita, 1993). This uses wind parameters, dispersal properties of the grain, and the size of the deposition basin to estimate the distance within which specific quantities of pollen within the basin would be likely derived from. For this study *Pinus* was used to calculate this distance as this is the most well dispersed grain with percentages of 70% and 30% for Loch an Eilein and Loch

Alvie respectively generating radii of 22100 m and 2432 m for the two deposition basins correlating to areas of 1533 km² and 18km². The former is too high and could be such due to the presence of Scots Pine around the margins of the loch impacting upon the deposition. Given the lower Loch Alvie values it seems that the 100 km² area estimate for comparison is the most suitable resulting in ERV 1 P-S from the full dataset and both open and 1 ms⁻¹ from the remainder the most representative PPEs.

4.5 Assessment of spatial properties in generating PPEs

An important aspect of any geographical study, especially one that is vegetation based, is the issue of spatial autocorrelation. This relates to the understanding that if the property of one point is known the value of the same property can be estimated at a point close by (Cliff and Ord, 1981). Consequently, if samples are close together they cannot be classed as independent and therefore violate a large number of statistical assumptions. Broström *et al.* (2004) suggested that a distance of 400 m should be sufficient to avoid the effect of autocorrelation and in most cases this distance was adhered to; although some points are closer than this and could affect the spatial properties. However, the 400 m threshold was obtained for sites within southern Sweden which have a different vegetation structure to Inshriach Forest; thus, is this distance applicable to all sites? Numerous factors can influence the spatial pattern of the vegetation which makes the autocorrelation issue site specific. Results discussed below show a test of systematically and randomly selected sites to understand the effect of this and the distance at which the spatial autocorrelation issue becomes evident. These are formed through subsets of the original 29 sites within 3 groups; 1000 m, 500 m and 200 m. Due to distance limitations each have a different number of sites included which are 12, 18 and 25 respectively.

Parameter estimation for the productivity estimates and the background component are achieved via maximum likelihood analysis (Prentice and Parsons, 1983). Using probability density functions (pdf) distributions the maximum likelihood score is achieved when the 'assumed' corresponds to the actual or natural outcome (Pickles, 1985; Bunting *et al.*, 2004). In calculating the PPEs the pdfs are estimated from the field data (pollen and vegetation) with estimates of pollen productivity and background obtained from this. Increased fit between the data lowers the ML score and provides a more robust estimate of the parameters. Because the pdfs are obtained from the input data both differences in the number of sites and the composition of these will impact upon the ML scores between distance groups. Inevitably, inter-dataset comparison is hindered by this property making selection of the best PPEs difficult. Consequently, the form of the graph will be used to determine the inter-group comparison where as the intra-group will use both form and magnitude of the ML score curve to counteract erroneous selection of suitable PPEs from ML scores alone.

Estimates of RSAP were made using two approaches which relate to the form of the ML graph. Where an asymptote was reached PPEs were calculated as an average of scores from the RSAP to the maximum survey distance. In contrast, where an increase in ML score was identified after the minimum, PPE scores were taken as the values from the distance with the lowest ML score with no averaging to exclude any variation from the reduced fit between pollen and vegetation.

4.5.1 Selection of subgroup sites for pollen productivity estimation

4.5.1.1 Systematically selected sites

Subsets of systematically chosen sites consisted of points that were no less than 1000, 500 and 200 m away from their nearest neighbour. Due to the possible combinations 3 subsets were chosen for each distance class. In each instance, pollen productivity estimates were generated for each group using vegetation estimates calculated from basal area and canopy cover. Summary results are presented below with the best groups chosen from each distance category from the basal area and canopy cover groups.

4.5.1.1.1 1000 m distance

Considerable variation was evident in both the pollen productivity estimates obtained and the maximum likelihood function scores between the two groups used within this analysis. When basal area was used the variability was much greater between different collections of sites than with the canopy cover vegetation data. Figures 4.20 and 4.21 show both the maximum likelihood scores and the location of the sites used within the best subsets for basal area. As is evident, there is a substantial difference between the appearances of the maximum likelihood curves produced even though the sample points are evenly distributed over the site. Increased ML score subsequent to the minimum being attained in the BA.Sy.1000.2 subset would result in this information being disregarded in preference of subset BA.Sy.1000.1 even though the scores are the same and suggests an additional influencing factor.

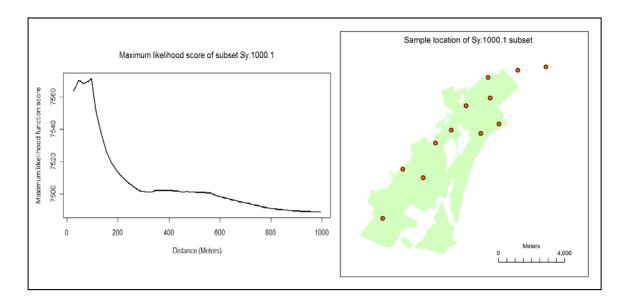


Figure 4.20: Details of sampling subset BA.Sy.1000.1. *Left*: Maximum likelihood function score with increasing distance from the sampling points. *Right*: A Map of Inshriach Forest showing the locations of the samples used within the analysis

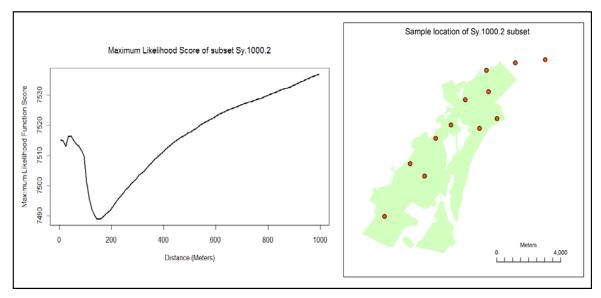


Figure 4.21: Details of sampling subset BA.Sy.1000.2. *Left*: Maximum likelihood function score with increasing distance from the sampling points. *Right*: A Map of Inshriach Forest showing the locations of the samples used within the analysis

Conversely when canopy cover is used the results show good conformity and form within the ML score graph. Although an increase is seen within the first 100 m a well defined asymptote with little subsequent fluctuation is evident.

Pollen productivity estimates for the subsets (Table 4.10) were reasonably consistent between Sy.1000.1 and Sy.1000.2 with differences accounted for by the local variation inevitable at the sites used within the analysis. Interestingly, there is a large disparity between the values obtained for the canopy cover data for all taxa but predominantly *Pinus*. Furthermore, there is considerable variation in the RSAP estimate relating to the lowest point of the maximum likelihood score. The larger distance recorded for subsets BA.Sy.1000.1 and CC.Sy.1000.1 relates to the asymptote being reached at this point and implies a more robust approximation.

G 4 ID	n:		D I		Moving window RSAP	RSAP Estimate	ML
Set ID	Pinus	Larix	Betula	Calluna	(metres)	(metres)	Score
BA.Sy.1000.1	17.9	9.5	15.2	2.6	365	800	7450
BA.Sy.1000.2	18.4	6	6.1	0.6	175	Not Reached	7490
CC.Sy.1000.1	3.55	1.96	3.25	0.49	345	300	7495

Table 4.10: Pollen productivity estimates relative to *Picea* generated from the three subsets of sites of 1000 metres apart. BA: Basal area; CC: Canopy over.

4.5.1.1.2 500 m distance

Composition of the subsets BA.Sy.500.1 and BA.Sy.500.2 were very similar in location however this is not reflected as the form of the graphs differ substantially (Figures 4.22 and 4.23). Difficulty arises in the decision process surrounding the most robust estimates that would be obtained from these two datasets as the BA.Sy.500.2 does not conform to the asymptotic requirements. The canopy cover set again provides a different form of graph showing a well defined asymptote and the loss of the stability within the initial 100 metres around the sample point.

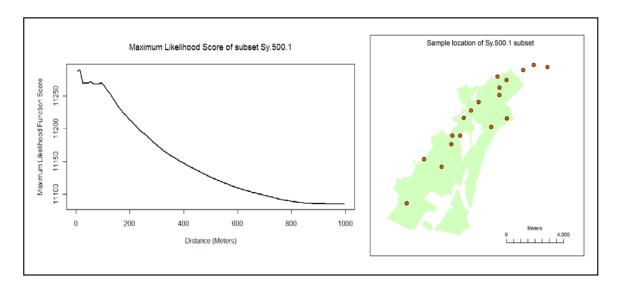


Figure 4.22: Details of sampling subset BA.Sy.500.1. *Left*: Maximum likelihood function score with increasing distance from the sampling points. *Right*: A Map of Inshriach Forest showing the locations of the samples used within the analysis

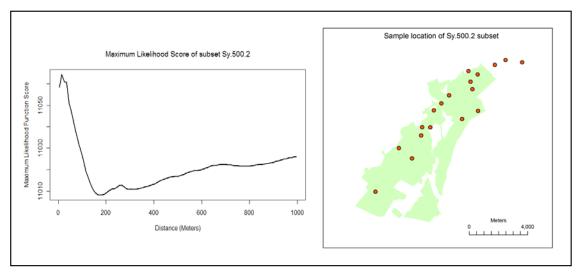


Figure 4.23: Details of sampling subset BA.Sy.500.2. *Left*: Maximum likelihood function score with increasing distance from the sampling points. *Right*: A Map of Inshriach Forest showing the locations of the samples used within the analysis

Consideration of the pollen productivity estimates, shown in Table 4.11, suggest that the form differences in the graphs are reflected within the values obtained from the datasets. Interestingly, the greatest difference is exhibited within *Larix* due to the inflated value from the canopy cover set which appears to relate to the vegetation measurement method. Stability within the *Pinus* estimates and distinct reduction from the 1000 metre dataset is surprising.

Set ID	Pinus	Larix	Betula	Calluna	Moving window RSAP (metres)	RSAP Estimate (metres)	ML Score
					Not		
BA.Sy.500.1	4.96	0.14	1.47	0.64	reached	850	11100
						Not	
BA.Sy.500.2	5.47	0.24	2.82	0.78	200	Reached	11010
					Not		
CC.Sy.500.1	4.37	22.42	1.91	0.47	reached	400	11433

Table 4.11: Pollen productivity estimates relative to *Picea* and relevant source area of pollen distances for sites not less than 500 meters apart.

4.5.1.1.3 200 m distance

Similar patterns exhibited with greater inter-sample distances are seen within the 200 metre dataset. BA.Sy.200.1 has the lowest maximum likelihood scores and reduces to an asymptote (Figure 4.24). The initial fluctuation in the scores could relate to the change in vegetation data from field sampled to aerial photograph derived. The BA.Sy.200.2 subset (Figure 4.25) fails to reach and asymptote and an increase following the lowest point is generated. The CC.Sy.200.1 group shows a gradual decline to a minimum at 300 metres subsequently increasing towards the limit of the survey distance.

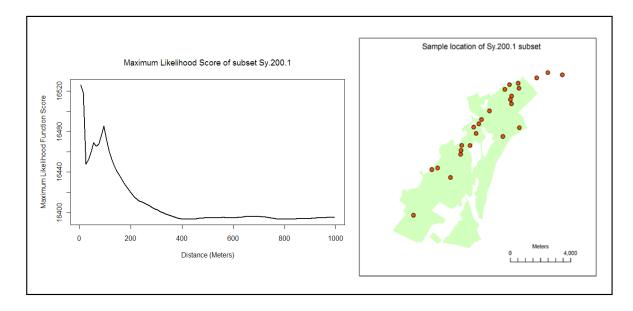


Figure 4.24: Details of sampling subset BA.Sy.200.1. *Left*: Maximum likelihood function score with increasing distance from the sampling points. *Right*: A Map of Inshriach Forest showing the locations of the samples used within the analysis

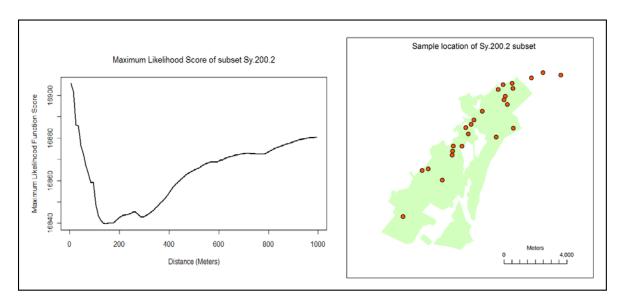


Figure 4.25: Details of sampling subset BA.Sy.200.2. *Left*: Maximum likelihood function score with increasing distance from the sampling points. *Right*: A Map of Inshriach Forest showing the locations of the samples used within the analysis

Pollen productivity estimates derived from the analysis, shown in Table 4.12, show considerable difference between the three subsets. *Pinus* has the biggest margin between the three groups with much higher estimates generated from the basal area derived values. Surprisingly, it is CC.Sy.200.1 and BA.Sy.200.2 that are correlated for all taxa despite the difference in spatial distribution.

Set ID	Pinus	Larix	Betula	Calluna	Moving window RSAP (metres)	RSAP Estimate (metres)	ML Score
BA.Sy.200.1	10.5	3	2.7	2.1	445	400	16400
BA.Sy.200.2	6.6	2.4	4.3	1.1	185	Not Reached	16840
CC.Sy.200.1	6.44	2.74	5.29	1.4	315	Not Reached	16227

Table 4.12: Pollen productivity estimates relative to *Picea* and relevant source area of pollen distances for sites not less than 200 m apart.

The low moving window distances for the RSAP for BA.Sy.200.2 arise from the uncharacteristic patterns produced from these curves and as the results are likely to be unrepresentative of the actual distance.

4.5.1.1.4 Summary

Variability is evident on both an inter- and intra-subgroup level which is less apparent when the canopy cover measurement of vegetation is used. With respect to the basal area values the 200 m group reflects the greatest difference between *Pinus* and the other taxa with this effect decreasing with increasing distance between the sampling points. Estimates from the 1000 m groups appear uncharacteristically high and could imply anomalous results. In addition, the relevant source area of pollen is little influenced by the nearest neighbour as there is no relationship identified between this distance and the sampling group. Variation amongst the other taxa does not reflect the systematic changes. In contrast, estimates generated from canopy cover measurements show little intra-group fluctuation with respect to *Pinus*. Similarly, other taxa show little systematic variation although a number of anomalous values are evident.

On the contrary, the amount of variation occurring with different combinations of sample points i.e. basal area group suggest that there could be an influence unaccounted for by the nearest neighbour distance alone. It appears that the properties of the pollen samples could have an overriding influence on the output from the subgroups. However, assessment of the vegetation properties in terms of openness and the amount of pine surrounding the site within 100 m of the sampling point show consistency between the subgroups and little difference between the distance classes; this is represented in Table 4.13. Furthermore, consideration of dissimilarity between the moss species used to obtain the pollen samples, discussed in section 4.2 reveal little difference in pollen concentration and therefore alternation in the combinations of these species within the subgroups would be unlikely to induce any variation into the results.

	Basal	vegetation larea erage	Vegetation structure			
Set ID	>50%	<50%	>50%	coverage <50%	Open	Closed
Sy.1000.1	9	3	8	4	5	7
Sy.1000.2	9	3	8	4	5	7
Sy.500.1	10	8	12	6	7	11
Sy.500.2	10	8	12	6	6	12
Sy.200.1	14	11	19	6	9	16
Sy.200.2	14	11	19	6	9	16

Table 4.13: Number of sites within each group showing the respective vegetation properties. *Left:* Percentage of *Pinus* vegetation within 100 m of the sampling point in basal area and canopy coverage. *Right:* Openness determined by the amount of arboreal vegetation surrounding the sampling sites.

4.5.1.2 Random selection of sites

In order to detect the impact of spatial patterning upon the pollen productivities a number of groups were constructed through random generation. The number of samples within each group was determined by the number of samples within the systematically derived groups removing the impact of sample quantity from the results and enable comparison of the ML scores calculated.

4.5.1.2.1 1000 m distance

Figures 4.26 and 4.27 show the location of the sample points included within the two random basal area datasets with associated ML score curves. Apparent from these figures are that some sites have a nearest neighbour well below the 1000 m distance of the systematic groups. However, the improvement in both the form of the maximum likelihood scores is distinctive. Both datasets experience a slight increase at the start of the graph, which relates to the linkage between the field and aerial photograph derived data, but follow with a smooth decline in values to an asymptote. Interestingly, the BA.Ran.1000.2 group shows the greatest conformation with the 'classic' graphs of pollen productivity studies.

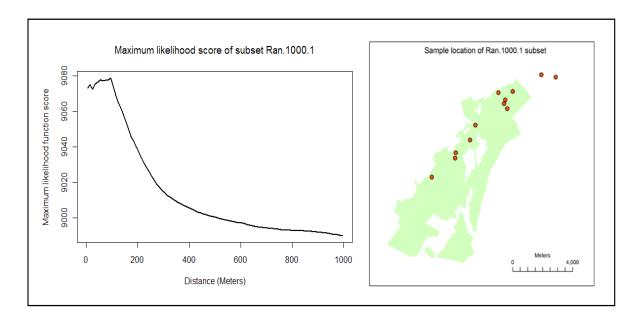


Figure 4.26: Details of sampling subset BA.Ran.1000.1. *Left*: Maximum likelihood function score with increasing distance from the sampling points. *Right*: A Map of Inshriach Forest showing the locations of the samples used within the analysis

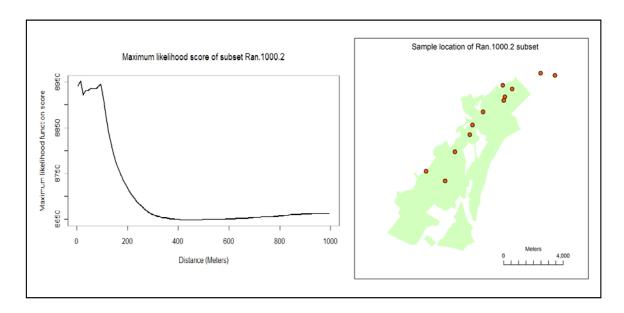


Figure 4.27: Details of sampling subset BA.Ran.1000.2. *Left*: Maximum likelihood function score with increasing distance from the sampling points. *Right*: A Map of Inshriach Forest showing the locations of the samples used within the analysis

Patterns shown in the basal area data groups are also reflected in the canopy cover with the CC.Ran.1000 graph showing a decrease in ML score monotonically with distance with an asymptote clearly evident. Also, the initial stability shown at the start of the transects in the basal area sets are not present.

Set ID	Pinus	Larix	Betula	Calluna	Moving window RSAP (m)	RSAP Estimate (m)	ML Score
					Not	Not	
BA.Ran.1000.1	3.1	4	2.5	2.1	reached	Reached	8980
BA.Ran.1000.2	11.2	2.8	4.8	1	455	390	8650
CC.Ran.1000	4.2	2.6	3.2	1.5	575	500	9456

Table 4.14: Pollen productivity and relevant source are of pollen estimates relative to *Picea* from the random 1000 m datasets. BA: Basal area; CC: Canopy cover

Pollen productivity and relevant source area estimates generated from the three datasets are shown in Table 4.14. Firstly, the productivity values of all species in the analysis show variation; *Pinus* clearly shows the greatest magnitude of variation with the largest values from the group with the lowest ML score. However, the relationship of the species also change with *Larix* being estimated as the highest producer in group BA.Ran.1000.1 and then one of the lowest in BA.Ran.1000.2.

Secondly, the relevant source area of pollen differs significantly between the two datasets even though the profiles of the declines are similar. It could be that the sampling distance was not large enough for BA.Ran.1000.1 to reach the estimated distance contributing to the difference in results.

4.5.1.2.2 500 m distance

Spatial distribution of sites within the groups of this distance class and the associated ML graph are shown (Figures 4.28 and 4.29). All basal area sample sets show a decline in value to an asymptote. In contrast, the canopy cover group shows a fluctuation in the maximum likelihood score close to the start of the transect with a subsequent increase in scores following the minima. However, the plateaus exhibited in the other groups from this distance class are not present.

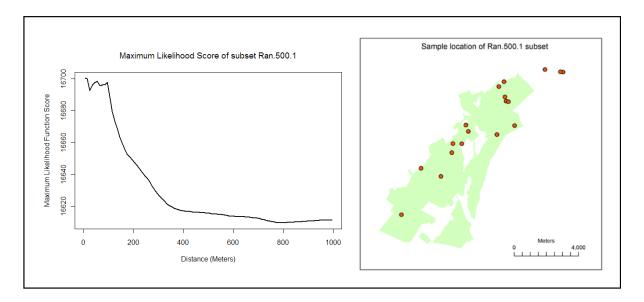


Figure 4.28: Details of sampling subset BA.Ran.500.1. *Left*: Maximum likelihood function score with increasing distance from the sampling points. *Right*: A Map of Inshriach Forest showing the locations of the samples used within the analysis

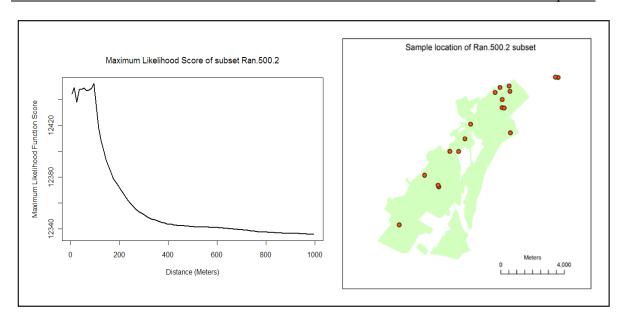


Figure 4.29: Details of sampling subset BA.Ran.500.2. *Left*: Maximum likelihood function score with increasing distance from the sampling points. *Right*: A Map of Inshriach Forest showing the locations of the samples used within the analysis

Productivity estimates (Table 4.15) show slight differences between the two datasets. *Pinus* is shown to be the greatest producer in BA.Ran.500.2 although the other sets show this to be of similar productivity with the canopy cover set implying that this is greater than *Pinus*. BA.Ran.500.2 shows inflated values for *Pinus* with the difference between this and *Betula* being much greater than previously seen in Ran.500.1. Variation occurring for *Larix* and *Calluna* show little difference.

Measurements for the relevant source area of pollen do not reflect this pattern with a large difference between the two figures, which is surprising after identification of the similarity between the profiles of the two curves. This implies that the BA.Ran.500.2 curve is still to achieve the asymptotic definition of the statistical analysis.

Set ID	Pinus	Larix	Betula	Calluna	Moving window RSAP (metres)	RSAP Estimate (metres)	ML Score
BA.Ran.500.1	4.1	3.2	4	0.9	445	800	12579
					Not		
BA.Ran.500.2	6	3	2.5	1.1	reached	850	12340
CC.Ran.500.1	3.3	2.6	4.1	0.9	275	Not Reached	12484

Table 4.15: Estimates of pollen productivity relative to *Picea* and relevant source area of pollen for the random dataset corresponding to the 500 metre distance class.

4.5.1.2.3 200 m distance

BA.Ran.200.1 decreased to a well defined asymptote, as shown in Figure 4.31, which could be associated with a greater degree of clustering amongst the sample points. In contrast, the BA.Ran.200.2 dataset showing a severe increase in maximum likelihood score following the minimum being achieved at 185 m (Figure 4.30 and Table 4.16). A similar pattern to that of the BA.Ran.200.2 pattern is identified in the CC.Ran.200.1 group in Figure 4.32.

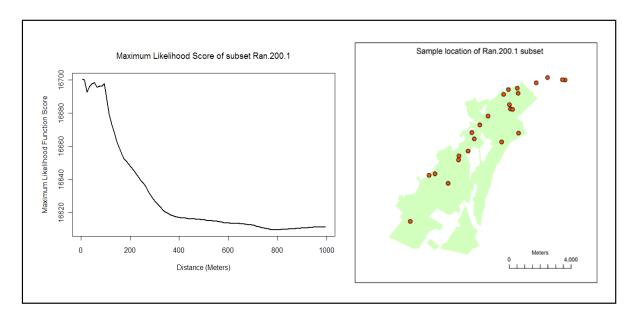


Figure 4.30: Details of sampling subset BA.Ran.200.1. *Left*: Maximum likelihood function score with increasing distance from the sampling points. *Right*: A Map of Inshriach Forest showing the locations of the samples used within the analysis

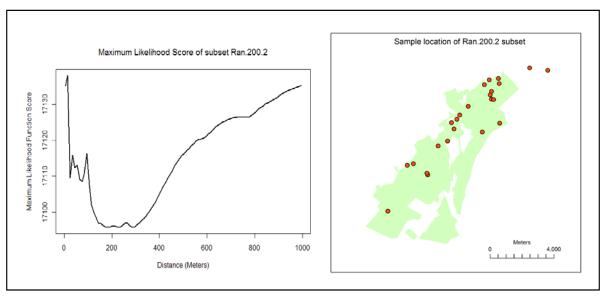


Figure 4.31: Details of sampling subset BA.Ran.200.2. *Left*: Maximum likelihood function score with increasing distance from the sampling points. *Right*: A Map of Inshriach Forest showing the locations of the samples used within the analysis

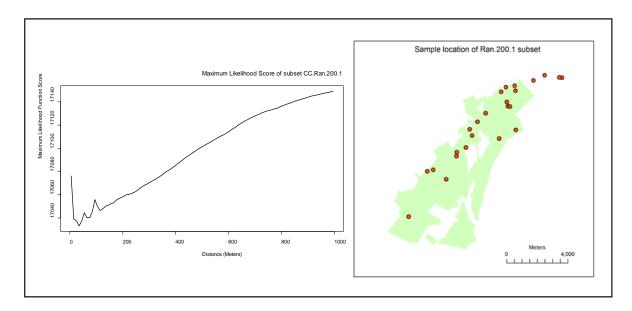


Figure 4.32: Details of sampling subset CC.Ran.200. *Left*: Maximum likelihood function score with increasing distance from the sampling points. *Right*: A Map of Inshriach Forest showing the locations of the samples used within the analysis

Differences between the pollen productivity estimates are limited apart from *Pinus* which shows large variability and much higher estimates than identified in other distance classes. Interestingly, the relationship of *Pinus* and *Larix* is reversed in the CC.Ran.200.1 with the latter as the highest

producer and *Pinus* much lower than previous predictions. Finally, estimates of relevant source area of pollen are fairly similar but given the appearance of the graphs it is anticipated that the estimates for the BA.Ran.200.2 and CC.Ran.200.1 datasets are a manifestation of their form rather than an accurate assessment of this distance.

Set ID	Pinus	Larix	Betula	Calluna	Moving window RSAP (m)	RSAP Estimate (m)	ML Score
BA.Ran.200.1	10.5	3	2.7	2.1	445	800 Not	16580
BA.Ran.200.2	6.6	2.4	4.3	1.1	185 Not	Reached Not	17000
CC.Ran.200.1	3.9	6.7	1.9	1	reached	Reached	17149

Table 4.16: Pollen productivity estimates relative to *Picea* and relevant source area of pollen distances for samples sites no less than 200 metres apart.

4.5.1.2.4 Summary

With respect to the form of the ML graphs the 1000 m and 500 m distance classes provide the least variation and correspond to the 'classic' form. In contrast, the 200 m distance provided poor representations with an asymptote rarely achieved. Comparison of the graph profile with the spatial properties of the sites included within the group show that there is a weak relationship between these two attributes. This is clearly seen within the 1000 m distance class where the greatest dispersion of sample points is found within BA.Ran.1000.2.

Variability between the pollen productivity estimates only principally occurs for *Pinus*, the values for the other taxa remain largely static. Potentially, this is a response to *Pinus* being the dominant taxon and therefore between site variability within the pollen vegetation data. Interestingly, at the 1000 and 500 m distance classes BA.Ran.1000.1 and CC.Ran.1000.1 produce concomitant results, yet at the 200 m class considerable difference is present. Consistency between the values of *Larix* and *Betula* is strong at all distance classes with *Calluna* showing more fluctuations, especially within the 200 m class.

4.5.1.3 Systematic versus random site selection

Regardless of the lower ML scores the systematic datasets produce the most variability in PPEs. For example, the 1000 m dataset produces very high estimates for all taxa not replicated elsewhere.

As these are in conjunction with the lowest ML scores of all groups tested the BA.Sy.1000.1 results should, theoretically, produce the most robust pollen productivity estimates. However, the lower number of sites will certainly influence this figure which makes use of this feature alone problematic when comparing the groups. Furthermore, the randomly selected sites consistently show *Pinus* as the dominant taxa. In contrast, the systematic sites show this to be more comparable with others especially *Betula*.

When averages are considered the systematic sites show a greater RSAP distance than the random counterpart. However, variation is inherent in this due to the method employed to estimate the RSAP and also the increasing ML scores following the minimum that occurs in some cases.

4.5.2 Statistical analysis

Variability between the PPEs produced from the inclusion of different data points is clear but the cause of this is not as evident. Statistical methods were applied to investigate the properties of the data, both pollen and vegetation, to elucidate the underlying factors influencing this pattern. Geostatistical methods were employed to assess the spatial independence of the whole dataset whilst multivariate analysis was used to focus upon the group specific properties (systematic and random).

4.5.2.1 Geostatistics of spatial autocorrelation properties

Geostatistical analysis was applied to both the pollen and vegetation data used to generate the PPEs from all 29 sites. Comparable analysis could not be undertaken on the systematic and random groups due to the low number of samples that do not meet the minimum threshold for a robust test. The aim of this analysis was to elucidate variation in spatial patterning within the groups but also between the pollen and vegetation distribution that could contribute to the different PPEs obtained.

4.5.2.1.1 Vegetation data at Inshriach Forest

A semi-variogram from the vegetation data for pine alone indicates a short range and thus similarity between sample points at only short lags (Figure 4.33). It was deemed appropriate to fit a nested model to the experimental variogram as there are two initial increases in semi-variance; firstly, a rapid increase to 0.07 at a distance of 160 m; secondly, a gentler increased to a sill of 0.085 at 500 m. Interestingly, once the sill has been attained there is a degree of fluctuation which is most prominent at 3000 m. Changes in the semi-variance could identify patches within the vegetation as periods of increase or decreased correlation. With respect to the feature at 3000 m this may relate to the extent of the woodland as its width at the northern extent matches this distance. The nugget

value, analogous to random variance, is high accounting for ~50% of the total semi-variance which could be associated with the lag size of 50 m being used when some points are only 10 m apart.

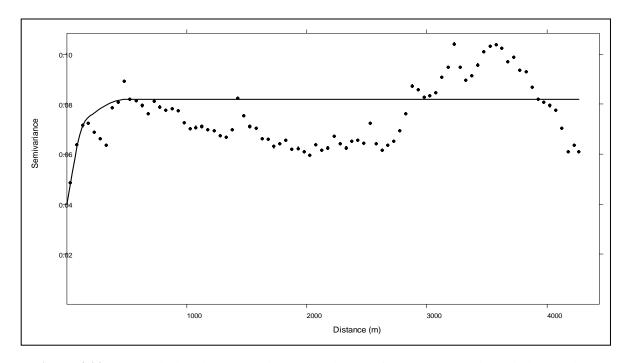


Figure 4.33: An omni-directional experimental variogram for *Pinus* vegetation within Inshriach Forest (points) using a 50 m lag. A nested variogram model (line) was fitted using two Spherical models with the formulas; Sill: 0.67, range: 160 m, nugget: 0.04; and sill: 0.085, range: 500 m, nugget: 0.

A degree of autocorrelation is also identified within the semi-variogram produced with larch vegetation data (Figure 4.34). A range of 440 m marks the limit of the autocorrelation with some short-lived fluctuations evident subsequent to this. Low nugget variance implies that most variation is accounted for within the model. Increased semi-variance values at 3000 m as seen in the *Pinus* data is also present within the *Larix* dataset which supports the conclusion of a major feature as the driver of this.

Semi-variogram analysis was undertaken on the remaining taxa within the woodland, however, these failed to show any spatial relationships. Scatter in the experimental variograms was too high to allow for a non-linear model to be fitted to the data points i.e. pure-nugget; thus no variation is encapsulated by the semi-variogram.

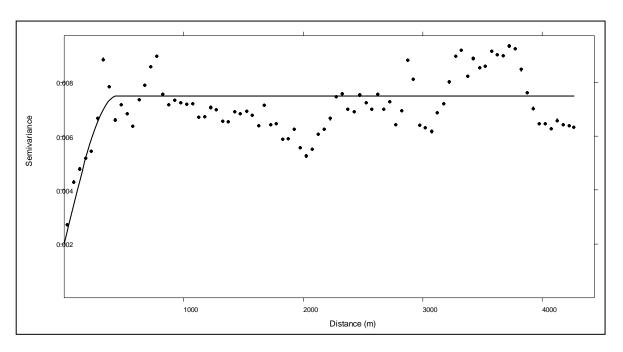


Figure 4.34: An omni-directional experimental variogram for *Larix* vegetation coverage within Inshriach Forest using a 50 m lag. A variogram model was fitted to the data points using a spherical model; sill: 0.0075, range: 440 m, nugget: 0.002.

An assumption of the semi-variogram model is that the data is isotropic in nature i.e. directionality is not evident but where this is not the case data is described as being anisotropic. Directional semi-variograms are employed to detect this and were used here with the *Pinus* and *Larix* vegetation data to assess the feature identified in the omni-directional analysis. Two bearings were used from the data points, 45° and 135° (transects are mirrored therefore 215° and 315° were not required), with a tolerance of 45° included to ensure that points were incorporated from the 0°, 90°, 180° and 270° transects originally creating the dataset. Not doing so would provide too few points for the analysis and impact upon the robustness of the results obtained.

Analysis of the *Pinus* vegetation data for the 45° transect shows a clear range at 200 m (Figure 4.35) with less variability than identified in the isotropic analysis. However, the peak in variance commencing at 3000 m is still present within the semi-variogram. In contrast, the 135° transect, although shows a degree of autocorrelation with the range of 200 m visible, the semi-variance subsequently decreases considerably as the lag distance increase. A number of anomalous points are also evident within this transect which could indicate faults within the dataset. A slight difference in the sill values of these two transects indicated that zonal anisotropy is present within the dataset, corresponding to differing levels of spatial variability.

Additional analysis was conducted with *Larix* vegetation data with the same transect bearings used (Figure 4.36). The degree of variability distinguishes the two transects; a clear sill is defined in the 45° transect; a sill is defined in the 135° although a large amount of fluctuation is evident in the semi-variance with a declining trend. Again, the peak in variance commencing at 3000 m is clearly visible in the semi-variance of the 45° transect whilst this is absent from the 135° transect.

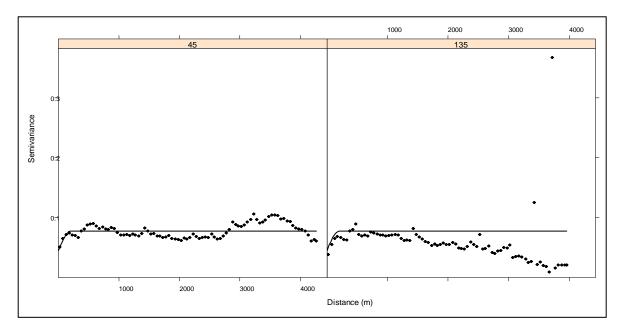


Figure 4.35: A directional experimental variogram using *Pinus* coverage values within Inshriach Forest (points). A spherical model was fitted to the variogram with features defined at, sill: 0.077, range: 200 m, nugget: 0.45.

Results of the directional variograms suggest that there is some zonal anisotropy present within the data with a slight difference in the sills of the two transects. A more prominent feature is that occurring at 3000 m which is associated with the north eastern (45°) transect only. This conflicts with the earlier conclusion that the width of the woodland was driving this feature as the 45° transect lies along the longer axis of the woodland. However, when the analysis is run with transects at 0° and 90° this feature occurs prominently on the former and not the latter. This implies that the width of the woodland is the cause of this decreased correlation as at the 45° analysis transect the 0° sampling transect is influencing the data due to the large tolerance with the combination of the two sampling transects muting this.

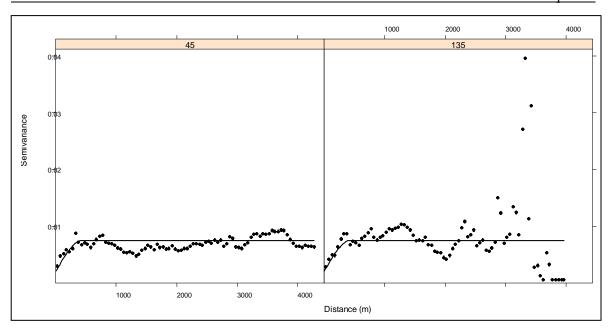


Figure 4.36: A directional variogram of *Larix* vegetation coverage in Inshriach Forest. A spherical model is fitted to the variogram with the sill: 0.0075, range: 440 m, and nugget: 0.002.

4.5.2.1.2 Site specific analysis

Presented here are results from site specific analysis carried out at two sampling locations using *Pinus* data only; S13 which is in the north eastern section of the woodland; S20 in a central location of the south western section of Inshriach. These sites were chosen due to their locations and vegetation patterning with the aim of detecting any differences within the two woodland sectors. Both omni-directional and directional variograms were calculated from the datasets available which consisted of field and database derived vegetation coverage.

S13 is characterised by a varied species composition and age classification which, with respect to this analysis, creates a heterogeneous structure (Figure 4.37 (a)). The omni-directional semi-variogram shows a strong range of 340 m which subsequently levels off with little fluctuation within the sill. Contrasting patterns are represented in the directional semi-variograms (Figure 4.37 (b)); the 45° transect shows a peak in variance at 500 m with subsequent decline of 0.15. The opposing transect at 135° has a shorter range of only 370 m and whilst still showing a declining trend after the range is attained this has a number of peaks. Correlation between the features of the semi-variograms and the vegetation patterns are tentative as no clear relationships can be determined. Similarities between the age structures of the pine patches could be creating a homogenous representation within the vegetation data such as that seen in the Glen More managed woodland investigated by Mason *et al.* (2007).

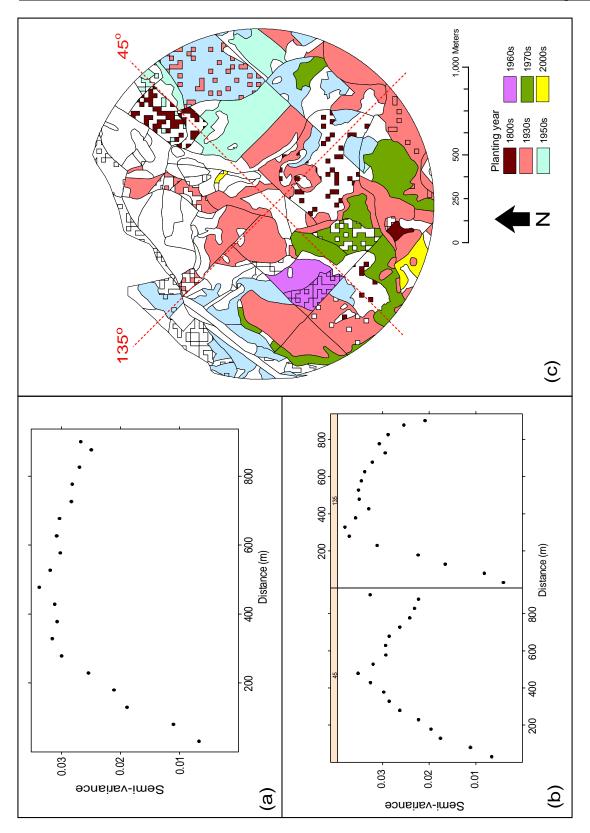


Figure 4.37: Omni-directional (a) and directional variograms (b) conducted on *Pinus* vegetation data at sample site S13. A map of the vegetation components is shown (c) with the location of the directional transects.

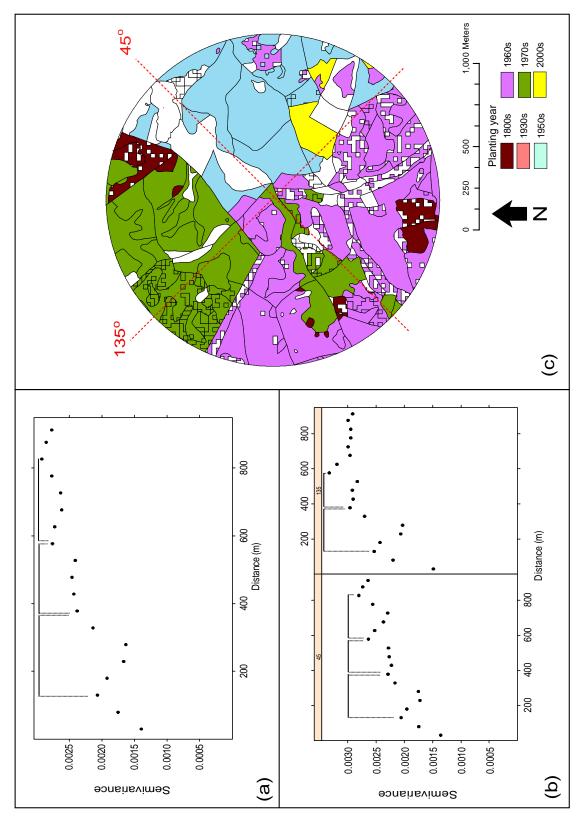


Figure 4.38: Omni-directional (a) and directional variograms (b) conducted on *Pinus* vegetation data at sample site S20. A map of the vegetation components is shown (c) with the location of the directional transects.

On the contrary, site S20 contains periodicity once the sill has been attained in both the omnidirectional and directional models. The former (Figure 4.38) has a range of 130 m with subsequent peaks with wavelengths of 300, 150 and 220 m. A decrease in amplitude occurs with progressive features. Although a similar periodicity is experienced in the directional semi-variograms the Along the 45° wavelengths of these features are shorter and more consistent (Figure 4.48 (a)). transect a range of 120 metres is followed by three peaks with wavelengths of 180, 190 and 160 m which is matched by a range of 140 m and two peaks of 140 and 200 m in the 135° transect. Unlike the omni-directional model the amplitude of these features does not exhibit trends. Differences in the patterns when compared with the models from S13 are demonstrated in the vegetation map of the sample area (Figure 4.38 (c)). Although pine dominates the area with only small patches of non-pine vegetation there are a number of mixed vegetation stands. These would be a contributor to the nugget variance as these features are below the 50 m lag used to construct the semivariogram. Distinction of the features controlling the periodicity in the semi-variograms is complex. Once again, although age structure can be determined similarities between the size of these patches and the wavelengths of the features are not present. Mason et al. (2007) attributed the periodicity at an older, managed stand in Glen More to the thinning regime that was undertaken in discrete patches, which could be the case here, with patches within age structures the driver. Confirmation of this is required through consultation with more detailed monitoring or forestry records.

4.5.2.1.3 Pollen samples

Additional variograms were conducted on the 29 modern pollen samples obtained from Inshriach to determine the level of autocorrelation in the dataset (Figure 4.39). A large nugget variance implies that variation within the samples is also occurring at distances shorter than 500 m which was the lag used within the experimental variogram. Analytical error can also contribute to this with the low number of samples available a potential source of this. Only 29 samples were used within the analysis which is below the advised number of 50 (Webster and Oliver, 1992; Burrough and McDonnell, 1998; Webster and Oliver, 2000). Fluctuations in the variance subsequent to the sill being achieved is indicative of further patterns within the pollen samples over 3000 m which could be related to scale changes in the vegetation patterns or the limit of the lag distances being attained. The range of 1800m shows a large correlation distance between samples implying a large separation required to counteract this.

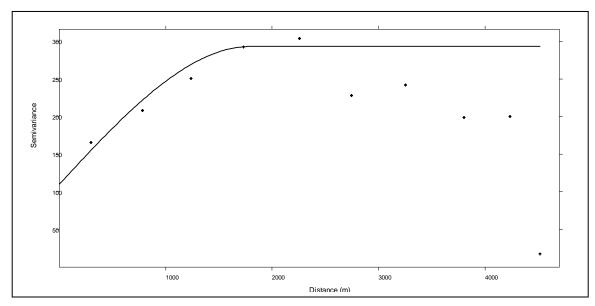


Figure 4.39: An omni-directional experimental variogram (points) with a lag of 250 m fitted with a spherical model for *Pinus* pollen percentages from 29 sites in Inshriach Forest. Sill: 293, range: 1800 m, nugget: 110.

4.5.2.1.4 Summary

There are a number of patterns that can be established from the application of statistical analysis. Firstly, within the vegetation data structure can be identified from the variograms. Differences between the peaks and troughs within the Larix (~500 m) and the Pinus (~1000 - 2000 m) variograms demonstrate the patch structure of the individuals (Legendre and Fortin, 1989; Cohen et al., 1990). As the former is only a minor component of the woodland it has an infrequent occurrence and in small patches whilst pine is the principle taxon with almost continuous stands. However, the nugget size of the pine semi-variograms implies that some variation is occurring below the scale of the lag threshold (50 m). A source of this is individuals or juvenile stands which would be scattered within open areas within which vegetation data was collected. Secondly, the presence of increased semi-variance at ~3000 m in all vegetation variograms describes the size of The width of Inshriach Forest is 3 km after which the landscape is open with the woodland. heathland the main community with only small, isolated stands of Scots pine. The dramatic change in vegetation explains the dominance of the feature in all the variograms used but also highlights the degree of information that can be obtained from the application of this analysis. However, the sampling regime could also be influencing this feature as only data from the woodland was used during this analysis and therefore this also describes the extent of the study area. Legendre and Fortin (1989), amongst others, stress caution when interpreting the form of the semi-variogram at high lags as these, being at the limit of the sampling distance can be distorted by insufficient sample inclusion. Clear demonstration of this occurs in the increased frequency of erroneous points after the 2000 m distance in both *Larix* and *Pinus* anisotropy semi-variograms.

Analysis using directional variograms distinguished the degree of anisotropy that is present within the vegetation patterns. The 45° transect shows the width of the woodland whilst the 135° corresponds to the length. The latter experiences increased correlation with distance in the *Pinus* variogram with the opposite true of the *Larix* semi-variogram which is related to the dominance of the former in the south west region of the site. It has been suggested by Legendre and Fortin (1989) that a controlling factor of the patterning identified are the physical properties and processes occurring within the landscape; however, within a managed landscape a degree of this removed with artificial control more prominent. Mason *et al.* (2007) compared spatial analyses from three areas of managed (Young Glen More) and semi-natural (Old Glen More and Abernethy) pine woodland in the Cairngorms. Results from this identified the least managed system as having the most random spatial patterning where as the young Glen More site was influence by the thinning regime providing a more homogenous stand.

In contrast, the pollen data does not experience the same degree of variation once the sill is attained. The range demonstrates spatial autocorrelation to a distance of 1800 metres in the *Pinus* profile. Consequently, a large degree of interdependence is identified between pollen samples, yet beyond this distance the samples are fully independent. Results therefore show that *Pinus* deposition is ubiquitous around Inshriach Forest. Dispersal properties on the *Pinus* pollen grains, high levels of productivity and dominance within the landscape all support the conclusion from the patterns extracted. However, a large proportion of this variation could have been induced into the model via the lag distance and the sampling regime. In this study only 29 points were used to explore variation over a 2000 ha area which is insufficient to ascertain robust patterns (Webster and Oliver, 2000). Production of pure-nuggets within semi-variograms of the remaining taxa can also be attributed to the sampling regime utilised within the study as this was not formulated for geostatistical analysis. On the contrary the method aimed to limit spatial autocorrelation within the samples to facilitate independence and enable statistical and ERV analysis. Unavoidably, this will also influence results of the *Pinus* pollen data but its effect is greatest in the sparsely occurring taxa due to frequency being below the lag distance (Webster and Oliver, 2000). Dungan et al (2002) define the terms "lag", "support" and "extent" and their importance within the preparatory processes and analysis. Inter-connection between each component and resultant impact upon features when sampling resolution varies has been frequently shown (Fortin et al., 1989; Qi and Wu, 1996; Fortin, 1999; Romshoo, 2004; Skøien and Blöschl, 2006). The most suitable sampling regime to counteract some of these issues is that of a nested-grid, to incorporate a number of scales

(Oliver and Webster, 1987) or a regular sampling grid (Meisel and Turner, 1998), and should be implemented in future studies applying such techniques. Where possible, information about the scale of the underlying processes to be investigated should be incorporated to ensure that a suitable sampling regime is undertaken (Skøien and Blöschl, 2006).

Unfortunately, the response of the pollen to anisotropy could not be explored due to the low sample numbers but this is something that requires investigation. An assumption of a number of quantitative models is the equal contribution of pollen from all areas around the basin (Sugita *et al.*, 1999; Sugita, 2007b; 2007c). Application of geostatistical analysis could provide an important tool to examine this in detail within a range of landscapes.

Finally, an assumption of the ERV and quantitative models is for omni-directional pollen contribution but anisotropy identified within the variograms of both the pollen and vegetation could invalidate this. Further analysis using predetermined sampling regimes and suitable methodology is required to investigate the potential of geostatistical analysis in palynology.

4.5.2.2 Multivariate analysis of sample inclusion

Multivariate statistics were employed to investigate patterns within the compositional properties of both the groups of sites and the samples. The former analysed data alone i.e. pollen or vegetation, whilst the latter was used to evaluate relationships between pollen and vegetation at individual sample points. Data from samples compiled to form the Ran.1000.1 and Sy.1000.1 groups were subjected to a Principal Components Analysis (PCA) and Redundancy Analysis (RDA) test. These two groups were identified due to (a) their limited spatial autocorrelation issues, (b) the substantial difference between the pollen productivity estimates, and (c) the randomly selected group showing more realistic values.

4.5.2.2.1 Principal Components Analysis (PCA) - Pollen data

The analysis was run in Canoco 4.5 (Ter Braak and Smilauer, 2002). A PCA analysis was chosen to detect patterns within the pollen samples after an initial Detrended Correspondence Analysis (DCA) identified the gradient for both datasets as being less than 4 S.D in length (Ran.1000 = 1.072; Sy.1000 = 1.511) therefore linear statistical methods were applied (Leps and Smilauer, 2003). Although an indirect analysis was undertaken environmental data were included but not used to determine the position of the axes. The data used the average distance weighted plant abundance within 100 m of the sample point as this has the greatest influence on the pollen assemblage at all sites. Scaling was applied to both pollen groups to focus on inter-species distances with centering by species to extract the patterns between samples based upon their species

properties (Pielou, 1984). As closed percentage data was used the data was log-transformed and centred by species and samples prior to analysis (Davis, 2002).

Figures 4.40 and 4.41 show sample-species biplots from PCA analysis of the Ran.1000.1 and Sy.1000.1 datasets, respectively. Within these plots the samples refer to the pollen sample sites and the species are counts of the 5 taxa used for the generation of pollen productivity estimates. The dispersal of points displayed within the Ran.1000.1 dataset implies a range of taxon values within the samples. Strong correspondence between axis 1 and the *Pinus* vector indicates that this is central to forming the axis. This describes 49% of variation (Eigenvalue (λ) = 0.49) which indicates *Pinus* is a strong determinant of the patterns formed. Axis 2 represents 22% of the variation (Eigenvalue (λ) = 0.22) and is highly correlated with *Betula* due to the low angle between the vector and axis 2. Sample 23 placed at the arrow of the *Calluna* gradient denotes a high value; similarly, samples 25 and 7 have high *Picea* and *Larix* counts respectively. The opposing direction of the *Pinus* and *Calluna* arrows signifies their negative correlation within the samples.

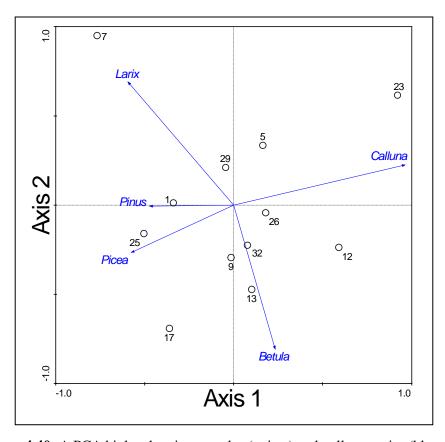


Figure 4.40: A PCA biplot showing samples (points) and pollen species (blue arrows) from BA.Ran.1000.1. Point identifications are shown and sample numbers i.e. 17 = S17

Figure 4.41 showing the multivariate plot for Sy.1000.1 exhibits clustering around the origin of the graph with only samples 7 and 34 showing extreme values. Furthermore, the clustering is centred on the *Pinus* vector showing that most samples are dominated by this taxon. Correlation between the length of the vectors for the taxa show that these are all represented by a similar spread of data. Eigenvalues for the axes show that the primary axis explains the most variation in the data points ($\lambda = 0.716$) whilst the second axis explains a large proportion of the remaining variation ($\lambda = 0.212$). Interestingly, the correlation identified between *Calluna* and *Pinus* above is not replicated and in contrast shows a no relationship as the vectors are placed at right angles to each other. A similar relationship is represented between *Pinus* and *Larix*.

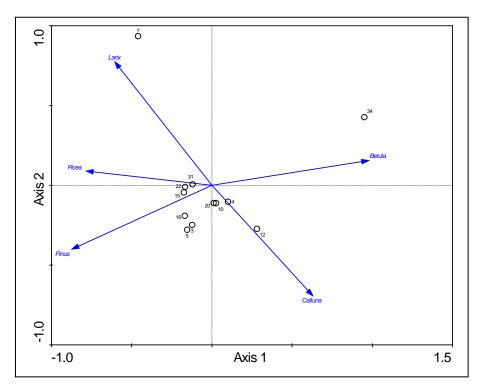


Figure 4.41: A PCA biplot of pollen samples (points) and species within these (blue arrows) for autocorrelation group BA.Sy.1000.1. Point identifications are shown and sample numbers i.e. 10 = S10.

As suggested by Leps and Smilauer (2003) an additional PCA was conducted on the vegetation data from the sites to identify patterns within the dataset. Figure 4.42 shows the biplot of the Ran.1000.1 data of vegetation based upon the distance weighted plant abundance within 100 metres radius of the sampling point. The principle axis represented 45% ($\lambda = 0.452$) of the variation in the data and the position of the *Picea* and *Larix* vectors along this axis signify a strong negative correlation between these features. In contrast, *Pinus* is highly correlated with axis 2 which has an eigenvalue

of 0.223. As with the pollen data there is a high degree of dispersion in the samples with extreme values frequently represented.

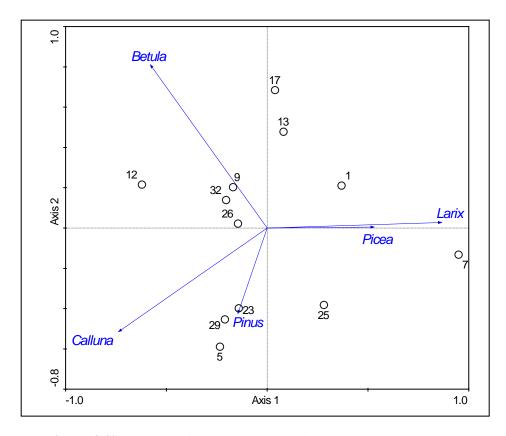


Figure 4.42: A biplot of pollen samples (points) and distance weighted plant abundance for the first 100 metres around the sample point (arrows) for autocorrelation group BA.Ran.1000.1.

Figure 4.43 shows the PCA biplot of the distance weighted vegetation data for Sy.1000.1. The diagram shows a strong linear gradient of samples parallel to the *Calluna* and *Larix* vectors which run orthogonal to the *Pinus* vector indicating a short range of values for this taxon. These are highly correlated with axis 1 which has an eigenvalue of 0.452. Axis 2, which is strongly correlated to *Pinus* and *Betula*, has an eigenvalue of 0.315. The positions of the vectors indicate that *Pinus* and *Calluna* have no relationship whilst *Pinus* and *Betula* are negatively correlated. Location of samples 7 and 34 correspond to their position within the pollen data.

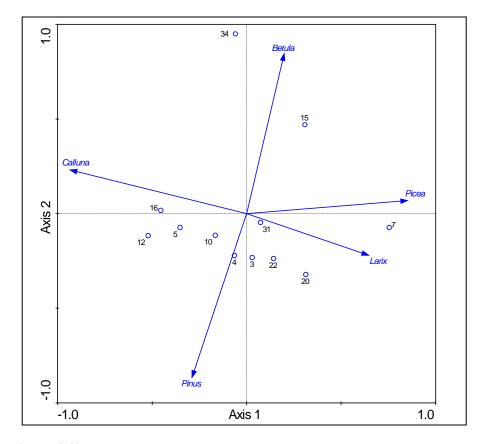


Figure 4.43: A biplot showing pollen samples (points) and distance weighted vegetation data within 100 metres of the sampling point (blue arrows) for autocorrelations groups Sy.1000.1.

4.5.2.2.3 Comparison of pollen and vegetation

Correspondence between pollen and vegetation patterns described from the multivariate analysis differs between the two datasets. Some of the dispersion shown within the pollen data for Ran.1000.1 is replicated in the vegetation data. Extreme values such as samples 7 and 17 are equally placed in each diagram. There are, however, some samples that show opposing patterns in the two variable datasets. For example, sample 1 is placed at the extreme of the *Pinus* vector in the pollen data but this is placed as below average in the vegetation plot. A similar relationship is seen for sample 23 which has a greater than average *Calluna* pollen value but this is *Pinus* in the vegetation plot, although in the direction also of *Calluna*.

The patterns emerging from the Sy.1000.1 dataset are complicated by the large degree of clustering between the variables. The only extreme values identified, samples 34, 12 and 7, plot in similar locations on both the pollen and vegetation diagrams. The limited range of values of the remaining

samples is replicated in the pollen and vegetation data which indicates that there is a relationship between the variables but low variation.

4.5.2.2.4 Redundancy analysis (RDA)

Pattern exploration within the pollen counts alone was achieved using principal components analysis; however, calculation of pollen productivity estimates is determined through relationships between the pollen and vegetation data. Hence, application of a direct multivariate technique, redundancy analysis, enabled this relationship to be investigated. As previously, the analysis was carried out in Canoco 4.5 (Ter Braak and Smilauer, 2002) with pollen counts and average distance weighted vegetation abundance within 100 metres of the sample point as the environmental data. Sample scaling was focused upon the species correlation with scaling applied to the species data; no centring was applied.

Figure 4.44 represents an RDA biplot for the Ran.1000.1 dataset. Location of the *Larix* vector along axis 1 indicates that these are strongly correlated in accounting for 40.2% of the species-environment relationship. However, the length of the *Pinus* vector indicates that this has a wider range of values represented as does *Betula*. *Calluna* proves the opposite of this pattern despite the concentration of points around the head of this vector. The Monte Carlo permutation tests did not indicate that the axes were significant (axis 1: p-value = 0.872; all axes: p-value = 0.516) indicating that the vegetation data does not fully explain the variation within the dataset.

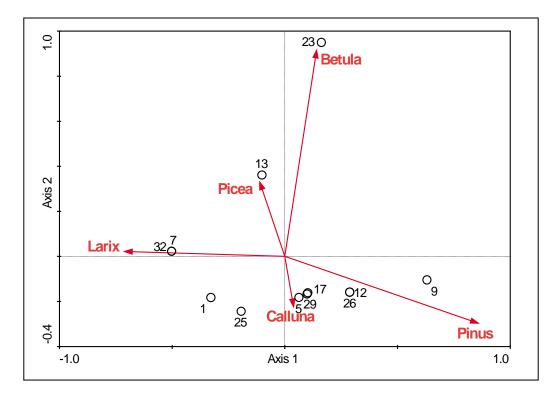


Figure 4.44: A RDA biplot of pollen samples and distance weighted vegetation data (red arrows) for groups Ran.1000.1

The RDA plot of Sy.1000.1 is shown in Figure 4.45. The location of the *Pinus* vector shows the correlation to the primary axis which describes 63.6% of the species-environment relationship. The length of this vector also indicates a range of values are found within the samples. However, the short length of the other taxa vectors show that the variance of these taxa in the samples is low and therefore may impede the analysis. Interestingly, the clustering that dominated the singular plots is not evident with a high dispersion of samples characterising the plot. In addition, the extreme values noted in the previous plots are still prominent features within the biplot. As with the Ran.1000.1 the axes are not identified as being significant as calculated through Monte Carlo permutation tests.

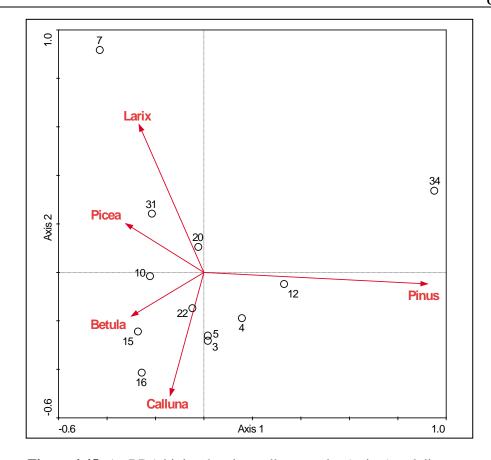


Figure 4.45: An RDA biplot showing pollen samples (points) and distance weighted vegetation data (red arrows) for autocorrelation group BA.Sy.1000.1.

4.5.3 Humpol modelling of the modern landscape

As with the previous pollen productivity estimates the Humpol software was used to model the present landscape around Inshriach to provide a 60km x 60km tile with pollen deposition simulated for four sites: two large lochs and two small sites. The map is the same as that used for the previous Humpol analysis.

Correlation between the pollen simulations from PPE groups from Table 4.17 and the observed assemblages is shown in scatter plots in Figure 4.46. Large and small deposition sites are combined in the diagram. Here the results show a strong linear relationship between all PPE groups and the observed pollen which is further supported by statistical analysis. Pearson's correlation coefficient test results have high p-values, for Ran.1000.1 and Ran.200.1 this is 1.0, implying that there is no statistical difference between the generated assemblages from Humpol and the observed data when the PPE groups are varied. However, when the actual values produced are assessed there are differences evident between sites.

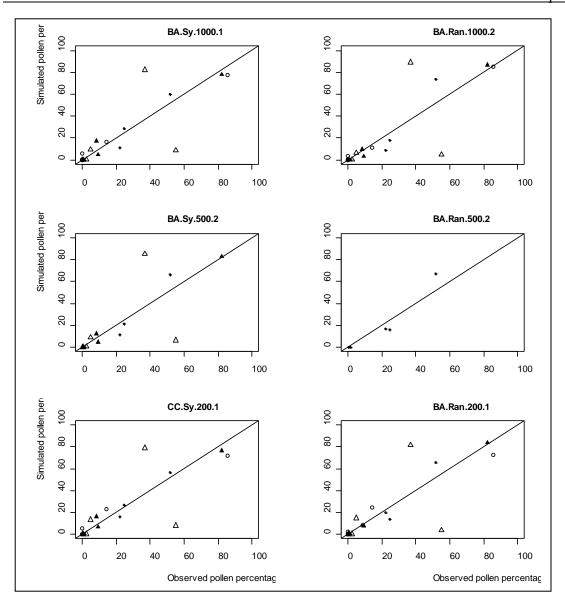


Figure 4.46: Scatter plots showing observed and simulated pollen percentages, using Humpol software, for four deposition sites within Inshriach. Different sites are represented by symbols; ●: Loch Alvie, ▲: Loch An Eilein, ○: Insh H1 (Forest Hollow), Δ: Lochan Geal

4.5.3.1 Large deposition sites

Assemblage simulation for Loch an Eilein and Loch Alvie compared well with the actual proportions largely irrespective of the PPE group. Averages of all taxa are consistent with the actual values with very low standard deviations. For example, at Loch an Eilein the simulated *Pinus* value is 81.3% in comparison to 82.2% actual representation with a standard deviation of only 6.4%. Similar patterns are present in the Loch Alvie dataset but with larger standard deviation calculations. Approximations for *Larix* and *Picea* were consistently good which could be associated with the low proportions of these taxa within the assemblages. *Calluna* experiences the poorest estimates with consistent underestimation of the actual value at both sites.

Difficulty arises in identifying the best performing PPE group at these sites as this is highly taxon specific. BA.Ran.200.1 has the greatest number of comparable estimates at both sites indicating that this could be one of the better performing groups. In addition, at Loch An Eilein BA.Ran.500.2 and BA.Sy.500.2 exhibit good correspondence whilst at Loch Alvie CC.Sy.2001 and BA.Ran.500.1 provide strong approximations.

4.5.3.2 Small deposition sites

Noticeable disparity occurs in results from Lochan Geal and Inshriach H1. Simulations from Lochan Geal fail to identify the relationship between *Pinus* and *Betula* with this being reversed. The best estimate for *Betula* at this site is 9.4% when the actual occurrence accounts for 55.1% of the assemblage. In contrast, the actual *Pinus* value of 37% is simulated by values of 61.7% and above. The mean of the simulation estimates are 5.5% and 81.4% for *Betula* and *Pinus* respectively. As a consequence of this poor correlation the remaining taxa also fail to accurately match the actual occurrences. In response, it is not possible to decide upon the most representative PPE group for this site.

At Inshriach H1 all PPE groups perform well when compared to the actual assemblage. High values of *Pinus* are reasonably represented with the simulated values providing a mean of 74.2% in comparison to the actual presence of 85.5%. Similarly, *Calluna* is well simulated by most groups with only an extreme value of 47.9% from BA.Ran.1000.1 inflating the mean. Unlike Lochan Geal the best PPE groups are difficult to determine because they all produce comparable results. However, BA.Ran.1000.2 and BA.Sy.500.2 provide the most exceptional out of all the PPEs tested.

4.5.4 LRA modelling of the modern landscape

As explained in Chapter 1, the LRA modelling software differs from that of Humpol as it uses the pollen sample to determine the vegetation patterns rather than fitting the vegetation patterns to the pollen. For this reason all pollen productivity estimates generated from the spatial autocorrelation groups were run with the REVEALS model to test the difference between outputs and with the results of the Humpol modelling. The aim was to differentiate between the PPE groups for use in the model whilst also assessing the influence of different PPE values.

4.5.4.1 REVEALS modelling

4.5.4.1.1 Lake sample sites

The REVEALS model was run with the surface samples (top 1 cm) from two short cores collected from Loch Alvie and Loch an Eilein. Tables 4.17 and 4.18 show some results of the simulations and the actual vegetation data as identified from the form of the ML scores when plotted against distance. Again, most sites show inflated values for *Larix* but also, in some cases, *Picea* when compared to the actual values. Interestingly, this effect is seen greatest in the BA.Sy.500.2 dataset where *Larix* is suggested as dominating 52.5% of the vegetation. Furthermore the errors associated with this dataset are much larger than those of the other PPE groups. CC.Sy.200.2 appears to be the poorest group and fails to correlate with any of the actual data presented in Table 4.18 as *Pinus* is not recorded. At the 100 km² area, deemed comparable to the sites, the results are poor. However, if this is compared with the 3600 km² area (the same as the Humpol grid) BA.Ran.1000.2 is identified as the best data set.

	Area of til	Inshriach		
OBSERVED	3600 km^2	400 km^2	100 km^2	32 km^2
Pinus	17.5	28.7	64.1	80.1
Picea	0.5	0.9	2.1	2.5
Larix	0.4	0.6	1.4	2.3
Betula	12.7	3.7	5.3	2.1
Calluna	68.7	66.1	27.2	13.1

Table 4.17: Vegetation percentages for Inshriach and the surrounding landscape estimated from the LCM 2000 dataset.

	BA.Sy.1000.1		BA.Ran.1	.000.2
	Mean		Mean	
	vegetation S.E.		vegetation	S.E.
	percentage	(%)	percentage	(%)
Pinus	26.8	15.5	19.1	12.8
Picea	12.4	6.0	5.5	2.7
Larix	9.5	11.0	14.5	15.3
Betula	4.8	1.0	6.8	1.4
Calluna	46.5	5.8	54.1	7.5

	BA.Sy.500.2			BA.Ran.500.2		
	Mean vegetation S.E.		_	Mean		
			vegetation	S.E.		
	percentage	(%)	_	percentage	(%)	
Pinus	14.5	32.8	_	31.0	18.7	
Picea	1.8	24.0		4.8	2.6	
Larix	52.5	43.3		11.7	13.7	
Betula	3.9	35.7		11.2	3.5	
Calluna	27.4	34.9	_	41.3	8.7	

	CC.SY.200.2			BA.Ran.200		
	Mean vegetation S.E.		N	Mean		
			veg	getation	S.E.	
	percentage	(%)	per	centage	(%)	
Pinus	0.0	0.0		31.8	18.7	
Picea	0.0	0.0		6.1	3.2	
Larix	0.0	0.0		14.4	16.3	
Betula	23.1	49.0		12.8	3.4	
Calluna	76.8	49.1	<u> </u>	35	6.5	

Table 4.18: REVEALS generated vegetation proportions from Inshriach based on surface samples from two lake cores and autocorrelation group PPEs.

The best results simulated from both the basal area and canopy cover PPE groups are those from BA.Ran.1000.1 and the BA.Ran.500.1 dataset (Table 4.19). When compared with actual regional vegetation values at 100 km² around Inshriach these all provide satisfactory results with the BA.Ran.1000.1 the most consistent. If compared with the 400km² observed data the BA.Sy.500.3 (Table 4.20) set provides exceptional correspondence with reasonably low error margins. This is especially true of the *Larix* and *Picea* estimates which are much more representative of the actual patterns creating an improvement in the assemblage as a whole. BA.Ran.1000.1 and BA.Ran.500.1 also show strong correspondence but to the 100km2 data set (Table 4.20). The error margins associated with these values appear to be large these are similar to the results of the PPE groups and reflect the errors incorporated from the actual PPE calculation and the data input within the model.

As this included only two sites for the calculation of the vegetation percentages this will automatically inflate the errors as the more sites available the more reliable the output.

	BA.Ran.1000.1		BA.Ran.5	500.1	BA.Sy.500.3	
	Mean vegetation percentage	S.E. (%)	Mean vegetation percentage	S.E. (%)	Mean vegetation percentage	S.E. (%)
Pinus	55.9	21.8	36.8	20.1	20.6	12.1
Picea	4.5	3.1	3.9	2.3	1.3	0.7
Larix	8.2	11.8	8.9	11.7	7.1	8.3
Betula	10.5	4.7	5.7	2.5	6.1	1.6
Calluna	20.9	7	44.7	11.3	65.0	7.1

Table 4.19: REVEALS generated estimates of vegetation coverage using basal area derived PPEs.

4.5.4.1.2 Moss sample sites

Considerable differences between the results obtained with the surface samples and the core samples from the two lochs cast doubt over the applicability of the sites to the modelling software. The results of these tests show that better results are obtained when data from only two sites are used to feed the model rather than 19 which is counterintuitive. The 29 moss samples used to generate the pollen productivity estimates were also used to determine the regional vegetation estimates, as a comparison to the lake sites.

	BA.Sy.10	000.1	BA.Ran.1000.2	
	Mean vegetation S.E. percentage (%)		Mean vegetation S.E percentage (%)	
Pinus	36.2	21.1	32.8 20.4	1
Picea	34.5	23.1	19.6 19.8	3
Larix	9.2	14.1	17.6 18.4	1
Betula	1.1	9.7	2.1 10.8	3
Calluna	19.0	19.2	27.9 21.4	1

	BA.Sy.500.2			BA.Ran.500.2		
	Mean vegetation S.E. percentage (%)		Mean vegetation percentage	S.E. (%)		
Pinus	25.0	26.2	_	48.7	25.0	
Picea	6.2	18.7		15.6	18.0	
Larix	53.5	32.1		13.1	16.1	
Betula	1.2	15.9		3.1	14.7	
Calluna	14.2	24.4		19.5	18.9	

	CC.SY.200.1			BA.Ran.200.1		
	Mean			Mean		
	vegetation	S.E.		vegetation	S.E.	
	percentage	(%)		percentage	(%)	
Pinus	0.0	0.1		43.7	22.9	
Picea	0.0	0.0		15.2	17.9	
Larix	0.0	0.5		15.8	17.6	
Betula	15.0	45.4		2.4	12.2	
Calluna	84.9	45.4		22.9	19.5	

Table 4.20: REVEALS model generated estimates of vegetation percentages within the regional landscape around Inshriach Forest from the autocorrelation test distance classes. Sy: Systematically selected groups; Ran: Randomly selected groups; S.E: Standard error.

Tables 4.20 and 4.21 show the results of this analysis with actual vegetation data from the landscape represented in Table 4.17. The best estimates are generated from the BA.Ran.1000.1 group with a *Pinus* value for 70.7% and *Calluna* of 7.9% closely matching those of the observed data. Overestimation of *Larix* and *Picea* is evident although these are not as significant as other groups. The poorest estimates are derived from the CC.Sy.200.1 which, like the previous lake

samples, showed zero values for some taxa questioning the reliability of the results. Finally, correlation between the two groups in the BA.Ran.500.1 set is strong with all taxa showing this relationship. However, error estimates associated with the canopy cover group are very large and cover the range of the mean vegetation proportions suggesting caution during interpretation.

	BA.Ran.1000.1		BA.Ran.500.1	.1
	Mean		Mean	
	vegetation	S.E.	vegetation S.l	E.
	percentage	(%)	percentage (%	5)
Pinus	70.7	25.0	56.1 25	.3
Picea	11.7	15.5	12.2 16	.3
Larix	7.4	12.2	9.7 14	.7
Betula	2.4	15.5	1.5 10	.8
Calluna	7.9	13.2	20.5 20	.1

Table 4.21: REVEALS derived estimates of vegetation coverage using canopy cover PPEs and moss samples for regional samples.

4.5.4.2 Summary

Overall, vegetation reconstruction using the LRA has proved to have mixed results. The estimates of the REVEALS models are promising producing analogous results to the observed data. Differences between the deposition locations did not impact on the groups producing the most comparable results when the lake core samples were used in preference of the moss samples. However, it is interesting that a greater number of lake surface samples reduced the quality of the results from the REVEALS model. This could be related to uneven sedimentation over the surface of the lake; by giving a false representation of the pollen rain this would induce error into the modelling software and the corresponding result.

Decision over the area of the landscape with which to compare these results with actual data is difficult to establish. Due to the small size of the deposition sites associated with the samples it would be instinctive to compare the results with vegetation data for Inshriach alone. On this basis the BA.Ran.1000.1 dataset would provide the most accurate results from the analysis. Equally, inclusion of such a large number of samples may allow detection of the regional patterns from the sites regardless of their size. If this is the case, to what distance is this achieved? If it reflects up to 100 km² around Inshriach then the BA.Ran.500.1 dataset provides a good approximation of the vegetation whereas further than this, up to 400 km² area, a number of the other groups also come into contention.

Calculation of the characteristic source area of pollen using the Ring source model of Sugita (1993; 1999b) gives some indication to the area that would be represented by the deposition sites. The software calculates the distance within which a selected pollen proportion would be derived from using parameter values such as wind and fall speed. This method estimates the greatest source area for the taxa included is just less than 1500 m. Although this is an approximation and some parameters cannot be fully accounted for this does suggest that the representative area for the moss samples would be just over the size of Inshriach itself, 2500 ha or 32 km². Consequently, BA.Ran.1000.1 and BA.Ran.500.1 provide the best estimates of the vegetation proportions and will be used to provide the parameters for further modelling.

4.6 Discussion

4.6.1 Representation of taxa in pollen and vegetation sampling

The majority of the 32 moss polster samples obtained from Inshriach are dominated by *Pinus* which seems inevitable given the proximity of the samples to the woodland and the quantity of natural and managed Scots pine woodlands within the regional landscape. Clear relationships between the pollen and vegetation are required if robust estimates of pollen productivity are to be obtained. Although some differentiation of community composition can be made based upon percentage/concentration of occurrence and species diversity in the pollen assemblages, the degree of openness due to the age structure of the woodland is indistinguishable. Even sites that are within open areas or are only dominated by juvenile Scots pine have between 20 - 50% *Pinus* pollen within the assemblage which could represent the regional composition alone or this pattern could have been influenced by the wind patterns and moss species within the region. This highlights the complexities associated with pine woodland and again questions the validity of using thresholds for defining pine presence.

4.6.1.1 Wind patterns

Distinct patterns between the pollen concentrations of the moss samples highlight potential effects of wind speed and direction combined with the woodland profile and location of samples therein. Investigations into woodland pollen deposition identify differential behaviour determined by the woodland edge, density of vegetation and height (Tauber, 1965; Andersen, 1974; Raynor *et al.*, 1974; Raynor *et al.*, (1974) released pollen above a canopy at increasing distances from the woodland. Interestingly, increased diffusion of the assemblage occurred as the airflow encountered the woodland edge even through the majority of the flow continued over the woodland canopy with no discernable decrease in wind velocity. Inevitably this increased deposition of pollen close to the woodland edge. Furthermore, some pollen was transported into the trunk space at this point but rapidly decreasing wind speeds within the woodland impeded long

distance transportation. Raynor et al. (1974) estimated that this effect would diminish after 60 - 80m into the woodland. Empirical work undertaken by Brown (1999) corroborated this when Poaceae pollen was found only up to distances of 100 m within a woodland when it was not present around the deposition sites. Factors affecting the degree of these processes proposed by Raynor et al. (1974) supported the previous findings of Tauber (1965), and Geiger (1950), that the amount of undergrowth and density of the arboreal stem are the main controls as this affects the penetrability of the airflows into the woodland. This effect can be used to explain some patterns exhibited within the pollen concentration data at the sample sites in Inshriach as the prevailing wind is predominantly westerly. Assessment of the concentrations, shown in Figure 4.1 in Section 4.2, shows a large proportion of sites on this western margin to have greater concentrations than those within the woodland. There are some exceptions to this which appear to relate to the density of the stems and the planting year, as older stands have undergone thinning allowing pollen laden airflows to penetrate further into the woodland. Furthermore, sites that are deep within the woodland also show high concentrations, such as samples 3 and 4, relating to the age of the stems and the openness. For example, sample 3 is surrounded by open bog woodland which will increase the dominance of the canopy airflows in contributing to the sample and in essence act as a woodland edge. This supports the need for patch-matrix investigations as the size and distribution of these areas can have an important influence. Orientation and profile of the woodland also controls the amount of pollen deposited. For example 31 has a high total concentration whilst being situated on the western margins whereas sample 34 has a low concentration even through it occupies a similar position. Both are within 100 m of the woodland edge, both are Hyloconium moss species, yet sample 34 lies in a portion of the woodland where the site is sheltered from the prevailing wind as it diverts around a protrusion, thereby lowering the concentration of grains within the air flow but also diverting this along the margins of the woodland rather than into it. In contrast, the margins at site 31 are almost perpendicular to the wind direction therefore this will strike the woodland and carry pollen to the site of deposition increasing the samples concentration.

The lack of pattern between samples with a location downwind of the woodland and *Pinus* pollen concentration is interesting. Intuitively, a relationship between these two components would be expected given the dominance of both Scots pine and Lodgepole pine within the woodland and topographic influences (Soepboer *et al.*, 2007). Previous studies have found a strong relationship between pollen composition and proximity to woodland stands with gradual decline in proportion with increasing distance from this (Turner, 1964; Caseldine, 1981; Tinsley, 2001). Modern pollen studies from Abernethy Forest by O'Sullivan (1973b) seem to suggest similar patterns to those found around Inshriach with little relationship between pollen proportions and canopy openness. However, the results of his analysis are represented as proportions of arboreal pollen and therefore

provide a difficult comparison. It is unlikely that wind patterns alone are responsible but also an influence of the vegetation structure or the strength of the regional pollen rain as identified within the ERV analysis. Given the structure of the vegetation and aerodynamic properties described above a correspondence between openness and regional-local pollen ratios seems realistic. For example, a site within a dense portion of Inshriach woodland would be strongly controlled by the local *Pinus* rain and to a lesser extent by the regional component as for samples analysed by Jackson and Kearsley (1998); in an open site the large amount of *Pinus* pollen would be derived from the air flows rather than the local, thus, the same assemblage could be obtained or at least mask the strong relationship between woodland proximity and pollen deposition identified in other areas.

4.6.1.2 Moss species

A number of studies have suggested that variation can be inherent between moss species used to provide the modern pollen samples, however this does not appear to be an influencing factor in Inshriach. Figure 4.1 shows the total pollen concentration of the samples in relation to the moss species and location. As discussed above the relationship is stronger with sample location than moss species alone. During sample collection decisions over the species used were controlled by presence at the site, which in turn is governed by the conditions prevailing at the site. Boyd (1986) went some way towards observing this by comparing three different moss species at each of four sites. The sites included birch woodland, pine woodland and open sites with differing degrees of arboreal presence. Although total concentrations differed, results from this test showed broad correlation between the pollen percentages of individual species with differences between sites clearly reflected. Similar conclusions were reached in a study by Bradshaw (1981) where both absolute and pollen in modern moss samples from South West England were compared with basal area within 20 metres of the sample point. Although Räsänen et al., (2004) identified that pollen composition in mosses differs from the representation in pollen traps the author went on to suggest that standardised sampling is the key. Although variation occurs dependant upon whether traps or moss are used, the species and the number of sub-samples if the methods are concurrent the errors should remain consistent.

4.6.2 Generation and application of pollen productivity estimates

If a large number of estimates can be obtained from a site will these all be representative so long as the number of sites is great enough, i.e. double the number of taxa included? Results here suggest that this could be the case but if the regional vegetation reconstructions from the LRA are considered it is evident that the differences from the pollen productivity estimates are recognised but are not fed through into the reconstructions.

4.6.2.1 Basal area versus canopy cover

The aim of this comparison was to determine the difference between the pollen productivity estimates should two different measures of vegetation abundance be used. There were similarities between the values obtained yet the two datasets differed in their estimates of the RSAP. Firstly, strong correlation between the canopy cover and basal area PPEs is evident in both the full set and spatial autocorrelation groups. Although in Sy.1000.1 this may not appear to be the case, the relationships and ratios between the taxa are highly comparable. This implies that although the magnitude of values changes the relationships between the pollen and vegetation are still identified within the analysis. It is difficult to compare the results to any other as limited analysis has taken place within this area. Although two studies in Sweden have used differing methods obtaining different PPEs, Broström et al. (2004) used basal measurements and von Stedingk et al (2008) canopy cover, the difference in environmental conditions could be a factor in this disparity complicating any conclusions associated with methods. In general, larger estimate of RSAP for the canopy cover data set suggests that this is related to the magnitude of the values used within the analysis. Estimates of basal area provide an accurate representation of the vegetation abundance yet these values are much lower than the coverage of foliage due to the structure of the species used within the analysis. As the ERV models use the relationship between pollen and vegetation within contiguous rings the results impact on the overall patterns with increasing distance. Consequently, with the larger canopy cover values, a larger number of rings will be included with steadily decreasing weightings before equilibrium is reached. To date there have been limited studies using a comparison of data acquisition methods for use within ERV analysis. This is obviously an area that requires more research as collection of the vegetation information to correspond to the pollen samples is a time consuming task and discourages others from obtaining such necessary information. Investigation into the most cost and time effective methods whilst still obtaining accurate estimates for application to the pollen modelling would be a valuable undertaking.

4.6.2.2 ERV model comparison

There are both similarities and differences exhibited by the application of the various ERV models and weighting functions. Similarities between the ERV 1 and 2 models are shown within the patterns and values of the ML graphs, whilst ERV 3 shows a similar form but much lower values in the basal area groups and inflated values in the canopy cover dataset. Similar relationships are exhibited in other studies and indicative of robustness in the dataset (Broström *et al.*, 2004; Soepboer *et al.*, 2007). Maximum likelihood scores of the two datasets do not vary indicating that the methodological changes do not affect the fit of the pollen and vegetation data yet the 'best' models can be distinguished. The lowest ML scores for the basal area group were obtained from ERV 3 whereas the canopy cover group preferred ERV 2. Identification of the most representative

ERV model is site specific and dependant upon the overall composition of the landscape and the heterogeneity. For example, separate studies carried out in the Swiss Jura and Swiss plateau both found ERV 1 to provide the lowest ML scores which reflects the local environmental conditions. Within Inshriach there is a large difference between the vegetation composition of the sites used within the analysis, but the proportions of the taxa do not change significantly especially *Pinus*. ERV 2 can be affected by large changes within the vegetation proportions at the site which do not occur with the canopy cover dataset supporting its suitability (Parsons and Prentice, 1981). Conversely, ERV 3 is suited to the basal area data as Sugita (1994) suggests that this model should be more appropriate for smaller scale studies, both spatial extent and in terms of the number of samples used, potentially explaining the better fit of this model to Inshriach given the study area covers around 2,500 hectares. ERV 1 is a poor fit because there is a large difference in the vegetation composition between sites which compromises the assumptions behind the model (Parsons and Prentice, 1981; Broström *et al.*, 2008). Consequently, all models have to be assessed at each site to ensure that a suitable model is used.

When weightings are applied, ¹/d and taxon-specific show equivalent patterns with comparable results identified at other sites (Nielsen, 2004; Mazier et al., 2008). In contrast, \(^1/d^2\) shows a very poor relationship when all models are considered with other studies highlighting similar situations predominantly via higher maximum likelihood scores and a shorter RSAP despite this being analogous to the leptokurtic nature of pollen dispersal (Broström et al., 2004; Bunting et al., 2005; Mazier et al., 2008). However, Calcote (1995) found the ¹/d² weighting to provide the best correlation from comparison with the taxon-specific function when undertaking studies in forest hollows of North America which could explain the low RSAP (50 m) estimates obtained. These differences potentially relate the ¹/d and the taxon-specific functions providing similar more gradual declines in applied weighting whereas the $^{1}/d^{2}$ has a much greater weighting to the first 20 – 30 m than the remainder of the sampling distance yet this will also be a consequence of the sampling distance used. Within this study a 10 m ring was used to weight the vegetation but others have used a much higher resolution. Mazier et al. (2008) employed a 1 m distance to the whole sampling radius whereas others applied an increased resolution within the immediate vicinity of the sampling distance, and increased this after 100 m when the difference between the weightings is minimal (Räsänen et al. 2007; von Stedingk et al., 2008). This latter approach seems the most suitable as the weighting of the vegetation closest to the deposition site is critical as this provides the strongest source to the sample. By increasing detail in this zone whilst reducing resolution with distance the computational processes involved will not be overly demanding.

Difficulty with the variation within the RSAP obtained from the two datasets is also found in deciding which is the most representative of the environmental conditions. No relationship is evident between the RSAP distance and the method of vegetation collection with differences only from opposing models. Similarly, the application of moving-window linear regression agrees with by-eye estimates in some models but differs in others, further affecting determination of this distance. At present, estimation by eye is a subjective process, especially when increases occur after the ML score minima as in this study. The alternative method employs a distance window to compare the mean and variance either side of its centre point and where this difference is minimal, at or close to 0 with a statistical significance of p = 0.05 level, the curve is determined as horizontal and RSAP established (Davis, 2002; Gaillard *et al.*, 2008). However, the moving-window method requires consideration as despite objectivity the size of the sampling window used in relation to the survey distance can influence the result obtained (S.Sugita, p*ers. comm.*). Gaillard *et al.*, (2008) found that increasing the window size corresponded to an artificial increase in the RSAP estimate. Also, the increases seen within some of the ML score curves will give a false representation of the distance if the gradients are similar either side of the minimum.

Using both determination methods the groups with the lowest ML scores (All site BA ERV3; autocorrelation groups at 1000 m) provide a range of distances of between 400 - 600 m. In open woodland studies such as the forest-tundra ecotone in Northern Sweden studied by von Stedingk *et al.* (2008) a distance of 400 m was identified. Similarly, Räsänen *et al.* (2007) obtained an estimate of 1 km for Northern Finland, again with a combination of closed and semi-open sample locations. One of the shortest distances from closed alder and willow woodland in Norfolk was around 150 m although the close proximity of the sites could be influencing this and therefore has to be used with caution (Bunting *et al.*, 2005). These distances concur with the range obtained at Inshriach suggesting that a distance of 400 - 600 m is a reasonable conclusion, yet a more definite value is difficult to reach given the variability in models and weighting functions, a strong control on distances obtained, and, with respect to this study, site combinations used to generate PPEs.

4.6.2.3 Pollen productivity estimates generated

Considerable numbers of pollen productivity estimates have been generated from the initial 29 moss sample sites at Inshriach. Detection of the most robust set is a difficult task given the lack of correlation between the groups. Comparison of the generated PPEs with previously published results show greater agreement with the autocorrelation corrected groups.

Original PPEs from the 29 sites for Inshriach generated high values for *Pinus* which are not reflected in other sites. Although the value from central Sweden is around this level the authors

suggest this is an overestimation of the actual value and is erroneous (von Stedingk *et al.*, 2008). Remaining values from the published datasets (Table 4.22) are all low and correspond well to the open values of the original PPEs and the majority of values from the larger distances in the autocorrelation groups. Other taxa do not generate the same magnitude of difference between the published and Inshriach values and in most cases all correspond, within the error margins, to the published estimates. However, it is the relationships between the values that are of importance in this case. Within the published dataset (Table 4.22) *Pinus* is lower than *Betula* in only one of the autocorrelation groups, BA.Ran.500.1 of the canopy cover set, in the Inshriach estimates with the remainder reflecting at best a one-to-one relationship.

Site Type	Study location	Pinus	Betula	Calluna	Picea
Moss	Central Sweden (1)	7.76	0.81	0.11	1
polsters	Southern Sweden (2)	3.17	4.94	2.61	1
T -1	Denmark (3)	0.3	-	0.34	1
Lake sites	Estonia (4) Swiss	1.42	1.42	-	1
	Plateau (5)	2.37	4.25	-	1
	Mean	7.8	3.5	1.1	1
Inshriach	Maximum	29.4	15.2	4.8	1
	Minimum	1.6	0.2	0.0	1

Table 4.22: Published pollen productivity estimates with *Picea* recalculated as the reference taxon in relation to the range of all calculated values obtained from Inshriach. (1) von Stedingk *et al.* (2008); (2) Broström *et al.* (2004); (3) Nielsen (2004); (4) Meltsov and Poska, in progress (from Broström *et al.*, 2008); (5) Soepboer *et al.* (2007)

PPEs from Inshriach compare well with the Southern Sweden set when the autocorrelation groups are deemed representative of the landscape. Environmental factors are similar between these two locations in terms of climate but the landscapes of the areas are different with values generated in Broström *et al.* (2004) from open and semi-open landscapes differing from the closed and managed state of Inshriach. Little comparison has been done to date regarding the productivity differences between the natural states of woodland and therefore this influence cannot be ignored. Inshriach is managed for commercial purposes but also for native flora and fauna regeneration. The former would have the greatest influence on productivity as growth is maximised to increase productivity in terms of timber yields. Consequently, thinning and brashing are undertaken to remove the

weaker individuals at defined periods after planting. It is only the most productive and therefore healthy timber that remains which would, theoretically, produce more pollen. Yet, there is also the issue of suppressed pollen productivity within dense woodlands. As Pardoe (2008) has shown within pollen monitoring studies the greatest amount of pollen production within a woodland is seen at its margins. Would this counteract the effects of increased production from healthy individuals?

Exaggerated *Pinus* values first obtained from the 29 sites and the Sy.1000.1 autocorrelation group are likely related to a combination of the vegetation structure at Inshriach and spatial properties of the sites, with the latter being dominant. Most samples were obtained from hollows in the woodland within which *Pinus* is by far the dominant taxon; consequently, the resultant PPEs are potentially subjected to enhanced deposition rates. Bunting et al. (2005) identified this in estimates for Alnus and Salix within wetland alder carr sites in Norfolk where the two species are highly dominant components of the surrounding vegetation. Small sites show a greater reflection of the local vegetation and at Inshriach this is densely stocked Scots pine and Lodgepole pine. This would increase the deposition of *Pinus* at the sites and inflate the values. Although there is evidence to suggest that pollen production of individuals would be reduced within a woodland context the amount would possibly counteract this. On the contrary, in more open sites where local *Pinus* deposition will be low due to fewer individuals, but heightened production, the regional component would contribute large amounts as this is a dominant regional component, as shown above. Theoretically this should relate to the biomass or proportion of those taxa within the vegetation and should be accounted for but what if the local rain is so extreme that it dominates the assemblage so much that there is an impact on the result of the ERV modelling. Is it that there are behavioural differences within the dispersal of pollen within a woodland context? If this is the case then this would be supported by the results as *Pinus* shows the greatest difference, possibly due to the airsacs. There is a small amount of difference between Betula and Calluna then Larix shows the least amount of change. This could relate to the impact of wind which would be greater in the open areas carrying more pollen within the canopy component. This would be greatest for *Pinus* which is carried easier and further and not as defined for Larix which is heavier and therefore requires a bigger change in the wind speed to be able to change the deposition rate. Calluna is interesting as lower productivity within the woodland is expected yet this is the case within the open sites. Consequently, relationships between the pollen and vegetation would be ambiguous creating the variability amongst the different groups identified above.

4.6.2.4 Spatial autocorrelation as an influence

Clear relationships between the spatial patterns and the PPEs are evident, especially within the basal area derived values. Overall, differences between the output of the systematically selected groups and the random groups can be detected. The form of the graphs appears to be unrelated to the spatial patterning of the samples. There is no pattern between increasing ML scores following the minimum being reached, and nearest neighbour distance suggesting site inclusion as a cause. As mentioned, direct comparison of ML score magnitude cannot be done which makes identification of the most suitable PPEs difficult.

The presence of interrelationships within some areas of pollen-vegetation relationships is fundamental to modelling, for example in the principles of the REVEALS model, but is a hindrance elsewhere, as with most geographical analysis (Gould, 1970). Effects of spatial autocorrelation are primarily detected in the *Pinus* values but the effects are fed into the other taxa during the modelling. Independence is required because pollen at a site is related to the amount of vegetation surrounding it and the PPE generated from the best linear relationship between the two; independence is also one of the assumptions underlying the ERV models (Prentice and Parsons, 1983). Using the analogy of the witch's hat of pollen contribution to a deposition site from Davis (2000) the relevant source area of pollen can be clearly identified as the peak. If, however, two sites are close together and this distance overlaps the intersected segment is essentially doubled as the same amount of pollen is being modelled as contributing to two sites; in reality this is not possible as the pollen contributed is halved. As the actual amount of vegetation required to produce the amount of pollen within the assemblage is overestimated this decreases the angle of the linear model, as high pollen is equated to higher vegetation, subsequently decreasing the PPEs obtained. Pinus is the main taxon affected as this is a major constituent of the vegetation and the pollen whereas other taxa do not occur in these frequencies and are not subjected to the same degree of autocorrelation. Clear evidence of this is found in the PPEs for Inshriach. In the 1000 m systematic group PPEs are the highest identified from all runs undertaken whereas the remaining groups, subjected to some degree of spatial autocorrelation have values less than 10. If this is the case, the high *Pinus* values are representative of the woodland, however further work is necessary to confirm this given the lack of correlation of these values with published results.

As the woodland under analysis is planted and managed the resultant spatial pattern is artificially controlled to obtain the highest yields over the shortest timeframe. Inevitably, being suited to the prevailing environmental conditions Scots pine is the dominant species which induces the spatial autocorrelation as, in most cases, the nearby compartment will also be planted with Scots pine. Consequently, the scale of this planting regime will determine the distance at which the samples

become independent. Similarly, within natural sites the patch-matrix structure of the vegetation will have a strong determining influence on the spatial autocorrelation properties making the level site specific. Although a natural system will not be fully random as taxa close by will have a greater influence on controlling patterns after gap creation it is more so than a managed system. Mason *et al.* (2007) used spatial statistics to compare woodland systems, two managed and one natural. In concluding, it was suggested that the natural system had a much more random patterns with the managed stands exhibiting an even-aged structure and larger correlation distance. Such difference could have implications on pollen deposition and sampling strategies from these woodlands as the structure is semi-planned. Furthermore, managed systems currently prevailing may not be representative of those in the past. If this is so this could have serious implications and limitations for the number of pollen based techniques requiring modern analogues. Hence, the spatial properties of each site need to be deduced, preferably before sampling, if this is to be avoided.

Semi-variogram results suggest that the pollen and vegetation data are reflecting different spatial scales. More importantly, the range of the pollen data is 1800 m, four times that reflected by the vegetation which implies that patterns within the vegetation are not reflected within the pollen. Environments dominated by pine are notoriously difficult for undertaking palynological studies and clearly geostatistical analysis of Inshriach Forest supports this conclusion. Thus, obtaining PPEs from this site could be problematic as distinguishing between the local and regional pollen rains is difficult. The distance of 400 m by Broström *et al.* (2005) has been used as a measure in subsequent studies (Mazier *et al.*, 2008; von Stedingk *et al.*, 2008), but unless tested representativeness remains unknown. Attempts at geostatistical analysis within this study imply that 500 – 600 m distance may be reasonable but the limited number of sites used may influence this result. Spatial structure and the RSAP distance are two dominant controls on the actual sampling distance that should be used, but these are site specific. Increasing the number of sites included within the analysis from double the number of taxa could allow spatial autocorrelation statistics to be performed. However, at least 50 points will be required to do this as suggested by Burrough and McDonnell (1998) which would significantly increase the data collection period.

Generation of multiple PPE sets in the same autocorrelation groups, in most cases, proved to correlate in the systematic but showed greater disparity in the random selections. Availability of sites will be a contributing factor to this pattern as within the random sets there is a greater deal of choice in the samples that can be included whereas the restrictions placed on the systematic group is limiting. Ultimately, changes in the mean and variance of the samples used in the analysis associated with the set will determine the output figures. Although a range of values may be

available in the full set this may not be fulfilled by the subsets stressing the importance of having a range of values (Broström *et al.*, 2008). As the ERV models used to calculate the productivity estimates are linear, variation within the pollen counts used to feed the model change the output but the inclusion of outliers will significantly alter the output of one group to another. This will become increasingly relevant if the landscape being modelled is significantly heterogeneous and samples sites record only the local vegetation i.e. moss polsters. For example, if some large values are not included within a group the gradient of the linear model, the alpha values, will appear reduced in comparison with those that have these incorporated.

4.6.2.5 Sampling design

Sampling design can have a large influence on the results obtained from a test further accentuating the spatial influences. Although previous studies suggest that a random technique should be employed for sample selection (Broström et al., 2005) this was not fully incorporated into this project. As an alternative, the initial design used within this study was a stratified-random approach to obtain a representative sample from all age classes, species composition and openness as vegetation information was available prior to sampling. The findings from Broström et al. (2005) highlight the differences that can occur from the use of systematic as opposed to random sampling by comparing the PPEs simulated from two hypothetical and one real landscape in both an open and semi-open scenario using different sampling techniques. Maximum likelihood scores show random sampling provides the lowest scores in the hypothetical landscapes. Conversely, in the actual landscapes the scores are more comparable and in the case of the semi-open landscape the systematic results produce a lower ML score which supports the results obtained within this study. Examination of the generated PPEs from the hypothetical landscapes identifies a greater disparity between the two sampling methods in the semi-open vegetation scenario whereas the open landscape has corresponding results. This variation in PPEs and comparability with changing landscape structure implies that sampling design is not the sole influence on the output having implications for the spatial autocorrelation argument discussed earlier. In the hypothetical landscapes where landscape structure is randomly created there is either no or limited spatial autocorrelation, whereas in a 'real' landscape there is the potential for much more. Consequently, although the sites can be randomly selected it does not automatically assign independence. As, Broström et al. (2005) state "PPEs are valid although obtained using a systematic sampling scheme", adding support to the view that sampling strategy may not be the sole influence on PPE diversity.

Also, transects were used to obtain the vegetation data in contrast to full landscape mapping as carried out in Broström *et al.* (2004). Although a similar strategy has been utilised previously (von

Stedingk *et al.*, 2008) this could affect the representation of taxa within the vegetation data and therefore the overall pollen-vegetation relationship. As pine is the dominant taxon it would have been influence more so than others which could account for the variability between the PPE groups. If over- or under-estimation is involved this would be greatest with increasing distance along the sampling transect and so would affect smaller hollows to a lesser extent. This site specific effect could therefore be contributing to the different PPEs obtained when subsets are used. Further tests into the influence of differing sampling regimes would be required

4.6.3 Simulations and PPE selection

Overall, the outputs from the two models are very promising. Interestingly, the best results from the two simulation suites differ complicating a conclusion of the most representative dataset for Inshriach. With the Humpol software the BA.Sy.500.1 group and ERV 2 P-S groups provide the best comparison with actual data, whereas the LRA produced good results when fed by the BA.Ran.1000.1, BA.Sy.1000.1 and ERV 3 P-S parameter groups (Table 4.23). Surprisingly, BA.Ran.1000.1 was one of the poorest performers within the Humpol model. Although comparison between the LRA and the actual data is complex due to difficulty in determining the exact source area for reconstruction the use of the moss samples ensures robust testing of the groups. Differences between the groups selected could be related to the approaches the models take. The Humpol software uses a forward-modelling approach to simulate pollen deposition using cells from an image of the landscape, whereas the LRA uses the pollen data to generate vegetation patterns. Although the same algorithm is used these different techniques will induce error. For example, the cell size of the grid in the Humpol model can determine the accuracy with which the results are obtained. Here the smallest cell size possible was used, 50m, without affecting computational power. This is further supported by differences in the output of the two models when different PPE groups are varied: Humpol has only a 3% difference in *Pinus* estimates between the ¹/d and taxonspecific weightings whereas the same PPEs in the REVEALS model have a difference of 11%. In the Humpol model the effects of the weighting are on a cellular basis and PPEs are directly applied to the vegetation estimates (Bunting and Middleton, 2005). REVEALS utilises this differently by first multiplying the weighting using the ring source model (Sugita, 1993; Sugita, 1994) and the PPE before applying it to the pollen counts.

	HUMPOL				
	BA Sy.500.1	ERV2 P-S	BA Sy.1000.1	BA Ran.1000.1	ERV3 P-S
Pinus	4.9	5.7	17.9	3.1	6.3
Picea	1.0	1.0	1.0	1.0	1.0
Larix	0.1	1.5	9.5	4.0	2.4
Betula	1.5	2.1	15.2	2.5	3.3
Calluna	0.6	0.7	2.6	2.1	1.1

Table 4.23: PPE groups used in the simulation models. These groups where selected as providing the most comparable results when compared with observed data (as shown in Tables 4.10, 4.11 and 4.14).

In addition, positional and categorisation errors associated with the remote sensing of the LCM 2000 dataset will contribute to the grid and are not taken into account within the modelling. Conversely, the LRA derives a covariance matrix from the errors associated with the parameters included and propagation of these during calculation of the vegetation proportions (Sugita, 2007b). Excluded from this analysis are errors incorporated from the community compositions generated for the comparison dataset. Any error from this will directly impact upon the output of the Humpol model as this is an attribute of the input grid whereas this provides the comparison data for the LRA model. In other previous studies using the Humpol software the Multiple Scenario Approach has been used where multiple landscapes are generated and used to simulate an output from which the best landscape can be selected as representative of the pollen assemblage (Bunting *et al.*, 2007). This approach could have been applied in this study to the vegetation composition of the landscape communities but this would not test the PPEs, to do this all remaining parameters had to remain static.

Larix is consistently seen as a poor performer in the modelling of the landscape using both the Humpol and LRA software. The effects of two factors are shown within the Inshriach dataset with respect to this. Firstly, Larix pollen grains are similar in features and size to Pseudostuga (Douglas Fir). Both of these species occur within Inshriach, simultaneously at some sites from which samples were obtained. Although every effort was taken to correctly identify the true Larix grains, due to uncontrollable effects i.e. breakage or crumpling, this is not always the case. Where doubt in identification occurred where both genera were present in the vegetation the tally was placed in a combined group but inevitably this will impact upon the counts of the Larix group. It is envisaged that this will not significantly affect the overall results but has to be considered as a source of error. At present the ERV models do not account for counting errors within the pollen data but perhaps

this is something that should be considered to make the output more statistically robust. Although the *Larix* example has been used here the same can be shown for other species; Scots pine and Lodgepole pine are both present in significant numbers at Inshriach yet the PPE is a combination of both these species which, again, will introduce an error term. Other studies have identified difficulties in accounting for this variability in the pollen samples and it is something that has been acknowledged as an un-quantified source of error within the estimates with and between project sites (Broström *et al.*, 2008).

Secondly, Larix is not a main constituent within the woodland at present and therefore occurs in relatively small stands throughout the earlier established areas of Inshriach. In the initial 34 site dataset *Larix* was identified at a range of values providing a good representation of the relationship between pollen and vegetation. Subsequent reduction to 29 sites removed some of these values, as for other taxa, and as a consequence this range was affected leaving a number of smaller values and two extreme values as seen in the pollen diagram in Figure 4.2. Inflated PPEs for this taxon occur when this site is included without some of the intermediate sites. This raises issues about the robustness of the PPEs for this taxon. However, not to include this within the sample would also affect the output as gradient would be shorter and estimates adjusted accordingly. At present, one of the constraints of the ERV models is that there is double the number of sites to taxa within the analysis which has been followed in numerous studies (Broström et al., 2004). Broström et al. (2008) states that, "the sites should be selected so that a long vegetation abundance gradient is obtained from most of the taxa selected for the analysis", which should perhaps be taken to mean the major taxa. If a long gradient is to be obtained for minor constituents of the vegetation then the number of sites required will be related to the degree of heterogeneity in the landscape and the taxa used. Furthermore, to undertake this would require a systematic element to the sampling strategy or prior analysis such as the simulation techniques of Mazier et al. (2008) and von Stedingk et al. (2008).

4.7 Conclusions

Estimates of pollen productivity at Inshriach are difficult to determine and not always representative of the environmental conditions prevailing at the site. Spatial patterning, dominance of *Pinus* and the samples included to generate the values are all factors that affected the results obtained in addition to the model and weightings used. Use of simulations to try and validate the PPEs potentially hindered the detection of the most representative group, with the best results obtained from groups that did not have the lowest maximum likelihood scores, or had clear evidence of spatial autocorrelation. However, PPEs are a necessary parameter to enable simulations to be undertaken and with disagreement between the Humpol and REVEALS models this is complicated

further. Consequently, the PPE set chosen for use within the remainder of the project is the BA.Ran.1000.1 group as this provided the most consistent results when used within the REVEALS model but tests with the additional spatial autocorrelation groups will also be undertaken. As this is the simulation software to be used within the project it is essential that confidence can be placed within the output.

Chapter 5: Vegetation history of Inshriach Forest

5.1 Introduction

This chapter is divided into two sections; core description and application of the modern analogue technique as a means of vegetation reconstruction. Results presented below outline pollen profiles obtained in addition to a number of site specific sedimentological analyses used to determine environmental change. Each section deals with short cores with a duration spanning a timescale of A.D. 1900 to the present day from four sites and a longer term representation from Lochan Geal representing change from c.3000 cal. BP to the present day. Standard intuitive interpretation of the assemblages is made before application of the modern analogue technique to provide a more rigorous but essentially 'traditional' interpretation.

5.2 Short-term vegetation change

5.2.1 Regional scale

Quantitative reconstruction of regional vegetation patterns requires larger sites to provide a more homogenous representation of patterns than smaller sites. Two large lakes (sensu Sugita, 1994) were sought for the analysis and provide the most suitable locations from the region. Figure 5.1 shows the location of these sites, Loch an Eilein and Loch Alvie in relation to the study area.

5.2.1.1 Loch an Eilein

A short core of 30 cm depth was obtained from a large loch, Loch an Eilein, situated on the Rothiemurchus estate at the north eastern extent of Inshriach Forest (Figure 5.1). The sediment comprised uniform clayey silt with no discernable features evident when extruded or sampled. ²¹⁰Pb determination was performed on the core using alpha spectrometry with an age-depth profile fitted to the core using both the CRS (Constant Rate of Sedimentation) and CIC models (Constant Initial Concentration). Figure 5.2 shows the profiles obtained from both these models. The CRS model was considered most appropriate for use at this site due to the non-monotonic change in unsupported ²¹⁰Pb with depth and is accepted as the more suitable of the two models (Oldfield and Appleby, 1984). Moreover, the similarity between the models supports the robustness of the chronology.

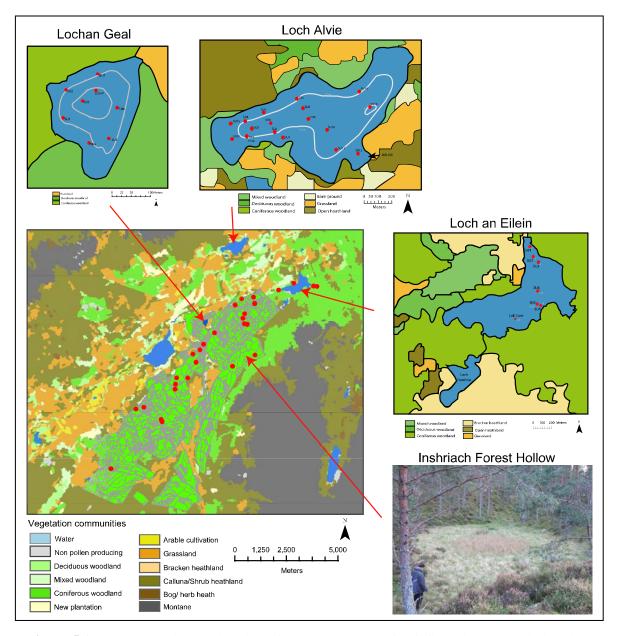


Figure 5.1: A map showing the location of modern moss and fossil field sites used within this study. Lake sites show basin morphology (where available) with core and surface sample locations.

Although the unsupported values for ²¹⁰Pb are high, previously dated sites by Jones *et al.* (1993) in the Cairngorms region also show this and they are not expected to signify error within the detection process. Interestingly, a slight inversion in dates occurs between 6 cm and 8 cm in the core with both models corroborating an age range from the 1940s. As this inversion is inherent in the raw unsupported ²¹⁰Pb values it is expected that this is a feature of the original ²¹⁰Pb measurements of the samples and not the dating models applied. A source for this could be increased sediment flux

from focusing or an increased atmospheric flux, with the former explanation considered most likely (Appleby, 2001).

Application of the correct depth model is required to determine an accurate age profile for the site as this, in turn, governs the selection of samples for use within the quantitative software. The CRS model was deemed a suitable choice for Loch an Eilein on consideration of the underlying assumptions; however, equivalent ages obtained from the opposing models increase confidence in the result. Appleby and Oldfield (1983) outline one of the main determinants as the degree of change in the unsupported ²¹⁰Pb profile with depth. As the CIC model assumes proportional ²¹⁰Pb incorporation with sedimentation rate when plotted against depth the unsupported 210Pb concentrations generates a monotonic profile. This was not the case at Loch an Eilein symptomatic of sediment accumulation changes responding to catchment scale events which were further accentuated by changes in the magnetic susceptibility profile both above and below the 7.5cm Furthermore, studies conducted to compare the application of the two models threshold. consistently support the use of the CRS model (Appleby and Oldfield, 1983; Appleby et al., 1990; Blais et al., 1995). During the study by Blais et al. (1995) the CIC model frequently provided younger determinations for known horizons than the CRS which the authors conclude as being caused by changes in the sedimentation rate diluting the ²¹⁰Pb flux. Although no large scale events are known to have occurred in the landscape surrounding Loch an Eilein felling was abundant during WWII possibly corresponding to the inversion of ²¹⁰Pb dates and magnetic susceptibility peak indicative of a large influx of material to the basin. Removal of woodland would increase the amount of mobile sediment and potential for further deposition reflected in the magnetic susceptibility record. Furthermore, steep slopes bound the basin margins at some locations which, if cleared, would accentuate this process. No quantitative estimates are available for the location of this felling or the total area affected which creates difficulty in connecting these features. However, a large task force was employed to undertake this work which implies that this was a large scale project with total Strathspey felling of 37,000 hectares which is 18 times that of the current extent of Inshriach (Dunlop, 1997; Foot, 2002). Subsequent designation of the Rothiemurchus estate as a nature reserve and construction of trails around the loch in the early 1960s would have sustained this increased allochthonous input to the basin with provision of extensive un-vegetated areas until sufficient regeneration provided stability (Lambert, 2004). In this study there are limited independently dated horizons to confirm the timing of this feature, which Appleby (2001) insists upon as an essential validation procedure for use of ²¹⁰Pb dating, creating increasing difficulty in explanation of these events. Further investigation would be required to determine the extent of this over the whole basin.

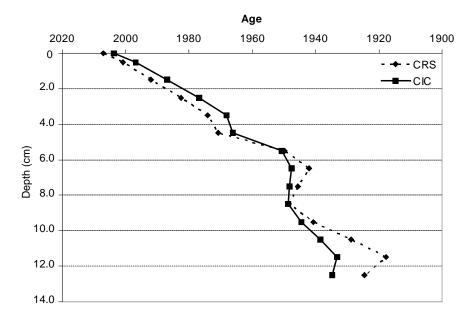


Figure 5.2: ²¹⁰Pb profiles added to dates obtained Loch an Eilein sediments. CRS: Constant Rate of Sedimentation. CIC: Constant Initial Concentration.

Spheriodal carbonaceous particles (SCP) were extracted from the sediment with the resultant profile shown in Figure 5.3. The maximum concentration of 550 g DM⁻¹ is shown at the surface of the core, with a rapid decrease in concentration to 2.5 cm depth followed by a slower decline from 150 g DM⁻¹ to 0 at 10.5cm. This does not conform to the normal regional patterns, principally due to the absence of a decline in concentration within the surface sediments (Jones et al., 1993; Rose et al., 1995). These patterns could be related to the temporal resolution of the samples influencing overall concentration of particles and resultant profile appearance (Rose, 2001). For example, the influx of allochthonous material at 7.5 cm is reflected in highly fluctuating SCP concentrations. At Loch an Eilein 1 cm contiguous samples were used which, although standardised, reflect a lower temporal resolution with depth and could induce some variation. The Clean Air Act of the 1970s that instigated the decrease in emissions occurs at a depth of 3.5 cm at Loch an Eilein which should be evident in subsequent samples but is not. If sedimentary processes identified from the ²¹⁰Pb profile are occurring this could diffuse the form of the SCP curve. Furthermore, the concentrations are considerably lower than those seen in other fossil studies both within the UK and other European countries where industrial areas are abundant (Wik and Renberg, 1991; Jones et al., 1993; Rose, 1995; Rose et al., 1999; Yang et al., 2001). Surface samples taken from Aberdeenshire and Inverness-shire proved to be abundant in SCPs due to the presence of industrial activity in these regions (Rose et al., 1995; Rose and Harlock, 1998). In contrast, the concentrations of Loch an Eilein correspond to those identified within remote regions such as Iceland, Greenland and the Arctic (Rose, 2001). Thus, the location of the basin coupled with the nature of the surrounding vegetation probably meant a low SCP input and some sedimentary mixing and smoothing generate a low concentration record.

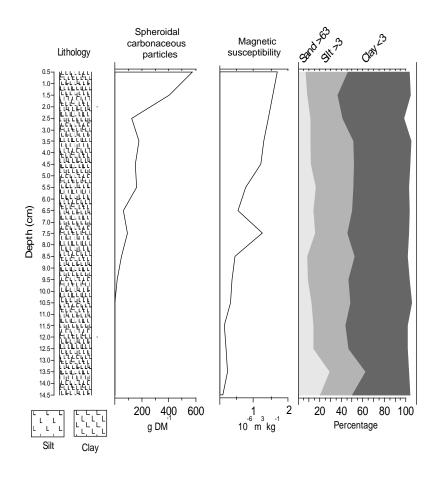


Figure 5.3: Sedimentological properties of the core extrude from Loch an Eilein.

Magnetic susceptibility is characterised by two zones delineated by a peak at 7.5 cm depth (Figure 5.3), corresponding to the inversions in the ²¹⁰Pb data indicative of an increased sediment input (Sandgren and Snowball, 2001). Below this zone, 15 – 8.5 cm, the magnetic susceptibility is low with consistent value of 0.5 10⁻⁶ m³ kg⁻¹; however, above 7.5 cm the trend is to higher values with a sharp increase to 1 10⁻⁶ m³ kg⁻¹ at 4.5 cm after which the increase continues but with lessened severity. This trend is not replicated in the particle size analysis, although there is a small increase in sand proportion of ~5%. Interestingly, the base of the profile at 15 – 12.5 cm contains increased percentages of sand comprising 30% of the sample at its maximum. This is not demonstrated in the reminder of the core as sand decreases towards the surface. Silt and clay components remain constant through the length of the core.

5.2.1.1.1 Pollen analysis

Figures 5.4 and 5.5 show a pollen percentage and a pollen accumulation diagram for Loch an Eilein respectively. CONISS (Grimm, 1987) was used to divide the pollen profile from zones each of which will be discussed separately:

LPZ LAE1 15cm - 12cm

Pinus dominates the assemblage constituting over 60% of the total land pollen (TLP) indicating a dominance of Pine woodland. A number of other native arboreal taxa are present including *Betula, Corylus* and *Alnus* although these occur in low quantities. *Juniperus* contributes to the pollen rain although fails to attain percentages greater than 5%. *Calluna* is the other predominant taxon with 10% TLP. Other heathland taxa occur within the zone including *Erica*-type, *Empetrum sp.* and low frequencies of Poaceae.

Changes in the pollen accumulation rate provide greater information than the pollen percentages alone. The main taxa contributing to the assemblage are *Pinus* and *Calluna* with higher portions from *Betula* and *Corylus*. Within LAE 1 heightened levels of non-arboreal taxa are also identifiable such as Poaceae, *Vaccinium* and *Erica*-type.

LPZ LAE2 12cm - 2cm

Pinus percentages are lower within this zone, ~50% TLP, although it is still the main element of the vegetation which reflects little difference in the dominance of this community. There are no changes in *Betula*, *Corylus* and *Alnus*. *Calluna* percentages are much higher in this zone attaining ~20% TLP possibly suggesting increased heath as other heathland taxa are consistent during the zone. A slight peak in both *Erica*-type and *Empetrum sp.* at 4.5 cm implies a temporary increase in diversity though that could reflect increased sediment input to the basin at 7.5 cm. There is no equivalent increase of other taxa i.e. Poaceae, *Erica*-type, *Calluna*, *Alnus* and *Corylus*.

Fluctuations are evident in the accumulation rates in all taxa at 8.5cm which corresponds to the inversion within the ²¹⁰Pb levels and suggest a change in the sedimentation rate or influx from the catchment. Although this is a short-lived event in most taxa increased levels prevail within the *Empetrum, Vaccinium* and Cyperaceae curves which could relate to their not being influenced by this event or their sustained influence from a allochthonous source. Interestingly, the levels of *Pinus* remain relatively static throughout the zone whilst other deciduous arboreal taxa show declining values i.e. *Alnus*, and *Corylus*.

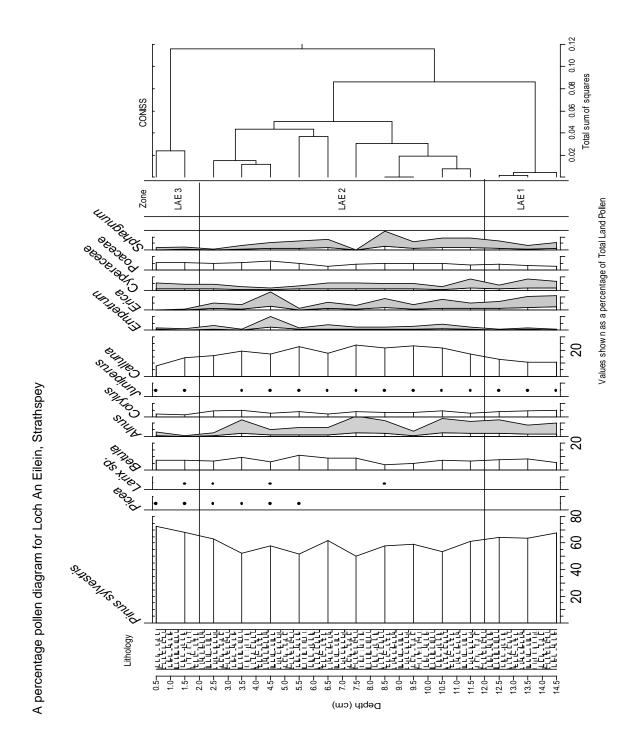


Figure 5.4: Pollen percentage diagram for Loch an Eilein with CONISS values marking horizon delineation. Dots represent presence below 1% TLP.

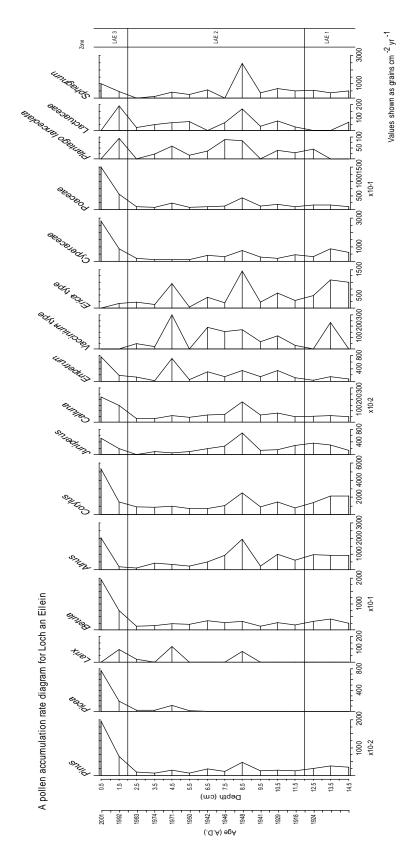


Figure 5.5: A pollen accumulation rate diagram for Loch an Eilein. Zones were obtained from CONISS using pollen percentages.

LPZ LAE3 2cm - surface

Characteristics of this zone replicate those seen at the base of the core in LAE1. High *Pinus* percentages occur with reduced *Calluna* percentages. *Juniperus* values are much lower than previously identified perhaps corresponding to increased density in these communities. *Picea* and *Larix* are present sporadically in quantities below 1% TLP but show a rapid increase in concentration as does *Betula*. Non-arboreal taxa such as Cyperaceae and *Erica* have consistent values probably representing the presence of waterlogged, marsh areas as can be seen to the north of the basin.

Rapid increases in pollen accumulation characterise LAE 3 with all taxa being influenced by the feature showing at least double the accumulation rates on the previous zone but more for arboreal taxa. For example, *Pinus* increased from a maximum of 480×10^{-2} grains cm⁻² y⁻¹ at 8.5cm to 1956 $\times 10^{-2}$ grains cm⁻² y⁻¹ at the surface.

5.2.1.1.2 Interpretation of landscape changes at Loch an Eilein

Only slight changes are evident in the pollen percentage profile from Loch an Eilein signifying minor variation of the vegetation patterns around the site since the 1900s. *Pinus* has dominated the landscape throughout this period exemplified in continual occurrence at high levels (>60% TLP). Similar features are identified when pollen accumulation rates are calculated for the site. The very high values for *Pinus* (90 – 1956 x10⁻² grains cm⁻² y⁻¹) indicate that dense woodland is present around the site as these values are only recorded in similar locations (Hättestrand et al., 2008). Recent examination of living tree cores taken from Loch an Eilein have identified a large proportion of existing stems having a mean age of 148 years which were planted during the 1700s and 1800s with negligible subsequent management (Fish pers. comm.). Presence of other native woodland taxa, Betula, Corylus and Alnus, suggest older stands with little active management or perhaps occupation of marginal zones. The quantities of *Betula* suggest a transition from sparse woodland present in the basal zones of the core to dense presence in the surface sediments. This increase in the upper sediments is seen in a number of taxa and therefore could be a feature of the sedimentation rate or within lake process. However, since the designation of the Rothiemurchus Estate and the Cairngorms area as a nature reserve native woodland regeneration has been encouraged and this would also increase the proportions of deciduous taxa. At present areas of heathland with Betula stands do occur around the site which supports a conclusion for an actual as oppose to statistical feature. Low diversity of non-arboreal taxa relates to the dominance of Calluna in the heathland communities and the inability for other taxa to colonise the dense canopy formed.

Reduced levels of *Pinus* during LAE2 could relate to utilisation of the woodland during the period prior and subsequent to WWI and WWII. Difficulty arises however in a definitive interpretation due to the dating inversions at this time. During this time both local areas of woodland were felled in addition to regional woodlands i.e. Inshriach and Glenmore, which would reduce the occurrence of this taxa in both the regional and local pollen rain. Simultaneous increase in Calluna can be related to the colonisation of the clear-felled regions by heathland and the community's expansion within the wider landscape. Low diversity in herbs and ruderals highlights the dominance of Calluna in this community. However, an initial period of increased diversity could relate to the juvenile stage of development where Calluna provides a more open structure, enabling more light penetration and increasing colonisation potential by other taxa (Barclay-Estrup and Gimmingham, 1969). Subsequent planting of the woodland in the wider landscape is the likely cause of changing patterns in LAE 3. Little large scale management has been undertaken at Rothiemurchus as its status as a nature reserve precludes this, with native woodland on the estate an essential element providing both environmental and commercial benefits. Similarity between this zone and the earlier LAE 1 may question whether the structure is fully natural but, the termination of the intensive management only occurred recently and requires time for the effects to be seen in the pollen record.

5.2.1.2 Loch Alvie

Loch Alvie is a large basin of 54 hectares situated to the north of Inshriach Forest. Although the basin is closed there is a small drainage inlet on the southern margin of the loch and a channel to the conjoining Loch Beag at the eastern extent which is a shallow basin. The average water depth of Loch Alvie is 10 m and a 30 cm core was taken at a depth of 14 m from the deepest portion of the lake, albeit not central to the basin. Stratigraphic changes were evident in the core when sampled as shown in Figure 5.6.

Magnetic susceptibility (Figure 5.6) was also conducted but results of this analysis show little variation over the length of the core with values fluctuating between 1 and 2 10⁻⁶ m⁻³ kg⁻¹. A sharp decline is evident at 10.5 cm depth but is not sustained and values revert to previous levels at 11.5 cm. This profile suggests a stable sedimentation to the sampling site with only minor and short lived changes (Sandgren and Snowball, 2001).

 χ_{lf}

Figure 5.6: Lithological changes and magnetic susceptibility measurements for Loch Alvie.

²¹⁰Pb and ¹³⁷Cs assay using gamma spectrometry was undertaken and initially the CRS model (Appleby and Oldfield, 1983) was applied to the points but two periods of rapid sedimentation punctuated the record and precluded correspondence with the ¹³⁷Cs peaks. Subsequent use of a CRS model with additional correction algorithm to account for these periods provided the best fit which is shown in Figure 5.7. The two periods of increased sedimentation are clearly identified within Figure 5.7 show strong association to the ¹³⁷Cs peaks from the nuclear testing fallout.

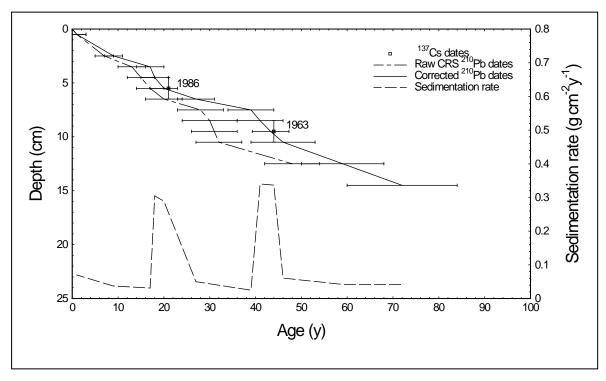


Figure 5.7: A ²¹⁰Pb derived age-depth model, ¹³⁷Cs profile and sedimentation rate for Loch Alvie.

Although a number of features of the regional SCP curve are present within that of Loch Alvie the concentrations recovered are low with a maximum of 350 gDM⁻¹ and disappearance of the curve at 15 cm depth, probably A.D. 1930. Thus, it is difficult to determine any significant features within the profile as this is close to the limit of detection of 100 gDM⁻¹ (Jones *et al.*, 1993). For example, increases are identified post-WWII *c.* 1945 and subsequently at *c.* 1970, the former showing an increase of 50 gDM⁻¹ whilst the latter increases by 250 gDM⁻¹. Comparison with previous studies suggests that these deviations are not large enough to imply atmospherically induced variation. Furthermore, the peak in concentrations at a depth of 4cm (*c.* 1990) could be related to reworking or re-suspension of the particles which could have occurred at previous horizons.

Dating of the sediment profile was problematic but has highlighted areas of increased sedimentation into the basin dated to the 1960s and 1980s. Changes in sedimentation would have affected the SCP record as the temporal resolution of each sample would have changed during this period. Consequently, the peaks identified within the SCP record could be an artefact of this. Although the clean-air act peak at 5cm depth corresponds to 1970s in the ²¹⁰Pb profile the earlier peak appears too late to represent the post-war industrial increase but does, however, correspond to increased sedimentation during the 1960s. Absence of changes in the magnetic susceptibility record alludes

to negligible catchment scale events and does not support this conclusion. An additional slight change in sedimentation rate change was identified c. 1980 in the 210 Pb profile which could be related to the construction of the A9 to the north of the site or modification of the existing minor road at the southern margins of the loch. Determination of the level of disturbance or sediment influx is complex and requires further analysis to elucidate the spatial extent and cause of this feature.

5.2.1.2.1 Pollen analysis

Three zones were identified from application of CONISS (Grimm, 1987) to a pollen diagram constructed for Loch Alvie. Pollen percentage and pollen accumulation rate diagrams are shown in Figures 5.8 and 5.9 respectively.

LPZ ALV1 14cm – 10cm

High percentages of *Calluna* characterise the zone with values ranging between 25% and 40% TLP indicative of extensive heathland. As *Erica* and *Vaccinium* are also found as subordinate components this probably represents the NVC H10 *Calluna vulgaris* – *Erica cinerea* heath (Rodwell, 1991a). In contrast, *Pinus* percentages are low and decrease over the course of the zone from 25% to 15% of TLP. The occurrence of shade intolerant taxa *Rumex acetosa*, *Plantago lanceolata* and Poaceae suggest that this would be open stands. *Betula* is present in quantities of 10% TLP and other arboreal taxa present in percentages >5% are *Alnus* and *Corylus* with *Salix* occurring sporadically but in quantities <1%. Cyperaceae, *Potentilla*-type and *Galium*-type occur in low quantities but continually present.

High accumulation rates are evident for *Pinus*, *Alnus*, *Betula*, Cyperacaeae, Poaceae and *Calluna* which are the dominant taxa within the landscape and around the basin. In this zone, ALV 1, there are equal and sustained levels of *Calluna* and *Pinus* with similar patterns exhibited in the Poaceae and Cyperaceae curves. Both *Erica* and *Rumex acetosa* show sharp declines from ~12cm but any connection cannot be suggested.

LPZ ALV2 10cm - 3cm

This zone is considered a transitional period with slowly declining *Calluna* percentages, 30% TLP to 10% TLP, with a contemporaneous increase in *Pinus* from 20% TLP to 40% TLP. *Betula* is present but shows little change. At the top of the zone *Picea* is present but at less than 1% TLP, possibly associated with planting and management of woodlands in the wider landscape. *Erica* values decrease but remain at 2% TLP throughout the zone. Poaceae shows no overall decline but fluctuates whilst Cyperaceae increases to 6% TLP. Similarly, *Sphagnum* increases to ~5%

TLP+spores and with stable *Alnus* implies the sustained presence of wetland communities. *Ranunculus flammula* is identified in low quantities but occupies wetland zones and could be associated with the alder woodland (Rodwell, 1991b). Lactuceae and *Galium*-type show some increase (Grime *et al.*, 1988).

High levels of variability are present throughout the zone in the pollen accumulation curve with only Poaceae showing relative stability. A peak in taxa associated with wetter environments is clear at 7.5cm and includes *Alnus*, *Corylus*, *Salix* and Cyperaceae. In addition, *Calluna* and some herbaceous taxa show similar increases. Subsequent to this horizon a large proportion of taxa show gradual declines in presence with *Pinus* and *Calluna* the most prominent reaching a minimum at 4.5cm corresponding to a period of increased sedimentation. Following this values increase within most taxa present with *Pinus*, *Alnus*, *Erica* and Poaceae showing the greatest change. *Larix* and *Picea* also peak to their highest values during this period.

LPZ ALV2b 3cm - surface

Pinus values comprise 40% TLP at the start of the zone but decline slightly at the surface whilst *Calluna* remains constant at 10% TLP. The decrease in the *Pinus* curve is concurrent with increases in both *Betula* and Poaceae both of which are important constituents with 10% and 15% TLP respectively, likely due to the colonisation of previously *Pinus* woodland dominated areas.

Within this zone, ALV 2b, lower accumulation values occur than those of the previous zone with all taxa responding to a decline in values. The deciduous taxa respond least to this decline with sustained values for *Betula* and *Corylus*. A similar pattern is exhibited in the Poaceae curve which could suggest that these are within the same community.

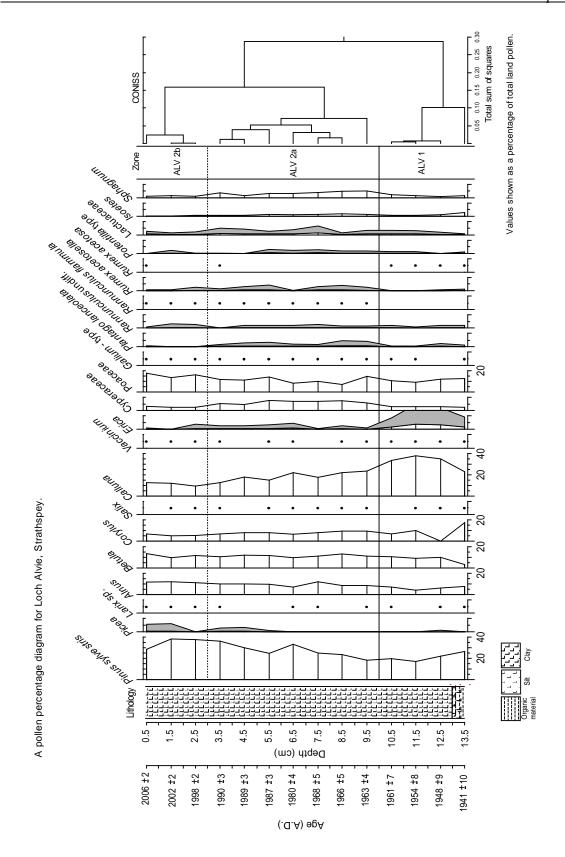


Figure 5.8: A pollen percentage diagram for Loch Alvie. Values are shown as a percentage of total land pollen (TLP) except aquatics (percentage of TLP+aquatics) and spores (percentage of TLP+spores).

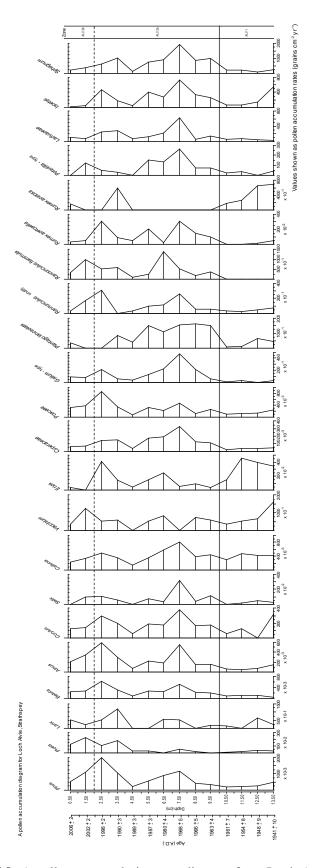


Figure 5.9: A pollen accumulation rate digrams from Loch Alvie. Zones were determined from pollen percentages using CONISS.

5.2.2 Interpretation of landscape changes at Loch Alvie

Contemporary landscape patterns reflect a largely open landscape comprising heathland and grassland with scattered woodland stands, predominantly Scots pine. It is suggested that this pattern has prevailed throughout the duration of the pollen record with fluctuations in the main components reflecting regional vegetation patterns. Although increases are identified c.1968 and later at c.1986 both effect all taxa in the assemblage and are consistent with an increase in sedimentation, which is known to influence PARs (Giesecke and Fontana, 2008). Figure 5.10 shows an Ordnance Survey map of the Loch Alvie area dating to A.D. 1903. There is a large proportion of rough grazing (Calluna heath) with scattered Scots pine which remains today. The presence of ruderals and light demanding taxa i.e. Plantago lanceolata in the pollen record are indicative of this (Birks, 1970; Shaw and Tipping, 2006). Prolonged presence of Calluna and simultaneous low Pinus values reflect this contemporary structure with increases in Calluna associated with felling of woodland during WWII (Dunlop, 1997). Subsequent planting regimes are reflected in the increased *Pinus* proportions with the rate associated with the establishment of the individuals, but are not shown within the pollen accumulation diagram. High quantities of Alnus probably derive from the presence of a wetland area to the southwest of the main basin which appears to have survived throughout the duration of the core. Salix, Corylus and other wetland favouring taxa are continually present but in varying quantities support this (O'Sullivan, 1973a). In the A. D. 1903 map this is identified as the channel area between Loch Alvie and the smaller Loch Beag with additional evidence of drainage channels in the surrounding area implying a previous marshland area under management for grazing or agriculture.

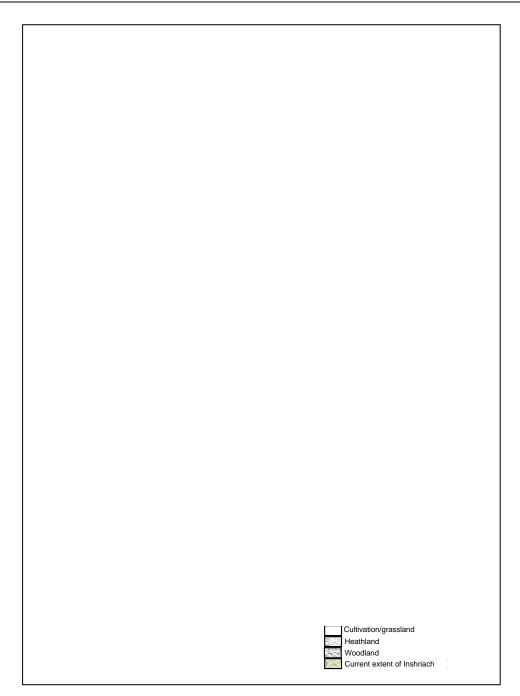


Figure 5.10: A 1903 County Series 1:10560 Ordnance Survey map of Loch Alvie. *Source:* Historic Digimap (an Edina service) © Crown Copyright and Landmark Information Group Limited 2009. All rights reserved (1903).

5.2.2 Local sites

Two small basins were sampled to provide a local representation of vegetation change for inclusion within the LOVE model (Sugita, 2007c). Profiles obtained from these sites span *ca.* 100 years of sedimentation.

5.2.2.1 Insh H1

Peat deposits were collected from a small depression at the edge of Inshriach woodland. The basin is 5 metres in radius with reasonably steep sides which are currently dominated by Scots and Lodgepole pine woodland with sporadic *Calluna* ground vegetation. The surface of the mire is characterised by Cyperaceae, *Molinia caerulea* and *Sphagnum*.

Total depth of sediment recorded was 180 cm at the centre of the basin with changes indicative of a slow transition from a limnic depositional environment to mire shown in Figure 5.11. Corresponding magnetic susceptibility and loss-on-ignition measurements supports this inference with a parallel decrease in magnetic susceptibility as organic content increases. Only the top 20cm was retained for analysis representing the most recent deposition associated with the management of the surrounding area. Within this the stratigraphy showed little deviation from peat with low humification and substantial amounts of macrofossils i.e. roots, *Calluna* fragments. Although some fluctuations are evident in the magnetic susceptibility record these are both short lived and questionable given the predominant organic composition of the sediments.

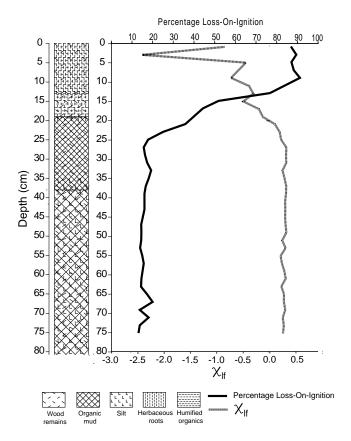


Figure 5.11: Core stratigraphy using Troels-Smith (1955) definitions and sedimentary analysis results from Inshriach Forest Hollow

Figure 5.12 shows the ²¹⁰Pb profile obtained using the CRS model (Appleby and Oldfield, 1978) with supportive independent evidence from ¹³⁷Cs. The top 20cm of sediment at the site represents equilibrium from the ²¹⁰Pb deposition and therefore contains the last 100 years deposition. Although an increase in sedimentation rate is identified over the most recent period, ca. 10 years, this corresponds to the most recent peat formation at the site. Some studies have shown dating of peat to be problematic with variability between age profiles obtained from different location within ombrotrophic mires (Oldfield et al., 1979). Investigations have shown that profiles extruded from hollows have higher ²¹⁰Pb inventories than those from adjacent hummock sites (Oldfield et al., 1979; El-Daoushy, 1988). Leaching has been proposed as a mechanism by which this occurs with profiles below the water table frequently exhibiting lower ²¹⁰Pb inventories (Oldfield *et al.*, 1979; Urban et al., 1990). However, additional studies have shown that little mobility of ²¹⁰Pb is evident in peat stratigraphy due to cation exchange even when water table variations are artificially induced (Lee and Tallis, 1973; Vile et al., 1999). Inshriach H1, although not an ombrotrophic mire, had a high water table with pools evident on the peat surface when sampled which could explain the low unsupported ²¹⁰Pb concentrations detected, although these are not considered low enough to compromise the results of the analysis (P.Appleby, pers. comm.). If fluctuations in the water table have occurred in the past this could influence the profile obtained from the core (Urban et al., 1990); however, correspondence of the CRS model derived dates with the independent ¹³⁷Cs profile increases confidence that any effect is minimal.

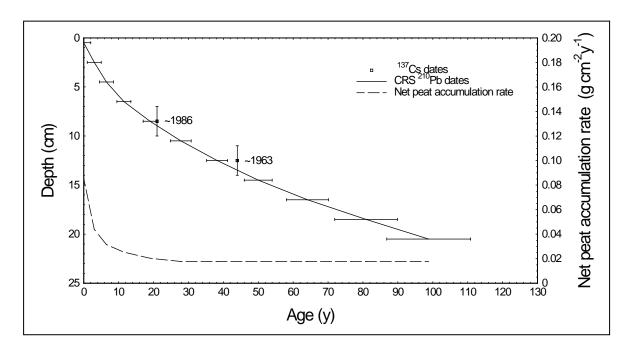


Figure 5.12: An age-depth model for Inshriach H1 Forest Hollow with sediment accumulation rate also expressed.

Results of the pollen analysis conducted at the site are shown in Figures 5.13 and 5.14, pollen percentage and pollen accumulation respectively, with zones defined using CONISS and discussed below:

LPZ IFH1a 20cm - 17cm

High proportions of *Sphagnum* in association with the sedimentological properties of the cores identify the transition of this site to a peat-forming basin. Low proportions of *Pinus* with associated high occurrence of *Calluna* indicate a heathland environment around the deposition basin. Low amounts of non-arboreal taxa are present during this zone e.g *Rumex acetosella* and *Ranunculus*-type, are also associated with the heathland communities. Both *Erica* and *Vaccinium* species occur but in low quantities suggesting the dominance of *Calluna* within the heathland community such as NVC 10 *Calluna vulgaris* – *Erica cinerea* heath (Rodwell, 1991a). Interestingly, the occurrence of *Larix* during this zone could be related to planting regimes in the surrounding woodlands due to its low occurrence (less than 1% TLP). The additional occurrence at 19.75cm is likely anomalous.

By far the dominant taxon identified in Figure 5.14 at this site is *Pinus* with levels of *Calluna* and Poaceae also major components of the accumulation. In the lower zone, IFH1 1a, *Pinus* is dominant with a large proportion of *Betula*, *Calluna* and Poaceae. Interestingly, the form of the *Plantago lanceolata* curve follows that of *Betula* which could suggest that these formed a single community.

LPZ IFH1b 17cm - 15.5cm

Sphagnum is much reduced within this subzone comprising ~5% TLP+spores. There are also decreases in *Betula, Alnus* and *Corylus* with the latter showing disappearance probably implying a drying of the wetland surface. In contrast, there is an increase of ~ 20% TLP in the *Pinus* with contemporaneous decreases in both *Calluna* and Poaceae inferring increased woodland present. Although *Erica* and *Vaccinium* species remain relatively unchanged the presence of the other non-arboreal taxa, *Ranunculus*-type and *Rumex* species, become more sporadic, perhaps related to increased shading by woodland stands.

This zone within the accumulation diagram shows the levels of *Betula* and *P. lanceolata* have declined rapidly and values of *Pinus*, *Picea*, *Calluna* and *Erica*-type have increased from the previous zone. *Corylus* declines considerable to only minor presence with accumulation rates of ~30 grains cm⁻² y⁻¹.

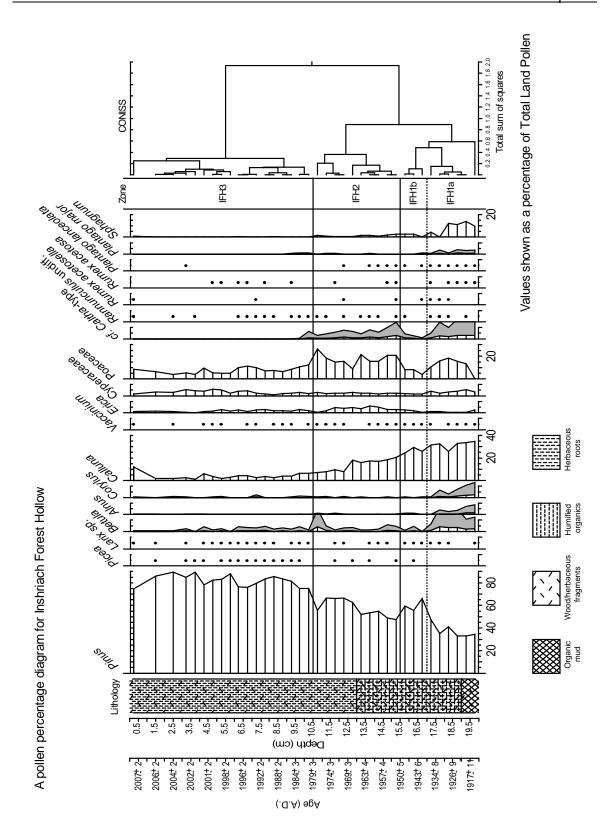


Figure 5.13: A pollen percentage diagram for Inshriach H1. Values are shown as a percentage of total land pollen (TLP) except aquatics (percentage of TLP+aquatics) and spores (percentage of TLP+spores). Points represent values <1%. Stratigraphy is represented using Tröels-Smith (1955) descriptions.

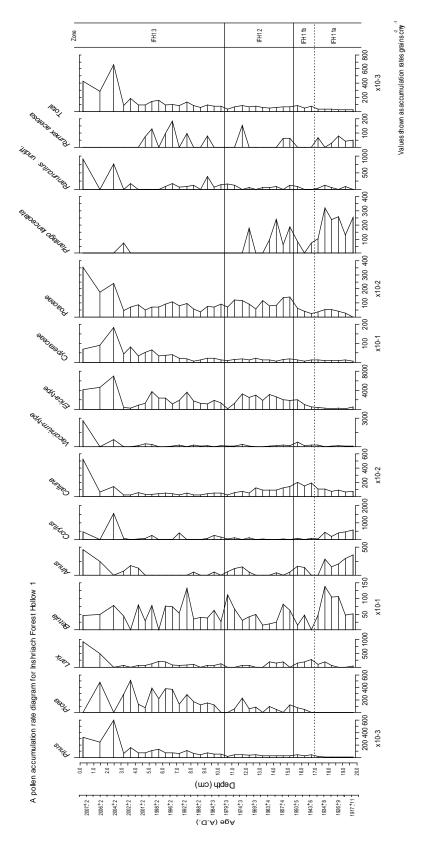


Figure 5.14: A pollen accumulation rate diagram for Inshriach Forest Hollow H1

LPZ IFH2 15.5cm - 10.5cm

This zone is characterised by increasing *Pinus* which comprises ~45% TLP pollen at 15cm, at the start of the zone, and reaches 60% at 11 cm. The exotic plantation taxa, *Picea and Larix*, are present during this zone but never attain percentages greater than 1% TLP. An associated and more pronounced decrease is apparent in the *Calluna* profile with a reduction of 15% TLP. Non-arboreal species that occur during the initial portions of the zone become more sporadic and eventually decline altogether from 13 cm depth. Some show little variation such as, *Erica*, Cyperaceae and Poaceae, with the latter rising to 15% TLP. These are predominantly associated with mire environments and probably derive from the local vegetation at the deposition site.

Sustained *Pinus*, *Picea* and *Larix* accumulation values are present throughout IFH1 2. Levels of *Calluna* show a gradual decline to 13.5cm at which point levels show a sharper decrease which is consistent with the planting of the *Pinus* woodland at the site. Levels of *Erica*-type and Poaceae are not influenced by this event.

LPZ IFH3 10.5 cm - surface

High and sustained quantities of *Pinus* dominate this zone with low values of other taxa throughout. *Pinus* values rarely deviate from 80% TLP whilst *Calluna* remains below 5% throughout the zone implying local closed woodland surrounding the deposition basin. A slight departure from this occurs at the top of the zone, at 0.25cm depth, with a rapid decline in *Pinus* values and increase in *Calluna* to 10% TLP. Although the values for *Erica* and Cyperaceae remain at levels previously attained Poaceae fluctuates around 5% with few other taxa occurring which demonstrate the poor diversity associated with the managed environment.

Zone IFH1 3 can be delineated into two subzones based upon the accumulation values. The first section of the zone 10.5 - 3.5cm is characterised by gradually increasing *Pinus* levels and rapidly increasing *Picea* levels. However, the *Pinus* increase does not reflect a change consistent with the newly planted areas reaching maturity. Cyperaceae is the only non-arboreal taxon to show this pattern which suggests a relationship to the peat surface. Above 3.5cm *Pinus* shows a dramatic increase in values from 100×10^{-3} grains cm⁻² y⁻¹ to over 590×10^{-3} grains cm⁻² y⁻¹ at a peak before declining towards the surface. Other taxa showing simultaneous increases are *Larix*, *Alnus*, *Calluna*, *Erica*-type, Cyperaceae and Poaceae.

5.2.2.1.2 Conifer stomata

Stomatal analysis indicates similar patterns to those of the pollen record. Figure 5.15, shows the *Pinus* pollen percentages, concentrations and stomata concentrations for the deposition site. Firstly,

the stomata show low concentrations until a depth of 12 cm after which a rapid increase is clear. Although concentrations remain high fluctuations do occur from 10 cm to the top of the core with a general decreasing trend throughout this.

Comparison with the pollen percentage data shows some correlation between the patterns. The initial low occurrence of stomata is associated with LPZ 1 and 2 of the pollen record; however, some increases in the stomata concentration in samples 11.25 and 12.5 cm are not reflected in the pollen data. At this point juvenile woodland would have been present around the site and therefore relates to their presence at the site but lack of maturity impairs their visibility in the pollen record. The high *Pinus* percentages of LPZ3 equate to fluctuations in the stomatal record which, in some instances, precede the declines in *Pinus* identified in the pollen record. In contrast, concentrations of *Pinus* pollen fail to show any agreement with the stomata patterns as features connected to local vegetation changes are difficult to determine within the record.

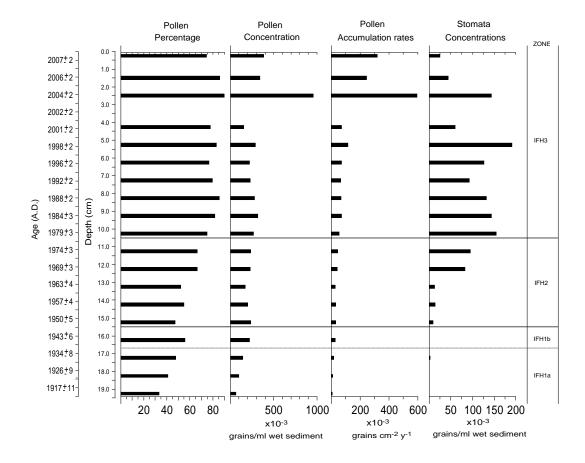
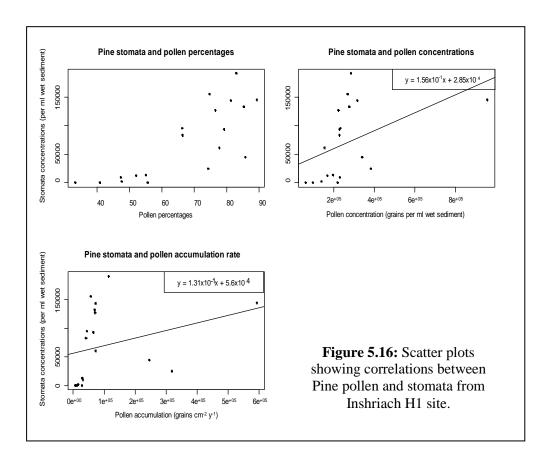


Figure 5.15: Stratigraphic changes in *Pinus* pollen and stomata concentrations at Inshriach Forest Hollow.

High pollen percentages do also correspond to the low stomata presence or total absence from the record, as seen at the intersection of the regression line at ~40% pollen, suggesting the influence of regional pollen. When linear correlation is undertaken between pollen and stomata concentrations this fit is with an r = 0.455 (Figure 5.16), primarily due to an outlier impacting upon the placement of the regression model which if removed would increase the correlation coefficient. A similar situation is shown in the pollen accumulation data which has an r = 0.294 which would improve if extreme values were removed. This also impacts upon the intersection between the regression line and implies that stomata are present in significant quantities whilst pollen is not present.



5.2.2.1.3 Interpretation of landscape changes at Inshriach Forest Hollow

Palaeoenvironmental analysis at Inshriach Forest reveals a transition from an open heathland landscape to a managed woodland system. At the commencement of the profile around A.D. 1908 ±12 the basin changes from a limnic environment with taxa indicative of waterlogged, but not submerged, conditions to peat formation. Low stomata counts during this time imply that the individuals contributing to the *Pinus* pollen profile are not within the immediate vicinity as Parshall (1999) suggests that stomata fall within 20 m of their source. Consequently, the *Pinus* presence in the pollen profile could be associated with extra-local or regional pollen deposition at the site rather

than local as suggested by Bennett (1984). However, the pollen accumulation rates are still high during this period with values of 69 x 10⁻² grains cm⁻² y⁻¹ which is above the >2000 grains cm⁻² y⁻¹ defined by Hicks (2001) to represent dense woodland presence. However, the range of PARs obtained from this site is much greater than those calculated from both fossil and monitoring studies previously conducted in woodland contexts (Koff *et al.*, 2000; Barnekow *et al.*, 2007; Huusko and Hicks, 2009; Kuoppamaa *et al.*, 2009). Consequently, it is difficult to conclude the location of woodland at this time from PARs and pollen percentages along. Historical data from A.D. 1873/74 and later in A.D. 1903 in Figure 5.17 identify the area surrounding Inshriach H1 as open heathland with Scots Pine which implies an open woodland structure around the site and both a local and regional source for the pollen within the lower sections of the profile. A large area of dense woodland occurs within the A.D. 1903 image to the north east of Inshriach H1 in an area previously defined as heathland suggesting the onset of planting in the late 1800s.

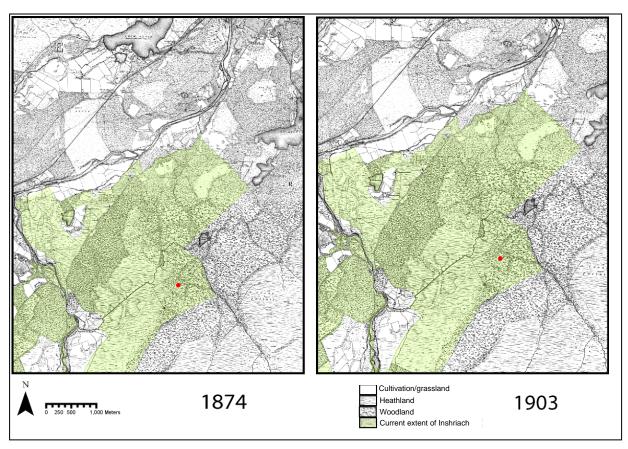


Figure 5.17: Historical County Series Ordnance 1:10560 survey maps showing vegetation change around Inshriach H1 Forest Hollow (red point). The green shading represents the current extent of the managed woodland. *Source:* Historic Digimap (an Edina service) © Crown Copyright and Landmark Information Group Limited 2009. All rights reserved. 1874/1903.

Increased *Pinus* is evident c.1930 (LPZ IFH1b) within the pollen percentage data and corresponds to the purchase of Inshriach and lands surrounding it by the Forestry Commission. During this time land was being acquired for plantations and management following World War I replenishing the limited resources available subsequent to the conflict (Mason $et\ al.$, 2004). Consequently, the purchase of Glenmore in A.D. 1923 and Inshriach in A.D. 1935 saw implementation of planting regimes focused around exotic, quick growing taxa that could provide large timber stocks (Dunlop, 1997). However, the opening of World War II initiated an immediate resurgence in woodland clearance with mass destruction in the Strathspey region (Dunlop, 1997). This is identified at 15.25 cm, corresponding to 1950 ± 4 , in the pollen record by a small reduction in *Pinus* pollen which is perhaps reduced due to its regional rather than local representation of the event.

Interestingly these features within the *Pinus* record are not identified within the PAR profile whilst the planting of *Picea* in the late 1930s is clearly visible in gradually increasing values. Two reasons could contribute to this feature either changes within the sedimentation rate influencing the calculation of PARs of the dominance of *Pinus* within the wider landscape is impacting upon the recognition of smaller spatial scale events. In a recent study Giesecke and Fontana (2008) highlighted the influences that can impact upon the calculation of PARs. Although predominantly focused around lake sites the authors concluded that in most cases there is little correspondence between the PARs at two sites within the same region and that the results obtained can be highly variable. Hicks and Hyvärinen (1999) found the contrary when they compared modern and fossil values from both lakes and peat locations but stressed that there are limitations to the method. Essentially, the most important factor in determining PARs is the accumulation rate and this makes the site selection the most important aspect of the study. If there are changes in the sedimentation rate then this can impact upon the results. At Inshriach H1 the influence appears to only affect *Pinus* which implies that this is a species specific factor and perhaps not one associated with the sedimentation at the basin.

The downward trend in *Pinus* pollen continues until c.1960 after which *Pinus* increases with a simultaneous decrease in *Calluna*. This strongly reflects the ploughing and planting of the area directly around the basin. Management documents from the time record Scots and Lodgepole pine being used following the removal of *Calluna* using a Cutherbertson plough. Initially, individuals are planted aged 1-2 years in rows 1.7-2 metres apart to allow for a high stem density with thinning every 6-10 years (Hibberd, 1991). As the woodland matures, density increases and *Calluna* cannot regenerate under the canopy resulting in features identified within the pollen record; declining *Calluna* and increased *Pinus* when percentages are used. Strong representation of the initial planting is clearly visible within the stomatal record with potential fluctuations associated

with the thinning cycle. Whilst Gervais and MacDonald (2001) show a correlation between Pinus stomata and pollen this is weak (r = 0.2) with high variability in the stomata concentrations which is similar to that evident within this study and others conducted (Hansen, 1995; Hansen $et\ al.$, 1996; Froyd, 2005). Consequently, the conclusion reached by Hansen $et\ al$ (1996) implying that stomata can only reflect presence or absence rather than provide density estimates, is supported by results from Inshriach. Results presented have shown particular difficulty in interpretation when both strong regional and local rains are contributing to the site. Dampening of actual changes and creation of artificial features increase complexity and lead to poor understanding of relationships present.

5.2.2.2 Lochan Geal B

Lochan Geal is a small closed basin, surface area 3.5 hectares, on the north western margins of the woodland. Depth of the basin ranges from 30 cm at a small shelf area to 13 m in the centre of the loch. A core of 30 cm was taken in 9.5 m water depth close to the centre of the basin with no stratigraphic changes apparent when the core was extrude or later examined and sampled. The sediments were comprised of a highly organic lake mud with silt and some clay. This is also shown in the high LOI values (Figure 5.18) which show minor changes over the length of the core.

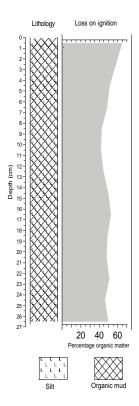


Figure 5.18: Lithostratigraphy (using Troels Smith) and loss on ignition data from Lochan Geal core B.

In addition, six surface samples were obtained from the margins of the loch to assess the effects of marginal vegetation. Figure 5.19 shows the pollen assemblages from these sites and their location and a simplistic representation of the marginal vegetation. Results of this analysis show little difference between the *Betula* and *Pinus* percentages within the samples which are the main fringe vegetation types. There are some minor variations within the remaining taxa but overall indications show good mixing within the basin.

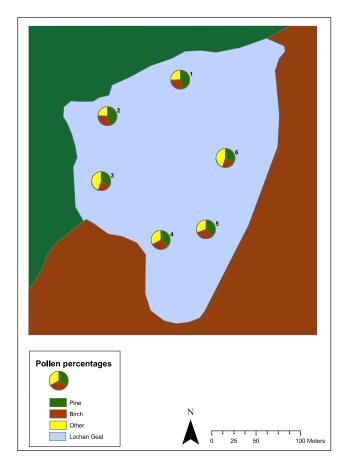


Figure 5.19: Location of surface samples obtained from Lochan Geal and their pollen percentages as calculated from Total Land Pollen.

Assessment of changes in the unsupported ²¹⁰Pb component of the sediments suggest a constant sedimentation rate over the duration of the core; However, low supported ²¹⁰Pb values and reduced atmospheric flux levels, imply that sediment scavenging processes may have affected portions of the core resulting in the low sedimentation rate. The ¹³⁷Cs profile also supports this supposition as it is diffused over a number of samples with an identifiable peak at 2.5 cm depth. This could correspond to the 1986 Chernobyl disaster but concurrent peaks are identified in both supported and

unsupported ²¹⁰Pb profiles implying a potential sedimentary aspect to this feature. A sedimentation rate corrected CRS model was applied to the ²¹⁰Pb profile with comparable results between that and the ¹³⁷Cs dates shown in Figure 5.20.

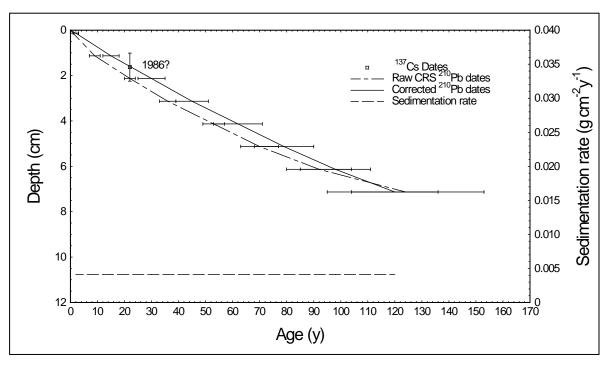


Figure 5.20: An age-depth profile for Lochan Geal (LGB) obtained from ²¹⁰Pb and ¹³⁷Cs assay. The CRS model was fitted to the data and corrected for sedimentation rate.

SCPs were analysed to provide a secondary dating method to complement the 210 Pb analysis. Figure 5.21 shows the profile obtained from contiguous samples. Although the commencement of the record is similar to those identified at other sites within the Cairngorms the remaining profile fails to correspond with regional features (Jones *et. al*, 1993). A sharp rise in concentration culminates in a peak at ~4cm corresponding to c.1945 with the subsequent peak at ~2cm depth correlating to the implementation of the Clean Air Act. However, this could be an artefact of redistribution from other areas of the lake or mixing of the profile. Concentration peaks at both 1cm and 2cm depth could be related to the 210 Pb and 137 Cs peaks identified during dating. Furthermore, concentrations are also low with respect to other studies that have been conducted within the region.

Loss-on-ignition results show little variation over the duration of the core corresponding to the sediment stratigraphy with a slight decrease in organic content from 65% to 50% although this level remains very high. This could be a reflection of the sampling interval as 1cm increments were used over the core despite the high sedimentation rate.

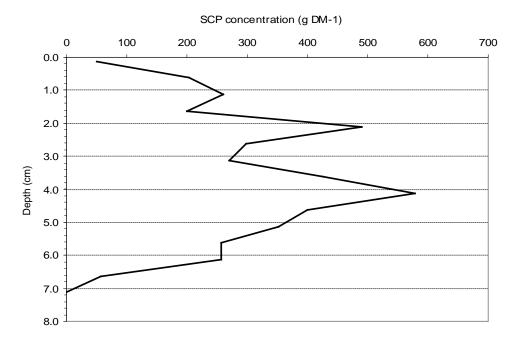


Figure 5.21: Spheroidal carbonaceous particle concentrations with depth from Lochan Geal

5.2.2.2.1 Pollen analysis

Two pollen zones were identified using CONISS (Grimm, 1987) with the delineation at 2.75cm depth. Figures 5.22 and 5.23 shows the pollen assemblages at Lochan Geal with zone characteristics described below:

LPZ LGB1 6.5cm - 2.75cm

Dominance of *Betula* characterises the zone with values attaining 50% TLP. In contrast, *Pinus* values are much lower and comprise only 20% TLP throughout. These values imply the local presence of a predominantly *Betula* woodland although some areas of mixed *Pinus-Betula* areas may have existed. Although small fluctuations can be seen within the profiles for these two taxa there are no discernable changes in this broad pattern. *Alnus* and *Corylus* are present in the pollen assemblage. *Calluna* and Poaceae are the main non-arboreal taxa indicative of some open areas around the site, supported by the presence of shade intolerant *Plantago lanceolata*, *Ranunculus*-type, *Rumex acetosella* and *R. acetosa*.

Accumulation rates for this site show reasonable stability over the duration of the core. In LGB 1 *Pinus* and *Betula* show the highest values with Poaceae also an important contributor. *Larix* also provides a large amount of pollen to the site which is associated with the plantations in the

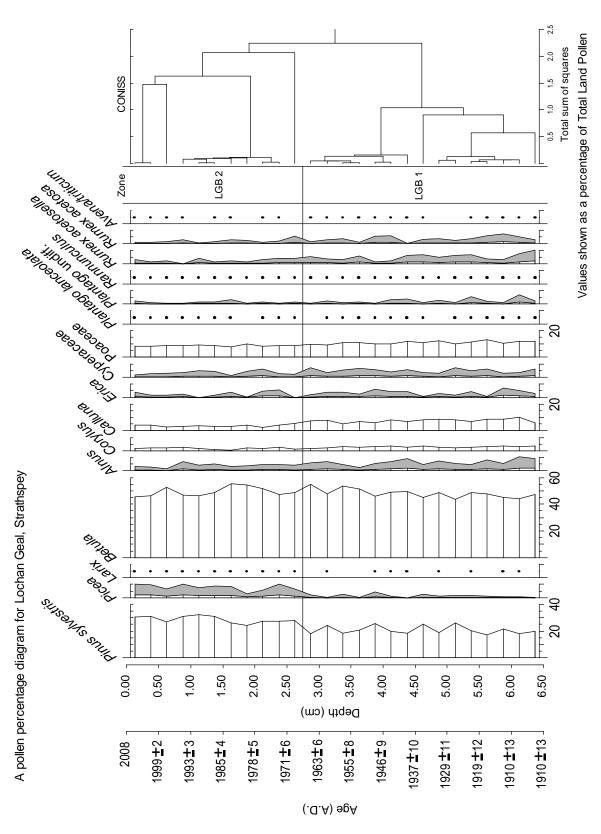


Figure 5.22: Pollen percentage diagram for Lochan Geal. Points represent values <1%.

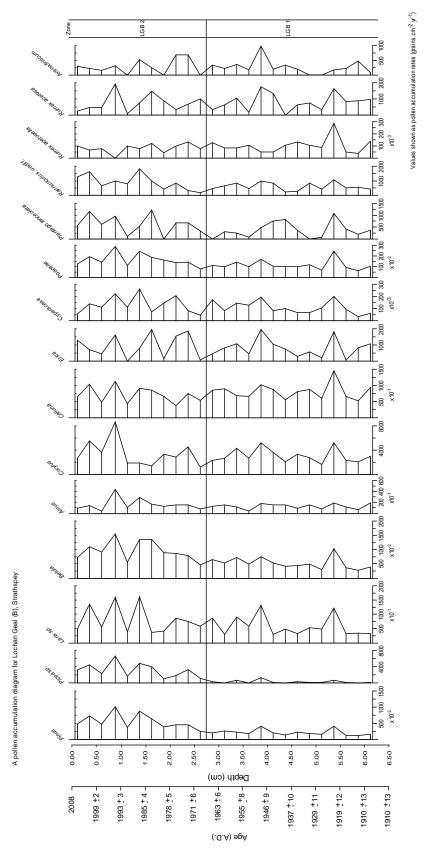


Figure 5.23: A pollen accumulation diagram for Lochan Geal.

surrounding landscape. A peak is evident in a large number of taxa at 5.5cm which could indicate a sedimentation change.

LPZ LGB2 2.75cm - surface

The main constituents of LGB1 show little change within this zone with the main contrast being the increased presence of exotic taxa including *Picea* spp. and *Larix*. Their low presence suggests sporadic local occurrence or a regional influx from the wider landscape. *Betula* values remain high with increased percentages of *Pinus* with values attaining 30% TLP. A reduction in *Calluna* is associated with this perhaps related to a closing or expansion of woodland areas. Interestingly, quantities of Poaceae, *R. acetosella* and *R. acetosa* show little decline suggesting a constant feature in the landscape independent of the *Calluna* decline.

Accumulation data for this zone shows increasing levels of *Pinus*, *Picea* and *Betula*. The increase in *Picea* values are likely associated with planting of this taxa within the managed woodlands. Variability is clear within the values and affects all taxa which inhibits correlation of peaks and troughs within the individual profiles.

5.2.2.2.2 Interpretation of landscape changes at Lochan Geal

It is possible from the radionuclide evidence that within lake processes have affected sedimentation at the core site. Furthermore, evidence from the SCPs does not conform to the regional profiles identified from a number of lakes around the Cairngorms region, including mountainous sites suggestive of a strong atmospheric flux. However, the pollen record shows little indication that changes in the sedimentation of the site has taken place during the time span reflected in the core. Betula and Pinus dominate around the site at present, with the latter occupying a much larger area and past fluctuations between these two components could be difficult to detect. However, the location of the Betula stems at the margins, and in some areas within, the lake will disproportionately represent this taxa accounting for the high percentages. Evidence of this was observed within the pollen assemblages with a number of *Betula* pollen clumps identified and when sampling large quantities of birch fruit were present on the loch surface. In addition, at present an area of pasture occupies a large track of land running to the south eastern margin of the lake. Continual Poaceae presence indicated in both the pollen percentage and accumulation diagram, in addition to other meadow indicating taxa, again implies the contemporary landscape have been stable for some time. Therefore, it seems likely that only minor changes have occurred within the arboreal vegetation patterns around Lochan Geal since ca. 1910±13. Ordnance survey maps support this with the A.D. 1903 image, Figure 5.24, showing a large proportion of dense woodland plantation to the south and east of the site, with a large area of heathland to the north of the basin.

The earlier map from A.D. 1874 identifies this region as heathland with fringes of mixed woodland around the basin again supporting the conclusion of planting from the late 1800s. Unfortunately, images are not available for this area for the 1910 – 1950 period of intense woodland utilisation and subsequent purchase of the area by the Forestry Commission. However, the areas not under woodland cover in A.D. 1903 but are so by the earliest records of the Forestry Commission a period which implies some woodland growth and expansion occurring in the duration of the pollen profile but is not evident. This is an interesting feature which could have multiple influences suggesting that either any planting was undertaken prior to A. D. 1910 or that the representation of local planting is diluted by the regional pollen rain, or that sediment focusing is an issue within the lake and is masking features within the pollen record. Evidence from the sedimentary profile fails to support the latter conclusion as continual sedimentation is apparent but ²¹⁰Pb conflicts this and is something that requires further investigation.

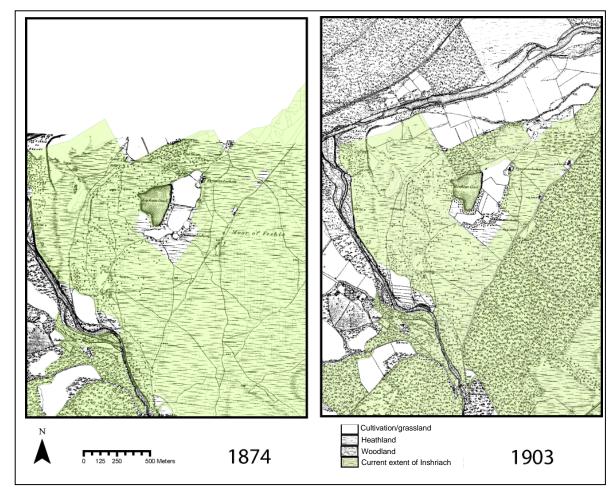


Figure 5.24: Historical County Series Ordnance survey maps 1:10560 showing vegetation change at Lochan Geal. Green shading represents the current extent of Inshriach Forest. *Source:* Historic Digimap (an Edina service) © Crown Copyright and Landmark Information Group Limited 2009. All rights reserved 1874/1903.

5.2.3 Discussion of recent vegetation change at Inshriach

Alternating patterns between *Pinus* and *Calluna* typify the regional vegetation changes of the recent historical period. The driving force of this change has been human intervention with utilisation of woodlands increasing heathland communities only to subsequently implement afforestation programmes and management. Comparison of the regional pattern of vegetation change is hampered by the lack of palaeoenvironmental studies which detail the historical changes within the region. A great deal of focus has been placed on longer term patterns for which the sampling and temporal resolution is too low to capture the detailed changes of more recent periods. O'Sullivan (1973a) did undertake a similar study in which mor humus profiles were obtained from sites at Abernethy for pollen analysis. Although a number of sites out of the eight examined do reflect an increase in *Pinus* from ca.1840 associated with planting a local vegetation signal predominates when the samples were obtained from woodland contexts. Furthermore, mixing and preservation are two issues raised by the author as affecting some of the sites influencing the resultant interpretations (O'Sullivan, 1973a). In spite of the potential errors the mor profile corroborates historical evidence that places this period, late 1800s – early 1900s, as one of the most intensive for woodland exploitation within the Cairngorms area (Carlisle, 1977; Smout, 2006). information relating to the Rothiemurchus Estate provides an insight into landscape management being undertaken as summarised by Smout (1999). These records show a strong focus on timber land management stimulating a high proportion of land being clear felled during the early 1800s with subsequent planting due to the 'exhaustion' of the woodlands. Loch an Eilein was a location for both activities with planting undertaken in A. D. 1863 on existing heathland areas utilising a number of fast growing and valuable tree species including larches, poplar, oak and Corsican pine (Smout, 1999). Although some exploitation of the woodlands has occurred since, predominantly focused on non-pine species, a large proportion of the stems planted in A.D. 1863 remain today as seen in the recent coring activities of Fish (pers. comm.). Cessation of large scale timber forestry had occurred by ca. 1850 in a number of areas in the Highlands, not just Rothiemurchus, after which the woodlands were utilised for sporting activities as timber forestry was no longer commercially viable (Mason et al., 2004). This pattern can be seen in the pollen records which realised small changes apparent over the last century or so.

Exploitation of the woodlands from the 1940s is not as distinctive in the larger sites, which is attributed to their regional picture and the predominance of regional pine. Inshriach H1 shows the influence these changes can have at the local scale emphasising the importance of site size in determining data presentation. However, the features identified at this site within the pollen percentage data is not replicated in the PAR representation as is the case at other sites. All sites are influenced by *Pinus* with very high PARs for this taxon. Interestingly, the site with the lowest

representation is Loch an Eilein despite the dominance of pine around the margins of the loch with Loch Alvie the highest values. Estimates of *Pinus* PARs from both monitoring and fossil studies have defined thresholds for the occurrence of this taxon in varying quantities. General consistency amongst a number of sites in northern Finland show that a dense woodland would generate PARs of >2000 grains cm⁻² y⁻¹ (Hicks and Hyvärinen, 1999) and >2500 grains cm⁻² y⁻¹ (Hicks and Sunnari, 2005). These estimates differ in relation to the size of the basin used which limits their applicability to analogous locations. However, their low value in relation to those from Inshriach implies that there is a greater productivity of *Pinus* in Inshriach or other biases have impacted upon the calculations. The former deals with the location of the studies used to generate these values with most sites concentrated around tree-line locations in northern Scandinavia. A study by Koff et al. (2000) in Estonia found similar levels overall with one site, lake Tänavjärv yielding much higher PARs which the authors suggest relates to the edge:surface ratio increasing the importance of marginal vegetation and sedimentary process. A more recent study by Sugita et al. (in press) compared absolute pollen productivity and concluded that there was little difference between taxa productivity at the limit of their range and at other locations. If this information can be applied to Inshriach it suggests that secondary biases could be influencing the PAR calculation.

A number of studies have highlighted the range of biases that can impact upon the calculation of PARs such as:

- basin size: a larger site will have a greater source area but reduced pollen loading as the marginal vegetation becomes less important in relation to the surface area of the lake receiving pollen (Prentice, 1985; Sugita, 1993).
- patterning of the vegetation: as discussed this influences the source area for the basin (Sugita, 1994).
- inlet transportation: although closed basins are preferred for most pollen studies the influence of slope wash has to be considered as shown in studies by Peck (1973) and Bonny (1978).
- within lake processes: changes in the sedimentation rate from focusing and redistribution can influence the PARs (Davis, 1973; Davis *et al.*, 1984; Kangur, 2009). This is not limited to lake sediments as changes in the humification of peat profiles can have a similar impact (Hicks and Hyvärinen, 1999; Sugita *et al.*, in press).

Comparison of pollen concentrations and PARs identifies some minor differences but the overall patterns remain consistent at Lochan Geal B and Loch An Eilein and implies that the sedimentation changes have had minimal impact upon the PARs here (Seppa and Hicks, 2006). Inshriach H1 shows the greatest difference as in the pollen concentrations a greater change in *Pinus* values

identified in relation to the planting and maturity of the woodland *ca*.1980. Here the change in sedimentation related to the transition from a sedimentary to peat deposition site could have influenced this. Similarly, at Loch Alvie the large decline in values at 4.5cm is associated with a large increase in sedimentation perhaps caused by inwash or slump at the coring site. These explanations fail to account for the high *Pinus* values in all cores and it is suggested that the dominance of pine not only around the sites but also within the region is the cause of this.

5.3 Long term vegetation reconstructions at Lochan Geal

Determination of the long term vegetation dynamics enables the current vegetation patterns to be seen in the context of both naturally and anthropogenically driven changes. This section outlines the late-Holocene history of Lochan Geal to elucidate changing vegetation patterns with additional application of the quantitative reconstruction models over longer timescales.

A core 118cm in length was extracted from Lochan Geal close to the centre of the basin where water depth at the core site was ~14 m, similar to the location of the shorter core, and was one of the deepest areas of the loch. The sediments were comprised of highly organic silt with no stratigraphic features identified when the core was initially extruded.

5.3.1 Chronology

An age-depth model was constructed for LG TAP, shown in Table 5.1 and Figure 5.25, using the median of the calibrated (using IntCal 04: Reimer et al., 2004) dating range as it has been shown to be more robust than the intercept method (Telford et al., 2004) showing a record from 3198 cal. Yr. BP to the present day. The model identifies a distinct change in sedimentation centred at 62cm with the upper portions showing a more rapid rate, although, the low number of dates makes dating the point of change difficult. As discussed in section 3.3.2.2, macrofossils were used where possible with those showing little indication of damage used in preference to reduce potential contamination from redistributed material (Björck and Wohlfarth, 2001). However, further caution is required as Oswald et al., (2005) showed little consistency between the age determination of different macrofossils with wood and charcoal fragments frequently providing estimates older than other material. Explanation for this is attributed to the slow growth of the trees which unavoidably increases the age prior to deposition which was also the conclusion of Gavin (2001) on analysis of charcoal derived ages. In addition, Bjorck and Wohlfarth (2001) suggest that wood undergoes more transportation and reworking than other macrofossils which could also increase the age determination from these fragments. At Lochan Geal only one sample, 115cm, contained wood whilst the reminder where comprised of Betula fruit and twigs, which provide unlagged estimates unless redistributed (Trumbore, 2000).

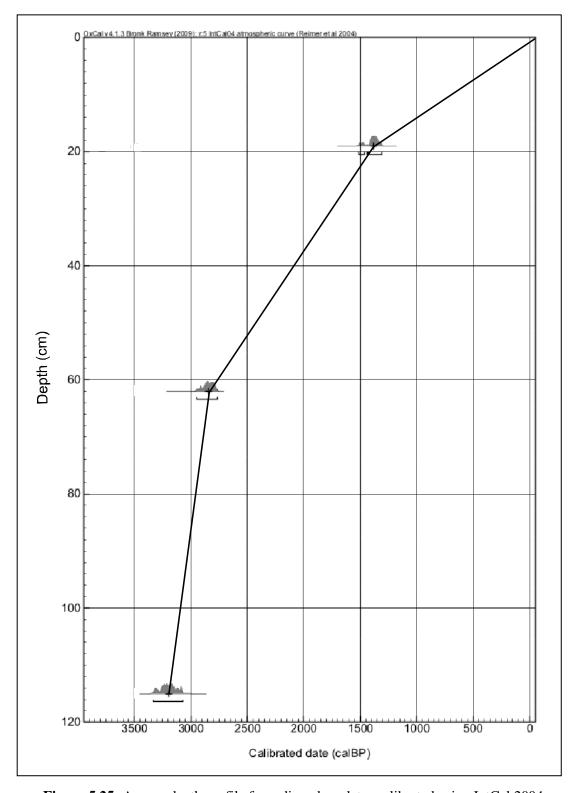


Figure 5.25: An age-depth profile for radiocarbon dates calibrated using IntCal 2004 (Reimer *et al.*, 2004) from Lochan Geal (LG TAP) and OxCal ((Bronk Ramsey, 1995). Crosses represent the median of the calibrated distribution with a linear model fitted to these points.

Laboratory Code	Sample Depth (cm)	¹⁴ C Age	Cal. Yr. BP median	Cal. Yr. BP age range	Material Dated
Beta-254879	19.5	1500±40	1383	1307 - 1516	Birch fruit
Beta-254880	62.5	2570±40	2198	1765 - 2946	Birch fruit
Beta-254881	115.5	3000±40	2841	3072 - 3335	Birch fruit

Table 5.1: Details of radiocarbon dating at Lochan Geal.

5.3.2 Sediment description and analysis

Loss-on-ignition (LOI), Figure 5.26, reveals a very high organic content with values consistently 90% with only three deviations from this. The main reduction in organic content occurred between 60 cm and 50 cm depth and whilst still containing ~55% organic material is a prominent feature within the profile. A similar event occurs close to the surface of the core from 20 cm and is a more gradual and sustained decline to ~70% organic content. Comparison of the features identified in the LOI curve to the magnetic susceptibility measurements is complex due to the variability in the magnetic data. Firstly, the core shows a diamagnetic pattern with major deviations indicative of inwash events and increased duration of events occurs from 10 cm to the surface. Secondly, the magnetic susceptibility of the core shows fluctuations until a peak at 80 cm. Above 60 cm depth the profile changes with rapid transitions variation in susceptibility but showing an overall increase culminating in a peak at 45 cm, and is identified as one of the largest influxes to the lake (Figure 5.26).

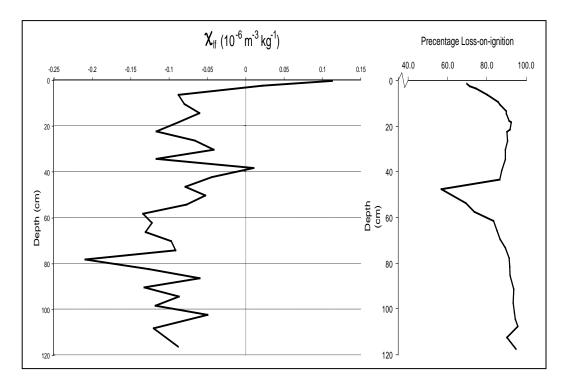


Figure 5.26: Magnetic susceptibility and loss-on-ignition curve for Lochan Geal.

5.3.3 Pollen and charcoal analysis results

Application of CONISS (Grimm, 1987) to the pollen diagram resulted in distinction of three pollen accumulation zones each of which are described below. Figure 5.27 and 5.28 shows the results of this analysis in pollen percentages and accumulation rates.

Overall, *Betula* is the dominant taxon within the zone attaining values of 70% TLP at its maximum presumably deriving from both the margins of the loch and the surrounding landscape. *Pinus* is the subordinate component attaining 20% TLP. A conspicuous feature of these taxa is that occurring at 80 cm depth where there is a brief point where *Pinus* doubles and there is a significant reduction of *Betula* a similar reduction occurs within the *Corylus* curve. Other arboreal taxa occur sporadically and only in low quantities. Non-arboreal taxa are diverse but many are present in only low frequencies. Cyperaceae, *Plantago lanceolata* and *Ranunculus*- type are the dominant taxa and have almost continuous presence throughout the profile.

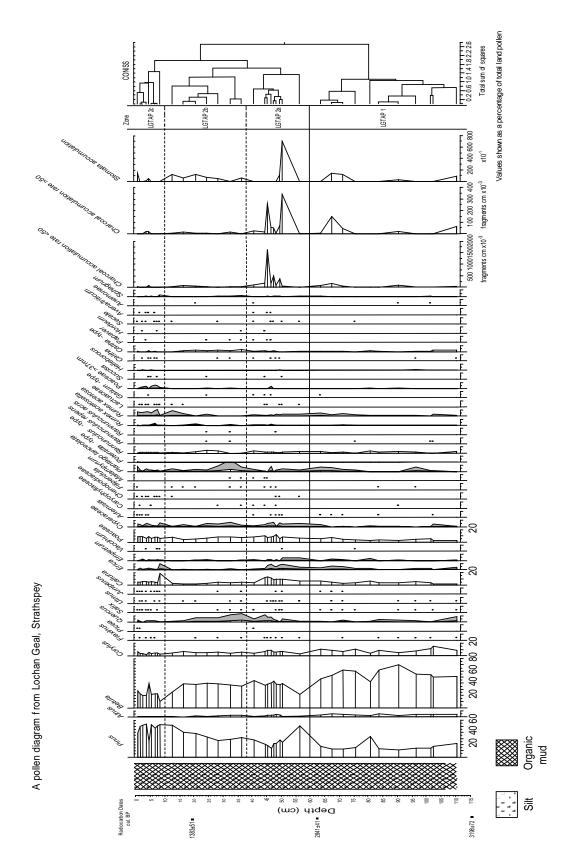


Figure 5.27: Percentage pollen diagram for Lochan Geal, Strathspey. Points represent values <1% TLP.

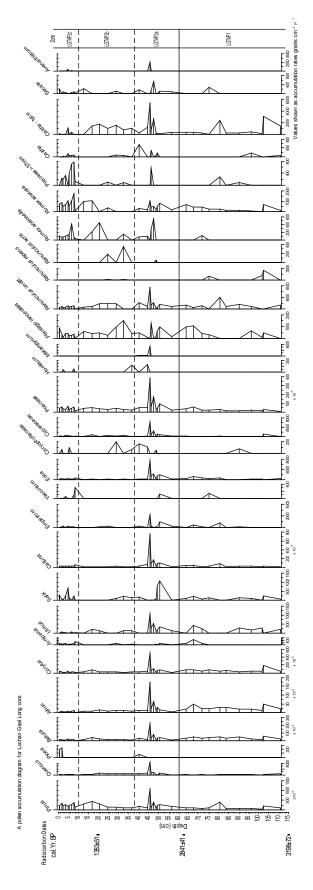


Figure 5.28: A pollen accumulation diagram for Lochan Geal Long core (LGTAP).

A peak in *Plantago lanceolata* occurs at 95cm but is not recognised in other taxa. In contrast, a later rise in the *P. lanceolata* profile, ~ 70cm, is simultaneous to rising *Pinus* and a peak in microscopic charcoal.

Within the accumulation data *Betula* is the greatest constituent of the assemblage with *Pinus*, *Calluna* and Poaceae also important taxa. Heightened levels of accumulation are noted until 105cm throughout most components of the pollen assemblage, it is only the heathland taxa that do not experience this. Also within this zone a peak in *Pinus* accumulation occurs at 80cm consistent with a peak in *Calluna* and other non-arboreal taxa. This occurs in conjunction with a peak in charcoal concentration and a rise in *Plantago lanceolata* levels.

PAZ LGTAP2a 60 – 38cm (2709 – 2000 cal. Yr. BP)

This zone is characterised by fluctuating *Pinus* and *Betula* values. A large decline in *Betula* values marks the opening of the zone with values falling to 20% TLP and simultaneous decline of *Corylus* values suggesting a combined effect. Concomitant with this feature is a peak in *Pinus* values of 55% TLP which is followed by a decline to a minimum at 45cm (c. 2200 cal. Yr. BP) of 15% TLP; Subsequently, values show some recovery whilst *Betula* experiences relative stability at ~50% TLP. *Calluna* and Poaceae show higher values than those of the previous zone achieving 10% - 15% TLP particularly at 45 cm or c.2200 cal. Yr. BP. Increases are also seen in other heathland representatives with *Erica*, *Vaccinium* and Cyperaceae showing slight changes which could signify increased diversity albeit on the basis of low frequencies. The presence of *Ulmus*, *Fraxinus* and increased *Corylus* values could be a reflection of the regional pollen influx rather than local changes. Reduction of *Rumex acetosa* and the presence of *R. acetosella*, *Ranunculus*-type and *Caltha*-type suggest a change within the open areas. The continued occurrence of *Plantago lanceolata* and increased representation of *Secale* suggest anthropogenic activity and relatively local cultivation.

Prominent increases in pollen accumulation rate characterise this zone between 50 – 45cm. Both the form and quantity of change is consistent between the constituents of the pollen assemblage. Relatively, *Calluna* and Poaceae experience the greatest increase in comparison to previous levels. Following this event the values return to quantities comparable with zone LGTAP 1.

Microscopic charcoal concentrations, both fragments g^{-1} and CHAR (Charcoal Accumulation Rate) demonstrate a large fire event with additional evidence from macroscopic charcoal between 50-45 cm with the longest axis of one fragment measured at 10mm. Sustained incorporation of smaller fragments are evident with exceptionally high quantities of the $<50\mu$ m class at 45cm, this occurred

around 2300 cal. Yr. BP. Furthermore, occurrence o a number of herbs and ruderals such as Lactuceae and *Cirsium* indicate a disturbed habitat.

The lower levels of this zone show an initial increase of *Pinus* to 30% TLP with *Betula* values stabilised at 40% TLP. Towards the end of the zone, from 20cm depth, values of *Betula* decline rapidly. Similarly, *Alnus* and *Corylus* are significantly reduced with their presence just attaining 5% TLP. Interestingly, *Calluna* and Poaceae show very little variation in values with presence still low at ~10% TLP for each taxon. High percentages of *Ranunculus*-type and *Caltha*-type grains are displayed reaching ~5% TLP at the start of the zone before declining, which could suggest a decline of open areas, a lower lake level or reduction in associated marginal habitats. The sustained occurrence of *Empetrum*, *Vaccinium* and *Rumex acetosella* highlights increased diversity in heathland areas. Furthermore, agricultural indicators (*Plantago lanceolata* and *Secale*) attain higher values suggesting sustained use.

High accumulation rates of *Plantago lanceolata* occur at the start of this zone and steadily decrease. This occurs in conjunction with increased non-arboreal presence i.e. *Rumex aceotsa*, *R. acetosella*, *Ranunculus acris* and *Caltha*-type. Levels of arboreal taxa are low but increases in *Pinus* occur from 25cm to peak at a depth of 15cm with values of ~500 x10⁻² grains cm⁻² y⁻¹. Other taxa remain relatively stable throughout the zone i.e. Poaceae, Cyperaceae, *Betula*, *Corylus* and *Alnus*.

Low concentrations of microscopic charcoal fragments are characteristic of the lower sections of this zone. However, high concentrations of *Pinus* stomata are evident which are coincident with increased *Pinus* percentages in the pollen profile, which could suggest a close relationship to *Pinus* presence around the margins of the lake.

Although short lived, an increase in *Calluna* at the opening of this zone is marked by increases to 20% TLP. Within the arboreal component *Pinus* is the dominant taxon attaining 50% TLP at its maximum. A substantial but transient decline in values is visible at 4.5cm depth (*c*.250 cal. Yr. BP) which is mirrored in an increase in *Betula* values of 20%. Towards the surface, there is a trend to decreasing *Pinus* values and increased deciduous taxa, notably *Betula* and *Corylus*, although the changes are of low magnitude. Increased diversity within the herbaceous taxa is observed with the sustained presence, for example, *Artemisia*, Chenopodiaceae and Lactuceae, which previously only showed sporadic occurrence.

Calluna accumulation rates do not show a pronounced increase as identified within the percentage profile, perhaps due to properties of the scale applied to the graph. However, there are increases in the herbaceous taxa including *Rumex acetosa*, *R. acetosella* and Poaceae >37μm. Both Poaceae and *Plantago lanceolata* have levels which are consistent with the previous zone. *Pinus* has a minor increase in values with *Picea* increasing presence in the surface layers of the zone. Deciduous taxa values decline with *Betula* only having accumulation rates of 14 x10⁻³ grains cm⁻² y⁻¹ which are much lower that levels previously attained.

As identified in the previous zone there are only low concentrations of charcoal with minor peaks equivalent to the depression in *Pinus* values. Similarly, *Pinus* stomata concentrations are low and reduced on levels attained in the previous zone.

5.3.4 Discussion

Interpretation of the changes in the pollen assemblage at Lochan Geal is made in relation to other environmental reconstructions and archaeological information.

Determination of the structure of the woodland communities is difficult to establish as *Betula* is identified as the dominant arboreal taxon but the interdependence between *Pinus* and taxon of deciduous communities implies that they were not fully mixed. The affinity of *Alnus* and *Corylus* to more fertile substrates than pine would separate these communities whilst birch could occupy a number of locations (McVean, 1953). Today, birch is present around the immediate margins of the basin which could have been their niche in the past, although the values imply that birch must have been seen in greater proportions in the wider landscape. Coincident fluctuations in *Pinus* and *Betula* at 80 cm are associated with a cessation of processes sustaining the dominance of birch. The occurrence of Poaceae, *Rumex acetosa* and *Ranunculus*-type imply that this is of the tall herb woodland of McVean and Ratcliffe (1962). Mixed woodland with *Alnus* and *Corylus* is a community that has frequently been identified in other palaeoenvironmental studies in Scotland (O'Sullivan, 1975; Dalton *et al.*, 2005; Froyd and Bennett, 2006; Shaw and Tipping, 2006) but which is less common in the present environment. Its presence may be inferred from the pollen data but low quantities imply that this is only a minor component of the landscape.

High levels of microscopic charcoal fragments also occur throughout this zone. Although indications suggest a regional signal, as micro fragments dominate the samples consistent with a much larger source area (Peters and Higuera, 2007). Table 5.2 outlines the definitions used in a

number of studies with the determination of local or regional source and identifies microscopic particles $>50\mu m$ as representative of local features. Application of this protocol to Lochan Geal would support the occurrence of local events for the increased charcoal concentration period from 3198 cal. Yr. BP – c.2300 cal. Yr. BP. This suggests *Betula* regeneration was facilitated by disturbance and fire. However, defining an anthropogenic or natural source to the charcoal presence is complex (Moore, 2000). Mackenzie (2002) suggests human settlement in the Cairngorms occurred from as early as 6000 cal. Yr. BP with suitable sites occupied predominantly associated with freshwater lochs. The author also suggests that grazing was practised whilst clearance was undertaken. Evidence of this seems to be displayed at Lochan Geal with open birch woodland supporting a grass-dominated understorey maintained by a grazing and fire regime.

Source	Local	Regional
Source	determination	determination
Clark (1988)	>50µm	<50µm
Clark and Royal (1995)	>100µm	
Peters and Higuera		
(2007); Patterson et al	>50µm	<50µm
(1987)		
Olsson et al (in press)	>250µm	<160µm
Blackford (2000)	>125µm	<20µm
Tinner (1998)	>50µm	<50µm

Table 5.2: Size thresholds for source area definition used in published studies.

Archaeological indications of settlement at this time are scarce and where found these are concentrated in the lowlands of the Spey Valley where fertile, alluvial soils are found (Henshall, 1963; Oram, 1997). Transhumance could have occurred sporadically throughout this period taking advantage of the sheltered location as the practice is common in the uplands (Halliday, 1993). A number of sites in Abernethy Forest, studied by Pratt (2007) show strong evidence for human activity with expansion of *Calluna* connected with increased charcoal presence. This is a time transgressive feature ranging from 5700 cal. Yr. BP at Tore Hill Moss to 2150 cal. Yr. BP at Forest Lodge. The higher location and early nature of the Tore Hill site is concluded as being a natural change associated with climatic deterioration whilst at the lower sites human activity is suggested as the agent of irreversible *Calluna* expansion from 3200 cal. Yr. BP corresponding to features at Lochan Geal.

Early human agricultural settlement is primarily concentrated in lowland locations where the climatic and edaphic conditions provide more suitable areas for settlement and agriculture (Tipping

and Tisdall, 2004). Climatic fluctuations enable the expansion of communities with contrasting settlement patterns between lowland and upland areas throughout the Holocene (Burgess, 1985; Edwards and Ralston, 1997). Burgess (1985) argued that climatic amelioration facilitated the utilisation of upland areas for both settlement and agriculture with subsequent abandonment when conditions could no longer support the community. Although there is a large body of evidence to support this conclusion there are also studies that show a considerable amount of agriculture, both arable and pastoral, continuing through the periods of climatic deterioration (Davies et al., 2004; Dark, 2006; Davies, 2007). Tipping et al (2008) compared an upland and lowland site in Sutherland but failed to identify any significant difference in the human activity indicators at this time. Similar features are seen at Glen Affric (Davies et al., 2004; Davies, 2007). A period of Betula dominance with several periods of heightened charcoal concentrations and pollen accumulation between ca. 3198 cal. Yr. BP and ca. 2200 cal. Yr. BP at Lochan Geal shows continued human activity which corresponds to periods of wetter and cooler conditions at sites both within the UK (Anderson, 1998; Hendon et al., 2001; Blundell and Barber, 2005; Langdon and Barber, 2005; Charman et al., 2006) and Europe (Van Geel et al., 1996). Charman et al. (2006) used testate amoebae profiles from a number of peat bogs within Britain to reconstruct fluctuations in water table levels as a proxy for precipitation levels. Figure 5.29 presents the regional composite data for northern Britain with patterns corresponding to the pollen zones of the Lochan Geal core. Throughout LGTAP 1 water tables show fluctuations of large magnitude with a significant rise occurring ca. 2700 cal. Yr. BP. If such features from the palynological record can be taken as indicative of human activity this supports the conclusion of Dark (2006) that abandonment of the uplands did not occur during deteriorating conditions but further investigations are necessary to validate this conclusion.

Correlation between the charcoal peak and increased quantities of Poaceae and *Plantago lanceolata* in both the pollen percentage and PAR diagram is highly suggestive of a fire event. Edwards and Whittington (2000) in a study at Black Loch, eastern Scotland, identified a positive correlation between charcoal and *P. lanceolata* throughout the duration of the profile. However, the authors went on to suggest caution in the interpretation of significant correlations between pollen presence and charcoal upon the basis of a single core due to intra-site variation in concentrations of both variables. If the relationship at Lochan Geal supports opening of the landscape a human agent could be argued as a probable source given the taxa involved. Furthermore, regeneration of vegetation subsequent to fire events is, to a large extent, dependant upon the range of taxa within the community preceding this (Hobbs and Gimingham, 1984) which could imply that open areas were already present around the site. Such presence is evident in the PAR profile.

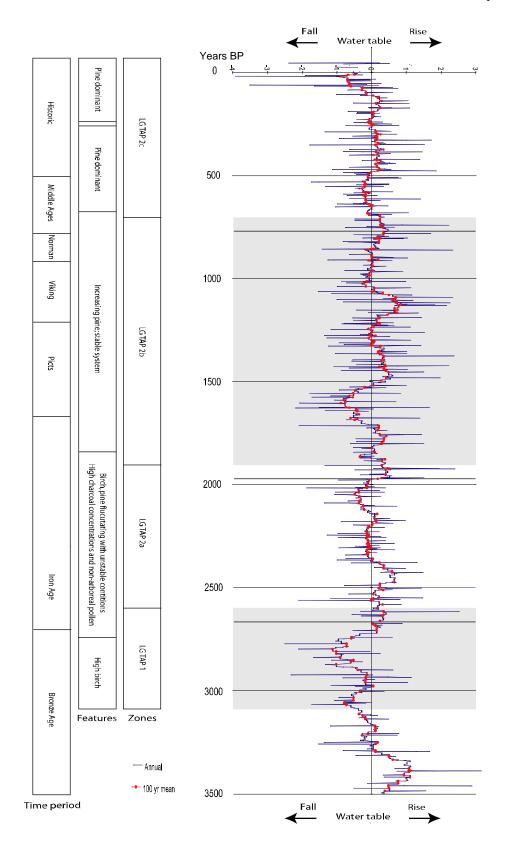


Figure 5.29: Water table fluctuations for Scotland (calibrated yrs BP) obtained from transfer functions applied to testate amoebae records. The figure is redrawn from data obtained from NOAA and previously published in Charman *et al* (2006).

Influences of grazing could also result in the diverse herbaceous taxa recognised in the pollen record. The taxa present during LGTAP 1 are also represented in the contemporary pollen assemblages that suggest an affinity with the present day environment. This is one dominated by pine, birch and a large area of pasture that is currently under low-intensity grazing. As mentioned, upland settlement is not highly recognised within the archaeological record close to Lochan Geal but this does not falsify anthropogenic activity as a cause of changes recognised in the palynological record. A number of Bronze Age and Iron Age sites are known from the area (Figure 5.30), including a large hill fort, Castle Law (Harding, 2004). Their utilisation of the Lochan Geal area cannot be discounted despite the distance to some of the sites. Although the presence of a number of anthropogenic indicator taxa, as defined by Behre (1981), occur at this time a number of studies have found difficulty in distinguishing the type of cultural landscape the assemblages represent (Gaillard *et al.*, 1992; Court-Picon *et al.*, 2005; Mazier *et al.*, 2006). Therefore, although anthropogenic activity appears the most likely candidate for the patterns of changes seen in the record at this time full details of the actual effects of the charcoal cannot be elucidated from the available data alone.

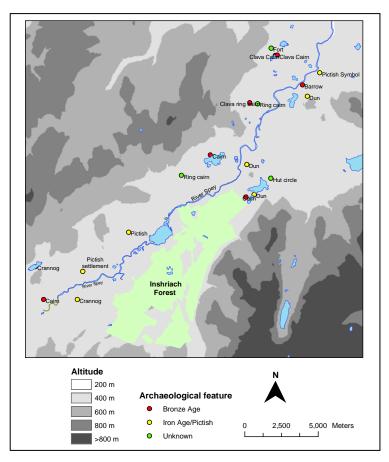


Figure 5.30: A map showing archaeological finds from the region dating from the Bronze Age and Iron Age.

Data obtained from Canmore online at http://canmore.rcahms.gov.uk

LGTAP2a 60 – 38cm (2709 – 2000 cal. Yr. BP)

The most discernible feature within this zone occurs between 45 - 50 cm with increased macroscopic charcoal and a great abundance of microscopic remains consistent with both a local and regional fire signal (Olsson et al., in press). For example, a fragment 1cm in length was found in the sediment at 40cm. Furthermore, the larger fragments are likely to have undergone significant breakage due to transportation over the steep slopes that surround the basin and therefore provide a conservative estimate for charcoal abundance. Numerous palynological features are associated with the charcoal peaks in the pollen diagram with a number of ruderals and light demanding taxa increasing in presence and diversity correlating to further opening of the landscape. The transient occurrence of *Malampyrum* is highlighted at this period which has been correlated to fire events at other sites (Innes and Simmons, 2000). A decline in Calluna, Erica and Cyperaceae is evident around 45 – 40 cm which could suggest heathland burning. Interestingly, there are no other relationships between the fire record and Calluna as has previously been identified at moorland and woodland sites (Innes and Simmons, 2000; Froyd, 2006; Pratt, 2007) but was not identified by Edwards et al. (1995). However, the decline in Pinus and increased Betula are the most distinctive palynological events associated with this. It is well known that Scots Pine is a fire sensitive taxon (Carlisle and Brown, 1968) whilst *Betula* is more resistant (Atkinson, 1992). Increases in stomata are recognised at this time which implies local presence of pine yet quantities cannot be derived as few studies have found a strong relationship between quantities and pollen stomata (Edwards et al., 1995; Hansen et al., 1996; Froyd, 2005; Shaw and Tipping, 2006). Consequently, the sequence of events may indicate that the fire was affecting areas occupied by pine as birch is a strong coloniser of newly created gaps consistent with the increased proportions in the pollen record (Grime et al., 1988).

All features identified in connection with the charcoal horizon could have been derived from sediment inwash. If the fire event was local, as supported by the fragment size of the particles, this would remove vegetation, increase instability and provide a source for sediment input. This is consistent with a reduced organic component and partly features in the magnetic susceptibility record. Edwards and Whittington (2001) studied a number of Scottish sites and identified heightened sediment input during the Iron Age attributed to increased human activity within the catchments. Consequently, although the pollen data may represent vegetation within the catchment the proportions of these components may be unrepresentative of actual patterns.

LGTAP2b 38cm -10cm (2000 cal. Yr. BP - 700 cal. Yr. BP)

A period of stability is identified with colonisation of pine and a decline of birch woodland. Reduced charcoal concentrations and lower sedimentation rates support this as a potentially local event (0.032 – 0.014 cm yr⁻¹). O'Sullivan (1976) identified a similar feature at Loch Pityoulish, in Abernethy, and suggested population reduction as the driver. At Loch Pityoulish this period of recolonisation spanned *ca.* 1450 – 900 cal. Yr. BP correlating to the period of charcoal reduction and *Pinus* expansion at Lochan Geal. Data from Barber *et al* (2000) notes a steady increase in wetness from *ca.* 1700 – 1000 cal. Yr. BP at Moine Morh in the western Cairngorms. Similarly Charman *et al* (2006) identify this as a period of higher water table depth at Mallachie Moss but significant variation was also indicated at Tore Hill Moss. Figure 5.29 shows this clearly with a sustained period of water table rise demonstrated throughout a large proportion of the LGTAP 2b zone. Effects of this climatic deterioration would also have exacerbated the social changes occurring at the time. Around 1000 Yr BP (A.D. 900) increased Viking raids are identified with resultant coalescence of Pictish tribes (Crone and Watson, 2003). Consequently, any centralisation would have been focused on more favourable lowland regions. These are concentrated to the far north of Inshriach forest near the coast and therefore it is not envisaged that this area was a foci for activity.

In contrast to earlier sections of this zone a peak of Calluna is indicative of an opening of the landscape at the boundary of zone c. Correlation to a Betula decline implies this area could have been utilised by human communities. However continued *Pinus* increase suggests that the whole area was not being utilised. Correspondence between the timing of this feature and the beginnings of the Medieval Climatic Anomaly between 1100 - 800 Yr BP (MCA: A.D. 800 - A.D. 1200) supports the supposition of marginal land utilisation due to climatic amelioration. Parry (1978) in a study of the Lammermuir Hills, southern Scotland, calculated the cultivation limits for differing periods in prehistory. During the MCA he suggested the limit rose to 450 m a.s.l. However, the increased wetness noted by Langdon and Barber (2005) and Barber et al. (2000), within the region shown in Figure 5.29, supports the presence of grazing in preference to arable cultivation. Furthermore, the sporadic and low quantity of cereal-type grains in the record permits only a tentative suggestion of localised crop growth. O'Sullivan (1974; 1975; 1976) investigated a number of sites around Abernethy Forest and established the first signs of human activity in the form of occasional *Plantago lanceolata* occurrence dated to 3900 cal Yr BP at Loch Garten and 3200 cal Yr BP at Loch Pityoulish with subsequent heathland expansion from 1500 cal Yr BP at a number of additional sites. Independent verification of these features are available from additional sites, for example studies in Abernethy and Lochnagar have provided support for the timing of heathland expansion with the former also identifying a strong increase in fire activity during this time (Dalton et al., 2005; Pratt, 2007).

LGTAP 2c 10cm – surface (700 cal. Yr. BP – present)

Pinus shows relative stability with only a slight reversion (4.5 cm) in otherwise high levels. Betula shows the reverse of this pattern with consistent but low presence within the record. Reduced amounts of charcoal at this time could have facilitated this succession but identifying a cause is difficult as these features occur at the end of the Little Ice Age (LIA). The LIA spans 600 – 100 Yr BP (A.D. 1350 – 1850), although it is in part a time-transgressive feature, and is associated with both sporadic and prolonged cold periods with increased rainfall and reduced evaporation (Lamb, 1966; Grove, 2004). A wet shift is identified in the Cairngorms dated to ca. 300 Yr BP (A.D. 1650) by Blundell and Barber (2005) and by Barber et al (2000), although Charman et al (2006) note this as only a minor deterioration. Water table deviations are only of small magnitude at this time (Figure 5.29) in comparison to those of earlier zones and in general the water table appears to be relatively stable. Evidence is available for the presence of human activity indicators such as cereals and grazed grassland species e.g. Plantago lanceolata, Secale, Avena/triticum, Rumex acetosa, R. acetosella and Ranunculus undiff. Lochan Geal is situated at 260 m a.s.l. which is considered as sub-marginal especially if unfavourable climatic conditions were prevailing. Although, it is plausible that land within or immediately surrounding the basin could have been the focus for human activity whilst permanent settlement was based in more sheltered locations the cereals and grassland taxa could be a reflection of more regional pollen influx but there is little indication of this from the PARs.

A feature of this period which is difficult to identify in the pollen record is the recent planting of coniferous woodland for management. In order to allow for this a large proportion of natural deciduous woodland was removed from the landscape and therefore this period would not only be evident within the coniferous taxa (Mackenzie, 2002). This began in the 1800s and therefore represents 200 years within the record yet is characterised in the pollen record by decreasing *Pinus* values and little change in the record of the arboreal species. Similarly, *Betula* follows a contrasting pattern to that expected and shows increasing values. These differences are most likely a response to the predominant sources of the pollen. Dominance of both pine and birch locally will have an overriding influence on the regional rain muting these patterns. This distinction infers that the land management frequently described in the literature may fall outside the source area of Lochan Geal. Consequently, it is likely that little direct management has been undertaken close to this site in the last 100 years. A greater temporal resolution would be required to provide further information but unfortunately the sedimentation issues highlighted from this period in LGB preclude this being analysed here.

5.4 Modern pollen comparisons

Multivariate analyses were used throughout this section to determine affinities between modern samples (29 moss samples from Inshriach Forest) and horizons from the core sample at all sites. Such an approach highlights analogous samples such as those from application of the modern analogue technique. All taxa with a presence of >1% TLP were included in the analysis from all locations. All analyses were conducted with species and sample centring and log transformation of the percentage values. This is to down-weight the overriding influence of *Pinus* and account for the closed dataset being used (Davis, 2002). Fossil samples are frequently included as passive samples to allow for a comparison based upon mapping of the samples (Hicks and Birks, 1996) but within this analysis all samples were included within the multivariate analysis however and could provide a source of variability in the results.

In addition to the multivariate analysis MAT technique was used (Analogue R package:(Simpson, 2007)) as a dissimilarity measure to identify the closest modern samples. Square chord distance was used to determine the degree of dissimilarity with an inclusion threshold of 0.15 as used by Overpeck *et al* (1985) with results of such horizons presented below.

As with the earlier section results from the large sites will be discussed first followed by the smaller sites and longer term changes at Lochan Geal. Differing techniques will be discussed simultaneously to allow for comparison.

5.4.1 Regional sites

Loch an Eilein

In the multivariate analysis an initial DCA returned an axis length of 1.33 units which substantiates the use of linear methods (Leps and Smilauer, 2003). Identification of two outliers obtained from birch woodland locations were removed from further analysis. Consequently, a PCA was run on pollen percentages from fossil horizons and 28 modern samples with species and sample centring and log transformation of the dataset as the values are closed (Davis, 2002). Results from this analysis, presented in Figure 5.31, show a strong distinction between the two groups with only a slight overlap. The concentration of points within the fossil group shows the lack of changes that have occurred over the time span of the core. There is however a comparable pair of samples identified where LAE 2.5 maps almost exactly with modern sample S2. The latter sample was obtained from open woodland of both birch and Scots pine and a dense *Calluna* ground flora. Samples also around this point include LAE 4.5 and 9.5 which also suggest a similar open structure. A reasonably strong connection is evident between LAE 0.5 and 1.5 with modern sample S12. The

location for this modern sample was Loch an Eilein and indicates that the ordination is identifying patterns within the dataset.

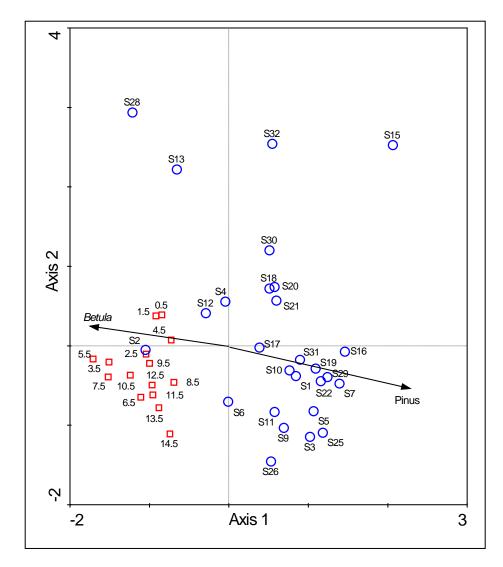


Figure 5.31: A PCA sample plot of modern pollen samples (blue circles) and fossil samples from Loch an Eilein (red squares). Eigenvalues: Axis 1 - 0.409; Axis 2 - 0.251. The arrows represent the species vectors for *Pinus* and *Betula*.

Dissimilarity analysis conducted on the data suggests that a number of analogues exist for horizons from Loch an Eilein (Table 5.3). A limited number of modern samples are consistently identified as suitable analogues which highlights the stability within the regional landscape over the time frame of the profile. These sites are predominantly dominated by Scots pine with little management intervention but sample S21 shows a clear distinction. In addition, three of the analogues matched to the upper sections of the core were obtained from the area surrounding Loch an Eilein. This sample was obtained from a spruce and Douglas fir dominated site which questions the representative nature of the analogues identified when these taxa are present in very low quantities,

if at all. This also has implications for the identification of equifinality as similar pollen assemblage could be produced from the different vegetation patterns. At Inshriach the dominance of pine does have to be taken into consideration as this will influence the analogues identified. None of the analogues selected from the multivariate analysis were identified here incorporating methodological and statistical bias into the results.

Sample Age	Depth (cm)	Modern Analogue	Dissimilarity coefficient	Site description
1992	1.5	S10	0.1374	LAE site. Pine, birch and Vaccinium
1983	2.5	S11	0.1128	LAE site. Pine with Vaccinium and Calluna.
1974	3.5	S12	0.0707	Old pine at LAE with Vaccinium.
1971	4.5	S12 S13	0.0371 0.1095	Old pine at LAE with Vaccinium Pine planted 1940s-50s, mixed age structure
1950	5.5	S13	0.1238	Pine planted 1940s-50s, mixed age structure
1924	12.5	S20 S21	0.0999 0.1326	Pine with bryophyte and grass flora Spruce and Douglas fir
	13.5	S21	0.0996	Spruce and Douglas fir. Grass flora
	14.5	S21	0.1258	Spruce and Douglas fir. Grass flora

Table 5.3: Summary of modern analogues defined for horizons from the pollen profile at Loch an Eilein.

Loch Alvie

A PCA of modern moss samples with the fossil horizons was attempted; however, no potential analogues were identified with a distinctive split between loch and moss samples (Figure 5.32). This is also indicated by the amount of variation accounted for by the primary axis, 59%, in contrast to the secondary axis, 8%. Reasoning for this relates to both the environment being recorded and the scale reflected within the samples as *Pinus* dominates the moss samples due to its close proximity with a few indications of largely open habitats.

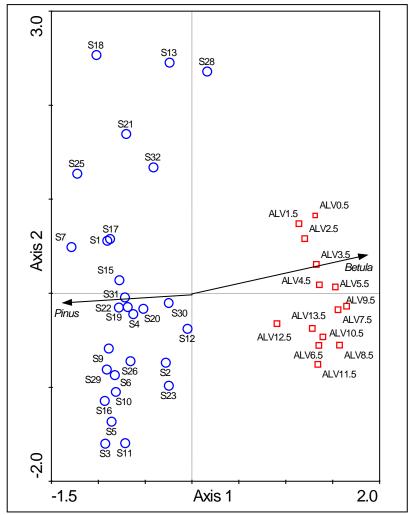


Figure 5.32: A PCA plot of modern samples (blue circles) and fossil samples (red squares) from Loch Alvie. Eigenvalues for the axes are: 1=0.593 2=0.081. Arrows represent species vectors for pine and birch pollen.

5.4.2 Local sites

Insh H1

Figure 5.30 shows a PCA diagram derived from pollen percentages of modern moss samples and fossil assemblages from Inshriach hollow. An initial DCA highlighted a linear relationship for the dataset with a gradient (1.215) of less than 4 S. D. units (Leps and Smilauer, 2003). In addition, samples S33 and S34 were identified as outliers within the dataset and removed from the PCA test.

One of the main features is the temporal split of the fossil horizons within the diagram; the top of axis 2 is dominated by the lower portions of the Inshriach H1 record and provides well distributed points; in contrast, the bottom of axis 2 the H1 samples are from the top levels of the core with a

greater degree of clustering with the modern samples. Furthermore, the position of the fossil samples relates to their stratigraphic position and the amount of *Pinus* in the samples. The vector shown in Figure 5.33 represents the direction of increasing *Pinus* values within the samples. At the arrow head samples are from the upper stratigraphic sections whilst in the opposite direction are the lower sections suggestive of decreasing *Pinus* quantities in these samples. Interestingly, the fossil sample, H1 19.75, corresponds to S12 which is well established pine woodland around Loch an Eilein with a strong *Calluna* understorey. Interestingly, higher stratigraphic sections such as 7.75cm, 8.25cm and 8.75cm plot with S15 which was obtained from juvenile open pine woodland with birch stems also present. The ground flora was represented by heathland taxa including *Erica tetralix*. This corresponds to a decline in *Pinus* stomata concentrations and could indicate that some thinning may have been conducted to provide a more open structure.

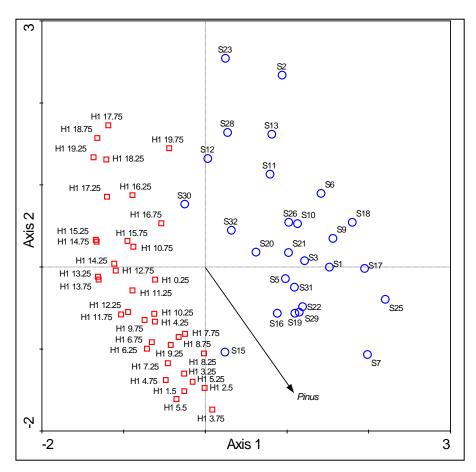


Figure 5.33: A PCA scatter plot of modern moss samples (blue circles) and fossil pollen samples from Inshriach Forest H1 (red squares). Black vector relates to *Pinus*. Eigenvalues: axis 1 = 0.398; axis 2 = 0.187.

As with Loch an Eilein issues of equifinality require consideration as a number of fossil samples are positioned close to an individual modern sample. Problems with the dominance of *Pinus* in the samples will be more prominent at the hollow site which will be a main contributor of this.

Table 5.4 shows the horizons found to have significant modern analogues defined through dissimilarity measures. The results identify two distinct vegetation types: pine woodland planted in the 1950s and older growth pine located at Loch an Eilein. An interesting sample is chosen as an analogue for 3.25 cm; an open, young pine structure with dense pine plantations surrounding the site after c.500 m. This could correspond to a period of thinning within the woodland or alternatively identify a potential problem with this technique as the pollen being incorporated from the plantations could be providing a false representation of the actual landscape. Interestingly, there is no correspondence between the analogues identified from the dissimilarity measures and those from the multivariate statistics. As the same data was used this cannot be attributed to methodological differences alone.

Sample Age	Depth	Modern Analogue	Dissimilarity coefficient	Site description
2007±2	0.25	S 1	0.1575	Pine, spruce, larch planted 1940s. Large, low density trees. Grass, bryophyte flora
2006±2	1.50	S10	0.1289	LAE site. Old pine, birch and Vaccinium
2004±2	2.50	S 30	0.0677	Open, young pine with old plantation surrounding. <i>Calluna</i> ground flora
2002±2	3.25	S 30	0.1224	Open, young pine with old plantation surrounding. <i>Calluna</i> ground flora
2002 ± 2	3.75	S5	0.1297	Pine planted 1956. Vaccinium and Calluna
2001 ± 2	4.25	S5	0.118	Pine planted 1956. Vaccinium and Calluna
2001 ± 2	4.75	S5	0.1068	Pine planted 1956. Vaccinium and Calluna
1998±2	5.25	S5 S9	0.1457 0.1469	Pine planted 1956. <i>Vaccinium</i> and <i>Calluna LAE</i> site. Pine and birch, <i>Vaccinium</i>
1998±2	5.50	S5	0.0818	Pine planted 1956. Vaccinium and Calluna
1979±3	10.25	S11	0.1445	LAE site. Pine, Vaccinium and Calluna.
1979±3	10.75	S12	0.14	LAE site with pine, Vaccinium and Calluna.
1969±3	12.25	S16	0.149	Open, young pine. Bryophyte and grass flora

Table 5.4: Dissimilarity coefficients for modern analogues identified at Inshriach Forest H1.

Lochan Geal B

PCA statistical analysis provided a strong dissimilarity between the two groups accentuating the strength of the *Betula* signal in the Lochan Geal samples. Figure 5.34 shows that S33 plots around

1.875cm and other higher stratigraphic samples whilst S34 plotted in the centre of all the samples below 3.125 cm in the core corresponding to the zonation in the pollen diagram. The former (S33) was taken from an area dominated by birch, mainly young, with a grass and herb ground flora. In contrast, S34 was taken from an area of older closed birch woodland with juniper also present suggesting a more closed structure prior to the 1940s. The location of samples S2 and S28, appear related to their high *Betula* values relative to the other samples and not due to structural comparison. It is, therefore, the lack of samples within the contemporary dataset which is driving the patterns evident within Figure 5.34. Such results convey the importance of a large and variable modern dataset if conducting the MAT approach.

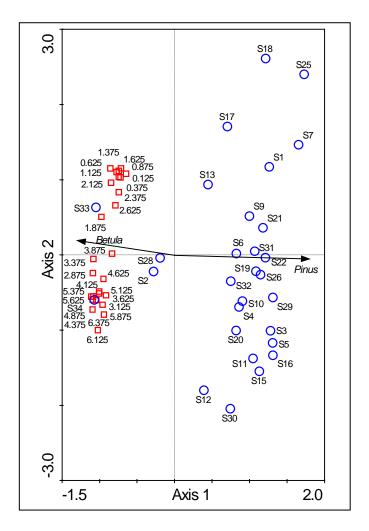


Figure 5.34: A PCA plot of LGB fossil horizons (red squares) and modern samples (blue circles). Eigenvalues for the axes are: 1= 0.695, 2= 0.099

Lochan Geal (TAP) long core

Ordination was undertaken on the LG TAP and modern moss samples (one outlier removed) to determine if any of the communities currently prevailing in Inshriach Forest are representative of the landscape around Lochan Geal in the past. A linear method, Principal Components Analysis (PCA), was carried out as the gradient was below 4 S.D in length (Leps and Smilauer, 2003). Scaling focused on samples to allow for proximity to represent similarity with species centring and division by standard deviation to allow for the dominance of *Pinus* values within the dataset.

Figure 5.35 shows the PCA plot from the ordination with the first two axes presented as these explained the most variation between the dataset with a number of features revealed. Firstly, a large proportion of the modern samples are not representative of the fossil landscape around Lochan Geal exemplified in the cluster of modern samples in the right of axis 1. Interestingly, mirroring this pattern at the left is a cluster of the LG TAP samples but a stratigraphic ordering can be distinguished. The majority of samples in the upper portions of the diagram are clustered at the origin and are correlated by their quantities and variability of herbaceous taxa and signify the stability within the upper portions of the core. Furthermore, samples from lower horizons are plotted around this zone indicating their relationship to the samples whilst also highlighting their dissimilarity. This distinction between the upper and lower portions of the LG TAP core further accentuates a change within the system at this time. Secondly, the mid section 50.5 - 44.5 cm samples (ca. 2200 cal. Yr. BP) which occur during a charcoal horizon form a distinct cluster. Furthermore, these are placed with modern sample S33, especially the sample from 48.5cm, which was obtained from open Betula woodland dominated by herb-grassland understorey with an open canopy despite a strong presence of *Betula* such as described by McVean and Ratcliffe (1962). This is a very interesting feature in contrast to the environment which currently prevails at the site and the analogue that was identified for the horizons immediately above those associated with this cluster. Furthermore, this highlights one of the strengths of the modern analogue technique in providing environmental information beyond the standard interpretation.

Finally, correspondence between the 8.5cm sample and the S2 modern sample shows that the landscape would have been predominantly open heathland with scattered birch and Scots pine. At the site S2 the trees were mature but suggestion of this being the case at Lochan Geal is tentative given issues of equifinality. Although *Calluna* levels are low in the LG TAP assemblage this was also the case at S2 with values ~10%. An artificially low presence of *Calluna* could be associated with the modern site despite its dominance of the ground flora (~60% coverage) due to the age of the vegetation. As *Calluna* follows an age cycle the early and most mature stages are periods within which little pollen is produced and therefore would affect the representation of the taxa

within the pollen (Gimmingham, 1960; Barclay-Estrup and Gimmingham, 1969). Although the moss samples are likely to smooth any annual variation in the pollen signal the relationship of the moss growth rate to that of the *Calluna* cycle is fundamental in capturing this. Elucidation of this would require further modern samples to be collected and additional comparisons made with the LG TAP samples.

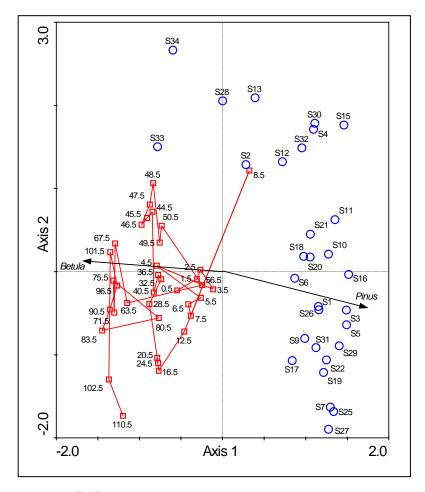


Figure 5.35: A PCA scatter plot showing LG TAP and modern samples from Inshriach Forest. Eigenvalues of axes: 1 = 0.661, 2 = 0.101

The samples placed in the lower left of the diagram from the basal samples of the core have no representation within the current environment. This relates to the modern samples being obtained from Scots pine dominated systems which is not the situation at Lochan Geal in the past when birch dominated.

MAT analysis selected few horizons for which analogues were available within the modern dataset presented. Table 5.5 shows a summary of the vegetation communities present at the sites. Although few conclusions can be drawn, the selected analogues indicate that the pine communities prevailing are a relatively new phenomenon. Furthermore, the distinction between the structure of 12.5 cm and the remaining two samples show discrimination between the age and structure of the woodland at these points.

Sample Age	Depth (cm)	Modern Analogue	Dissimilarity coefficient	Site description
c.A.D. 1750	3.5	S12	0.1477	Old pine at LAE. Vaccinium ground flora
c. A.D. 1700 c. A.D.	4.5	S12	0.0973	Old pine at LAE. Vaccinium ground flora
1300	12.5	S20	0.0879	Dense, young pine. Bryophyte ground flora

Table 5.5: Dissimilarity coefficients and detected analogue data for LGTAP fossil horizons.

5.4.3 *Summary*

Information provided by use of the comparative approach varies both between sites and their ages. Large proportions of the modern samples used were obtained from the main woodland of Inshriach and therefore predominantly reflect pine communities. It is clear that affiliation between modern samples and those of the cores reflect the changing density of pine woodland. Schofield *et al.* (2007) found this relationship when birch samples were analysed using similar multivariate techniques but this was in an open environment in Greenland where there is little arboreal pollen within the regional component. Consequently, poor results are obtained from Loch Alvie and Lochan Geal B as these sites are not dominated by pine woodland to the extent of that at both Loch an Eilein and Insh H1. At the latter site structural differences, enforced by age, were clearly identified when a suitable analogue was available. Even though the woodlands of Loch an Eilein have previously been managed, and nearly destroyed, the current lack of management is demonstrated in its structure and evident distinction from Inshriach Forest at present.

Associations identified from the Lochan Geal TAP core were more variable given the longer time frame. The most significant feature is the lack of modern analogues suited to the conditions prevailing in the past. No analogues were identified for the portions below c. 2500 cal. Yr. BP, whilst only one for the upper sections from c. 1600 cal. Yr. BP to the present day. As the modern

samples were obtained from managed woodland contexts it is clear that these do not reflect the range of vegetation patterns prevailing at present but the species may have been expected to be the same. Overpeck *et al.* (1985) defend the need for a range of samples to be used within the modern analogue set to ensure that environmental distinctions are accounted for. In a recent study Ortu *et al.* (2008) compile a dataset of 3000 modern samples yet still failed to find some suitable analogues. However, this investigation was focused on Late-glacial reconstruction which proves difficult due to the lack of available locations to acquire modern samples. Clearly, dominance of birch in the past is not reflected in the present landscape as although some samples are from this environment they were only affiliated with a limited number of horizons at the main charcoal feature and there may be analogies elsewhere.

An aspect applicable to all lake sites is the representative nature of the analogues to the sampling basin. Pollen deposition in lakes and moss sites differ and therefore representation of individual taxa varies. However, Gaillard *et al.* (1994) produced good results with comparisons of modern moss samples and lake fossil sites, but went on to suggest that it was the size of the basin that was the contributory factor not the environment. Pollen samples from a pinewood context would reflect this more so than other landscapes due to its enhanced dispersal properties. Consequently, scale of representation of the sampling site and taxa involved has to be considered prior to data collected and during analysis (Mazier *et al.*, 2009). Furthermore, a range of sites is required to extract suitable information for the samples. Limitations placed on the sampling strategy focuses the collection on Inshriach and the open heathland surrounding it. This gives samples at the extremes of the openness spectrum as oppose to samples throughout this range. As a consequence, it is likely that there are analogous modern sites for some of the horizons where these were not found. Such issues with sample set size and representation is further discussed in Chapter 7.

Differences between the analogues selected for the fossil sites corresponding to the analytical method highlights methodological factors. Multivariate analysis is frequently applied to pollen data to distinguish patterns with environmental data and between fossil and modern sites (Gaillard *et al.*, 1992; Gaillard *et al.*, 1994; Court-Picon *et al.*, 2005; Mazier *et al.*, 2006). Within the latter method, often one of the datasets are included passively (commonly the fossil set) to exclude this data from contributing to the axes positions and the eigenvalues (Hicks and Birks, 1996). This technique was not undertaken within this study and therefore can be contributing to the dissimilarity in results from the multivariate approach and the analogue approach. This would require an investigation to exclude this as a cause of variability.

5. 5. Conclusion

Analysis of the pollen profiles indicates minor changes over the recent timeframe presented by the short cores. The lack of destructive management that has been undertaken since the late 1800s when forestry was a mainstay of a large number of estates is well defined in a relatively stable pollen record. Although a large degree of woodland utilisation is recorded during periods of conflict these are not distinctive within the pollen profiles which could be due to this being masked by continued regional pollen influx. Longer time scales show increased diversity of landscapes that have prevailed around Inshriach prior to management. Increased birch occurrence indicates that the trend towards pine dominance is a recent one and perhaps influenced by human interaction.

Despite the mixed results obtained from the modern analogue approach promise is shown for the application of this to the Inshriach area. Where similarities in the modern and past landscapes were identified distinctions between structural details were detected. Inclusion of a greater range of samples will inevitably increase the number of associations and the detailed information obtained. Further consideration of this analysis will be discussed in Chapter 7.

Chapter 6: Regional and local vegetation reconstruction of the Strathspey region using the modelling approach

6.1 Introduction

Validation of the quantitative techniques using present landscapes only is not sufficient to permit confidence in fossil landscape reconstructions. Investigations of past ecosystems frequently discover pollen assemblages that show variation from those of the present day. This is especially the case of Inshriach which has seen a transition from semi-natural to fully managed woodland. Moreover, the patch-matrix structure of the landscape has been highlighted as a likely source of variability in estimations of relevant source area of pollen for deposition basins impacting upon the performance of the quantitative models (Bunting *et al*, 2004). Consequently, time slice reconstructions at Inshriach aim to fully test the application of the LRA model to changing vegetation structure around the deposition sites.

Horizons were chosen based on a number of criteria shown in Table 6.1 with the additional constraint of ensuring no two landscapes were same. By fulfilling a number of these criteria the model could be tested with a diverse range of conditions with full knowledge that appropriate data were available for comparison with the results. In these situations, as previously shown in Chapter 5, the models were run with only 5 taxa – *Pinus*, *Picea*, *Larix*, *Betula*, *and Calluna* – as they provided the only PPEs specifically for Inshriach. Consequently, simulated vegetation proportions and those of the comparison dataset were calculated from these 5 taxa only to provide corresponding datasets. Two exceptions occur where regional comparison data is unavailable, highlighted in Table 6.1, due to a lack of large scale datasets for the periods in question.

	Time slice	Regional vegetation data	Patch- matrix	Openness	Age structure
	1	•			•
Inshriach	2	•			•
H1	3			•	
	4			•	
	1	•	•		
Lochan	2	•	•		
Geal	3		•		
	4				•

Table 6.1: Criteria used to determine time slices for modelling comparison at Lochan Geal and Inshriach H1. Time slice 1- Present; 2- 1989; 3- 1960; 4- 1950

Results presented below are vegetation reconstructions from both the REVEALS and LOVE models providing regional and local descriptions for each time slice respectively. Regional estimates are obtained from combined core samples from Loch Alvie and Loch an Eilein with the local reconstructions for two basins, Lochan Geal and Inshriach H1 forest hollow. Profiles from these sites were all dated using ²¹⁰Pb as outlined in Chapter 5. Samples chosen to feed the model were identified from the closest sample to the horizon as possible. Where this condition was not achievable the horizon dated slightly older than the desired time slice was used to ensure that the pollen released during the period of interest was included within the pollen sample providing a representative comparison for the observed data. Estimates of relevant source area of pollen (RSAP) for the local reconstructions can be predefined in the model but if this value is too low the software automatically initiates a detection process which is constrained by taxon proportions being no greater than 1 but no less than 0. However, this is inclusive of error margins for the estimates allowing some negative values to be obtained which require correction; the results present throughout are the corrected estimates and are shown as a percentage of all 5 taxa where negative values are assumed to be zero.

In concluding Chapter 4 the PPEs of the BA.Ran.1000.1 dataset were chosen as the most representative for the current form at Inshriach Forest. However, in addition to these results the reconstructions from other groups are discussed in the following chapter. The aim of this is to express the range of variability inherent between the PPE groups tested.

6.2 Regional reconstructions

The results presented are estimates of vegetation proportions from the REVEALS model for the time slices identified. As reconstructions for the contemporary landscape were analysed in the previous chapter they will not be discussed in detail; however, the most comparable results are presented in Table 6.2 to allow for comparison with other reconstructions shown. Also, Table 6.3 shows the actual vegetation data for both 100km^2 and 400km^2 area around Inshriach using two data sources for the present and time slice 2; Land Cover Map 2000 (LCM 2000) and Land Cover of Scotland 1988 (LCS 88).

	BA.Ran.1	000.1	BA.Ran.500.1				
	Mean		Mean	_			
	vegetation	S.E.	vegetation	S.E.			
	percentage	(%)	percentage	(%)			
Pinus	55.9	21.8	36.8	20.1			
Picea	4.5	3.1	3.9	2.3			
Larix	8.2	11.8	8.9	11.7			
Betula	10.5	4.7	5.7	2.5			
Calluna	20.9	7.0	44.7	11.3			

Table 6.2: REVEALS generated vegetation proportions from Inshriach based on contemporary surface samples from two lake cores.

	Area of tile centred on Inshriach Inshriach			Area centr Insh	Inshriach		
LCM 2000 OBSERVED	$\frac{400}{\text{km}^2}$	$100 \\ \text{km}^2$	32 km^2	LCS 88 OBSERVED	$\frac{400}{\text{km}^2}$	$100 \\ \text{km}^2$	32 km^2
Pinus	28.7	64.1	80.1	Pinus	27.4	59.6	80.1
Picea	0.9	2.1	2.5	Picea	0.7	1.8	2.5
Larix	0.6	1.4	2.3	Larix	0.0	1.2	2.3
Betula	3.7	5.3	2.1	Betula	6.0	7.1	2.1
Calluna	66.1	27.2	13.1	Calluna	65.4	30.2	13.1

Table 6.3: Vegetation percentages for present day Inshriach and the surrounding landscape estimated from the LCM 2000 (first presented in Table 4.5 pp. 117) and LCS88 dataset.

6.2.1 Time slice 2 - 1989

There are a number of samples that show clear comparison with the actual estimates of vegetation whilst others fail to generate accurate figures (Table 6.4). Overall, the best results are obtained from the random groups regardless of the data collection method employed. It is the BA.Ran.1000 group that provides the closest comparison to the actual data when the 100km^2 area is considered (Table 6.3); reasoning for this distance is given in Chapter 4, with the assumption that the basin size of these two sites has not changed significantly in the intervening period. All taxa achieve strong correlation between the two datasets with *Pinus* providing the greatest disparity of 10%, which although large is still within the error margins calculated by the model. This suggests that the landscape in 1989 was dominated by a greater proportion of heathland community than the present landscape. Arboreal components are the minority with *Larix* showing the greatest reduction; however, difficulties with the PPEs for this taxon could also be affecting the result.

	BA.Ran.s Mean vegetation	S.E.	BA.Ran.16 Mean vegetation	S.E.		BA.SY.500.1 Mean vegetation S.E.			BA.SY.1000.1 Mean vegetation	
	percentage	(%)	percentage	(%)	_	percentage	(%)	_	percentage	S.E.
Pinus	27.2	11.2	49.3	12.8		12.2	34.5		20.1	7.0
Picea	1.6	1.4	2.2	2.1		0.9	2.1		5.2	4.0
Larix	2.7	4.6	3.0	4.5		34.0	42.6		3.1	5.1
Betula	4.4	2.2	9.8	4.7		6.6	17.8		3.8	1.3
Calluna	64.1	11.8	35.7	9.4	_	46.4	36.2	_	67.9	7.3

	CC.Ran.s Mean vegetation percentage	500.1 S.E. (%)	CC.Ran.10 Mean vegetation percentage	900.1 S.E. (%)	CC.SY.5 Mean vegetation percentage	vegetation S.E.		000.1 S.E.
Pinus	32.8	23.0	36.3	16.7	16.6	6.3	20.3	6.7
Picea	1.5	2.1	2.2	2.0	1.0	0.8	1.0	0.9
Larix	3.3	7.1	4.5	7.5	0.3	0.4	2.9	4.6
Betula	4.2	5.1	7.7	4.0	6.1	1.9	3.5	1.2
Calluna	58.2	23.9	49.3	15.1	76.0	4.6	72.2	8.4

Table 6.4: REVEALS reconstructions from 1989 representing regional vegetation coverage percentages for all values tested.

6.2.2 Time slices 3 and 4 - 1960 and 1950

Lack of comparison data for the regional element of these horizons places difficulty on defining the most representative reconstructions. Consequently, the BA.Ran.1000 results are those presented in Table 6.5 as they provide the strongest correlation with the previously tested horizons. Also, estimates from the remaining PPE groups fall within the error margins of the BA.Ran.1000 values for all taxa.

	1960		1950
BA.Ran. 1000.1	Mean vegetation percentage	S.E. (%)	Mean vegetation S.E. percentage (%)
Pinus	34.3	15.0	24.8 16.1
Picea	0.7	0.8	0.6 0.9
Larix	4.4	6.3	7.1 13.5
Betula	10.5	2.6	6.0 1.5
Calluna	50.1	10.8	61.6 14.9

Table 6.5: Regional vegetation percentage reconstructions using the REVEALS model and PPE group BA.Ran.1000.1 for time slices 3 and 4

The 1960 reconstruction highlights a reduction in *Pinus* proportions and concomitant increase in *Calluna*. Low error margins could suggest that the accuracy of the results is similar to those of the previous time slices. Estimates of the *Larix* coverage is much lower than the present day estimates but is marginally higher than the 1989 values. Determination of the cause of this is difficult as it could relate to the initial planting of this taxon and faster growth rate or it could be an artefact of the PPEs and modelling accuracy. Without suitable comparison data definitive conclusions cannot be drawn. By 1950 the estimates for *Pinus* are further reduced and *Calluna* increased implying a predominantly heathland landscape. The *Larix* figure appears to be high given the increase in open community representation. The figure of 7.1% resembles that of the contemporary vegetation structure although the large error margins of 13% imply that this figure could also be close to 0.

6.3 LOVE reconstructions

Results presented below are derived from a number of PPE values used within the model. In all cases the regional estimates that were used to feed the model, presented above, were obtained using equivalent PPEs. During the time slice model runs basin size for the two deposition sites remained constant (5m radius for Inshriach H1; 100m radius for Lochan Geal). At present, no data are available to infer any changes in basin size at either site through time. Although Lochan Geal is a closed basin there is the potential for this basin area to fluctuate but any small changes over the reconstruction period would not significantly alter the surface area of the basin. A similar situation is envisaged for Inshriach H1 hollow as this occupies a confined depression with little indication that significant changes in the deposition environment have occurred. Initial RSAP distance was set at 50 m for Inshriach H1 and 100 m for Lochan Geal which relate to empirical results for forest hollows and small lakes within closed woodland contexts (Calcote, 1995; Sugita et al., 1999b). However, if the RSAP is larger than the input distance the model will calculate a more realistic value incorporating the basin size and vegetation properties in an iterative process outlined above. In addition, tests were run with increased input RSAP distances calculated from the characteristic source area of pollen model. This produced estimates of 100 m for Inshriach H1 hollow and 400 m for Lochan Geal. These are much larger than those originally estimated as it assume homogeneity in the vegetation patterns these distances are more appropriate for these sites as they are based upon the dispersal characteristics of the vegetation constituents present at the sites and therefore account for different dispersal properties of the grains.

Results for these runs are presented in tables which state the simulated mean vegetation coverage and standard errors for these estimates. The additional column gives the observed vegetation coverage from within the RSAP which was obtained from the Inshriach forestry records where possible.

6.3.1 Time slice 1 - Modern

6.3.1.1 Inshriach H1 Forest Hollow

Varied reconstructions were produced from PPE parameter substitution. Two experiments were used with both moss samples and those from the lake sites providing the regional estimates. The former produced poor results with constant underestimation of *Pinus* in the output potentially related to the high local representation, which was more prevalent in the canopy cover derived estimates, and will not be considered further. The reconstructions obtained from the lake samples repeatedly provided comparable results to the observed and are discussed here.

The BA.Ran.1000.1 group reconstruction, shown in Table 6.6, gives the strongest correlation with the actual vegetation although the error margins are large and could impact upon this result; similarly, the canopy cover equivalent provides reasonable correspondence and had lower error margins although the basal area results produced a closer approximation to the observed vegetation proportions. In the remaining groups, not shown, the relationship between *Pinus* and *Calluna* is not accurately represented with the latter consistently overestimated, in some cases this is as much as ~55%.

BA.Ran.1000.1					CC. Ran.1000.1				
	Corrected Observed vegetation DW				Observed DW				
RSAP = 830m	coverage	S.E.	vegetation		RSAP =	coverage	S.E.	vegetation	
830111	(%)	(%)	(%)		310	(%)	(%)	(%)	
Pinus	80.8	43.6	99.2		Pinus	70.2	105.4	98.4	
Picea	0.0	1.0	0.0		Picea	0.0	2.2	0.0	
Larix	0.2	0.4	0.0		Larix	0.4	0.8	0.0	
Betula	0.0	8.6	0.0		Betula	0.0	11.3	0.0	
Calluna	19.0	11.6	0.8		Calluna	29.6	36.3	1.6	

BA.Sy.1000.1				CC.Sy.1000.1				
	Corrected vegetation		Observed DW		Corrected vegetation		Observed DW	
RSAP =	coverage	S.E.	vegetation	RSAP =	coverage	S.E.	vegetation	
530m	(%)	(%)	(%)	920	(%)	(%)	(%)	
Pinus	45.1	25.2	99.2	Pinus	46.3	23.6	98.2	
Picea	0.0	7.0	0.0	Picea	0.0	0.5	0.0	
Larix	0.2	0.5	0.0	Larix	0.3	0.5	0.0	
Betula	0.0	5.5	0.0	Betula	0.0	3.8	0.0	
Calluna	54.5	28.9	0.8	Calluna	53.6	29.9	1.8	

Table 6.6: Local vegetation reconstructions for Inshriach H1 forest hollow. The most comparable results are represented by BA.Ran.1000.1 and CC.Ran.1000.1. The weakest correlations are shown in BA.Sy.1000.1 and CC.Sy.1000.1. RSAP = Relevant source area of pollen radius in metres. DW = Distance weighted vegetation data using the Prentice-Sugita algorithm.

Calculated distances for the RSAP are PPE dependant and show no standardisation with distances ranging from 50 to 920 m and proved to show better correspondence when calculated by the model. Interestingly, within the canopy cover set the larger radii were obtained from the random PPE groups with the reverse true of the basal area set. This is represented in the dissimilarity between the RSAP for the groups shown in Table 6.6.

6.3.1.2 Lochan Geal

Results from Lochan Geal are poor in comparison to those highlighted from Inshriach H1. Reconstructions using both moss and lake samples to determine regional proportions are comparatively unsatisfactory yet it is the latter results that will be discussed below as these are marginally superior.

Despite BA.Ran.1000.1 being identified as the principle PPE group the results are considerably poorer than some of the other groups shown in Table 6.7. In some instances the values for *Pinus* are 0 with *Betula* as high as 92% which is almost the reverse of the actual vegetation patterns at the site. Variability between groups is evident in the *Picea* reconstructions with values ranging between 0 and 40% of total vegetation which substantially overestimate the actual coverage; *Larix* and *Calluna* are accurately modelled in all cases due to low actual presence. Table 6.7 contains the best vegetation coverage estimates from the CC.Sy.1000.1 and BA.Ran.500.1 groups which were chosen having the highest *Pinus* value although this remains a significant underestimation.

Inconsistency between the RSAP distances is again illustrated within different PPE groups. The randomly selected groups frequently provide the largest distances with the BA.Ran.1000.1 a distance of 1100 m. The lowest distance is 410 m from the BA.Sy.500.1 group. Estimates of the RSAP using the characteristic source area of pollen algorithm implies a distance of ~400 m to be suitable for this site which is close to the estimate provided by the CC.Sy.1000.1 group as shown in Table 6.7. However, when the RSAP was defined, at 400 m, the results showed no improvement from those calculated from the software.

	BA.Ran.	500.1.		CC.Sy.1000.1				
RSAP = 700m	Corrected vegetation coverage (%)	S.E. (%)	Observed DW vegetation (%)	RSAP = 620	Corrected vegetation coverage (%)	S.E. (%)	Observed DW vegetation (%)	
Pinus	6.1	11.6	62.4	Pinus	8.4	7.6	63.7	
Picea	14.6	3.5	0.0	Picea	11.7	2.7	1.5	
Larix	1.0	0.5	0.1	Larix	1.3	0.6	0.0	
Betula	78.7	7.8	34.8	Betula	78.4	6.8	32.9	
Calluna	0.0	10.9	2.7	Calluna	0.0	11.1	2.0	

	BA.Ran.1000.1			CC.Sy.500.1				
	Corrected vegetation		Observed DW		Corrected vegetation		Observed DW	
RSAP =	coverage	S.E.	vegetation	RSAP =	coverage	S.E.	vegetation	
1100m	(%)	(%)	(%)	630	(%)	(%)	(%)	
Pinus	0.0	24.3	61.5	Pinus	0.0	12.9	63.7	
Picea	10.4	3.2	0.0	Picea	8.1	4.0	1.5	
Larix	0.6	0.3	0.1	Larix	0.1	0.1	0.0	
Betula	89.0	21.5	34.8	Betula	91.7	78.7	32.7	
Calluna	0.0	5.4	3.7	Calluna	0.0	23.3	2.1	

Table 6.7: Local vegetation reconstructions for Lochan Geal. The most comparable results are represented by BA.Ran.500.1 and CC.Sy.1000.1. The weakest correlations are shown in BA.Ran.1000.1 and CC.Sy.500.1. RSAP = Relevant source area of pollen radius in metres. DW = Distance weighted vegetation data using the Prentice-Sugita algorithm.

6.3.2 Time slice 2 – 1989

Results below, and for the remaining time slices, describe the results of the LOVE model using lake samples only as the moss samples are unrepresentative of the regional environment for time slices other than the present day.

6.3.2.1 Inshriach H1 Forest Hollow

The BA.Ran.1000.1 group was considered one of the weakest overall with despite all PPE group estimates being comparable to the actual vegetation, potentially connected to the dominance of *Pinus*. Differentiation between the groups is determined by the error margins associated with the values. For both methodological PPE datasets the randomly selected groups have the larger error margins but this is greatly accentuated when the canopy cover dataset is considered in some cased being as large as 137% for *Pinus*. The best correspondence is achieved from the groups shown in Table 6.8. Although some groups provided stronger correlations between estimates the increase in the error margins, discussed above, supported this choice.

	CC.Sy.1	.000.1			CC.Sy.	500.1	
RSAP = 1140m	Corrected vegetation coverage (%)	S.E.	Observed DW vegetation (%)	RSAP = 1260m	Corrected vegetation coverage (%)	S.E.	Observed DW vegetation (%)
Pinus	98.8	19.6	99.1	Pinus	99.4	19.1	99.0
Picea	0.8	0.9	0.0	Picea	1.0	1.0	0.0
Larix	0.3	0.4	0.0	Larix	0.0	0.1	0.0
Betula	0.0	1.9	0.0	Betula	0.0	2.7	0.0
Calluna	0.0	19.7	0.9	Calluna	2.3	22.1	1.0

	BA.Ran.	1000.1			BA.Ran.	500.1	
RSAP = 1060m	Corrected vegetation coverage (%)	S.E.	Observed DW vegetation (%)	RSAP = 820m	Corrected vegetation coverage (%)	S.E.	Observed DW vegetation (%)
Pinus	99.1	72.1	98.0	Pinus	98.9	82.5	98.1
Picea	0.7	1.1	0.0	Picea	0.9	1.2	0.0
Larix	0.2	0.2	0.0	Larix	0.2	0.3	0.0
Betula	0.0	6.0	0.0	Betula	0.0	2.9	0.0
Calluna	0.0	11.5	1.9	Calluna	0.0	23.9	1.9

Table 6.8: Local vegetation reconstructions for time slice 2 at Inshriach H1 forest hollow. The most comparable results are represented by CC.Sy.1000.1 and CC.Sy.500.1. The weakest correlations are shown in BA.Ran.1000.1 and BA.Ran.500.1. RSAP = Relevant source area of pollen radius in metres. DW = Distance weighted vegetation data using the Prentice-Sugita model.

Generated RSAP distances had no recognisable controls underlying the variability irrespective of whether this was predefined or calculated by the model. Estimates were larger than the modern day ranging from 120 - 1260 m with the larger distances obtained from the better performing PPE groups i.e. systematically selected.

6.3.2.2 Lochan Geal

Improvements in the model are detected when compared with those from the modern time slice although the results remain discouraging. Firstly, a change in the *Pinus – Betula* relationship is evident with estimates for the former attaining 25% in the best PPEs, Table 6.9. Although one group simulated *Pinus* at 2% coverage most of the groups have increased *Pinus* percentages yet this is still below the actual value of ~75%. Secondly, *Calluna* is unsuccessfully modelled, in all groups this remains at 0 when the actual vegetation coverage for this taxon is ~6%. Finally, error estimations in some instances are large, more so in the randomly derived PPE estimates. Consideration of all results highlights CC.Sy.1000.1 and BA.Ran.500.1 as providing the most

comparable results to the actual vegetation patterns, especially for *Picea* and *Larix*, with the lowest error range. Interestingly, the BA.Ran.1000.1 output was too poor to be considered as one of the best performing groups.

RSAP distances are all high for this site with comparable estimates between the best performing PPEs. Distances range from 790 - 2620 m although the extremes of these ranges are not representative of the mean which is calculated as 1633 m. This is much greater than the 400 metres suggested by the characteristic source area radius with potential for vegetation patterns affecting this or changes in basin size.

'	CC.Sy.1000.1				BA.Ran.500.1				
RSAP = 1540m	Corrected vegetation coverage (%)	S.E. (%)	Observed DW vegetation (%)		RSAP = 1530m	Corrected vegetation coverage (%)	S.E. (%)	Observed DW vegetation (%)	
Pinus	24.6	6.3	76.0		Pinus	23.1	24.9	76.0	
Picea	8.1	2.6	12.5		Picea	10.0	4.1	12.5	
Larix	0.2	0.3	0.1		Larix	0.2	0.2	0.1	
Betula	67.1	7.7	4.6		Betula	66.7	31.5	4.6	
Calluna	0.0	13.2	6.9		Calluna	0.0	16.4	6.9	

	CC.Sy.500.1				BA.Sy.500.1				
RSAP = 1590m	Corrected vegetation coverage (%)	S.E. (%)	Observed DW vegetation (%)		RSAP = 790m	Corrected vegetation coverage (%)	S.E. (%)	Observed DW vegetation (%)	
Pinus	12.1	12.9	76.0		Pinus	2.6	17.8	75.7	
Picea	5.9	3.6	12.5		Picea	5.1	2.5	13.9	
Larix	0.0	0.0	0.1		Larix	1.8	3.2	0.1	
Betula	82.0	83.7	4.6		Betula	90.7	40.0	3.9	
Calluna	0.0	19.8	6.9		Calluna	0.0	44.8	6.4	

Table 6.9: Local vegetation reconstructions for time slice 2 at Lochan Geal. The most comparable results are represented by CC.Sy.1000.1 and BA.Ran.500.1. The weakest correlations are shown in CC.Sy.500.1 and BA.Sy.500.1. RSAP = Relevant source area of pollen radius in metres. DW = Distance weighted vegetation data using the Prentice-Sugita algorithm.

6.3.3 Time slice 3 – 1960

Again, reconstructions presented below are based upon regional estimates generated using pollen samples from lake sites. Also, observed vegetation proportions are stated as both vegetation and mature vegetation to account for some individuals present but not contributing to the pollen rain. In

this case the ages at which maturity was estimated is shown in Table 6.10 with sources used to arrive at this decision.

	Flowering age (years)				
Source	Pinus	Picea	Larix	Betula	
Carlisle and Brown (1968)	10 - 12	-	-	-	
Longman (1984)	-	-	-	5 - 15	
Wareing (1959)	5 - 10	20 - 25	10 - 15	5 - 10	
A. Fletcher (pers. Comm)	10 - 15	20	15	5	
Ages for study	10 - 15*	20	15	5	

Table 6.10: Flowering ages used to determine vegetation coverage contributing to the pollen rain. * Lodgepole Pine 10yrs was used and Scots Pine 15yrs used on the advice of A. Fletcher (*pers. Comm.*)

6.3.3.1 Inshriach H1 Forest Hollow

Age induced difference between the actual vegetation and the mature vegetation are present in the observed dataset. Interestingly, a wide range of values for the *Pinus* and *Calluna* values that dominate this vegetation are generated from the PPE parameter values whilst the remaining taxa show stability and a good level of correspondence potentially due to low occurrence. This distinction can be made in relation to the use of random or systematically derived PPEs. The former are defined by higher estimates of *Pinus* and larger error ranges for all taxa whilst the latter have larger *Calluna* estimates with low errors accompanying the values. Comparison of these simulated results with observed data accentuates this discrepancy with the random groups showing reasonable association with data inclusive of all vegetation whereas the systematic groups provide a strong correlation with the mature vegetation percentages only. Table 6.11 shows the best correspondences for these situations which imply a potential weakness with the random PPE groups including the BA.Ran.1000.1 dataset. In addition, to the poor mean estimates the error margins are large accounting for over 50% of the mean value.

Once again the range of RSAP is large with the smallest at 100 m and largest at 1690 m. However, it is the reconstructions with the smaller RSAP that have the poorest correlations with the actual datasets. This is especially true of the sites that compare to the mature vegetation only where no RSAP distance is below 1300 m.

	BA.Ran.500.1								
RSAP = 1000m	Corrected vegetation coverage (%)	S.E. (%)	Observed DW vegetation (%)	Observed Mature vegetation (%)					
Pinus	44.9	31.4	88.6	16.4					
Picea	0.7	0.9	0.1	0.6					
Larix	0.5	0.5	0.1	0.6					
Betula	0.0	2.6	0.0	0.0					
Calluna	54.0	43.3	11.2	82.3					

	BA.Ran.1000.1								
RSAP = 950m	Corrected vegetation coverage (%)	S.E. (%)	Observed DW vegetation (%)	Observed Mature vegetation (%)					
Pinus	73.5	46.8	88.8	15.1					
Picea	0.9	1.1	0.1	0.5					
Larix	0.5	0.4	0.1	0.6					
Betula	0.0	7.2	0.0	0.0					
Calluna	25.1	23.8	11.1	83.8					

	CC.Sy.1000.1								
RSAP = 1690m	Corrected vegetation coverage (%)	S.E. (%)	Observed DW vegetation (%)	Observed Mature vegetation (%)					
Pinus	33.4	8.9	90.4	10.9					
Picea	0.5	0.5	0.0	0.4					
Larix	0.5	0.4	0.0	0.0					
Betula	0.0	1.6	0.0	0.4					
Calluna	65.2	27.5	9.5	88.3					

	BA.Sy.1000.1								
RSAP = 1360m	Corrected vegetation coverage (%)	S.E. (%)	Observed DW vegetation (%)	Observed Mature vegetation (%)					
Pinus	30.7	11.6	90.5	10.2					
Picea	1.9	2.9	0.0	0.4					
Larix	0.5	0.4	0.0	0.0					
Betula	0.0	2.2	0.0	0.4					
Calluna	67.0	26.3	9.4	89.0					

Table 6.11: Reconstructed vegetation coverage for Inshriach H1 forest hollow for 1960. The results represent those that are comparable to the mature vegetation and those all observed vegetation (see text for further details). DW = Distance weighted

6.3.3.2 Lochan Geal

Application of the LOVE model fails to produce comparable results to the actual vegetation patterns at Lochan Geal. However, PPEs used have similar outputs in both magnitude and relationships, for example underestimation of *Pinus* and overestimation of *Betula*. Interestingly, all groups also failed to accurately represent *Calluna* in the reconstructions with estimates of 0. When the mature vegetation is assessed this taxon comprises 15% – 20% of the total vegetation coverage but much lower when all vegetation is calculated. Difficulty arises in determination of the best results from this site. If all vegetation is considered BA.Sy.1000.1 has the most accurate reconstruction for *Picea* with small error margins yet CC.Ran.1000.1 and BA.Ran.500.1 provide the best *Pinus-Betula* relationship. If only mature vegetation is included the two latter groups again present very accurate results with the addition of CC.Ran.500.1 as shown in Table 6.12. Again, BA.Ran.1000.1 is not identified as one of the better performers from the groups tested.

Radii for the relevant source area of pollen differ between the groups. Most calculate a large radius for the basin with estimates between 670 - 1030 m with an uncharacteristic result of 340 m from the CC.Ran.1000.1 group. There is no correlation between this distance and the better performing groups as previously identified.

	CC.Ran.1000.1								
	Corrected			Observed					
RSAP =	vegetation	S.E.	Observed DW	Mature					
340m	coverage (%)	(%)	vegetation (%)	vegetation (%)					
Pinus	7.7	21.1	60.5	0.0					
Picea	2.9	1.9	18.2	0.0					
Larix	0.0	0.3	0.6	0.0					
Betula	89.4	36.6	20.7	100.0					
Calluna	0.0	19.1	0.0	0.0					

BA.Ran.500.1							
RSAP = 1030m	Corrected vegetation coverage (%)	S.E. (%)	Observed DW vegetation (%)	Observed Mature vegetation (%)			
Pinus	13.5	14.5	68.0	23.1			
Picea	3.4	1.9	13.4	0.0			
Larix	0.0	0.0	0.4	0.0			
Betula	83.1	35.2	13.4	56.9			
Calluna	0.0	18.7	4.7	20.0			

BA.SY.1000.1							
RSAP = 850m	Corrected vegetation coverage (%)	S.E. (%)	Observed DW vegetation (%)	Observed Mature vegetation (%)			
Pinus	1.7	3.8	67.7	16			
Picea	12.2	6.5	14.0	0.0			
Larix	0.0	0.0	0.4	0.0			
Betula	86.1	70.0	13.6	63.8			
Calluna	0.0	10.5	4.3	20.2			

CC.Ran.500.1								
Corrected Observed								
RSAP =	vegetation	S.E.	Observed DW	Mature				
670m	coverage (%)	(%)	vegetation (%)	vegetation (%)				
Pinus	14.1	30.3	67.6	9.0				
Picea	3.5	2.3	14.7	0.0				
Larix	0.0	0.0	0.5	0.0				
Betula	82.4	60.1	14.4	75.6				
Calluna	0.0	31.3	2.9	15.4				

Table 6.12: Reconstructed vegetation coverage Lochan Geal for time slice 3 (1960). The results represent those that are comparable to the mature vegetation and those all observed vegetation (see text for further details). DW = Distance weighted vegetation using the Prentice-Sugita algorithm. RSAP = Relevant source area of pollen estimate in metres from the edge of the sampling basin.

6.3.4 Time slice 4 – 1950

As with previous results these are represented from regional estimates from lake samples. Reconstructions from Lochan Geal were obtained from the use of two contiguous samples spanning the sampling data as no one sample could be deemed representative. Tests were undertaken to determine differences between results from this and those using single samples with none discovered for the main calculations with difference only inherent in the error margins.

6.3.4.1 Inshriach H1 Forest Hollow

Distinctive from the previous horizon is the significant increase in estimated and observed *Calluna* percentages. Reconstructions from the pollen assemblage fail to accurately represent this change although results of BA.Ran.500.1 produce a reasonable attempt shown in Table 6.13. Again, BA.Ran.1000.1 is considered the poorest reconstruction due to overestimation of *Pinus*. Of the results not shown estimates for *Calluna* coverage ranged between 48 - 76% with most values positioned around the higher end of this range. Simultaneous fluctuations in *Pinus* have a range between 23% - 51% much inflated on the 0 estimate from the actual data. Large error ranges are also associated with these results consistent with those of previous time slices.

	BA.Ran.	500.1		
	Corrected		Observed	
	vegetation		DW	
RSAP =	coverage	S.E.	vegetation	F
540m	(%)	(%)	(%)	
Pinus	36.7	27.7	0.2	F
Picea	0.7	0.8	0.0	F
Larix	0.0	0.3	0.0	L
Betula	0.0	2.1	0.0	Е
Calluna	62.6	46.8	99.8	(

BA.Ran.1000.1							
	Corrected vegetation		Observed DW				
$\begin{array}{c} RSAP = \\ 440m \end{array}$	vegetation (%)						
Pinus	74.5	41.0	0.0				
Picea	1.0	1.0	0.0				
Larix	0.0	0.5	0.0				
Betula	0.0	4.0	0.0				
Calluna	24.5	28.1	100.0				

Table 6.13: Vegetation reconstructions showing the highest (BA.Ran.500.1) and weakest (BA.Ran.1000.1) correlation to the observed vegetation data at Inshriach H1. DW = Distance weighted vegetation data using the Prentice-Sugita algorithm. RSAP is radius of the relevant source area of pollen in metres from the basin edge.

Estimates of relevant source area seem small given the estimated openness of the landscape with a range from 170 - 750 m. The distance for the BA.Ran.500.1 dataset is 540 m, which is slightly larger than estimates when closed woodland dominated the landscape.

6.3.4.2 Lochan Geal

The relationship between *Pinus* and *Betula* is again unsuccessfully represented by the reconstructions. In some instances the estimates for *Betula* are ~90% of vegetation coverage which, when compared, with the actual vegetation in terms of total and mature individuals is unrealistic. As previously identified, the *Calluna* component of the vegetation is acutely underestimated by the model. Table 6.14 shows the results from CC.Sy.1000.1 and BA.Ran.500.1 which represent the strongest and poorest reconstructions respectively.

CC.SY.1000.1						
	Corrected			Observed		
RSAP = 880	vegetation coverage (%)	S.E. (%)	Observed DW vegetation (%)	Mature vegetation (%)		
Pinus	12.9	3.8	70.2	66.3		
Picea	2.8	1.4	11.9	1.5		
Larix	0.0	0.0	0.4	0.1		
Betula	84.4	8.3	1.3	2.2		
Calluna	0.0	14.9	16.3	27.7		

BA.Ran.500.1							
Corrected Observed							
RSAP =	vegetation	S.E.	Observed DW	Mature			
1030	coverage (%)	(%)	vegetation (%)	vegetation (%)			
Pinus	12.7	14.9	80.7	83.1			
Picea	3.4	1.9	13.2	2.4			
Larix	0.0	0.0	0.1	0.2			
Betula	83.8	36.5	4.6	10.8			
Calluna	0.0	19.0	1.4	3.4			

Table 6.14: Vegetation reconstructions showing the highest (CC.Sy.1000.1) and weakest (BA.Ram.500.1) correlation to the observed vegetation data at Lochan Geal. DW = Distance weighted

The lowest calculated distance for RSAP is 820 m with the largest extended to 1320 m yet most estimates are concentrated in the lower end of this range showing some consistency between groups.

6.4 Summary and discussion

Estimates of regional cover, $\sim 100 \text{ km}^2$ area around the deposition site, show an increase in woodland since the 1950s in the landscape which reflects the known woodland history. Intensive felling during the 1940s, accounting for the high simulated *Calluna* values, was followed by a large planting scheme implemented by the Forestry Commission at the start of the 1950s (Dunlop, 1997).

In total the woodland areas of Scotland increased from 6% in 1960 to 16% by 2000 (Foot, 2002). Land use was a combination of owned land, previously planted and subsequently felled, and newly acquired old growth woodland and heathland areas (Foot, 2002). Initially, pollen contribution from this new planting would be low until maturity was reached accounting for the much higher woodland values in the 1989 (19 years) and contemporary estimates (47 years). Planting was initially comprised of so-called 'exotic' species i.e. Sitka spruce, European larch but also a high proportion of Scots pine (Foot, 2002). Figures from the National Inventory of Woodland and Trees (Smith and Gilbert, 2001) highlight increased planting of these taxa with peaks between 1960 and Interestingly, Sitka Spruce and Lodgepole Pine show the greatest increase with both European and Japanese Larch only minor constituents in comparison. Dunlop (1994) states that, during a survey between 1979 - 1982, non-indigenous conifers occupied 27% of woodland area (~5300 ha) within the Strathspey region, with Scots pine occupying 70% (~14000 ha) in response to the planting regimes. This information correlates to increases identified in the REVEALS reconstructions for the 1950s to the present day with the greatest changes evident between the 1960s and the contemporary landscape. However, the fluctuations in the *Larix* reconstructions do not correspond to variations in planting potentially because this has been minimal over this period comprising at most 1% of stock planted per age class (10 year span) and only 3% of total woodland within the Highland region since 1950 (Smith and Gilbert, 2001) which is too low to be detected within the regional pollen record when the rain encompasses ~100km² around Inshriach. Although this could suggest errors within the PPEs or model it must also be acknowledged that it is a reflection of regional data and therefore the spatial scale of the pollen and reconstructions may not be sufficient to sense these patterns. A similar situation is evident for Betula with little change in overall planting yet increases in the reconstruction level suggestive of natural regeneration.

Simulations from the LOVE model were variable in terms of the estimated RSAP at each time slice and the correspondence to observed vegetation. Details of the recent vegetation change at Lochan Geal and Inshriach H1 cannot be confidently outlined due to this variability. Further discussion of these results is presented in section 6.4.2.

6.4.1 Performance of the REVEALS model

Reconstructions of the regional vegetation composition are highly promising using the REVEALS model. Simulations of the present and 1989 horizons produced highly comparable results to the actual vegetation patterns which allow confidence in the results for the remaining time slices for which observed vegetation data was unavailable. Furthermore the identification of BA.Ran.1000.1 providing the most representative estimates from both time slices 1 and 2 is encouraging. Similar validation studies have been undertaken in southern Sweden using samples from numerous large

lakes greater than 100 ha (Sugita, 2007b; Hellman et al., 2007; Hellman et al., 2008). Given the limited number of taxa used within this study the results of Hellman et al. (2008) suggest potential improvement with additional taxa when appropriate PPEs are available. Reduction of error margins in the Inshriach results is achievable by inclusion of additional lakes as in some cases the large error margins can conceal any variability between PPE groups and sites. Hellman et al. (2008) investigated effects on sampling design on the output of the models finding that fewer sites produced the same mean vegetation output and reduced error margins were achievable by inclusion of more sites or increased samples from fewer sites. Sugita (2007b) also showed this pattern but in relation to basin size. When smaller sites were used the error margins increased but vegetation coverage estimates were the same as larger sites. Unfortunately, ability to achieve these optimum criteria for the model is dependant upon the study region and any within lake processes. For example, a number of deposition basins within Inshriach were discounted due to previous human actions and tests carried out using numerous cores from Loch an Eilein failed given poor sediment accumulation at the coring sites. Inevitably, these points raise concern as to the ability of only two sites to present a robust portrayal of the regional landscape. Furthermore, the sites used were on the lower limits of the large lake size identified by Sugita (1994) which will incorporate some site specific variability. Additional samples would enable more general patters to be distinguished and potentially alter the output of the model. This could be challenging in some areas but with sufficient validation it appears that a low number of sites can produce representative reconstructions.

Decisions over the area used for comparison with observed vegetation data which were raised in Chapter 4, are still significant here and this questions the best PPEs and results from the model. Although use of the characteristic source area distance for the taxa support the decision to use 100km^2 this is an approximation based upon vegetation homogeneity and can be subjected to errors due to the site specific pollen transportation mechanisms. This relates to the strength and dominance of the prevailing wind, vegetation height and patterning and topographic variation which are not considered within the generic model and therefore could influence this result. Furthermore, processing methods used including classification of aerial images, digitising and community composition assignment in the observed data should be acknowledged as error sources with potentially significant influence

6.4.1.1 Sources of error

Two regional datasets were available to provide comparison data, Land Cover Map 2000 and Land Cover of Scotland 1988, which were both constructed from the classification of aerial photographs. As mentioned in Chapter 3, there are many errors associated with this technique which have to be

assessed when the resultant database is used. With respect to this project any errors can affect judgement of the most representative results which, in this case, can impact on subsequent modelling if PPEs are chosen on this basis. Both databases have errors associated with them which can have potential implications for the modelling results.

Firstly, the LCM 2000 is a vector dataset constructed from the classification of aerial photographs from 1998/1999 for the whole of the UK. Thematic Mapper images from summer and winter were combined for each region to ensure coverage that would provide maximum discrimination between 20 predefined broad habitat communities (Fuller *et al.*, 2002). However, only 46% of all data was obtained from target sources – those that provided clear images and the best spectral definition – requiring some pre-processing of images to remove cloud cover (Fuller *et al.*, 2005). Quality of the images to be classified is a key source of error in the final database but no further details are given in the report as to the areas that have this potential error source and therefore full account of this cannot be taken. An area that is more relevant is from the classification process and the assignment of pixels to the broad habitats. Comparison of the LCM 2000 data with field surveys undertaken for the Countryside Survey 2000 (Barr *et al.*, 2003) provided a source of evaluation although Fuller et al (2002) stress that the results of the comparison are not an accuracy assessment. For Scotland this process found only 47% comparability with the field survey when the Broad Habitats were used; sources of this difference are due to a number of factors suggested by Fuller *et al.* (2002):

- Minimum mappable unit (MMU) was 0.5 hectares in the LCM 2000 but 0.04 hectares in the field data
- Bog had the largest misclassification due to poor distinction from open and dense dwarf shrub
- Boundary placement for semi-natural communities was difficult to achieve in both the LCM 2000 and field survey.
- Montane habitats were defined by altitude (>600m) which overestimated this community when compared with field data

As Fuller *et al.* (2005) suggest the broad habitats were defined for vegetation analysis rather than mapping which induces a large proportion of this error as distinction of these groups are not discernible on images. Furthermore, with the MMU being 0.5 ha any woodland stands or openings in woodland are combined into the surrounding area. Consequently, this will induce errors into the area calculations used for the comparison data with the main impact in the dwarf heath proportions. Subsequent community composition assignment distinguishes these groups by *Calluna* proportions and therefore overestimation of this taxon may occur through false representation of bog by dwarf

heath which has a *Calluna* value 20% greater. Finally, deciduous woodland areas showed high proportions of misclassification with designation primarily as coniferous woodland with others dwarf heath. The latter is a response to the high amounts of grass within the heathland communities which gives a very similar spectral signature to that of the *Betula* stands. Again, this will underestimate the amount of *Betula* within the comparison data but also increase *Pinus* and *Calluna* estimates.

Data from the Land Cover for Scotland 1988 (The Macaulay Institute, 1988) map has similar errors associated with it with regards to the classification procedure:

- Ground area is underestimated in areas of high relief as limited geo-rectification was carried out on the aerial photographs prior to classification.
- Misclassification of natural ground vegetation classes is large at 14.7% although data as to which class this is assigned is not given.
- Mixed woodland shows high errors (due to false assignment of pixels to the correct group via commission and omission) of 14.7% with both coniferous and deciduous forms
- Positional and feature error equates to 39.56 m although this is site specific as it is related to the boundary placement of features which is less well defined within highland locations.

The effects of these errors are less easy to determine in terms of impact on the vegetation data used for the comparison information than the LCM 2000. Misclassification would have the greatest effect although the confusion matrix (outlining the omission and commission data for each class) was not available and therefore determination of actual classes assigned inhibits estimation. However, the most important features are those errors associated with topography and position of features. When these data are used to represent regional vegetation coverage the degree of topographical variation will significantly impact upon the correct estimation of the Montane community coverage. Conversely, at the local scale when this information is used to supplement the Forestry Commission data the positional and feature error will become more significant as the topographical variation is limited. Interpretation errors are given by the database constructors relating to four levels and gives correspondence between mosaic composition of the producer and validator (The Macaulay Institute, 1988). Errors range from 4% for level 1 to 25.3% for level 4 with the authors suggesting that the best error estimates are levels 2 or 3, 13.3% and 19.5% respectively, between the two extremes. However, application of error levels to different portions of the dataset is problematic which hinders utilisation of the information.

In addition to errors encountered from the construction of the vegetation cover datasets are those from formulation of community composition. As mentioned in section 4.5.3 in relation to the Humpol maps the definition of the communities creates difficulty in accurate species composition. Table 6.15 shows the community groups from the two regional databases and their association in species composition, reflecting the generalisations that are made with respect to the community determination and composition. As previously suggested finer distinctions of the vegetation are not possible using spectral analysis without using hyperspectral images and necessitate simplification and will inevitably induce error into the calculations. Those areas identified will also show local variation in their floristic composition not recognised within the general application of community composition data. However, the low taxon diversity in the modelling will moderate this as only major taxa have been used, had it been that minor components of the vegetation were included the effects of this would have been greater.

LCS 88	LCM 2000	NVC Classification
Blanket bog/ peat vegetation	Bog	M19 (Calluna vulgaris – Eriophorum vaginatum blanket mire): 41% Calluna, 24%
Undiff. Heather moor	Open dwarf heath	Erica, 23% Poaceae H12 (Calluna vulgaris – Vaccinium myrtillus heath): 61% Calluna, 15% Vaccinium, 7% Erica
Dry heather	Dense dwarf heath	H12 (Calluna vulgaris – Vaccinium myrtillus heath): 61% Calluna, 15% Vaccinium, 7% Erica
Wet heather	_	H16 (Calluna vulgaris – Arctostaphylos uva- ursi heath): 61% Calluna, 15% Vaccinium, 7% Erica
Montane	Montane	H12 (Calluna vulgaris – Vaccinium myrtillus heath): 61% Calluna, 15% Vaccinium, 7% Erica
Undiff. Broadleaved woodland	Deciduous woodland	20% Betula/50% Betula
Undiff. Mixed woodland	Mixed woodland	40% Pinus; 40% Betula
Coniferous plantation	Conifers	92% Pinus; 2% Betula; 2% Larix; 3% Picea *
Coniferous semi-natural	_	75% Pinus
Open canopy (young)	New plantation	10% Pinus
Arable	Arable	100% Cerealia
Grass	Grass	100% Poaceae

Table 6.15: Representation of regional vegetation groups by the NVC classification system. Where vegetation percentages are given field data was used. * signifies data obtained from the Forestry Commission records for Inshriach.

6.4.1.2 Composition of community groups

Table 6.15 shows the correspondence between community groups of the LCM 2000 and LCS88 with the NVC categories or species percentages used to represent these. Inevitably, the detail of the NVC classifications cannot be included within the community groups, as outlined above, which will be the main factor affecting the calculation of vegetation proportions. For example, the heathland distinctions of the two regional datasets are not included and are represented by a combination of two NVC classifications and field observations. Amalgamation of these was employed to reduce the effects of misclassifications during the construction of the datasets, mentioned above, with errors inherent from over- or under estimation of the main constituents counteracted. This does however increase the simplification of the landscape and the proportions of *Calluna*, being a main constituent of this class, will be the main taxon affected.

Estimation of the arboreal communities was inherently more complex as true combinations of taxa, predominantly relating to the mixed woodlands, are difficult to accurately establish. Section 3.1.4 outlines the criteria for the determination of community structure for these groups and the rationale for this, but issues relating to simplification of the landscape once again are important. Mixed woodlands, by their definition, have a number of constituents with varying degrees of presence determined by life strategy and environmental factors i.e. soils, water, light and nutrient availability. The taxa to be most affected by this are *Pinus* and *Betula*, which were deemed components of the mixed woodlands but also the latter as a constituent of the broadleaf/ deciduous woodland. It is envisaged that the errors associated with the latter groups will be the most significant in affecting the results of the comparison data as the mixed woodland was not present in large quantities and at the extremes of the 100km² area; therefore, *Betula* will have the greatest errors.

With respect to the comparison data for the results of the LOVE model the errors will be site specific. Inshriach H1 will be affected by the heathland approximations as this community dominates the wider landscape surrounding the site. Lochan Geal will be affected by both the arboreal and heathland errors as there are large stands of woodland and areas of heathland within a predominantly grassland landscape. These errors will be more significant for Lochan Geal and could be a potential contributor to the poor results gained from this site. However, it must be stressed that the primary data used for these comparisons were obtained from the Forestry Commission data and only when the RSAP was larger than the extent of the woodland (Lochan Geal: 600 m, Inshriach H1: 600 m) were these sets used with a significantly lower weighting applied. Error margins are not presented for these datasets as determination of this would be unreliable given the complexity of factors involved. Variations between potential community constituents would be a large undertaking and the cut-off values for the composition would be hard

to establish and ultimately create large errors margins that would render the data unusable. A compromise for any future work would be to weight the different combinations in likelihood of occurrence using additional landscape features which could give lower errors and perhaps a better representation of the vegetation patterns.

6.4.2 Performance of the LOVE model

A striking distinction can be made between the results from the two deposition basins using the LOVE model. In addition, links can be made between model performance associated with the time slice being reconstructed, PPEs and species included. Reconstructions from Inshriach H1 were very strong overall with vegetation changes reasonably well matched by model results. On the contrary results from Lochan Geal were poor regardless of the PPEs used or time slices. The difference in depositional environment between the two sites clearly affects pollen accumulation.

6.4.2.1 Inshriach H1 forest hollow

Reconstructions are reasonable for time slices 1 and 2, but subsequent results are poor in comparison despite the simplified landscape components. A distinction can be made between these two groups: during time slices 1 and 2 the landscape around the deposition basin was high density, closed woodland; for time slices 3 and 4 the landscape was open heathland. However, in 1960 this area was ploughed and planted with Scots pine and Lodgepole pine woodland. Interestingly, the model fails to identify this from the pollen record. Furthermore, the model identified the presence of mature vegetation but does not distinguish changes in stem density. The greatest density would have occurred around time slice 2 (1989) after which thinning was employed to remove the poorer performing individuals. A number of influences could be contributing to these results:

1 - Modelling is not applicable to open landscapes

Changes in vegetation structure are clear between open and enclosed landscapes and transitions have been accurately modelled using previous algorithms (Mazier *et al.*, 2008; Poska *et al*, 2008). Similarly, validation of the REVEALS model has shown that it can recognise changes in vegetation landscapes between open and semi-closed conditions. Sugita (2007c) used hypothetical landscapes to simulate landscape openness with the LOVE model producing accurate results as percentages of open areas (represented by Poaceae) varied from 33%, 60% and 88% of the total landscape. However, little empirical work using the LOVE model has been undertaken to address changes in landscape characterisation. In such situations the input data is far from perfect and 'real' landscapes differ significantly from hypothetical ones. For example, in hypothetical situations vegetation height is treated as uniform which is not the case in reality. At Inshriach H1 changes from a landscape dominated by tall arboreal vegetation to heathland of only ~50cm in height could have a

significant influence on the pollen dispersal and deposition properties such as changes in wind speed. At a regional level this may not be significant as modelling studies show good approximations (Hellman *et. al.*, 2007; Soepboer *et. al.*, 2010); however at small spatial scales this effect could have a greater control over deposition patterns that are currently unaccounted for. Previous studies dismissed the use of theoretical dispersal algorithms representing high release point sources in favour of ground source release as the former were unrepresentative of empirical work as vegetation coverage is an amalgamation of numerous point sources which mutes some of the patterns identified (Turner, 1964; Kabailiene, 1969; Janssen, 1972; Tinsley and Smith, 1974; Raynor *et al.*, 1975; Caseldine, 1981). However, as the LOVE model deals with a much smaller spatial scale these characteristics could have a greater influence. For example, if pollen of the same size and shape is released in similar atmospheric conditions but from different source heights the time taken and distance at which the grains are deposited will differ. There will be further effects from changes in wind velocity and obstacles will interfere with the theoretical deposition properties (Gregory, 1973). This is something that requires further investigation to determine whether they do have any significance (Jackson and Lyford, 1999).

2 - PPEs not representative of the environment

Under estimation of *Calluna* and over estimation of *Pinus* could imply that the PPEs used are too high for the open woodland reconstructions. Interestingly, the flowering intensity of Calluna is reduced in woodland environments (Gimmingham, 1960) where most PPEs sites where situated which, if this was the case, would see Calluna overestimated within the modelling of the open environment. Secondly, Calluna shows a cyclical pattern of growth and maturity, a mixture of which typifies mature heathland (Barclay-Estrup and Gimmingham, 1969). Associated with the different stages of development are degrees of flowering; the early and degenerate phases (oldest) have the lowest or no flowering whilst the building and mature phases have the greatest density of individuals and thus most flowering (Barclay-Estrup and Gimmingham, 1969). Thus, if most sites in open areas were dominated by building or older growth heather the PPEs would be over estimated and subsequently under estimate the taxon in any vegetation reconstructions. mentioned in section 4.5.2.3, this can impact on the PPEs obtained from the sites but also potentially affect the applicability of the estimates to other landscapes which differ in heathland composition. This further requires the temporal resolution to be addressed as this will control the degree to which this feature could be detected within the pollen assemblage. For example, a moss sample with only 1-2 years growth would be more likely to reflect this than a sediment sample covering 10 years deposition. The flowering of *Pinus* is more complex as the advantage given to managed woodland individuals could increase productivity (as poorer performing individuals are removed to allow advantages to stronger stems) yet older individuals with abundant light availability, so called granny pines, also see increased productivity (Steven and Carlisle, 1959). Errors linked to PPE calculation discussed in Chapter 4 appear significant here as the implications of this are that between group variations induced from parameter changes are large. Consequently, error from the PPEs appears to be inbuilt rather than a function of the vegetation composition around Inshriach H1; this will be discussed further in Chapter 7.

3 - Regional vegetation data not representative

The dataset used to represent the regional landscape for time slices 3 and 4 was the LCS 88 as this was the oldest large scale data available. Inevitably, the difference between this dataset and that which the time slices cover will incorporate error as this was a period of intensive planting and management in the region (Dunlop, 1994). During this time older, native stands of Scots pine were removed to allow planting of 'exotic' taxa seen in the present woodland in both Inshriach and Glenmore (Dunlop, 1997). Although the scale of planting in relation to the comparison area (100km²) or locally ~2km² is small the changes are significant enough to be recorded within the pollen record affecting the representativeness of the comparison data. A further source of error, and potentially more important, is derived from the threshold for woodland identification set at 2 hectares for inclusion as a parcel (The Macaulay Institute, 1988). Although presence of individuals was noted in the community classification determination, the actual area occupied by this was difficult to establish and site specific. Furthermore, as these occurrences were predominantly within open heath context any misclassification would increase the proportions of Calluna estimated from the landscape. This is most significant at Inshriach H1 hollow as the area is dominated by heathland with mature stands of Scots pine that has never been under a management regime. If these areas are adjacent to the site of deposition they would be sufficient to change the results of the modelling considerably as the deposition bog (Inshriach H1) behaves as a point source and therefore is greatly influenced by vegetation immediately surrounding the site (Birks and Birks, 1980; Sugita, 1993).

4 - Maturity ages not accurate enough

Correction of the available vegetation data was necessary in order that this accurately represented the vegetation contributing to the pollen rain. A number of sources were consulted to provide a general age class for the maturity of the main species included within the woodland which is shown in Table 6.10 pp. 256. However, this generalises a species and individually determined age which has a number of characteristics, both in terms of growth and environment, influencing commencement of this process (Wareing, 1959). In addition, delineating the start of this process is inevitably challenging, especially given the number of individuals within the woodland and different conditions prevailing. For example, individuals planted in 1960 would be included

whereas those in 1961 would not despite being of similar age with the potential to flower. Furthermore, individuals are 1-2 years old when planted after being raised in nurseries which will incorporate additional error. The consequence of this is inaccuracy in the proportions of vegetation included in the comparison data and thus false interpretation of the results. Yet, because this is a very difficult time frame to accurately represent, errors are unavoidable but have been kept at a minimum.

In summary, the changing landscape patterns at Inshriach H1 that were modelled show a split between closed and open landscapes. The greatest potential for the poor correlation of the simulated and actual results lies with the comparison data both in terms of the maturity level and the regional datasets. Quantification of these error sources is difficult but the latter would potentially have the greatest influence on the results. As most previous model results successfully detect an opening of the landscape it suggests that the errors from the model are minimal in this case, but more so from the PPEs.

6.4.2.2 Lochan Geal

In contrast, the consistently poor simulations obtained from Lochan Geal are interesting. Potential explanations for these results are:

1. Model is not representative

This explanation has to be considered as there are limited empirical results available to suggest that the LOVE model works within different environments and further tests are required to identify any potential faults. However, both the results from the Inshriach H1 forest hollow and the large lakes suggest that this may not be the case. Algorithms used in the two models are essentially the same and have been used within earlier modelling software which were validated for use within numerous environments (Nielsen, 2004; Nielsen and Odgaard, 2005; Von Stedingk and Fyfe, 2009; Hellman *et al.*, 2007). Furthermore, the model was specifically designed for use with lake sites and therefore should be representative.

2. Differential sedimentation and mixing

Transport of pollen and basin size are two of the major controls on the assemblage composition obtained from sites and are issues that have been addressed in detail in previous chapters. Due to the small surface area of Lochan Geal (4.5 ha) it is dominated by the local pollen rain which permits its use for the local modelling of this study, however, this aspect of the lake in addition to its location could also be having a detrimental affect on the results. Around 33% of the margin of the lake supports a fringe of natural birch whilst the reminder is planted pine woodland which occupies

steep slopes around the basin on the western, northern and eastern sides. Inevitably, a large proportion of the pollen released will be directly deposited onto the surface of the basin as noted elsewhere (Berglund, 1973). This was identified in surface samples taken from Lochan Geal although the differentiation between the two zones was not strong enough to alter the modelling appreciably and replicate the patterns observed from use of the core samples within the model. However, there are two scenarios that could affect this deposition: firstly, the prevailing wind is from a westerly direction, Figure 5.17, which would carry the regional pollen rain but also incorporate pollen from the Scots pine immediately surrounding the basin. However, as Lochan Geal occupies a small depression some of the pine woodland will be protected from this wind and the pollen from exposed vegetation will be combined into the regional pollen rain. The second scenario is associated with an alternative wind direction, easterly, which has been suggested by Steven and Carlisle (1959) as occurring more commonly during pollen release. If this is the case, the wind would transport more Betula pollen onto the surface of the lake, also bringing Poaceae and Pinus from the surrounding woodland. However, the pollen from the woodland occupying the margins of Lochan Geal would be carried away from the site and therefore not contribute to the assemblage.

3. Differential pollen release

Investigations into pollen deposition within lacustrine situations have identified processes that mix pollen deposited on the surface of the lake prior to being deposited on the basin floor (Davis, 1968). Thus, multiple assemblages obtained from different areas in the lake should, theoretically, produce the same pollen composition when sampled, but this is not always the case. A number of processes can occur within the lake to distort this which are dependant on site specific factors. Davis and Brubaker (1973) initially identified impacts of circulation within lakes upon the pollen profiles. The authors assessed pollen profiles and monitored Ambrosia and Quercus pollen input to a small basin, Frains Lake with an area of 6.7 ha, and identified differential sedimentation associated with the flowering time in accordance with the overturning of the lake. Quercus was the earliest species to flower and deposited evenly over the basin whilst Ambrosia, flowering 3 months later, was concentrated within the littoral regions of the lake as sinking was prohibited by both the buoyancy of the grain and the stratification of the lake. As sediments are then redistributed during autumn overturning the Ambrosia laden littoral sediments are moved to the deeper portions of the lake distorting the actual relationship between these two taxa. Davis and Brubaker (1973) supported this by measurements of pollen proportions within the redistributed sediments which suggest that the Ambrosia values are increased by a factor of 11 whilst the Quercus proportions only 25%. Kabaleine (1969) noted similar processes and suggested the behaviour of *Betula* as being similar to Ambrosia at Frains lake. This was later supported by Brush and Brush (1972) who conducted tests on the buoyancy of grains and noted swelling of *Betula* which increased suspension on the lake surface. However, these tests where not carried out in conjunction with *Pinus* which, due to its saccate form, remains buoyant for considerable periods of time (Pohl, 1933). Two recent studies that have assessed the relationship between *Pinus* and *Betula* produced differing results. Firstly, Punning et al (2003) placed traps in a small lake in Estonia and identified that only *Pinus* was affected by re-suspension and only at negligible levels. However, the stratification of the lake did slow the settling velocity. In contrast, Kangur (2009) analysed sediment cores from a short transect from the edge to the centre of small basin and found that lake level increase reduced accumulation of *Betula* at the margins whilst the centre of the basin experienced the reverse. He concluded that an increase in lake depth through time increased the energy during overturning and enabled a greater amount of sediment to be redistributed. This conclusion of Kangur (2009) could represent the patterns reflected at Lochan Geal implying that *Betula* is re-suspended during overturning before *Pinus* is flowering and its pollen deposited on the lake surface. Such a process also has the potential to vary through time which increases complexity for the interpretation of pollen profiles, whether used in simulations or not.

4. Within lake processes

The term 'sediment focusing' was first used by Likens and Davis (1975) to describe the movement of sediment from the shallow regions of a lake to the deepest area. Since this paper a number of studies have been conducted to improve understanding of this phenomenon. There are three principal features which impact on the degree of sediment redistribution:

- i. Lake morphology: Lehman (1975) investigated morphological controls on patterns of sedimentation and found that as the basin filled, for some shapes, the changing shape of the basin affected the sedimentation. Davis and Ford (1982) corroborated this with empirical evidence from Mirror Lake with the additional finding that the sediment redistribution is transgressive and dependant upon morphology and water depth.
- ii. Water depth: shallow lakes are more susceptible to wind disturbance and have limited stratification. A number of studies have shown that deeper lakes, especially when stratification occurs, show uniform sedimentation (Pennington, 1974; Beaudoin and Reasoner, 1992; Mieszczankin and Noryskiewicz, 2000). Furthermore, the ratio between margins and lake area also appear significant as an increase in the littoral region increases susceptibility to movement which will be proportionally greater in lakes that have a higher ratio (Beaudoin and Reasoner, 1992).
- iii. Exposure: Wind driven currents are important in providing energy to entrain and move sediment from one region to another. Parallel increases in the size of the lake and degree

of exposure allow for greater energy and potential for redistribution (Larsen and MacDonald, 1993). Odgaard (1993) found that episodic periods of increased wind speed to be most effective in transportation of sediment rather than a sustained lower speed as greater energy is available to entrain sediments.

These factors are not mutually exclusive and occur to differing degrees depending upon site specific factors. For example, Larsen and McDonald (1993) highlighted basin morphology and wind shelter to be the main features for sites to be used within high resolution studies. However, a final consideration is the type of material within the basin as the density of this will determine the resistance to movement. For example, a lake dominated by allochthonous sedimentation will consists of greater inorganic material which requires greater energy for transportation. In contrast, a more productive lake will have a greater organic content with lower density allowing for easier redeposition. In addition, Bengtsson *et al.* (1990) suggests that the recently deposited sediment that has greater water content will be most susceptible to movement.

The complexity of this relationship is stressed by the potential causes of the patterns identified in the pollen accumulation at Lochan Geal. Hilton (1985) tabulated information on sedimentary processes from numerous lakes in the USA, Canada, and parts of Europe in an attempt to determine the controls on sediment redistribution. Results suggest that lakes of similar size and depth to Lochan Geal are primarily controlled by the intermittent mixing from stratification. The amount of shelter provided by the location of the lake, the shallow slopes to the basin and its depth preclude major impacts of turbidity currents or wave action as dominant controls. Ascertaining the occurrence of stratification in Lochan Geal is difficult from the information currently available, however, assessment of correlation between lake area, depth and stratification class has been undertaken by Gorham and Boyce (1989) which implies that Lochan Geal should undergo some annual stratification. Furthermore, the high organic content and associated mobility will aid sediment redistribution via this process supporting within lake processes as the likely driver.

6.4.2.3 Species differentiations

Picea and *Larix* show the poorest correlation and the greatest amount of variation between time slices and PPE groups. This is associated with the strength of the PPEs, discussed in Chapter 4, and highlights the error induced into the model when representative PPEs are not included. The remaining taxa showed some slight variability but overall performed well within the model. Although *Calluna* reconstructions were poor for the recent reconstructions within Lochan Geal this is a response to the vegetation representation within the lake with better performances over the longer time frame. In addition, the strong presence and correlation of pine and birch will control

the visibility of this taxon in the pollen record and its subsequent reconstructed value. Hellman *et al.* (2007) further imply that lower species diversity in the landscape being modelled could increase the poor performance of the model which perhaps influences the amount of *Calluna* to the *Pinus: Betula* relationship at Lochan Geal. For example, as the values are percentages these are highly dependant on performance of the other taxa within the model.

6.4.2.4 Instability in best performing PPEs

Unpredictability in the results of the PPE groups mirrors that seen within the regional tests shown in Chapter 4. Although BA.Ran.1000 was selected as the most representative data set from the original validation the performance of this group within the time slices is highly variable. Few inferences can be made from the Lochan Geal tests but the patterns are still evident at Inshriach H1 although not to the same degree. Here BA.Ran.1000 produces good reconstructions for the time slices 1 and 2, although the latter has very high standard errors, but fails to accurately represent time slices 3 and 4. Within the latter two slices it is the PPEs from systematically selected sites that consistently produce improved correlations and reduced error estimates. Furthermore, changes in the density of woodland structure also fail to be accurately modelled. A number of explanations for these patterns can be taken into consideration:

- Errors associated with the pollen productivity estimates are inducing the differences as they
 are not fully representative of the landscape or to lake deposition sites;
- Differences in pollen productivity are exhibited in different landscape conditions i.e. managed woodland, natural woodland and open structures. Consequently, application of unrepresentative PPEs can generate misleading results;
- Pollen productivities are not static through time. This is an assumption underlying pollenvegetation models and could invalidate all simulation software if falsified.

Given the nature of the PPEs the initial explanation seems to be the most likely within this study. The impacts of having PPEs that are unrepresentative of the environment are highlighted by these results and stress the importance of having robust parameter data available when undertaking modelling without prior validation. As mentioned previously, indications are that differences between vegetation structure of the landscape have a degree of influence on the PPEs obtained. Such details require further studies in an attempt to understand the behavioural differences of pollen dispersal and deposition in relation to this to ensure that representative PPEs are used when reconstructions are being undertaken. The final explanation also has merits for a potential influence on the reconstructions. It is known that pollen productivity can respond to temperature changes on an annual basis (Barnekow *et al.*, 2007) but it is envisaged that the smoothing effect of

sedimentation will reduce the impact of this upon any palaeoenvironmental studies. Furthermore, management i.e. coppicing, grazing or fire from naturally or anthropogenic forcing can also be a factor for influencing pollen productivity.

6.4.2.5 Time slices and relevant source area of pollen

Selection of the time slices for the historical reconstructions intended to maximise changes in the vegetation structure, age class and openness of the landscape, with the aim of assessing changes in the performance of the model and relevant source area of pollen distance. However, results from this study are difficult to interpret with respect to these factors as the variability induced from the PPE groups and poor performance at Lochan Geal obscure any patterns.

At Lochan Geal the horizons reflected both changes in age structure but also vegetation patch size as time slices 3 and 4 were dominated by large, monocultural stands. Estimates of relevant source area of pollen (Table 6.16) show the distances from all PPE groups and those judged most representative. Time slice 2 clearly has inflated estimates when all and selected sites are considered with a low standard deviation indicating a simultaneous cause. Interestingly, when patch size decreases in time slices 3 and 4 it is only the latter where RSAP distance increases. Both this and time slice 2 have woodland comprised of young individuals which could indicate a relationship with height rather than the patch-matrix structure. Previous simulation studies have identified a number of factors that influence RSAP distances; vegetation patterning is considered the main control and has been supported by a number of simulation studies. For example, Nielsen and Sugita (2005) identified an increase in RSAP with simplification of the landscape indirectly increasing patch size due to generalisation of vegetation components. Recent tests to investigate this by Hellman et al. (2009a) used evenness as a measure of the ecological patterning within hypothetical landscapes and concluded that a greater unevenness increased the RSAP distance. Both are in response to a greater distance required to find equilibrium between the pollen and vegetation data (Sugita et al., 1999). Unfortunately, the quality of results from Lochan Geal precludes discussion of these with respect to available information as although significant variation occurs within the result the association of this to vegetation patterning alone would be inappropriate.

LG	All PP	E groups	Selected groups		
Time slice	Mean (m)	Standard deviation (m)	Mean (m)	Standard deviation (m)	
1	685	223	660	57	
2	1609	583	1535	7	
3	938	516	725	290	
4	1002	179	955	106	

Inshriach H1	All PPE groups		Selected groups		
Time slice	Mean (m)	Standard deviation (m)	Mean (m)	Standard deviation (m)	
1	568	304	570	368	
2	826	407	1200	85	
3	813	552	1213	35	
4	455	234	540	0	

Table 6.16: Estimates of relevant source area of pollen (metres) for local vegetation reconstructions generated from the LOVE simulation model (Sugita, 2007b). Sites were selected upon the best correlation to the actual dataset. Time slice 1 – Present; 2 – 1989; 3 – 1960; 4 – 1950.

Inshriach H1 was used to address degree of openness and age structure. Prior to the 1960s (time slice 3) the landscape was open with juvenile Scots pine whilst time slices 1 and 2 represent enclosed woodland with differing density associated with age class. Inshriach H1 has a general trend of increasing RSAP distance with opening of the landscape, although time slice 4 counteracts this trend, more distinctively shown when the selected PPE data is used. The transition from time slice 1 to 2 is dramatic with a doubling of this distance. As with Lochan Geal this time frame is associated with a reduction in age of the stand surrounding the deposition site as oppose to structural changes. Interestingly, there is little further increase as the landscape is largely open (heath land dominated) in time slice 3 and remains so into time slice 4 despite the dramatic reduction in RSAP distance. As with Lochan Geal vegetation height could play a crucial role in the deposition at the basin. Vegetation pattern and coverage remains static in the immediate vicinity of the deposition basin in time slices 1 and 2 with only age of the stands showing variation. Height difference between individuals of Scots pine of 20 years and 48 years of age is 2 – 10 m and 10 – 22 m respectively, which is dependent upon yield class (Forestry Commission, 1981). Inevitably, the

wind patterns will be adjusted between the two heights and even more so with its full replacement by herbaceous vegetation inducing non-uniform dispersal mechanisms within the landscape.

Currently, height differences are not accounted for within the simulation models with uniformity assumed between different vegetation patterns. However, successful identification of openness has been achieved by earlier software with increases in RSAP associated with 'open' landscapes. Recent simulations undertaken by Hellman et al (2009) identified a difference in results when 'open' taxa differed, potentially indicating a further control on the RSAP. When patch size of Poaceae was increased to represent openness a contemporaneous increase in RSAP was identified but, in contrast, when *Calluna* was used no variation was identified. The author argues that this relates to the evenness of the landscape in response to both patch size changes and cover proportion. The low estimate of RSAP at Inshriach H1 from 1950 could be attributed to this source of variation as the landscape would be expected to have a high evenness value due to its pure dominance by Calluna heath with low species diversity. Increased disturbance from planting in 1960 and subsequent growth of woodland would disrupt this and potentially contribute to the increased RSAP identified, further influenced by increased evenness within the contemporary, mature woodland which would be structurally homogenous (Summers et al., 1999). Again, these are tentative suggestions given the limited dataset currently available from Inshriach, but the results from Hellman et al., (2009) highlight additional factors that could severely impact upon the ability to accurately estimate RSAP in past landscapes and requires expansion.

A further consideration is the actual calculation of the RSAP estimates by the model as considerable variation occurred between the vegetation and simulated pollen data from these sites preventing independent approximation. Tests to define the RSAP prior to modelling using the characteristic source area of pollen algorithm (Sugita, *unpublished*) failed to improve the output implying that this was perhaps too low which instigates the iterative technique. The LRA software uses an iterative process based upon the results of the modelling whereby the components and/or their errors can be no greater than 1 or less than 0 (Sugita, 2007b). Should the calculations of the vegetation proportions be incorrect for any reason i.e. PPEs, pollen values or poor regional results, this will impact upon the RSAP estimates and resultant variations a demonstration of this influence. However, estimation of the RSAP is problematical due to the complex interaction of factors outlined throughout this study, consequently, distances obtained from the modelling software, when the results are accurately generated, are the best estimates at present.

6.5 Quantitative modelling of long-term vegetation changes at Lochan Geal

Application of the models to longer timescales is the foremost aim of the quantitative techniques. Therefore, the LRA suite was applied to Holocene sediments obtained from Lochan Geal. Despite the poor performance of the same site over the historical period samples extracted from a secondary core from the site proved to have significantly improved results. Firstly, the surface sediments were used to validate the core with comparisons to contemporary data. Subsequent modelling of numerous horizons from the present day to 3100 cal. Yr. BP was undertaken using PPEs from Inshriach and southern Sweden (Sugita *et al.*, 1999b; Broström *et al.*, 2004). Due to the limitations on taxon numbers of the Inshriach data set the southern Swedish values were used to increase taxon diversity in the model results. Therefore, the model was run with 5 taxa from both the Inshriach and southern Sweden values to allow for comparison with further runs using the southern Sweden values for 14 taxa.

The pollen data were used within the REVEALS (version 4.2.2.) and LOVE (version 3.1.7.) software of the LRA group. Although the same algorithm was used in earlier versions the developments enable time windows to be used in contrast to single horizons. When dealing with past landscapes this allows for some error within the dating profiles for each site and amalgamation of a number of samples from one site to increase pollen counts and improve the reconstructions. At Lochan Geal the time slices were chosen based on known historical events, features within the pollen diagram and availability of regional data. For example, the 1700s and 1800s were chosen as these periods encompass the extinction of Capercaillie within the region with time slices prior to this giving an indication of habitat availability for existing populations. To enable the regional vegetation changes to be modelled actual pollen counts were taken from the European Pollen Database for sites included within the study by Birks (1975) and the original publications for the remaining sites (O'Sullivan, 1970; 1973; 1976) information on these are shown in Table 6.17. As a limited number of lacustrine palaeoenvironmental studies have been conducted in the region some mire sites were included from these studies. Additional data were used from Loch Alvie and Loch an Eilein where possible with the use of the surface samples for this time horizon.

Although these sites are required to quantitatively reconstruct the vegetation at Lochan Geal there are issues with the chronological control at some of these sites, although now calibrated using Intcal 2004 (Reimer *et al.*, 2004). At the short core sites (Ryovan, CAC1 and CAC3) only two ¹⁴C bulk dates were obtained which are subject to potential errors from contamination, counting error and interpolation. Similarly, at the Abernethy sites (Alt na Feithe, Loch Enich and Abernethy) the predominant aim of the studies was to investigate the pine decline and as such pine stumps were used for the ¹⁴C analysis. As these are found in a particular horizon this limits the control to the mid

and lower sections of the profile. Furthermore, the Alt na Fiethe site is a peat bog and pollen concentrations will be subject to a strong local input from the surface vegetation which will influence some taxa. Finally, although Loch Pityoulish is constrained by 8 ¹⁴C dates (1 is dubious) they are again bulk samples. These potential errors have to be considered to enable unbiased interpretations of the resultant profiles to be made and raise issues for the application of this methodology to areas where raw data cannot be collected in sufficient quantity or when perfect datasets are unobtainable.

	LRA Time slices (cal. Yr BP)									
Site name	0-100	100- 200	200- 300	550- 650	1550- 1650	1950- 2050	2300- 2400	2700- 2800	2950- 3050	3050- 3150
Ryovan	•	•		•						
CAC1	•	•	•	•						
CAC3	•	•	•	•						
Alt na Feithe	•		•	•	•	•	•	•	•	
Loch Enich	•			•					•	
Loch Pityoulish	•	•	•	•	•	•	•	•	•	•
Abernethy	•			•	•	•	•		•	•
Loch Alvie	•									
Loch an Eilein	•									

Table 6.17: Sites used within the REVEALS model to determine the regional pollen rain around Lochan Geal. Site references: Ryovan, CAC1, CAC3 (O'Sullivan, 1973a); Loch Pityoulish (O'Sullivan, 1976); Abernethy (Birks, 1970); Loch Enich, Alt na Feithe (Birks, 1975); Loch Alvie, Loch an Eilein (this study).

6.5.1 Modelling with locally obtained PPEs

PPEs calculated in this study were used to run the model with only the 5 main taxa. The PPEs and fall speeds are the same as those from the BA.Ran.1000.1. dataset used and presented in Chapter 4.

6.5.1.1 Contemporary validation

Results from the regional and local reconstruction are shown in Table 6.18 with the associated contemporary information from the LCM2000 and forestry records respectively. Interestingly, the scale at which the regional reconstructions compare to the actual data is much larger, 100km radius, than previously seen. Although sites of similar size to Loch Alvie and Loch an Eilein were included Loch Pityoulish is much larger. Also mire sites may be classed as having a larger RSAP due to their open nature which would also influence this distance. Similar sites were used from

O'Sullivan (1970) where short cores were taken from soil and peat profiles indicating that these could also have large source areas.

Individually, taxa perform well in the REVEALS model when compared with observed data. *Betula* is the only taxon which is over represented in the local but under represented in the regional reconstructions. This taxon has been know to produce erratic representations from PPE studies (S. Sugita, pers. comm., O'Sullivan, 1973a) which could be a problem if this taxon is to be used in future studies. *Calluna* is over represented which could be a response to the use of mire sites as if this occurred on the bog surface inflated proportions would be modelled for the regional level. Error margins for all taxa are high, especially when considered relative to the mean vegetation coverage values. In most instances, for all taxa but *Calluna*, inclusion of the error margins could equate to mean values of zero for the REVEALS results which are unrealistic at this site. However, inclusion of a greater number of larger sites has the potential to reduce these margins further (Sugita, 2007b; Hellman *et al.*, 2008).

DECIONAL	Estimated	Estimated S.E.		LCM 2000		
REGIONAL	vegetation	(%)	$10000~\mathrm{km}^2$	400 km^2	100km^2	
Pinus	17.0	22.8	17.6	28.7	64.1	
Picea	1.5	26.0	0.6	0.9	2.1	
Larix	0.1	2.0	0.4	0.6	1.4	
Betula	1.8	11.0	12.7	3.7	5.3	
Calluna	79.9	28.8	68.8	66.1	27.2	

LOCAL RSAP = 1320m	Estimated vegetation	S.E. (%)	Distance weighted vegetation percentage
Pinus	47.6	19.4	61.8
Picea	1.4	0.9	0.0
Larix	0.0	0.0	0.1
Betula	50.9	14.0	34.5
Calluna	0.0	0.0	3.6

Table 6.18: Results from the contemporary validation of REVEALS (upper) and LOVE (lower) reconstructions for Lochan Geal using LG TAP.

Comparison of the LOVE results with the distance weighted vegetation within the RSAP (1320 m) show reasonable consistency between the values. Although the differences are much larger than identified regionally the values fall within the standard error estimates for the calculated values. The underestimation of *Calluna* can be, in part, attributed to its high presence in the regional calculations. The *Betula* discrepancy could be related to its marginal location at Lochan Geal with heightened pollen contribution to the lake surface or processes mentioned in section 6.4.2.2. Failure to identify this marginal birch in the Forestry Commission records used to obtain the observed vegetation data would further accentuate this.

6.5.1.2 Long-term reconstructions using Inshriach PPEs

A total of nine additional horizons were used for vegetation reconstruction over the duration of the core based upon the availability of regional data and interest. Figure 6.1 shows the results of these reconstructions, both regional and local, with pollen percentage data presented for comparison.

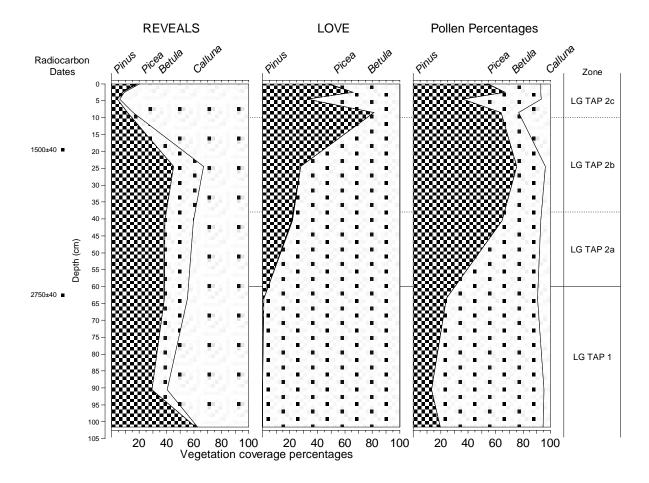


Figure 6.1: LRA reconstructions and pollen percentages (as a proportion on the 5 taxa only) from Lochan Geal. PPEs used are those from Inshriach.

The regional results show a dominance of *Calluna* in the wider landscape from 90.5cm (3100 cal. Yr. BP) with values showing a significant increase at c. 1600 cal. Yr. BP subsequent to which values of ~90% are attained. *Pinus* is the predominant arboreal taxon comprising 20 - 40% of the vegetation whilst *Betula* has values between 0% and 10%. Clear stability of the components are shown between 95 cm and 25 cm (3100 - 1600 cal. Yr. BP) with *Pinus* the dominant taxon. Declining pine values from 25cm (1600 cal. Yr. BP) are reversed in the top 4 cm of the reconstruction with a tripling of the arboreal component predominantly composed of *Pinus*. The first occurrence of *Picea* is also identified during this period consistent with known planting of the taxon.

Representations by the LOVE model show strikingly different changes in the vegetation data in comparison to the regional levels. Firstly, the record is dominated by *Betula* until 65 cm which is *c*. 2600 cal. Yr. BP, during which it comprises 100% vegetation coverage when only 5 taxa are included. The 65 cm horizon marks a critical threshold at the site with establishment and increase in *Pinus* coverage modelled which, similarly, attains a dominant proportion by 10 cm (700 cal. Yr. BP). Sustained *Pinus* presence ends with a rapid reduction in values from 80% to 30% at 5 cm (*c*.375 cal. Yr. BP). Although values increase by ~20% following this, the feature is short lived and returns to 50% coverage at the surface.

Figure 6.1 also shows pollen values as a percentage of the five taxa included within the reconstructions. Comparison of the vegetation coverage estimates and the pollen assemblage show that the main trends are identified. Firstly, in the period before 60cm depth (c. 2500 cal. Yr. BP) the pollen data present the local picture of the vegetation estimates with only small quantities of *Calluna*, all of which is accounted for by the regional component even when increased values are seen at 10cm (700 cal. Yr. BP). This is also evident in the *Pinus* curve as reconstructed local vegetation values are significantly lower than would be attributed through standard interpretation. Finally, the rapid fluctuation in *Pinus* can be attributed to local features due to coeval changes in the pollen and local reconstructions but not presence regionally.

Error margins associated with the LOVE results are much lower than the comparable estimates from the REVEALS model. This pattern is consistent with that seen within the historical period modelling discussed in Chapter 5 and therefore suggests the PPEs as the cause of this error. However, some errors will perpetuate through from the REVEALS results and as these are high will be detrimental to the LOVE results and perhaps result in estimates much larger than attainable if a greater number of sites were used.

6.5.2 LRA modelling with previously published PPEs

A limitation of using PPEs derived from the local area is the restriction to only 5 taxa for the reconstructions. Figure 6.2 shows the occurrence and importance of a larger number of taxa throughout the c. 3000 year span of the record. In order that increased diversity could be achieved within the modelling, previously published PPEs from southern Sweden were applied with all other data used for the initial modelling remaining static. Taxa included and PPEs used are presented in Table 6.19. Initial validation was undertaken to determine the suitability of the values to this analysis to examine whether they could be used with some confidence given problems of applying PPEs for different regions (Broström $et\ al.$, 2008).

	Pollen productivity					
Taxa	Values used Values relative to used <i>Picea</i>		BA.Ran.1000.1 values	Fall speed	Source	
Poaceae	1	0.6	-	0.035	Broström et al. (2004)	
Pinus	5.7	3.2	3.1	0.031	Sugita et al. (1999)	
Picea	1.8	1	1	0.056	Sugita et al. (1999)	
Larix	5.7	3.2	4	0.126	Inshriach	
Betula	8.9	4.9	2.5	0.024	Sugita et al. (1999)	
Calluna	4.7	2.6	2.1	0.038	Broström et al. (2004)	
Quercus	7.6	4.2	-	0.035	Sugita et al. (1999)	
Alnus	4.2	2.3	-	0.021	Sugita et al. (1999)	
Corylus	1.4	0.8	-	0.025	Sugita et al. (1999)	
Plantago lanceolata	12.8	7.1	-	0.029	Broström et al. (2004)	
Poaceae >37µm	3.2	1.8	-	0.06	Broström et al. (2004)	
Cyperaceae	1	0.6	-	0.035	Broström et al. (2004)	
Ericaceae	4.7	2.6	-	0.038	Broström et al. (2004)	
Ranunculus acris type	3.8	1.2	-	0.014	Broström et al. (2004)	

Table 6.19: PPEs and fall speeds from Southern Sweden used for the diverse reconstructions and references for these figures.

6.5.2.1 Contemporary validation process of the LRA

The validation process took the form of that used for previous model runs. Table 6.20 shows the results of REVEALS and LOVE model with the observed data from the contemporary data sets.

The regional results show a high correspondence to those of a 100 km radius around Inshriach (10000km²) and are very comparable to those obtained from the use of PPEs calculated from the site in this study. Furthermore, the reconstruction coverage for *Betula* at the regional level is

underestimated as was seen from the previous validation. Similarly, error margins are high which supports the conclusion that site inclusion is a main driver in these values.

			LCM 2000		
	Estimated	S.E.	10000	400	
REGIONAL	vegetation	(%)	km ²	km ²	100km^2
Pinus	19.9	24.4	17.6	28.7	64.1
Picea	1.8	26.0	0.6	0.9	2.1
Larix	0.1	2.6	0.4	0.6	1.4
Betula	1.1	7.3	12.7	3.7	5.3
Calluna	77.1	28.9	68.8	66.1	27.2

LOCAL			Distance weighted
RSAP =	Estimated	S.E.	vegetation
1320m	vegetation	(%)	percentage
Pinus	63.6	21.2	61.8
Picea	1.9	1.1	0.0
Larix	0.0	0.0	0.1
Betula	34.5	8.5	34.5
Calluna	0.0	0.0	3.6

Table 6.20: Results of the contemporary LRA model for the 5 main taxa using previously published PPEs from southern Sweden.

Reconstructed values of the local area are exceptionally good in comparison to the observed data and are an improvement on the results obtained when local PPEs are used. *Pinus* reconstructions are within 2% of the observed values and the *Betula* values are directly equivalent. Standard errors for the estimated values are high but are an improvement on those of the area PPE values used with the *Betula* only 8.5%. Low estimates for *Picea* and *Calluna* are a concern with the former potentially related to the PPE for the taxon and the latter an influence from the regional values.

The calculated RSAP for these taxa is equivalent to that obtained when the Inshriach PPEs are used. This is attributed to the similarity of the PPES but also the calculation process of the model that is employed if the estimated distance (user defined) is too low.

6.5.2.2 Long-term reconstructions of 5 taxa

To facilitate a comparison of the published PPEs and those from Inshriach when used in the model software the long-term analysis with only 5 taxa was run with the published PPEs. Results of this

analysis, shown in Figure 6.2, show a strong correlation to those seen in Figure 6.1 with the same patterns identified as alluded to in the validation process. Quantitative reconstructions of the taxa do show some variation with *Betula* estimated in slightly lower proportions and *Pinus* higher which is, in part, due to the interconnection between these taxa associated with the use of percentages. As previously identified, *Calluna* present within the Lochan Geal assemblage is fully accounted for by the regional pollen rain and therefore was not present around the site at this time.

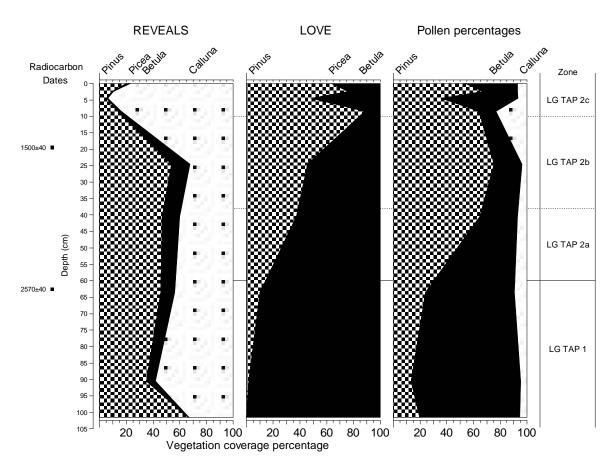


Figure 6.2: LRA reconstructions and pollen percentages (as a proportion on the 5 taxa only) from Lochan Geal. PPEs used are those from Southern Sweden.

Similarities between the RSAP estimates are also exhibited between the two PPE parameter sets as shown in Table 6.21. Consistency is evident to a depth of 40.5 cm (2000 cal. Yr. BP) below which the estimates show considerable differences of ~300 metres at every time slice. This is potentially related to the dominance of *Betula* in these horizons as it is only this taxon which shows significant differences in PPE value between the two parameter sets.

Time slice		RSAP estimate (m)		
Depth	yrs. BP	Sweden	Inshriach	
0.5	0	1310	1320	
2.5	150	1220	1200	
4.5	250	1370	1430	
8.5	600	700	650	
24.5	1600	1860	1780	
40.5	2000	1490	1550	
63.5	2750	970	1290	
90.5	3000	1570	1720	
101.5	3100	1380	1620	

Table 6.21: Estimates of relevant source area of pollen calculated from the LOVE model for the two PPE parameter groups used for the analysis.

6.5.2.3 Long-term reconstructions with increased taxon diversity

The summary diagram, Figure 6.3, shows the reconstructed vegetation coverage for some of the main constituents at Lochan Geal. The wide range of taxa within both the wider landscape and around the deposition site throughout the 3000 year time frame of the reconstructions is clear.

Regional vegetation proportions indicate both *Pinus* and *Betula* as only minor constituents of the landscape with the former comprising between 10 - 20% coverage and the latter only 5%. *Pinus* is the only taxon to show any changes in coverage throughout the time frame with slightly inflated values at the base, c. 3000 cal. Yr. BP, and increased values within the most recent 250 years consistent with planting of this taxon. Significantly, *Corylus* and Cyperaceae are modelled as being major constituents of the vegetation from c.3000 - c.250 cal. Yr. BP. Whilst *Corylus* has estimates consistently around 20% coverage Cyperaceae shows more variability with distinct increases in coverage at 63.5 cm (2750 cal. Yr. BP) and 24.5 cm (1600 cal. Yr. BP) of ~30% in both instances. *Calluna* follows a similar pattern to these taxa although in reverse. At the base of the profile coverage is estimated to be ~20% which increased slightly at 90.5 cm (3000 cal. Yr. BP). Although this decreases to become a minor component a rapid and large expansion occurs from 24.5 cm (1600 cal. Yr. BP) with only recent contraction. Values of Poaceae also follow this pattern, although at a lesser magnitude, with the only difference identified at the top of the profile where an increase in coverage is experienced.

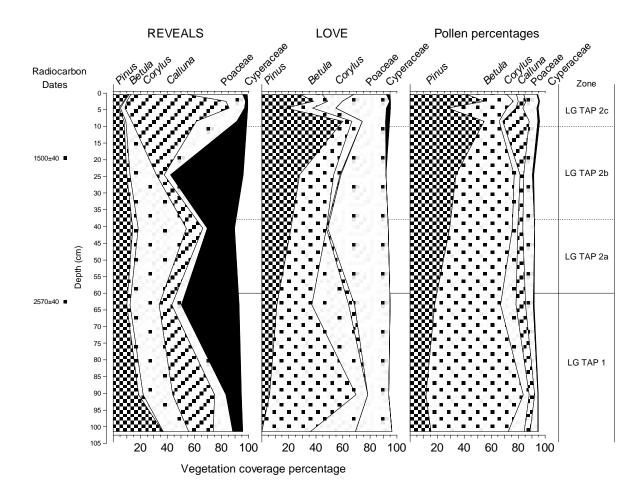


Figure 6.3: A summary of the LRA reconstructions and pollen percentages from Lochan Geal calculated from the 12 taxa included in the analysis. PPEs used are those from Southern Sweden. Some taxa are excluded for clarity therefore values do not

Reconstructions of the local vegetation change occurring at Lochan Geal show distinct differences from those of the regional patterns. Firstly, *Pinus* and *Betula* are identified as important vegetation components at the site. *Pinus* shows gradually increasing values from the base of the profile to reach a maximum of 65% at 8.5 cm (600 cal. Yr. BP) prior to showing an unstable decline to 30% coverage at the present day. In contrast, *Betula* has a dominant proportion at the base of the profile, ~65%, which declines to ~20% at 63.5 cm (2750 cal. Yr. BP). Following a period of stability the amount of *Betula* coverage declines, mirroring the fluctuations in the last 500 years identified in the *Pinus* record, to present levels of ~15% coverage. Locally initial *Corylus* levels are high, comprising ~30% of the vegetation coverage throughout LGTAP1. At 40.5 cm (2000 cal. Yr. BP) *Corylus* is absent with a rapid decrease identified prior to this horizon. Subsequent recovery is shown in LGTAP2c but the taxon only attains its highest levels at the present day (20%), which are

still lower than previous presence. Non-arboreal taxa are not as prominent around Lochan Geal as within the regional landscape. *Calluna* is only represented as a minor constituent, rarely attaining 5% coverage, with its maximum levels around 63.5 cm (2750 cal. Yr. BP). Cyperaceae shows similar patterns with increased representation over the upper 25cm of the core corresponding to the last 1600 years. Poaceae is the only taxon which does not follow this trend with high values throughout the profile. Coverage is estimated as ~15% or greater with two peaks at 40.5 cm (2000 cal. Yr. BP) and 4.5 cm (250 cal. Yr. BP), the latter of which is coeval with a decrease in the arboreal component of the vegetation.

Differences between the reconstructed vegetation proportions and presence in the pollen record are exemplified when comparisons are made between the two datasets. Figure 6.3 shows the pollen assemblage as a percentage of taxa included within the reconstructions (some of which are not shown in the summary diagram but can be seen in the appendix). The change in importance of *Corylus* and non-arboreal taxa in the vegetation communities is very clear. This is especially true of Cyperaceae yet consideration also has to be given to increased representation of this within the regional profile due to the use of some mire sites and its presence in such environments. However, *Calluna* does not show any local representation despite its high percentages in the pollen record due to the dominance of this in the regional record as explained in section 6.5.1.1. Reconstructed levels of the arboreal components are demonstrable in the pollen data as *Pinus* and *Betula* dominate. A feature that is identified as purely local by the reconstructions is that near the surface, 4.5cm, which identifies a decrease not only in *Pinus*, which is clear in the pollen record, but also *Betula* which is obscured in the pollen record by the high regional proportions of this taxon. Expansion of *Corylus* and Cyperaceae are noted as a response to this which would be an artefact of data presentation using percentages.

6.5.3 Interpretation of LRA profile

A purpose of the LRA approach is to apply correction factor to the main constituents of the pollen assemblage to account for differential production and dispersal. Inevitably this affects the interpretations that can be made from profiles. Table 6.22 provides a summary of conflicting observations made when this method is applied to Lochan Geal. Differences are identified primarily with respect to the proportions of non-arboreal communities in comparison to their arboreal counterpart. For example, the regional expansion of *Calluna* in LGTAP 2b is striking in the zone whilst poorly distinguished in the pollen profile. A further difference occurs between the dominants of the woodland. Although pine and birch are clearly dominant in both the pollen profile and the LRA, the latter also identifies hazel as a major constituent of the local landscape at Lochan Geal.

Zone	Standard interpretation	LRA interpretation
LGTAP 2c	High pine and low birch apart from short	Regional: Low arboreal component (10%
10 - surface	punctuation where this is reversed.	coverage) of which pine is dominant.
	Increased grasses, herbs and ruderals.	Calluna is main component but gives way
	Short-lived <i>Calluna</i> peak.	from 3cm to Poaceae increase.
		Local: Arboreal fluctuations between
		pine, birch and hazel. Poaceae increases
		when arboreal shows transient decrease.
		Cyperaceae has heightened levels.
LGTAP 2b	Although increasing pine and decreasing	Regional: Initial increase and dominance
38 – 10cm	birch values are reasonably stable.	of Cyperaceae replaced by explosion of
	Heathland and herb taxa still present.	Calluna and Poaceae to a lesser extend.
	Peak in <i>P.lanceolata</i> values.	Declining arboreal component
		predominantly hazel.
		Local: High Poaceae levels. Expanding
		pine and hazel. Birch shows no change
LGTAP 2a	Increasing pine and decreasing birch starts	Regional: Hazel retains and increases
60 – 38cm	but reverses at charcoal level. High	dominance. Other taxa stable apart from
	heathland presence at charcoal horizon	Cyperaceae which decreases slightly.
	but low levels before this.	Local: Pine and birch increase. Hazel
		decreases to zero. Poaceae increases.
LGTAP 1	Birch dominant but interdependent from	Regional: Pine and hazel co-dominant,
110 – 68cm	pine. Poaceae, Ranunculus-type and	birch has low presence. Calluna and
	Plantago lanceolata all present.	Cyperaceae extensive
		Local: Birch and hazel dominant with low
		pine levels. Poaceae high presence but
		Calluna low levels.

Table 6.22: Summary details of interpretations made relating to landscape change at Lochan Geal from pollen data alone (*left*) and vegetation reconstructions from use of the LRA (*right*).

These conflicting interpretations are discussed below:

The importance of *Corylus* is increased in comparison to the pollen percentages alone, thus this suggests that *Pinus* and *Betula* woodland was dominant with *Corylus* as a co- or sub-dominant of the *Betula* woodland due to its high values (Birks, 1969). Changes detected in the presence of *Betula* and *Corylus* at 90cm are indicative of local changes as regional levels remain stable. Correspondence between *Betula* and the charcoal horizon could support a link with anthropogenic origins as birch is known to colonise newly burned areas and facilitates its expansion (Atkinson, 1992). However, this is identified at ~90cm but not so with the second horizon at ~65cm which makes this conclusion problematic. Similarly, the dynamics of *Corylus* in the LRA profile in conjunction with the openness indicators and charcoal could be indicative of community expansion or coppicing and as such human presence but is tentative. Presence of *Corylus* in the Scottish

woodlands has been noted (Roberts *et al.*, 1992; Tipping, 1994; Mackenzie, 2002) but its presence within the pollen record can be questionable and variable. For example shade can reduce flowering (Rackham, 1980) and coppicing makes it more prolific (Edwards and MacDonald, 1991) creating ambiguous interpretations and makes comparison with other studies problematical.

Poaceae becomes a major component of the vegetation profile attaining values of 25% coverage whilst only ~5% in the pollen record and heightens the importance of openness indicators. Such patterns in addition to the arboreal dynamics further support the presence of human communities in the area and therefore the interpretations made upon the pollen data alone. As upland landscapes were primarily reserved for transhumance, grazing is the most likely land use (Halliday, 1993). As such these areas are transient and less visible within the archaeological record than permanent settlement which restricts the information available from additional sources to support any inferences made.

The influences of climatic change and human activity were discussed in section 5.3 and further influences are identified in the regional LRA results through a peak in Cyperaceae. A second peak of similar magnitude also occurs in zone LGTAP2b. These two periods are consistent with climatic changes identified regionally but also locally at Mallachie Moss. Here, Langdon and Barber (2005) identified two periods of increased wetness at 2800 and 2000 cal. Yr. BP punctuated by a drier phase. A strong correlation between these events and the Cyperaceae horizons is clear and therefore could imply common forcing. Inevitably, as some of the regional data feeding the model results is taken from mire locations the climatic changes will be accentuated in these environments. However, this does enable climatic variation to be considered on a site specific basis; for example, during the first of these events a decline in *Betula* is evident on a regional and local scale but at the second the local response is not detected.

Stable *Betula* but increasing *Pinus* and Poaceae characterise the LRA output for this zone suggesting some utilisation of the landscape via human agents without inhibiting woodland regeneration. This contradicts the conclusions reached when pollen data alone was interpreted in Chapter 5 which showed rapidly decreasing *Betula* values and potential utilisation of the resource. In the LRA reconstructions *Corylus* appears to be affected by fire due to simultaneous decline in *Corylus* pollen and the charcoal horizon. This was also a correlation seen by Tallis and Switsur (1990) in the Peak District but Edwards (1990) did not find a corresponding relationship and questioned this conclusion. Furthermore, Vera (2000) and Svenning (2002) state that the growth of hazel can be stimulated by fire which would provide an opposing relationship to that seen at Lochan

Geal. This provides further support to an anthropogenic source for the decline and suggests clearance of hazel perhaps for utilisation of the resource for building or fuel (Edwards, 1999). In addition, Quelch (1997) discusses some features of hazel. For example natural coppicing can be instigated by light grazing but if this becomes too intensive can kill the taxa. If the reconstructions are representative these factors could be contributing to such dynamics and it is likely that Betula and Corylus woodland would have prevailed providing pasture areas as was seen in the 1700s (Smout et al., 2005). The gradual decline and eventual loss could be a response to grazing pressure and an inability to regenerate implying a coincidental occurrence with the charcoal horizons. Alternatively two other factors could be considered: natural changes such as the increasing amounts of *Pinus* could be creating shade and inhibiting regeneration of the *Corylus* community instigating its decline due to its inability to reproduce under such conditions (Rackham, 1980; Vera, 2000); increased Corylus levels are experienced regionally which would reduce values at the local level but could be subject to error if the regional values are not fully representative of the actual changes occurring. Increased temporal resolution would aid interpretation by providing more detail on the declining values. Furthermore, better defined spatial characteristics from a network of sites would help identify the relationship between Corylus, Betula and other taxa to determine community composition and the likelihood of this conclusion.

A clear difference in the representation of Poaceae between the records (pollen percentages and the reconstruction) locally to Lochan Geal demonstrates the under representation of open area indicators in the pollen profile. Although an increase in diversity of open area ruderals and herbs can be inferred from the pollen profile alone the full extent of the grassland area is only appreciated when the LRA results are consulted. Groenman-van Waateringe (1993) showed an increase in flowering of grasses on colonisation of recently open ground. Within the profile the expansion of Poaceae commences in conjunction with the charcoal horizon indicating that this was not a driving factor of this feature. The subsequent decline of Poaceae this could reflect onset or intensification of grazing which was demonstrated by Groenman-van Waateringe (1993) to reduce flowering and therefore presence in pollen profiles.

LGTAP2b 38cm –10cm (2000 cal. BP – 700 cal. Yr. BP)

The most distinctive feature of the LRA reconstructions occurs in the regional representation and shows the rapid expansion of *Calluna*. This feature was first identified in the Abernethy region by O'Sullivan (1974; 1976) and was dated to 1500 ¹⁴C yr. BP. These sites were used to feed the regional model and therefore its accentuated presence within the results in unsurprising. However, independent verification of this feature at a number of other sites (Dalton *et al.*, 2005; Pratt, 2007) indicate that this is a regional as opposed to local feature and therefore should not falsely influence

the modelling results and could support the inference of population expansion and increased land utilisation (O'Sullivan, 1976). Occurring during the MCA this also supports the use of upland locations during favourable climatic conditions. This contradicts the interpretation of the pollen profile as the *Calluna* peak can be fully attributed to the regional rain through the application of correction factors. The coverage of *Pinus* and lack of *Calluna* locally can be attributed to dense woodland casting unsuitable condition for ground flora growth and flowering or grazing within the woodland prohibiting *Calluna* establishment (Rodwell, 1991b).

An additional feature of the LRA reconstruction is the continued high presence, albeit declining slightly, of grassland indicators in the local reconstruction. Marginally reduced from the previous zone they still equate to 30-40% open land and with comparison of present day levels indicate a more open landscape in the past. As mentioned, there is an area of grazing currently at the margins of the loch and the uplands have frequently utilised for transhumance (Halliday, 1993; Armit and Ralston, 2003; Davies *et al.*, 2004; Tipping *et al.*, 2008) and it is not until the 18th Century when some of the areas used were permanently settled (Smout *et al.*, 2005). Expansion of *Pinus* represents a period of relative stability with the opportunity for woodland to regenerate indicative of reduced activity. However, grazing cannot be discounted due to declining Poaceae because a reduction in flowering can be initiated by this land use (Groenman-van Waateringe, 1993). Interestingly, this period spans A.D. 300 – 1300 during which Pictish tribes were present in the area but where centralised in lowland valleys (Burgess, 1985; Ralston and Armit, 1997; Crone and Watson, 2003). Restricted use of this area for only low intensity and sporadic grazing would have maintained the open areas but not expanded them and also enabled some degree of woodland regeneration.

Features seen in the pollen profile mostly reflect the local vegetation structure at Lochan Geal. Results from the LRA show a very low arboreal component within the regional landscape, which at this time is predominantly heathland. It is envisaged that this can be attributed to hill farming expansion of the $18^{th} - 19^{th}$ Centuries which saw cattle and sheep numbers increased by tenant farmers on a large scale (Thomson, 2002). In contrast, the local landscape is a mix of arboreal and open areas, predominantly pine, at the start of the zone which decreases to be replaced by grassland. In contrast, to the pollen diagram the LRA clearly shows all arboreal taxa to be influenced by this decline. The start of this zone correlates to the Little Ice Age A.D. 1550 – A.D. 1800 (Lamb, 1966; Grove, 2004), whilst the arboreal decline occurs towards the end. During this period climatic and historical records confirm increased rainfall (Figure 5.28) and reduced temperatures. Impacts of

such conditions are demonstrated in the reduced cultivation limit in the Lammermuir Hills which Parry (1978) estimates as 210 m at this time. Abandonment of many areas in preference of sheltered, lowland locations has been suggested (Grove, 2004) but there are difficulties in concluding the lack of activity from the pollen record (Dark, 2006). Deterioration of climatic conditions could have inhibited natural regeneration which would facilitate grassland expansion without a human agent but additional details are required to investigate this period further.

6.5.4 Sources of error

Robust chronological control is a main determinant of reliable output from the model. Within this study AMS dates were used to derive the Lochan Geal chronology but the regional sites differed in their dating methods which has implications for the results of the model. For example, the focus of Birks (1975) was to address preservation of pine stumps within the area with few dates located in the upper portions of the profiles with the assumption of linear sedimentation. Sites used from O'Sullivan (1973) applied bulk radiocarbon dating to the profiles of which some were derived from soil horizons. A recent release of the LRA programs aims to reduce variation from this component enabling time frames to be used with multiple samples from all sites to covering the period used (S. Sugita pers. comm.). This development gives greater flexibility to the user through less stringent time slice distinction and facilitates inclusion of more samples, creating lower error margins. Two critical features to the data obtained are the sampling resolution and horizons used. In most studies the former is the optimal to fulfil the objectives of the study in the allotted time frame. The latter has a greater impact upon the resultant output and definition of this time fame is crucial to the accuracy of the reconstruction. In this study 100 year windows were used which seems reasonable given the errors associated with the dating techniques and data available. Adjustment of this could provide differing results if more data was available to reduce this frame and has to be considered on a project specific basis.

6.5.5 *Summary*

Both the pollen profile and LRA reconstructions show a degree of human activity in the record at Lochan Geal, however, the details of the changes differ between the two. The dominance of birch in the past is clear and only recent succession has changed this structure. Changes appear to have been largely natural but humans must also have been involved although evidence for community settlement or presence around the basin is highly limited at present. A number of archaeological artefacts have been recovered from the region but predominantly date from the early Bronze Age and Iron Age (RCAHMS 2009) and are located in the Spey valley. If communities were utilising the landscape at Lochan Geal would climate changes force abandonment of the land or contraction to the Spey valley? Cowell (1981) suggests that any climatic changes only emphasise existing

problems and are therefore not considered the driver of abandonment. Additionally, Tipping (2002) has argued that during times of climatic deterioration communities occupying marginal areas would be unwilling to abandon areas with adaptation and modification enabling continuation. Support for this comes from Dark (2006) in which analysis of site altitude and abandonment was conducted and showed no linkage which indicates a more complex interrelationship than a simple response to climate change.

6.6 Conclusion

Time slice investigations were not as revealing as desired with respect to changing vegetation structure due to the poor results from the Lochan Geal site. Difficulty in correlating vegetation changes at Inshriach H1 forest hollow further complicates patterns with respect to this. However, results seem to suggest that the vegetation height is an additional contributing factor to determination of the RSAP. The single age form of the woodland could be a controlling influence with more natural, uneven stands being less so. Changing stand height could have a bearing on the heterogeneity in terms of composition of the canopy pollen rain. It is known that the air flows over the vegetation control incorporation and deposition of this component and therefore a more heterogeneous structure i.e. age and openness is more likely to have different component than an even structure. In their simulation work Bunting et al. (2004) fixed all features and varied the patch size of one taxon. Doing so changes the heterogeneity of the landscape when the patch size is modified. In contrast, simultaneous changes in the patch size of the vegetation components relative to each other would not appreciably change the heterogeneity which could restrict RSAP changes. These are tentative comments due to the weakness in the modelling output as in the case of Lochan Geal the information feeding the model is not fully illustrative of the vegetation. Reduced confidence in the modelling output will inevitably impact on the calculations of the RSAP as estimates are obtained from error prone data. Further empirical studies to address the issue of vegetation structure and in particular heterogeneity are required to confirm the results of the simulation studies of Bunting et al. (2004).

In addition, implications of poor parameter data are seen in the degree of variation exhibited when the PPE groups are used within the model. This highlights the need for robust PPE data and further investigation into the controls on this parameter group. Whilst PPE collection and analysis is being undertaken rigorous tests should be applied with multiple reconstructions used to ensure their use over longer timescales. Without such tests the results of the model reconstructions could be ambiguous and hinder interpretation rather than aid it. Furthermore, the number of taxa included within the reconstructions can determine the information derived from the results. Too few, and the interpretations could provide an erroneous representation of the landscape.

Chapter 7: Discussion

7.1 Pollen productivity estimates

Estimates of pollen productivity are an essential parameter for the quantitative models tested within this thesis. An accurate representation of the landscape being modelled by these values is required to limit the source and magnitude of errors incorporated and perpetuated through the model. The calculation of these parameters is still a relatively new technique and the dataset of values is currently insufficient to facilitate generalisations to be made and in many ways this study perhaps raises more questions than it answers.

7.1.1 Considerations for PPE generation

Recently, Broström et al. (2008) compiled existing PPE data and provided technical information to enable increasing numbers of collection studies to be undertaken. In this paper a number of conditions for suitable datasets were discussed including the specification that the number of sites required had to be double that of the taxa under review. Ultimately, this aims to generate data points with a range of vegetation and pollen values to identify correctly the relationship between the two variables. At Inshriach, initially 29 data points were selected for calculation of PPEs for 5 taxa, yet resultant PPEs were most suitable for modelling when only 12 sites were used to obtain these values. Such a situation seems counterintuitive as the greater the size of the sample group, the better the understanding of the population. A number of variables influence this outcome such as the type of landscape being modelled and the spacing of the sites which raises a new question: can generalisations be made? Every landscape is different in relation to the vegetation patterning, community structure and the underlying processes regulating these patterns and as such methodological requirements will be affected. Taking Inshriach as an example a number of PPE groups were generated with the inclusion of a different number of sites and their location. Dominance of pine within the landscape, as reflected in PAR values from the fossil record, could have been the driving factor of this feature as previous studies have been conducted in landscapes which have a diverse range of taxa. As a large proportion of the background component was *Pinus* the distinction between local and regionally derived portions could have blurred, resulting in the erratic PPEs or spatial autocorrelation. PPEs calculated for southern Africa by Duffin and Bunting (2008) derive a higher value for Poaceae/Cyperaceae than all other taxa. As with Inshriach these dominate the pollen assemblages with Poaceae having an average of 56% TLP at all but two sites but validation data is not presented as to the suitability of this value to the site and therefore conclusions over connections between these two features cannot be made. However, suitability of such sites for quantitative studies is highlighted by these results and further analysis is required in similar or monoculture areas to investigate this further.

An additional requirement given by Broström et al. (2008) was the random nature of site selection. This was not fully utilised in this study (see Chapter 3) as to address some of the initial aims of this project specific conditions had to be met. As additional datasets are collected and more specific questions are generated such freedom may become more difficult to achieve. Understandably, independence of samples is a prerequisite to comply with the assumptions for statistical analysis which is achievable by determining the spatial pattern of pollen deposition. In a test of sampling regimes Broström et al. (2005) concluded that although a random regime provided consistently better results, the performance of the systematic results was dependant upon the vegetation patterning of the landscape. Essentially, the distribution of taxa within the landscape influences the relationship of pollen to vegetation and the significance of spatial autocorrelation to the results. Therefore, not only does the patterning influence the RSAP but also the data collection and subsequent analytical processes. There is therefore a real need to understand the underlying spatial patterning of vegetation and pollen. Within this study geostatistical methods have been applied to both datasets to try and elucidate this. Although the limited success of the pollen dataset hampered the formulation of definitive conclusions the methods applied show considerable promise. Investigation of the spatial patterning of both aspects in the landscape will benefit the data collection for the ERV analysis in two ways: defining the range of spatial autocorrelation and assessing the accuracy of the pollen in reflecting the vegetation data. The former relates to the independent nature of the pollen samples which is required for the statistical analysis. Although 400 m has been defined as a representative range (Broström et al., 2004), given the issues involved and the variability of vegetation structures and patterns this is site specific.

Determination of the optimal representative range prior to sampling could ensure independence and facilitate the use of a systematic strategy. The second advantage will be to assess the applicability of the site for the generation of PPEs. For example, at Inshriach Forest the regional dominance of *Pinus* masked the local relationship between pollen and vegetation as identified in the geostatistical analysis which undoubtedly influences calculation of PPEs. By modelling the full spatial patterning that exists in the vegetation the spatial variation can be accounted for in the sampling regime to ensure a much clearer and thorough examination of the likely relationships that exist. However, geostatistical analysis requires a large dataset which, most likely, is much greater than the required surface samples for PPE generation and would demand longer field time. An alternative method that has been utilised in two studies involved the use of simulation software. Mazier *et al.*, (2008) and von Stedingk *et al.*, (2008) used maps of their study areas to design the sampling regime for the

fieldwork element. By modelling pollen deposition at random locations the most suitable sites were used to provide a representative range of values for the desired taxa. By doing so, the influence of a systematic sampling regime can be tested prior to the sampling being undertaken which can facilitate use of a systematic strategy to address more specific questions in the future.

7.1.2 The validation process: what makes a representative set of PPEs?

A decision over whether the PPEs calculated for the study site are representative of the landscape is a question that has to be addressed in all studies obtaining such data using validation tests. This proved to be an essential step in defining the best set for Inshriach due to the range of PPEs derived from the analysis. Recently, Hellman *et al.* (2008) compared the PPEs derived from southern Sweden and Denmark and found considerable differences between the two groups individually and combined, predominantly within the herbaceous taxa highlighting the importance of validation. Causes for this difference are still unknown but it is likely that methodological factors could be an influence. Previously published studies have generated PPEs based upon single datasets and therefore any variations derived from creating subgroups from them are not available. As a result few of these studies present a validation in conjunction with the PPEs when the dataset is first published (Broström *et al.*, 1998; Bunting *et al.*, 2005; Mazier *et al.*, 2008; von Stedingk *et al.*, 2008). Within these the results obtaining the lowest ML score were compared with established datasets to determine similarity and difference. In most cases these have gone on to provide reasonable approximations when used in modelling but the variability has not been examined to establish the most appropriate PPEs.

Within this study two approaches were used to validate the PPE groups: forward modelling and the REVEALS model. Two additional studies have used simulations to aid identification of the most suitable PPEs: Räsänen *et al.* (2007) in Fennoscandia and Soepboer *et al.* (2008) in the Swiss plateau both used forward modelling simulation to compare with modern observed pollen deposition. However, at Inshriach differences were detected between the results of these approaches as the Humpol model was less susceptible to changes in PPE values than REVEALS. As a result of this each method selected a different PPE group as the most representative of the site. Consequently, what method should be used as a validation procedure? If available an independent sample dataset should be applied to the model intended for use within the subsequent reconstructions at the site. As carried out in this study multiple spatial and temporal scales should be addressed to investigate the stability of the values under differing conditions. The most time consuming aspect to this procedure is the data collection which may be out of the scope of some studies with respect to time and financial constraints. In such a situation a validation should be conducted on contemporary samples which can be collected during the initial sampling procedure

for the PPE dataset. Ideally, additional samples will be collected to those used for the PPE calculation but, again, where this is not possible a sub-set can be derived from the available samples in a cross-validation technique.

7.1.3 How many more PPE sets are required to facilitate general application of quantitative models?

As more PPEs are generated more questions will be raised but there has to be a limit for practical purposes. As mentioned studies have shown differences when reconstructions obtained using PPEs from different regions are compared (Nielsen, 2004; Hellman et al., 2008). Such effects are greater within low diversity reconstructions where the impact of a poor reconstruction is significant for the remaining taxa due to the use of proportions (Sugita, 2007b). Although differences can be incorporated from the variability of the observed data the results highlight the problems surrounding the representative nature of the PPEs. To date, there is still no conclusive understanding of why there is a difference between the PPEs from this region with numerous potential effects suggested by Broström et al. (2008) including: methods used differ between studies as there are not standardised processes in place for collection of vegetation data based upon both coverage and presence/absence and alternative approaches; climate has proven to be a driver of pollen productivity (Barnekow et al., 2007) but such influences are difficult to quantify and further studies are necessary to develop understanding with respect to this variable: PPEs for genera based upon different species have the potential to be influenced by different reproductive strategies (von Stedingk et al., 2008) but the taxonomic precision of pollen analysis will be the prohibitive factor in accounting for this. These problems raised above underline the need and urgency for broadening the environments from which PPEs are obtained as this has the potential to be the main limiting factor to the approach. At present the number of taxa which have corresponding PPEs is low, 15 tree and 18 herb taxa (Broström et al., 2008), hence there are limits on the taxon diversity that can be modelled and ultimately the information generated. As shown in this study, a change in the number of taxa included within the model can significantly influence the interpretations of the results. Constraints placed by the range of taxa for which PPEs are available, largely site specific, will have to be considered. As most samples are calculated relative to Poaceae where PPEs are unavailable these can, in theory, be substituted from other sites but then varying environmental influences have to be addressed (cf. Hellman et al., 2008).

Another main consideration has to be the time frames to which the quantitative models will be applied and if the PPEs can be regarded as an actual reflection at the time. At present an assumption of the modelling is that PPEs are stable or constant through time (Sugita, 2007c; Sugita, 2007b; Broström *et al.*, 2008). Although climatic changes have been of limited magnitude in

relation to the remainder of the Quaternary short-lived fluctuations such as the Little Ice Age and Medieval Climatic Anomaly provide problems in recreating environments different from the present and recent past. The impact of temperature changes on the pollen productivity of some taxa has been shown (Hicks, 1999; Sjogren et al., 2006; Barnekow et al., 2007). Huusko and Hicks (2009) found that although PAR fluctuations were evident in traps they were poorly replicated in the fossil record due to the smoothing effect of the sedimentation rate and sampling regime which creates difficulty in quantifying the influence of this factor. Furthermore, additional studies have suggested that this is only applicable for taxa at the limit of their range as they become more susceptible to fluctuations in marginal habitats (van der Knaap et al., 2001; Kuoppamaa et al., 2009). Consequently, reconstructions based on PPEs uncharacteristic of the contemporary conditions risk producing erroneous results, especially if the site is or has been located close to a taxon limit. Analyses to detect correlations between pollen abundance and vegetation density have been conducted in Greenland (Schofield et al., 2007) and Siberia (Pelánková et al., 2008; Pelánková and Chytrý, 2009) but these studies were not focused on collection of PPEs. Although Pelánková and Chytrý (2009) found a strong correspondence between climate and taxa response their study highlighted a variable relationship between the presence of vegetation and pollen. For example, the proportion of Larix was significantly reduced when Pinus or Picea was present but did not correspond to changes in *Larix* presence in the landscape.

Finally, what determines the number and taxa included in the reconstructions? Here, comparison of the 5 taxa reconstruction and those using 12 taxa exhibited considerable differences, which was also the case in Hellman et al (2008). Consideration, therefore, has to be given to the threshold for taxon inclusion. At Inshriach the 5 main taxa comprised an average of 75% TLP and the diverse reconstructions incorporated taxa contributing 95% TLP (on average). Caseldine and Fyfe (2006) presented similar statistics with simulations based on taxa providing at least 95% TLP but few other studies state this value. Publication of these in addition to the number of taxa should be examined in order to facilitate result interpretation and comparison. Optimising the information that can be obtained with potentially limited data upon parameter values will be an area for future work whilst more details are gathered relating to the consequences of variations in PPEs. Recently, the formation of a network, LandClim a NordForsk Network, aims to reconstruct vegetation for inclusion in climate models. In order to generate suitable maps plant functional types or PFTs (Prentice *et al.*, 1992) have been utilised which enables a greater diversity of species to be incorporated into the reconstructions. Thus available PPEs have to be assigned to each PFT equivalent potentially increasing errors.

7.2 LRA Modelling

Application of the quantitative techniques at Inshriach provided mixed results, in part due to the PPE problem. Dominance of Scots pine influenced the sampling locations for the modern material and limited the diversity of the pollen assemblage. Existing methods for qualitative and semi-quantitative analysis provided equally valid interpretations and this casts doubt on the value of attempting a quantitative modelling approach in such an environment.

7.2.1 Can quantitative techniques be used to address structural questions?

Given the results obtained from Inshriach Forest questions surrounding the influence of vegetation structure upon pollen representation remain. No strong relationship between RSAP and vegetation patterning was detected but, as mentioned, the nature of the data did not facilitate this. Consequently landscape heterogeneity and its influences remain a focus for future research. At Inshriach heterogeneity was derived from both taxon patterns but also age class differences which may not be conducive to detecting structural differences. Landscapes under management may not be suitable for modelling as they have a predominantly uniform structure (Mason *et al.*, 2007). These differ from non-managed systems with respect to species composition and structure (Kuuluvainen *et al.*, 1998) within the stands and the degree of connectivity in the landscape, due to removal of the natural disturbance regimes (Peterken, 1999). Differences in pollen dispersal between such woodland contexts have not been extensively investigated and therefore limitations in the representation of models to such environments could exist which makes structural investigations difficult. Therefore, comparative studies should be conducted within natural/semi-natural contexts to investigate this issue further.

Determining patterning of vegetation is an issue that presents problems both spatially and temporally, especially for landscapes under disturbance regimes (cf. Gillson, 2009). In order to fully understand any system these two elements need to be investigated concurrently (Manning *et al.*, 2009). However, the current form of the LRA models does not enable questions of spatial patterning to be addressed, as the RSAP is treated as a homogenous area. Nor does it allow temporal linkages to be made. Inclusion of a further step would be required to develop this tool in the model. Such a method for spatial patterning is available in the Humpol technique which uses species' ecological requirements, DEMs and other available data to provide 'plausible' scenarios. However, the need for empirically driven rather than model data is important to validate such results. A second possible method would be the use of high spatial resolution sites which will provide overlaps in their RSAP (cf. Pratt, 2007). Geostatistical or visual analysis could be used to derive scenarios by combining the spatial information obtained from the site structure.

7.2.2 Influences on the LRA modelling performance

If these models are to be widely available an important requirement will be the education of users as to the limitations and potential influences on the model output. As with most modelling studies accurate determination of the uncertainty incorporated into the output is necessary, however large, from which informed interpretations can be made. Such uncertainty is derived from the PPEs, chronological control, number of sites included and any processes active at these sites that may manipulate the data. Recently, Hellman et al. (2008) published details of model requirements to produce valid results. In their work, sampling design, PPE dataset and taxa included were investigated to determine their influence on the results obtained. Firstly, the sampling design is crucial to obtaining the best reconstructed values as a representation of the regional pollen rain is essential to provide accurate estimations at the local scale. A number of tests have shown that increased numbers of sites lower the standard errors but the estimated mean does not vary (Sugita, 2007b; Hellman et al., 2007; Hellman et al., 2008). An initial constraint of the model was to have numerous large sites (Sugita, 2007b) but these results confirm that basin size is not a stringent condition provided the number of sites can delimit the regional pollen rain enabling wider application of the models. Secondly, both studies found errors due to inappropriate PPEs, as discussed in section 7.1.2. Finally, suitable protocols have to be established to ensure that full validation has been undertaken prior to use of the model output (Hellman et al., 2007).

Validation studies of the LOVE model (Sugita, 2007c) are fewer than those for the REVEALS model but unpublished results show an equally good performance between the two (S. Sugita, *pers. comm.*). Essentially, similar methodological factors raised for the REVEALS model will be applicable for LOVE. However, the results at Inshriach demonstrate a need to test this model further. Issues may arise from the scale of the investigations used to determine the underlying principles of the algorithms. These are formulated based upon regional studies addressing processes occurring over large predominantly regional scales. At a more local spatial scale the influences of vegetation height and structure on pollen deposition become more important, which may complicate the assumptions of the model. For example, filtering of the pollen rain by arboreal vegetation surrounding the site may skew pollen representation (Tauber, 1965; Raynor *et al.*, 1974). If occurring, the importance of these influences would have been heightened in Inshriach due to the dominance of woodland around the site and may not be as applicable in open or semi-open contexts. However, vegetation change is not static and therefore knowledge of this has important implications for reconstructing past systems where this situation is likely to occur.

An important aspect in the application of the LRA is the use of multiple datasets which require robust chronologies. Not only does this allow for the proxy records to be matched but it also

highlights potential sedimentary processes that may influence the sedimentation at the basin. An area where this may have implications is with the use of databases to collate the data to be included. If a study has been undertaken with a specific purpose the data may not be compatible for use in models. For example, at Inshriach, sites were used from Birks' (1975) study which focused on the pine decline and concentrated the dating horizons around this period. Therefore, a large proportion of the remaining core had relatively poor chronological definition. Furthermore, as with most scientific studies the improvement in dating methods has been rapid both with advances in old techniques and formulation of new ones; consequently, some data to be included may require additional analyses to ensure that the chronology can be relied upon. In response to some of these issues, the LRA models have been adapted to include time periods rather than single horizons. The ability to allocate pollen samples to 10 - 100 year periods facilitates the use of database results where the inclusion of samples is pre-determined.

7.2.3 Alternative interpretative methods

Three techniques were used throughout the project: quantitative software (LRA and Humpol), modern analogue (applied through multivariate techniques), and the standard 'intuitive' interpretation. All have benefits but their applicability is driven by the ultimate objectives of the project carried out. Initially the standard interpretive techniques provide a good intuitive representation of changing landscape structure. On the understanding that a range of spatial scales can be incorporated into the assemblage and influence the temporal variation general changes are effectively identified. The additional benefits gained from the use of quantitative or semi-quantitative techniques are the defined representation of spatial scale. As such, the LRA can be used to address smaller scale questions where as the MAT approach enables general patterns to be established.

7.2.3.1 MAT

As with the LRA the modern analogue approach has a number of beneficial aspects to obtaining quantitative information from pollen assemblages. To date these have predominantly been utilised within palaeoclimatology to derive regional temperature and precipitation regimes (Prentice *et al.*, 1996; Ortu *et al.*, 2008), but more recently applied to anthropogenic landscapes (Gaillard *et al.*, 1992; Gaillard *et al.*, 1994; Court-Picon *et al.*, 2005; Mazier *et al.*, 2006; Mazier *et al.*, 2009). Reconstructions of vegetation patterns using this method remain more elusive due to difficulties averaging data when multiple analogues are identified (Jackson and Williams, 2004), but this niche is now filled by the LRA approach.

Results at Inshriach were highly variable primarily in response to the use of two techniques in implementing this approach. Overall, use of dissimilarity matrix identified an increasing number of modern analogues when compared to the multivariate approach, despite equivalent data being used. Comparable samples selected also appeared to provide good representations of landscape cover when estimates of landscape characteristics were made from known historical patterns. However, some failings were identified and driven by two factors: the limited range of modern analogues available from the site which was partly a response to the dominance of *Pinus* within the sample masking the presence of subordinate individuals, and that the spatial extent reflected in the modern samples is not equivalent to that of the fossil sites investigated.

The MAT approach does not necessarily provide a less labour- and time-intensive alternative to the LRA. Although the requirement for high pollen counts is removed (Lytle and Wahl, 2005), a large modern dataset is crucial to provide a suitable range of samples for comparison. A poorly selected dataset enhances the probability of type I (inappropriate analogues selected) and type II (suitable analogues overlooked) errors influencing the procedure (Jackson and Williams, 2004). Inevitably, the size of this modern dataset will be determined by the questions being addressed within the study and its location. Where numerous studies have previously been undertaken a large database of modern samples provides a good basis (Guiot, 1990; Huntley, 1990; Williams et al., 2001; Nakagawa et al., 2002; Ortu et al., 2008), for example North America alone encompasses 4500 available modern samples (Jackson and Williams, 2004). Data collection during individual projects is beyond the target which necessitates the availability of such databases to expand this and enable suitable numbers of modern sites to be freely available in a number of regions. Secondly, the dissimilarity coefficient and cut-off value used to determine the analogues selected is an area that is critical to the whole approach (Overpeck et al., 1985; Gavin et al., 2003; Wahl, 2004; Lytle and Wahl, 2005). Overpeck et al. (1985) showed the benefit of signal-noise methods i.e. square-chord distance, which has received wide spread application (Jackson et al., 2000; Williams et al., 2001; Ewing, 2002; Nakagawa et al., 2002; Cheddadi et al., 2006). Such methods use a weighting mechanism to increase the importance of rare taxa in determining the analogues. Prior to this no or equal weighting was applied (Prentice, 1980). The cut-off horizon is significant in the determination of suitable analogues and the level of type I and type II error introduced. As Wahl (2004) explains, these two are not mutually exclusive therefore defining the correct level will significantly influence any results obtained. Pollen count size and the number of taxa that are included determine this level in part, and therefore the decision will remain site specific (Overpeck et al., 1985; Wahl, 2004). To ensure an objective level is derived statistical analysis is conducted prior to MAT results being obtained.

An aspect which requires further investigation is the lack of consideration for pollen productivity and dispersal issues. Recent studies employing the MAT technique take these into consideration in that analogous modern sites are used i.e. basin size and type to reduce errors associated with basin changes. In a study of anthropogenic landscapes Gaillard *et al.*(1994) suggested differences between the basin sizes of the modern and fossil sites was a contributory factor to the non-analogue situations encountered. This is attributed to the scale at which pollen captures the vegetation communities as appearances and process differ at varying levels (Delcourt *et al.*, 1983). Some studies fail to take this into account which is perhaps due to the difficulties of finding analogous sized basin in a wide range of environments. In addition, the assumption of stability in basin size through time necessary for the LRA approach becomes applicable with respect to this issue and encompasses greater limitations.

Ultimately, the main concern with this technique is the lack of suitable analogues for some time periods or situations i.e. Late Glacial and anthropogenic environments and the knowledge that it is not possible to 'prove' that communities that existed in the past are directly comparable to those of today. With respect to climate, current environments do not provide the temperature regimes that have prevailed in the past, especially the Late Glacial, which will become more prominent with warming trends and increasing CO₂. A further argument for the use of this technique to derive climate information is the importance of additional factors in determining vegetation structure and landscape patterning. Although climate has a demonstrable influence over the distribution of communities there is a structure of spatial and temporal interconnections that also drive some of these changes. For example spatially differentiated abiotic influences such as soil structure and water availability will combine with biotic processes such as competition and disturbance regimes (Jackson and Overpeck, 2000). Temporally the presence of past vegetation patterns will determine current ones to some degree, as local plant occurrence has a greater influence on regeneration after gap creation (Belyea, 2007). Linkages between climate and pollen distribution can therefore be complex and not replicated in the almost simplistic approach of sample matching. In relation to determining anthropogenic landscapes this problem is exacerbated by the number of taxa that can occur within a range of communities which widens ecological envelope (Court-Picon et al., 2005). Furthermore, multivariate analysis based upon modern pollen samples and a range of environmental factors show the influence on soil properties, nutrient availability, pH and topography (Hjelle, 1999; Court-Picon et al., 2005). In summary therefore, patterns derived from a single study area are difficult to apply to other sites.

7.2.3.2 Forward modelling simulation

In addition to the LRA models there are some forward modelling examples (PollScape, Sugita et al. (1999b); HumPol, (Middleton and Bunting, 2004; Bunting and Middleton, 2005) which use simulation software to create 'landscapes' from which pollen deposition can be simulated. Such an approach can be used to test some of the fundamental principles of palynology (e.g. Bunting et al., 2004) or to compare with actual pollen profiles for hypothesis testing (Gaillard et al., 2008). Soepboer and Lotter (2009) utilised this method to address conflicting theories by applying models to determine the degree of openness within the Swiss Plateau to test the 'open-pasture' theory of Vera (2000). This is an area where utilisation of quantitative models provides an important perspective on past openness developing the standard approach of the NAP:AP ratio as a crude measurer of openness. Similar studies have addressed change in cultural landscapes: Fyfe (2006) investigated upland spread of cultivation in Dartmoor, and Caseldine et al. (2007) simulated the opening of the landscape in western Ireland using both theoretical composition and 'real' landscapes. Recently, Gillson and Duffin (2007) adopted this approach within a management context in the Kruger National Park whereby hypothetical situations were created to obtain an algorithm to characterise the pollen-vegetation relationship. When applied to past pollen profiles the algorithm classified the range of variability in arboreal vegetation proportions and highlighted that current management limits - application of thresholds of potential concern - had not been crossed within 1600 – 5000 years and current patterns were not at critical levels as perceived by park managers.

Caseldine *et al.* (2008) discussed the potential consequences of providing singular definitive scenarios and alluded to techniques defining 'plausible' conditions. They suggested that the aim of these should be to discount particular vegetation constructions as opposed to finding definitive scenarios, and the Multiple Scenario Approach aims to address this. Bunting and Middleton (2009) describe this approach which is a development of the previous forward-modelling software through inclusion of LANDSCAPE, which allows the construction of multiple landscapes (absolute numbers of landscapes totalling $10^4 - 10^5$) through iteration of simple initial conditions i.e. topography (DEM), aspect, soil properties and species ecological information. By adopting the MAT methodology suitable landscapes are selected from dissimilarity measures used to compare actual pollen assemblages to those simulated from all of the landscapes and is described as the Multiple Scenario Approach (MSA). Similarities between the application and principles of this software with the previous simulations models are evident (Bunting *et al.*, 2007; Pratt, 2007; Bunting *et al.*, 2008) but the model provides a greater representation of the uncertainty involved within the reconstruction approach as a whole from selection of a range of landscapes.

Although both simulation models (Humpol and Landscape) differ from that of the LRA the underlying algorithms are comparable and some assumptions are similar. However, limitations of the method differ as has been discussed earlier. Firstly, results from Chapter 4 show that although parameters (PPEs) can be variable this is not consistently exhibited in the output of the model. At Inshriach the results obtained from the LRA were more sensitive to differences amongst the PPE datasets than those of the forward-modelling. As the principal aim of the latter method is to construct multiple landscapes the danger is to alter the landscape, either in form or composition, to fit with the desired pollen data whilst disregarding errors in the parameter data. The implications of this are that erroneous results are obtained from the modelling which in turn impact upon the interpretations made. As with most modelling studies it is crucial to undertake a suitable validation process to ensure that this is not the case, either with the parameter set or resultant modelling. Secondly, the resolution (pixel size) of the simulation maps can influence the results obtained. Bunting et al. (2004) noted this in a number of simulations used to detect influences on the RSAP distance; however this is a factor that is going to be problematic to overcome. Different scales have been used in studies published to date: 10 m, Caseldine and Fyfe (2006), Gillson and Duffin (2007), Bunting et al. (2008), Hellman et al (2009b) and Soepboer and Lotter (2009); 25 m, Caseldine et al. (2007) and Hellman et al. (2009a); 50 m, Fyfe (2006) raising issues for the comparability of these results. Standardisation of the cell size used within the simulations could be introduced but data availability may limit the application of this. Thirdly, consideration has to be given to the chronological control when multiple sites are used (Pratt, 2007). To date, most forward-modelling studies have been conducted on single profiles, but the benefits of using multiple cores to further spatially constrain the results will necessitate this. Finally, insufficient landscape size to represent both the extent of local and regional pollen rains will underestimate the level of background within the simulated pollen assemblages. Caseldine et al. (2007) discussed this issue in relation to simulations generated for Achill Island, Ireland, and stressed the importance of accurately assessing the background component prior to generating the simulation maps. Nested grids can be used within the MSA and therefore this can be included within the model (Bunting and Middleton, 2009), however, it is the responsibility of the user to ensure that this is represented when species composition and topography is accounted for.

7.2.3.3 Future of modelling studies within palynology

As has been eluded too within the above discussion all methods of pollen interpretation, both qualitative and quantitative, have their advantages and disadvantages. The application of suitable techniques should primarily be made upon a study and site specific basis. However, the benefits of some of these techniques do overlap and they can be combined to provide a complementary

analysis structure. This involves a number of steps with different techniques applied to optimise the benefits of each technique:

- 1 Standard 'intuitive' interpretation: The benefit of this approach is centred upon the experience of the analyst in interpreting the ecological preferences of taxa identified at the site. Key periods and taxa can be determined and an evaluation of the site for application of quantitative techniques can be made. Potential indicator taxa may also be identified from the minor components that would not be suitable for inclusion in the modelling due to low proportions to gain a more detailed insight into composition.
- 2 Landscape Reconstruction Algorithm: Identifying the local and regional components of the pollen assemblage and the application of the correction factor is the main benefit of this approach. Definition of these components can have important implications for the interpretation of changes occurring at a site and is an invaluable development within pollen analysis. Application of this to periods of interest defined during the initial interpretation can provide an alternative perspective to changes occurring. For example during periods of rapid change the influence of background can be removed to detect the magnitude and reality of these local effects.
- 3 *Modern analogue technique*: Once the spatial extent represented by the site has been established MAT can be employed to infer vegetation patterning and attributes at the site. By understanding the spatial representation this can be incorporated into the site selection for the modern analogue samples. As the analysis has been undertaken this removes the requirement for definitive analogues and enables general characteristics to be defined including an understanding of the spatial patterning of the community elements.

7.3 Applications of palaeoecology and quantitative techniques

Allocation of correction factors derived from pollen productivity differences and filtering of spatial scales provides an alternative to the current methods available. Although it is understood that pollen productivity is species specific and basin size influences the representation of the landscape (Jacobson and Bradshaw, 1981) the LRA sub-models provide a composite correction to the pollen assemblages. Consequently, the benefit of the LRA approach is to achieve a representation of spatial scales within the landscape from which greater detail and understanding can be obtained. Furthermore, provision of a different perspective can alter the interpretations made from the assemblages but caution has to be taken at present given the current limitations. In response to this defined hypotheses can be formulated and suitable sites chosen to address these.

7.3.1 How does palaeoecology aid conservation and landscape restoration?

Awareness that human dominance of the environment is altering the natural landscape and processes acting within it has heightened the need for management. Conservation programmes are implemented to maintain existing landscapes and direct some to a more 'natural' state. However, defining what constitutes a 'natural' state and the sites requiring such management are difficult to resolve (Birks, 1996). Palaeoecological investigations provide a mechanism by which the criteria can be assessed over a longer time frame. Defining the naturalness of the landscape, however, can be achieved through application of baselines. In a study of forest history in southern Sweden Lindbladh et al. defined this goal as 'the ecosystem present before human influence became pronounced on the landscape' (2007 pp. 284). In some instances these conditions cannot be accurately defined (e.g. Bradshaw et al., 2003; Jackson and Hobbs, 2009) and it has been suggested that cultural landscapes should not be discounted because of their origins as the communities produced can become valued habitats (Foster and Motzkin, 2003). Furthermore, Gillson and Willis (2004) stressed that ecosystems are unique entities at specific points which are impossible to replicate; a point which was reiterated by Jackson and Hobbs (2009 pp. 567): "restoration to a historic standard is anachronistic". Conversely, it has been argued by a number of authors that an envelope of change should provide the reference to assess the degree of temporal variability (Foster and Motzkin, 2003; Dearing et al., 2006a; Jackson and Hobbs, 2009). By doing so, the dynamic nature of the system can be considered rather than a single, static point in time (Froyd and Willis, 2008). Incorporating this information can inform and focus directives based upon the sensitivity of the landscape when seen in the context of long-term trends. Willis and Birks (2006) and Dearing et al. (2006b) emphasised this and suggest that landscapes with increased sensitivity to invasions and disturbances should be given greater conservation status. Only the long term view of the landscape can provide this information, as monitoring timescales are too short to describe the full range of variability.

Concerns over the ability of proxy records to provide such detailed information have arisen, although Swetnam *et al.* (1999) identify the benefits of historical and long-term data in understanding the system despite the limitations and state:

"...the record of the past is often brief, fragmentary, or simply unobtainable for the process or structure of interest" (Swetnam *et al.*, 1999, pp. 1201).

Issues of taphonomy, temporal and spatial resolution are not new to palaeoecological debates (Davis, 1973; Birks and Birks, 1980; Havinga, 1984; Davis, 2000), but technological and theoretical advances may help to address some of these. At Lochan Geal impact of sedimentary processes

affecting the short core became more apparent when the LRA model was used and compared to observed data. There is a strong argument that such situations may not always be detected, especially if suitable validations are not undertaken, and that sites that have been previously studied in detail should be used in these models. This will ensure that suitable information is used in the model and the derived interpretations are valid. If funds and time are limited incorporating previously analysed sites would be a valuable undertaking as, if suitable sites are selected i.e. well chronologically constrained, this would ensure that the model can be applied.

7.3.1.1 How can palaeoecology aid woodland management?

Government strategies have responded to calls for action with respect to the declining natural status of British woodlands with a focus for increasing biodiversity within plantations. The UK Biodiversity Action Plan (Anon, 1994) is concerned with the promotion of biodiversity and development of sustainable use of resources. Plantations, although they can promote biodiversity in their own right (Quine and Humphrey, 2003; Brockerhoff et al., 2008; Quine and Humphrey, In press), provide monocultures that fail to encapsulate the characteristics of the natural stands. Furthermore, in the past plantations have been established on sites such as peatlands, which are themselves 'hotspots' for biodiversity (Quine and Humphrey, 2003). Following the UK BAP the UK Forestry Standard (Forestry Commission, 2004) detailed plans for sustainable forestry within the UK whilst benefiting socially, environmentally and economically. These and similar policies have addressed the need to reduce the non-native species used within forestry and encourage the use of native taxa with less invasive management techniques. Benefits from these approaches are to create habitats that are suitable for native flora and fauna that are currently endangered from native woodland loss. Restoration of plantations of ancient woodland sites is an area that has been championed by The Woodland Trust (Pryor et al., 2002) promoting higher species diversity and habitat provision. As addressed above, the palaeoecological perspective would be a valuable contributor to defining the nature of such woodland systems prior to intensive human intervention. This would not provide a definitive end point but would define characteristics and an indication of response to forcing factors in the past that could inform management plans.

One of the taxa identified by the UK BAP as requiring intervention was the Capercaillie which, as mentioned in Chapter 2, inhabits open pine woodland with a strong *Vaccinium* ground flora and requires habitat areas of ~300ha (Kortland, 2006; Stevenson, 2007). A recent EU funded project highlighted the need to increase Capercaillie numbers with focus upon managing grazing, controlling predators and increasing viable habitat for 6 metapopulations within Scotland, one of which is in Strathspey (EU LIFE Project, 2002; Project, 2007). Intervention required the management of woodland areas to provide suitable open leks and optimal thinning of the stems to

provide enough light to provide an ericaceous ground flora. Palaeoecological perspectives have the potential to provide information on previous habitat structures when Capercaillie populations flourished. Results from this study show that the landscape around Inshriach has previously been dominated by open birch woodland with a relatively recent transition to pine woodland around the site. Unfortunately, details surrounding the spatial patterning and density of woodland cannot be obtained from the pollen data which is the information required to fully understand the former habitat of the Capercaillie. Further investigations that could perhaps increase the information available would require a network of smaller sites, i.e. forest hollows, to enable overlaps in the source areas and increase information as to the spatial structure. Application of additional analysis such as plant macrofossils (*sensu* Birks and Birks, 2000) would support the detection of local presence of both pine and blaeberry, especially as the latter is often poorly represented in the pollen record (Broström *et al.*, 2008). This was identified within the contemporary samples taken from Inshriach but not the lake sites which advocates the use of small, forest hollows for such studies.

It is not just the stand scale where palaeoecology can provide a useful perspective for future management. A development plan to implement the UK BAP is the Forest Habitat Network approach (Anon, 1994; Scottish Executive, 2006) with the aim of reducing fragmentation by addressing issues at the landscape scale in addition to the stand scale. By planting new woodlands in addition to enhancing and conserving smaller areas the aim is to connect stands to create larger areas of woodland. Creation of larger woodlands encompassing both old growth stands and native plantations are encouraged to provide suitable sized habitats for a number of the native fauna i.e. Capercaillie, Scottish Crossbill (Hampson and Peterken, 1998; Humphrey et al., 2006). However, there is ongoing debate as to how this approach should be implemented as Humphrey et al. (2006) stress the danger of using an approach that is too simplistic for the landscapes being considered. For example, plantations on previously un-forested areas have responded differently to those that have been planted on ancient woodland sites (Quine and Humphrey, 2003). Therefore, planting areas without consideration could prove to be counterproductive. In addition, the patch size of the different communities (open and forested) has implications for the habitats and use of the landscape by the flora and fauna the interventions aim to protect (Ratcliffe et al., 1998). Utilising the palaeoecological record would give an indication as to previous levels of woodland cover, if any at a site, and the relative proportions of components. Selection of sites can be achieved to meet with the specific objectives as to the scale required to obtained information about the landscape history. Investment in planning and investigative studies would conserve resources in the future and provide an important insight to past changes applicable to development of management strategies.

7.3.2 Can quantitative techniques provide an additional perspective?

Use of the LRA at Lochan Geal shows the potential contribution that the LRA model can make to differentiating between local and regional changes. Interpretative differences were based upon distinct features at the local scale which were masked by regional patterns when standard interpretation was used. Benefits of this approach could be achieved within conservation as at present there are two broad areas for concern: (1) which areas require management and to what level? (2) what are the implications of future climatic variation? Details of these issues have been addressed above but can quantitative analysis enhance the information obtained from intuitive palaeoecological interpretation alone?

Difficulty of defining baselines as management targets have been addressed above and Lindbladh et al. (2007) highlighted the importance of scale in establishing this level. Ecosystem change occurs at a range of scales in response to forcing factors and internal processes (Delcourt et al., 1983). Encapsulating the processes occurring at these different levels within the palaeoenvironmental data is required to fully understand interaction and community development (Gillson and Willis, 2004). The foundations to achieve this are provided through the application of the LRA, despite being within the relatively early stages of development. Disentangling the records of the regional and local pollen rain enables vegetation reconstruction on differing scales which is dependant upon the size of the basin used. Inclusion of multiple sized sites within a single field area would distinguish the manifestation of vegetation patterns within the pollen record. Furthermore, Manning et al. (2009) suggest that simultaneous investigation of temporal and spatial scales in ecology will enhance understanding and facilitate management. Similar strategies should be pursued in palaeoecology to provide analogous data. To date, limited studies have investigated the spatial representation of pollen deposition (Binney et al., 2005; Waller et al., 2005) with no assessment of difference in spatial scale. Continued management and development of Forest Habitat Networks could benefit from the LRA modelling technique if such spatial patterning was also incorporated. Again, this heightens the demand for further investigation of the spatial relationships between pollen and vegetation if these techniques are going to benefit the wider community.

Future projections for climate presented by the IPCC (IPCC, 2007) give a range of potential scenarios. With each, the impact on vegetation will be unique and to some degree unpredictable. Shifting ranges of current taxon limits and associated ecosystems presents an obstacle to the modern analogue approach. Williams and Jackson (2007) suggest that the number of 'no-analogue' situations will only increase with continued climatic variation. Again, it is the LRA approach that could provide the tool to overcome this issue as reliance upon suitable communities prevailing could be lost. However, this is dependant upon future findings in relation to variations in PPEs. It

has been shown that the variability of PPEs at ecotone limits could invalidate the use of this approach in such systems. Until a greater number of data sets have been acquired and analysis conducted the full potential cannot be assessed.

A limitation to the application of these techniques, primarily within conservation, is the increased costs involved to provide suitable data. A hierarchy of work packages are involved and the LRA requires increased field time, significantly so if PPEs are required, plus the availability of robust chronologies for sites. MAT necessitates the collection of a wider range of modern samples. MSA only requires good chronology if multiple sites are utilised. Consequently, the necessary data provision could be outside the budget availability for some management studies. As mentioned, the aim of the project will define the approach that is taken and the individuals included. Furthermore, enhanced participation in and use of databases will be required to reduce such costs and enable wider employment of these techniques.

7.3.3 Wider context of the modelling approach within palaeoecology

More generally, modelling in palaeoecology has implications for understanding future environmental changes whether being incorporated into management schemes or used within GCMs i.e. LandClim. The role of these models in providing additional information from that already gained from qualitative interpretations has to be considered. Swetnam et al. (1999) have argued that the filtered information received from the palaeoecological record provides a patchy reflection that cannot be fully related to current environmental processes. Although this is an issue with the data feeding the models does this have implications for the application of these techniques on imperfect data? More recently, Belyea (2007) suggested that a qualitative representation of the past may be the only information we can expect to obtain from palaeoenvironmental records. Both of these papers imply that complexity inherent within the prevailing systems cannot be established for the past. A consideration for future research would be to incorporate a more defined spatial element to the modelling software. Inclusion of numerous datasets within the LRA model provides some progress towards this but the scale of the processes involved have to be effectively characterised through initial geostatistical investigation. Inevitably, this would involve a high spatial resolution for any study and therefore problems with financial and time constraints arise. In such situations, use of databases e.g. European Pollen Database, will become more important to encapsulate this variability (Fyfe et al., 2009). However, the erroneous elements included through extrapolation of data points would be reduced and additional information relating to the scale of changes would become more apparent. If greater spatially definition could be embedded into the analytical methods the landscape could be studied to include a number of processes occurring over differing spatial extents. Such detail will facilitate stronger cross-disciplinary links beneficial for formulating research objectives and encouraging data dissemination.

An additional issue that has been raised in relation to a number of palaeoenvironmental modelling techniques is that of temporal changes. Changes which have occurred in the past are important in determining prevailing patterns, and this is especially true of ecology (Swetnam *et al.*, 1999; Gillson, 2009). Few models take into account the linkages between horizons and in contrast treat each as a separate entity. Using the HumPol software Caseldine and Fyfe (2006) successfully incorporated this element into the decision process to aid landscape scenario selection. Encapsulating the temporal connectivity may provide an important stage in determining landscape change if processes of current ecosystems can be deemed representative of the past. Spatial connectivity, characteristics closer to a point are more likely to share attributes (Legendre and Fortin, 1989), influence the patterning of the landscape and could provide an understanding of similar temporal connections. Fundamentally, the degree of spatial autocorrelation can influence the succession following disturbance as those taxa closer to the newly created open area have a greater advantage (Belyea, 2007). If such links can be identified spatially, for the present, this has the potential to be applied temporally.

7.4 Limitations of the quantitative techniques

Despite their separation within this discussion the three techniques described are inter-linked in their approach i.e. LRA and MSA; MAT and MSA. Fundamental principles are associated with all of these approaches which are difficult to limit: uniformitarianism and equafinality.

Uniformitarianism – 'the present is the key to the past' - is a principle that underlines all of the techniques discussed. Assumptions of the correction factor approaches rely upon the stability of pollen productivity and that if obtained from the current landscape is representative of the past. The forward modelling approach when used for 'real' landscapes assumes that the ecological requirements of species have not changed. Similarities between that and the assumptions of the MAT approach are evident in that the modern landscapes are expressions of those in the past. Essentially, these assumptions have repercussions for application of the approaches to climate regimes different from those prevailing at present i.e. the Late Glacial. As Bunting and Middleton (2009) discuss modern ecological information is heavily based upon modern monitoring studies rather than descriptive processes and tolerances, consequently boundaries of the MSA are stretched when not used within full interglacial conditions (Bunting and Middleton, 2009). This is further limited by the requirement of PPEs from analogous cold climate locations. Even so, the MAT technique relies upon environmental conditions of the past prevailing at some location today and

that a suitable pollen assemblage has been obtained from this area. This provides a more stringent limitation to the approach and is the main contributor to the non-analogue situation. A second fundamental issue is the degree to which anthropogenic activity has influenced patterns. Landscapes are dynamic systems which can respond in non-linear ways to external forcing factors (Mayer and Rietkerk, 2004). Increasing intensity of human activity throughout the Holocene, especially since the agricultural revolution and more recently the Industrial Revolution, has seen dramatic changes within natural systems (Messerli *et al.*, 2000). Therefore, consideration has to be given not only to the presence of anthropogenic communities but also the influence of these in modifying natural processes. Only then can the decision over whether such systems are truly representative be made.

Equifinality is ubiquitous in all geographical disciplines and palaeoecology is no exception. In consideration of the application of quantitative techniques it relates to the provision of multiple pollen assemblages from the same vegetation patterns and vice versa. Identifying one approach where this issue is more prevalent is difficult as despite the different methods the end point is similar. Using discrete analogues the MSA and MAT techniques often identify a number of compositions that are similar to the landscape being investigated. Moreover, within the MSA the identification of suitable analogues can be further fed into the iterative process to increasingly define the 'plausible' landscape. When circumstances arise using MAT to determine climatic parameters, for example, the best analogue is taken or a combination of data from the closest matches (Overpeck et al., 1985; Nakagawa et al., 2002; Cheddadi et al., 2006). Although, intuitively, this appears conducive to identification of the 'actual' landscape such detailed reconstructions may mask the potential composition and hamper understanding of the processes. As these approaches only compare the product rather than constructional processes the issues surrounding equifinality are more apparent (Haines-Young and Petch, 1983). Acknowledgement of the possible scenarios will decrease the exactness but will demonstrate the complexities of the system and contribute to understanding of the formation processes. In contrast, the LRA deals with this influence in a different manner through provision of a mean value and error. Presentation in this format allows for assessment of the uncertainty of the analysis whilst fully appreciating the potential vegetation compositions

Finally, an issue that has been frequently touched upon is scale. Each fragment of the system being represented by the pollen, and the sample itself, is influenced by different scales. As a result a hierarchical interaction of patterns and processes is created (Gillson, 2009) and the representation of the landscape reconstructed by the pollen record may not reflect the full range of variability (Mayer and Rietkerk, 2004). In essence, a pollen sample taken from different areas will not only vary based

upon the size of the deposition basin but also the landscape characteristics. Therefore, if a distribution regime is active the scale at which this occurs will determine its presence in the palaeoenvironmental record. Development of the LRA uses this understanding and, to some extent, can adapt the pollen view to required scales. However, the patterns and processes of past landscapes cannot be fully distinguished and this will impact upon the results.

Chapter 8: Conclusions

This thesis has outlined a number of investigations into the use of quantitative models within palaeoecology as a development of standard reconstruction techniques. A number of areas have been addressed in relation to this but more questions have been raised than the project aimed to answer.

8.1 Summary of results in relation to the initial aims

This section outlines the main points raised in relation to the aims and objectives of the study.

Pollen productivity estimates

- Methods of vegetation data collection within the initial area around the sample point showed little difference in the PPEs calculated. This suggests that opportunities to find less labour and time intensive methods could be sought without compromising the results obtained.
- Open and enclosed (woodland) sites show differences between PPEs but additional factors could be influencing the results given the nature of the main vegetation components and therefore further studies are required to investigate this further.
- Variations in the spatial patterning of the sample points influenced the PPEs obtained. Geostatistical analysis indicated that the monoculture structure of the woodland or the dispersal properties of pine could be influencing the pollen representation and masking variations in the vegetation.

Quantitative modelling using the LRA

- Patch-matrix relationships could not be investigated as the site did not facilitate this. However, the importance of understanding this influence has been stressed and should be a prime focus for future research.
- Pine woodlands are highly challenging environments in which to utilise the models and was highlighted by the variability in model output from the time slice results. Again, investigations into to defining the underlying cause and opportunities to counteract this would be beneficial as this feature has implications for the application of the model to past landscapes.
- The number of taxa included within the model has to be considered carefully as this can influence the details obtained from the modelling. Stating the proportion of pollen from the assemblage included within the modelling would be beneficial to the wider community and potential users of the results.

Comparison of interpretation techniques

All techniques have associated benefits and detriments and constraints on the methods employed will be both financial and operational. Results from this study would support a combination of techniques to utilise the benefits from each approach but, again, the limitations of the project will dictate this. If one method had to be selected then the LRA provides a strong candidate as the distinction of regional and local pollen rains transforms interpretations. However, availability of robust PPEs are a large driver of the potential for utilisation.

8.2 Implications of this study

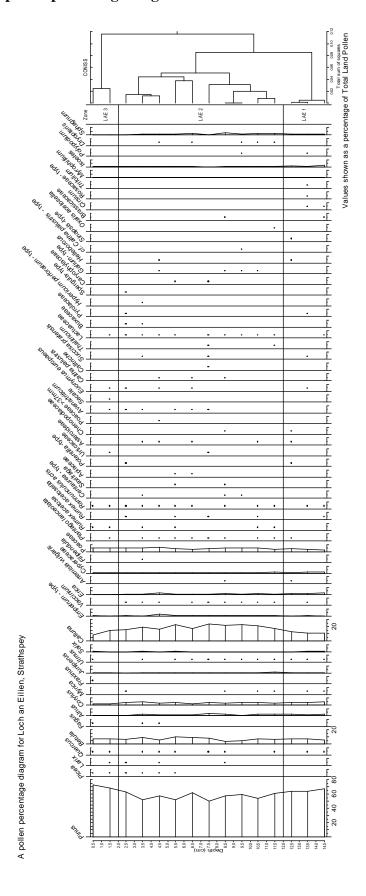
Quantification of pollen data is a strong focus for current research and the results presented in this thesis have shown that the models can strongly influence the conclusions derived from palaeoecological analysis. However, these techniques are not universally applicable as there are areas that are yet to be fully understood by the palaeoecological community. For example, landscape characteristics strongly influence the relationships between pollen distribution and vegetation presence. It is acknowledged that collection of PPEs is highly developmental but investigations into the influence of contrasting landscape structure, climatic regime and methodology are highly encouraged as initially stated by Broström *et al.* (2008). Dynamic systems, such as ecosystems, have multiple states that require analogous information which may not be fully represented by the contemporary landscape. If steps are not taken to understand distinctions between landscapes with respect to their pollen-vegetation relationships temporal application of the models could be severely limited.

Application of quantitative techniques has the potential to be valuable to conservation and management of landscapes in the future as this becomes of increased importance. Management is undertaken at a range of scales and the LRA provides a potential tool to target studies at the most applicable range. Although single, definitive representations appear to be beyond the scope of the models at present understanding the dynamics of the system and response to forcing factors temporally is a valid exercise. Limitations to this are the restrictive quantity of parameter data that is required to feed the model. However, this would facilitate greater communication between the organisations directing conservation management plans and the palaeoecological community. Creating such links could help focus policies based upon long-term, site specific characteristics to restore and manage systems and not provide static representations of specific periods.

8.2.1 Suggestions for further work

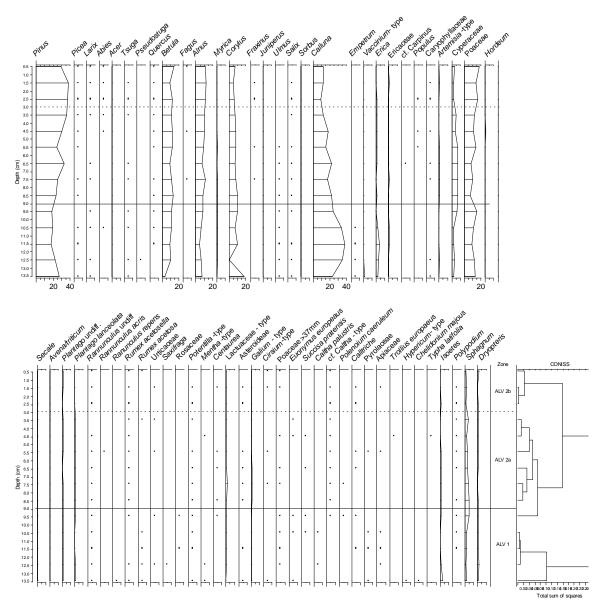
Simplistic models are required as a starting point but development is necessary to represent complex system that prevails. However, there are some fundamental issues that need to be addressed with existing models and parameter collection before increasing complexity can be added to the models. Firstly, greater investment is needed to understand the relationship between pollen and vegetation in a range of environments. For example, differences may be exhibited between managed forests and natural woodlands that could influence the application of contemporary values to past landscapes. Obtaining PPEs from such areas will provide a larger dataset with which to highlight potential influences on different outcomes. This is an area of work that is ongoing and is, to some degree, limited by the time required to undertake such studies. Secondly, understanding the spatial extent and resolution of pollen deposition is necessary if this factor is going to be accounted for within interpretations and future models. This study has highlighted a number of areas where the spatial precision is fundamental to understanding the system as a whole. Understanding the reflection of this in the pollen record would develop knowledge of past ecosystems and forge links with ecologists.

A.1.1 Full pollen percentage diagram for Loch an Eilein



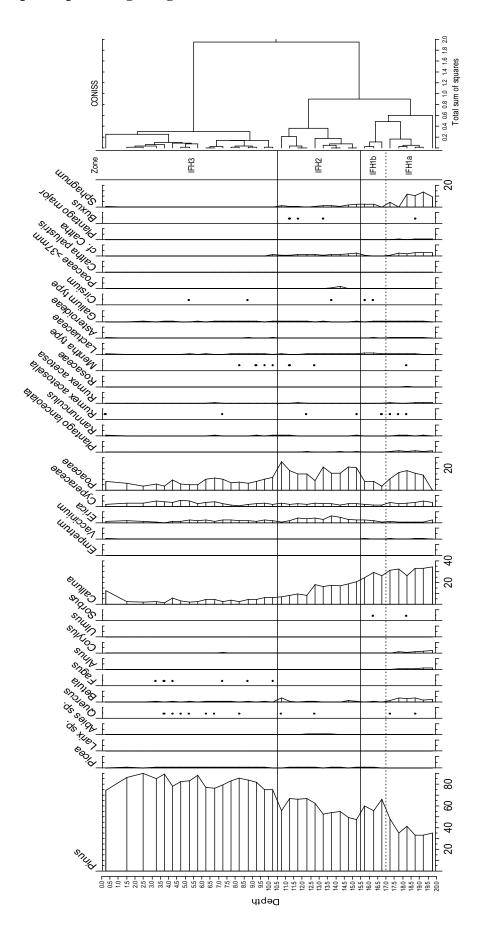
A1.2. Full pollen percentage diagram for Loch Alvie

A pollen diagram from Loch Alvie, Strathspey

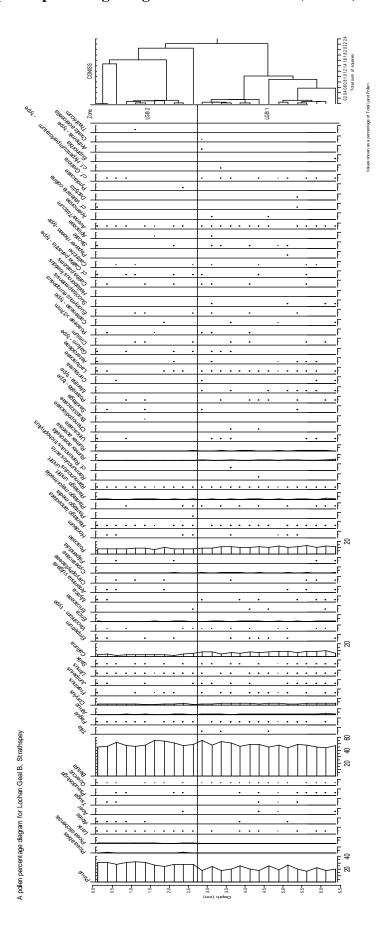


Values shown as a percentage of Total Land Pollen

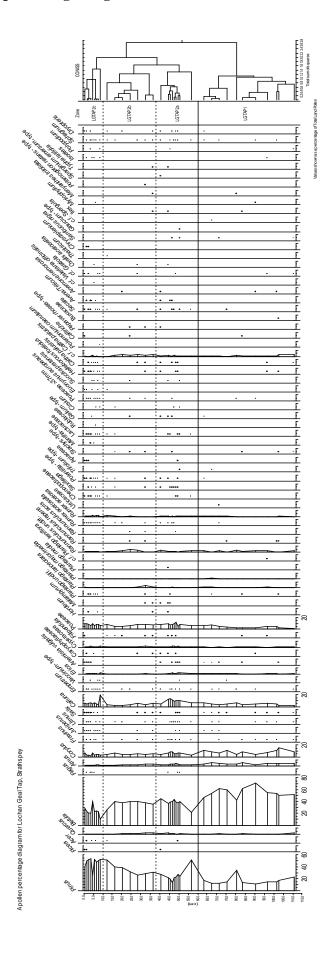
A1.3 Full pollen percentage diagram for Inshriach Forest Hollow



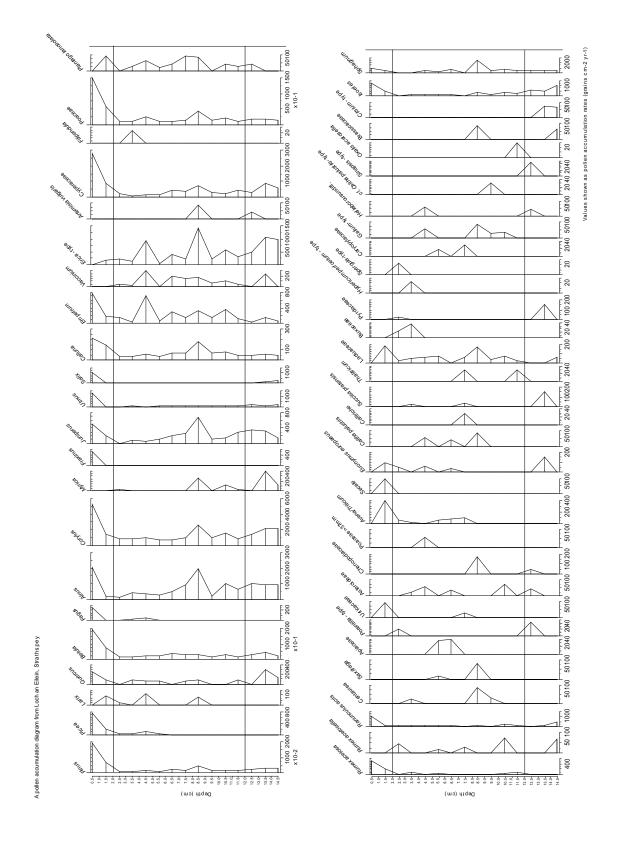
A1.4. Full pollen percentage diagram for Lochan Geal (Core B)



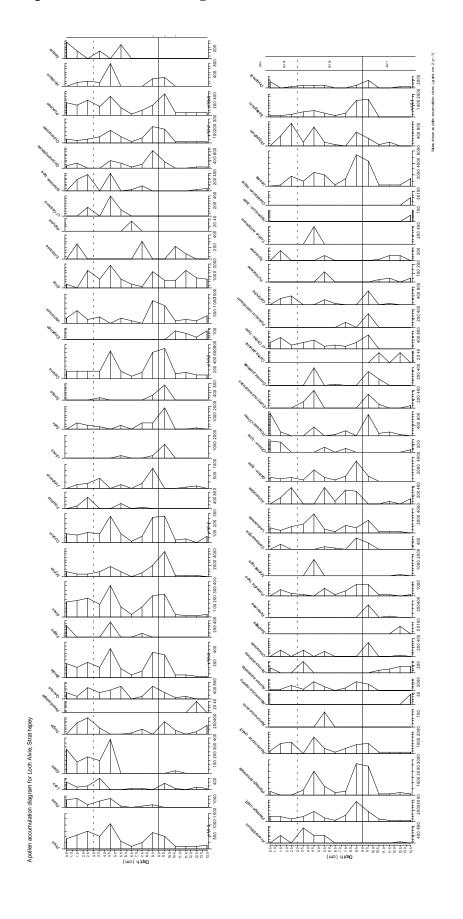
A1.5 Full pollen percentage diagram for Lochan Geal (TAP)



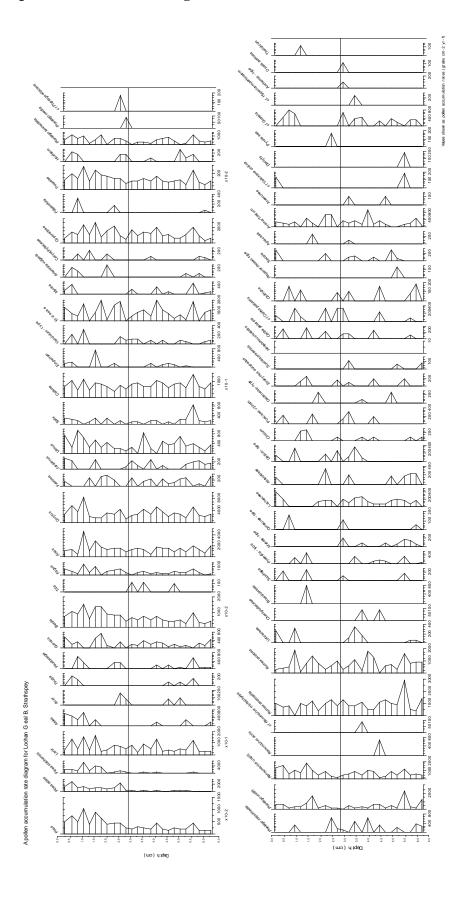
A2.1 Full pollen accumulation diagram for Loch an Eilein



A2.2 Full pollen accumulation diagram for Loch Alvie

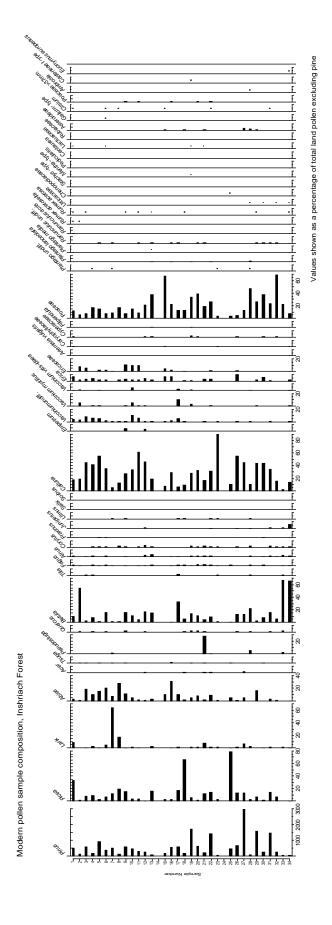


A2.3 Full pollen accumulation diagram for Lochan Geal (Core B)



A2.4 Full pollen accumulation diagram for Lochan Geal (TAP)

A3.1 Pollen percentage diagram for modern moss samples taken at Inshriach forest calculated to exclude *Pinus* values.



References:

- Ali, A. A., Higuera, P. E., Bergeron, Y. and Carcaillet, C. (2009) Comparing fire-history interpretations based on area, number and estimated volume of macroscopic charcoal in lake sediments, *Quaternary Research.* **72**, 462 468
- Ammann, B., and Wick, L. (1993). Analysis of fossil stomata of conifers as indicators of the alpine treeline fluctuations during the Holocene. *In* "Oscillations of the alpine and polar tree limits in the Holocene." (B. Frenzel, Ed.), pp. 175 187. Palaoklimaforschung.
- Andersen, S. T. (1970). The relative pollen productivity and pollen representation of North European trees and correction factors for tree pollen spectra. *Dansmark Geologiske Undersøgelse II RÆKKE* **96**.
- Andersen, S. T. (1974). Wind conditions and pollen deposition in a mixed deciduous forest I: Wind conditions and pollen dispersal. *Grana* **14,** 57 63.
- Anderson, D. E. (1998). A reconstruction of Holocene climatic changes from peat bogs in northwest Scotland. *Boreas* **27**, 208-224.
- Anderson, N. J., Bugmann, H., Dearing, J. A., and Gaillard, M. J. (2006). Linking palaeoenvironmental data and models to understand the past and predict the future. *TRENDS in Ecology and Evolution* **21**, 696 704.
- Anon. (1994). Biodiversity: The UK action plan. Her Majesty's Stationary Office.
- Appleby, P. G. (2001). Chronostratigraphic techniques in recent sediments. *In* "Tracking Environmental Change Using Lake Sediments Volume 1." (W. M. Last, and J. P. Smol, Eds.), pp. 171 203, The Netherlands.
- Appleby, P. G., Nolan, P. J., Gifford, D. W., Godfrey, M. J., Oldfield, F., Anderson, N. J., and Battarbee, R. (1986). ²¹⁰Pb dating by low background gamma counting. *Hydrobiologia*, **143**, 21 27.
- Appleby, P. G., and Oldfield, F. (1978). The calculation of lead-210 dates assuming a constant rate of supply of unsupported ²¹⁰Pb to the sediment. *Catena* **5**, 1 8.
- Appleby, P. G., and Oldfield, F. (1983). The assessment of ²¹⁰Pb data from sites with varying sediment accumulation rates. *Hydrobiologia* **103**, 29 35.
- Appleby, P. G., Richardson, N., and Nolan, P. J. (1992). Self-absorption corrections for well-type germanium detectors. *Nucl. Inst. and Methods* **B**, 228 233.
- Appleby, P. G., Richardson, N., Nolan, P. J., and Oldfield, F. (1990). Radiometric dating of the United Kingdom SWAP sites. *Philosophical Transactions of the Royal Society of London Series B* **327**, 233 238.
- Armit, I., and Ralston, I. (2003). The coming of Iron 1000 BC 500 AD. *In* "People and Woods in Scotland: A history." (T. C. Smout, Ed.), pp. 40 59. Edinburgh University Press, Edinburgh.
- Armit, I., and Ralston, I. B. M. (1997). The Iron Age. *In* "Scotland: Environment and archaeology 8000BC AD1000." (K. J. Edwards, and I. B. M. Ralston, Eds.), pp. 169 193. John Wiley and Sons, Chichester.
- Atkinson, M. D. (1992). *Betula pendula* Roth (*B. Verrucosa* Ehrh.) and *B. Pubescens* Ehrh. *Journal Of Ecology* **80**, 837 870.
- Aylor, D. E. (1978). Dispersal in space and time: aerial pathogens. *In* "Plant disease: an advanced treatise." (J. G. Horsfall, and E. B. Cowling, Eds.), pp. 159 180. Academic Press, New York.
- Barber, K. E., Maddy, D., Rose, N., Stevenson, A. C., Stoneman, R., and Thompson, R. (2000). Replicated proxy-climate signals over the last 2000 yr from two distant UK peat bogs: new evidence for regional palaeoclimate teleconnections. *Quaternary Science Reviews* **19**, 481.
- Barclay-Estrup, P., and Gimmingham, C. H. (1969). The description and interpretation of cyclical processes in a heath community I. Vegetational change in relation to the *Calluna* cycle. *Journal Of Ecology* **57**, 737 758.

- Barclay, G. J. (1997). The Neolithic. *In* "Scotland: Environment and archaeology 8000BC AD1000." (K. J. Edwards, and I. B. M. Ralston, Eds.), pp. 127 150. John Wiley and Sons, Chichester.
- Barnekow, L., Loader, N. J., Hicks, S., Froyd, C. A., and Goslar, T. (2007). Strong correlation between summer temperature and pollen accumulation rates for *Pinus sylvestris, Picea abies* and *Betula spp.* in a high-resolution record from northern Sweden. *Journal of Quaternary Science* 22, 653-658.
- Barr, C. J., Bunce, R. G. H., Clarke, R. T., Firbank, L. G., Gillespie, M. K., Howard, D. C., Petit, S., Smart, S. M., Stuart, R. C., and Watkins, J. W. (2003). Methodology of Countryside Survey 2000 module 1: Survey of broad habitats and landscape features. Final report. Centre for Ecology and Hydrology, Cumbria.
- Beaudoin, A. B., and Reasoner, M. A. (1992). Evaluation of differential pollen deposition and pollen focussing from three Holocene intervals in sediments from Lake O'Hara, Yoho National Park, British Columbia, Canada: intra-lake variability in pollen percentages, concentrations and influx. *Review of Palaeobotany and Palynology* **75**, 103 131.
- Behre, K.-E. (1981). The interpretation of anthropogenic indicators in pollen diagrams. *Pollen et spores*, 23, 225 245.
- Bell, M., and Walker, M. J. C. (2005). "Late Quaternary environmental change: physical and human perspectives." Pearson Education Limited, Essex.
- Belyea, L. R. (2007). Revealing the Emperor's new clothes: niche-based palaeoenvironmental reconstruction in the light of recent ecological theory. *The Holocene* **17**, 683-688.
- Bengtsson, L., Hellström, T., and Rakoczi, L. (1990). Redistribution of sediments in three Swedish lakes. *Hydrobiologia* **192**, 167 181.
- Bennett, K. D. (1984). The post-glacial history of *Pinus sylvestris* in the British Isle. *Quaternary Science Reviews* **3**, 133 155.
- Bennett, K. D. (1994). Confidence intervals for age estimates and deposition times in late-Quaternary sediment sequences. *The Holocene* **4,** 337 - 348.
- Bennett, K. D. (1996). Late Quaternary vegetation history of the Cairngorm mountains. *In* "The Quaternary of the Cairngorms: Field Guide." (N. F. Glasser, and K. D. Bennett, Eds.). QRA.
- Bennett, K. D. and Hicks, S. (2005) Numerical analysis of surface and fossil pollen spectra from northern Fennoscandia. *Journal of Biogeography*. **32**, 407 423
- Berglund, B. E. (1973). Pollen dispersal in south eastern Sweden. *In* "Quaternary Plant Ecology." (H. J. B. Birks, and R. G. West, Eds.), pp. 117 129. Blackwell Scientific, Oxford.
- Beug, H.-J. (2004). "Leitfaden der pollenbestimmung für Mitteleuropa und angrenzende Gebiete." Verlag Dr. Friedrich Pfeil, München.
- Binney, H., Waller, M. P., Bunting, J., and Armitage, R. A. (2005). The interpretation of fen carr pollen diagrams: The representation of the dry land vegetation. *Review of Palaeobotany and Palynology* **134**, 197 218.
- Birks, H. H. (1969). "Studies in the vegetational history of Scotland." University of Cambridge.
- Birks, H. H. (1970). Studies In Vegetational History Of Scotland.1. Pollen Diagrams From Abernethy-Forest, Inverness-Shire. *Journal Of Ecology* **58**, 827-837.
- Birks, H. H. (1975). Studies in the vegetational history of Scotland IV. Pine stumps in the Scottish blanket peats. *Philosophical Transactions Of The Royal Society B-Biological Sciences* **270**, 181 223.
- Birks, H. H., and Birks, H. J. B. (2000). Future uses of pollen analysis must include plant macrofossils. *Journal of Biogeography* **27**, 31.
- Birks, H. H., and Mathewes, R. W. (1978). Studies In Vegetational History Of Scotland.5. Late Devensian And Early Flandrian Pollen And Macrofossil Stratigraphy At Abernethy Forest, Inverness-Shire. *New Phytologist* **80**, 455-&.
- Birks, H. J. B. (1977). The Flandrian forest history of Scotland: a preliminary synthesis. *In* "British Quaternary Studies: Recent advances." (F. W. Shotton, Ed.), pp. 119 135. Clarendon Press, Oxford.

- Birks, H. J. B. (1989). Holocene isochrone maps and patterns of tree-spreading in the British Isle. *Journal of Biogeography* **16,** 503 540.
- Birks, H. J. B. (1994). Did Icelandic Volcanic-Eruptions Influence The Postglacial Vegetational History Of The British-Isles. *Trends In Ecology & Evolution* **9**, 312-314.
- Birks, H. J. B. (1996). Contributions of Quaternary Palaeoecology to Nature Conservation. *Journal of Vegetation Science* **7**, 89.
- Birks, H. J. B., and Birks, H. H. (1980). "Quaternary Palaeoecology." Edward Arnold, London.
- Björck, S., Bennike, O., Possnert, G., Wohlfarth, B., and Digerfeldt, G. (1998). A high-resolution ¹⁴C dated sediment sequence from southwest Sweden: age comparisons between different components of the sediment. *Journal of Quaternary Science* **13**, 85 89.
- Björck, S., and Wohlfarth, B. (2001). ¹⁴C chronostratigraphic techniques in palaeolimnology. *In* "Tracking environmental change using lake sediments: physical and chemical techniques." (W. M. Last, and J. P. Smol, Eds.), pp. 205 245. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Blackford, J. J. (2000). Charcoal fragments in surface samples following a fire and the implications for interpretations of sub-fossil charcoal data. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology* **164**, 33 42.
- Blackford, J. J., Edwards, K. J., Dugmore, A. J., Cook, G. T., and Buckland, P. C. (1992). Icelandic volcanic ash and the mid-Holocene Scots pine (*Pinus sylvestris*) pollen decline in northern Scotland. *The Holocene* **2**, 260 265.
- Blackmore, S., and Barnes, S. H. (1986). Harmomegathic mechanisms in pollen grains. *In* "Pollen and spores: form and function." (S. Blackmore, and I. K. Ferguson, Eds.), pp. 137 149. Academic Press, London.
- Blais, J. M., Kalff, J., Cornett, R. J., and Evans, R. D. (1995). Evaluation of ²¹⁰Pb dating in lake sediments using stable Pb, *Ambrosia* pollen and ¹³⁷Cs. *Journal of Paleolimnology* **13**, 169 178.
- Blundell, A. C., and Barber, K. E. (2005). A 2800-year palaeoclimatic record from Tore Hill Moss, Strathspey, Scotland: the need for a multi-proxy approach to peat-based climate reconstructions. *Quaternary Science Reviews* **24**, 1261 1277.
- Bonny, A. P. (1978). The effect of pollen recruitment to the seston and sediment of some English Lake District lakes. *Journal of Ecology* **66**, 385 416.
- Boyd, W. E., and Dickson, J. H. (1986). Patterns in the geographical distribution of the early Flandrian *Corylus* rise in southwest Scotland. *New Phytologist* **102**, 615 623.
- Bradshaw, R. (1994). Forest response to Holocene climate changes: equilibrium or non-equilibrium. *In* "Climate change and human impact on the landscape: studies in palaeoecology and environmental archaeology." (F. C. Chambers, Ed.). Chapman and Hall, London.
- Bradshaw, R. H. W. (1981). Modern Pollen-Representation Factors For Woods In Southeast England. *Journal Of Ecology* **69**, 45-70.
- Bradshaw, R. H. W., Hannon, G. E., and Lister, A. M. (2003). A long-term perspective on ungulate-vegetation interactions. *Forest Ecology and Management* **181**, 267.
- Bradshaw, R. H. W., and Mitchell, F. J. G. (1999). The palaeoecological approach to reconstructing former grazing-vegetation interactions. *Forest Ecology and Management* **120,** 3-12.
- Breeze, D. J. (1997). The great myth of Caledon. *In* "Scottish Woodland History." (T. C. Smout, Ed.), pp. 46 51. Scottish Cultural Press, Dalkeith.
- Bridge, M. C., Haggart, B. A., and Lowe, J. J. (1990). The history and palaeoclimatic significance of subfossil remains of *Pinus sylvestris* in blanket peats from Scotland. *Journal of Ecology* **78,** 77.
- Brockerhoff, E., Jactel, H., Parrotta, J., Quine, C., and Sayer, J. (2008). Plantation forests and biodiversity: oxymoron or opportunity? *Biodiversity and Conservation* 17, 925.
- Bronk Ramsey, C. (1995). Radiocarbon calibration and analysis of stratigraphy: The OxCal program. *Radiocarbon* **37**, 425 430.
- Broström, A., Gaillard, M. J., Ihse, M., and Odgaard, B. (1998). Pollen-landscape relationships in modern analogues of ancient cultural landscapes in southern Sweden A first step towards

- quantification of vegetation openness in the past. *Vegetation History and Archaeobotany* **7**, 189-201.
- Broström, A., Nielsen, A., Gaillard, M.-J., Hjelle, K., Mazier, F., Binney, H., Bunting, J., Fyfe, R., Meltsov, V., Poska, A., Räsänen, S., Soepboer, W., von Stedingk, H., Suutari, H., and Sugita, S. (2008). Pollen productivity estimates of key European plant taxa for quantitative reconstruction of past vegetation: a review. *Vegetation History and Archaeobotany* **17**, 461.
- Broström, A., Sugita, S., and Gaillard, M. J. (2004). Pollen productivity estimates for the reconstruction of past vegetation cover in the cultural landscape of southern Sweden. *The Holocene* **14**, 368-381.
- Broström, A., Sugita, S., Gaillard, M. J., and Pilesjo, P. (2005). Estimating the spatial scale of pollen dispersal in the cultural landscape of southern Sweden. *Holocene* **15**, 252-262.
- Brown, A. G. (1999). Biodiversity and pollen analysis: modern pollen studies and the recent history of a floodplain woodland in S-W-Ireland. *Journal Of Biogeography* **26**, 19-32.
- Brown, I. M., and Clapperton, C. M. (2002). The phyical geography. *In* "The ecology, land-use and conservation of the Cairngorms." (C. H. Gimmingham, Ed.). Packard Publishing Limited, Chichester.
- Bruneau, P. M. C. (2006). Geodiversity: Soils. *In* "The nature of the Cairngorms." (P. Shaw and D. Thompson, Ed.). The Stationary Office Edinburgh, 43 53
- Brundtland, G. H. (1987) The UN world commission of environment and development: Our common future, Oxford University Press, Oxford
- Brush, G. S., and Brush, L. M. (1972). Transport of pollen in a sediment-laden channel: A laboratory study. *American Journal of Science* **272**, 359 381.
- Buller, A. H. R. (1909). "Research on Fungi." Longmans, England.
- Bunting, M. J. (2002). Detecting woodland remnants in cultural landscapes: Modern pollen deposition around small woodlands in northwest Scotland. *Holocene* **12**, 291-301.
- Bunting, M. J. (2003). Pollen-vegetation relationships in non-arboreal moorland taxa. *Review of Palaeobotany and Palynology* **125**, 285-298.
- Bunting, M. J., Armitage, R., Binney, H. A., and Waller, M. (2005a). Estimates of 'relative pollen productivity' and 'relevant source area of pollen' for major tree taxa in two Norfolk (UK) woodlands. *Holocene* **15**, 459-465.
- Bunting, M. J., Gaillard, M. J., Sugita, S., Middleton, R., and Broström, A. (2004). Vegetation structure and pollen source area. *Holocene* **14**, 651-660.
- Bunting, M. J., and Middleton, D. (2005). Modelling pollen dispersal and deposition using HUMPOL software, including simulating windroses and irregular lakes. *Review of Palaeobotany and Palynology* **134**, 185-196.
- Bunting, M.J., Middleton, R., and Twiddle, C. L. (2007). Wetland records of a coastal cultural landscape in north-west Scotland: an application of the Multiple Scenario Approach to landscape reconstruction. *In* "Archaeology from the wetlands: recent perspectives." (B. Barber, C. C., M. Cressey, A. Crone, A. Hale, J. Henderson, R. Housley, R. Sands, and A. Sheridan, Eds.), pp. 109 117. WARP Occasional Paper 18, Society of Antiquaries of Scotland.
- Bunting, M. J., and Middleton, R. (2009). Equifinality and uncertainty in the interpretation of pollen data: the Multiple Scenario Approach to reconstruction of past vegetation mosaics. *The Holocene* **19**, 799.
- Bunting, M. J., Twiddle, C. L., and Middleton, R. (2008). Using models of pollen dispersal and deposition in hilly landscapes: some possible approaches. *Palaeogeography, Palaeoclimatology, Palaeoecology* **259,** 77 91.
- Burgess, C. (1985). Population, climate and upland settlement. *In* "Upland settlement in Britain: The second millennium BC and after." (D. Spratt, and C. Burgess, Eds.). B.A.R., Oxford.
- Burrough, P. A., and McDonnell, R. A. (1998). "Principles of Geographical Information Systems." Oxford University Press, Oxford.
- Calcote, R. (1995). Pollen source area and pollen productivity: Evidence from forest hollows. *Journal of Ecology* **83**, 591.

- Campbell, J. B. (2002). "Introduction to Remote Sensing." Taylor and Francis, London.
- Carlisle, A. (1977). The impact of man on the native pinewoods of Scotland. *In* "Native pinewoods of Scotland: proceedings of the Aviemore symposium." (R. G. H. Bunce, and J. N. R. Jeffers, Eds.), pp. 70 77. NERC, Cambridge.
- Carlisle, A., and Brown, A. H. F. (1968). Biological flora of the British Isle, *Pinus sylvestris* L. *Journal of Ecology* **56**, 269 307.
- Caseldine, C., Fyfe, F., Langdon, C., and Thompson, G. (2007). Simulating the nature of vegetation communities at the opening of the Neolithic on Achill Island, Co. Mayo, Ireland the potential role of models of pollen dispersal and deposition. *Review of Palaeobotany and Palynology* **144**, 135 144.
- Caseldine, C., and Fyfe, R. (2006b). A modelling approach to locating and characterising elm decline/landnam landscapes. *Quaternary Science Reviews* **25**, 632-644.
- Caseldine, C., Fyfe, R., and Hjelle, K. L. (2008). Pollen modelling, palaeoecology and archaeology virtualisation and/visualisation of the Past? *Vegetation History and Archaeobotany* **17**, 543 549.
- Caseldine, C. J. (1981). Surface pollen studies across Bankhead Moss, Fife, Scotland. *Journal of Biogeography* **8,** 7 25.
- Caseldine, C. J. (1989). Pollen assemblage-plant community relationships on the Storbreen glacier foreland, Jotunheimen Mountains, southern Norway. *New Phytologist* **111**, 105 118.
- Chamberlain, A. C. (1975). The movement of particles in plant communities. *In* "Vegetation and the atmosphere Volume 1." (J. L. Monteith, Ed.), pp. 155 203. Academic Press, New York.
- Charman, D. J., Blundell, A., Chiverrell, R. C., Hendon, D., and Langdon, P. G. (2006). Compilation of non-annually resolved Holocene proxy climate records: stacked Holocene peatland palaeo-water table reconstructions from northern Britain. *Quaternary Science Reviews* **25**, 336 350.
- Cheddadi, R., Vendramin, G. G., Litt, T., Francois, L., Kageyama, M., Lorentz, S., Laurent, J. M., de Beaulieu, J. L., Sadori, L., Jost, A., and Lunt, D. (2006). Imprints of glacial refugia in the modern genetic diversity of *Pinus sylvestris*. *Global Ecology and Biogeography* **15**, 271-282.
- Clark, J. S. (1988). Particle motion and the theory of Charcoal analysis: Source area, transport, deposition and sampling. *Quaternary Research* **30**, 67 80.
- Clark, J. S., and Royall, P. D. (1995). Particle-Size Evidence For Source Areas Of Charcoal Accumulation In Late Holocene Sediments Of Eastern North-American Lakes. *Quaternary Research* **43**, 80-89.
- Cliff, A. D., and Ord, J. K. (1981). "Spatial processes: models and applications." Pion, London.
- Clymo, R. S., and Mackay, D. (1987). Upwash and downwash of pollen and spores in the unsaturated surface layer of *Sphagnum*-dominated peat. *New Phytologist* **105**, 175 183.
- Cochrane, M. A. (2000). Using vegetation reflectance variability for species level classification of hyperspectral data. *International Journal of Remote Sensing* **21**, 2075 2087.
- Cohen, W. B., Spies, T. A., and Bradshaw, G. A. (1990). Semivariograms of digital imagery for analysis of conifer canopy structure. *Remote Sensing of Environment* **34**, 167.
- Comanor, P. L. (1968). Forest vegetation and the pollen spectrum: An examination of usefulness of R-value. *Bulletin New Jersey Academy of Science* **13,** 7 19.
- Coppin, P., Jonckheere, I., Nackaerts, K., and Muys, B. (2004). digital change detection methods in ecosystem monitoring: a review. *International Journal of Remote Sensing* **25**, 1565 1596.
- Court-Picon, M., Buttler, A., and de Beaulieu, J.-L. (2005). Modern pollen-vegetation relationships in the Champsaur valley (French Alps) and their potential in the interpretation of fossil pollen records of past cultural landscapes. *Review of Palaeobotany and Palynology* **135**, 13 39.
- Cowell, A. H. (1981). Marginal land and climate: a comment. *In* "Consequences of climate change." (C. D. Smith, and M. Parry, Eds.), pp. 135 140. University of Nottingham Press, Nottingham.

- Cowie, T. G., and Shepherd, I. A. G. (1997). The Bronze Age. *In* "Scotland: Environment and archaeology 8000BC AD1000." (K. J. Edwards, and I. B. M. Ralston, Eds.), pp. 151 168. John Wiley and Sons, Chichester.
- Crone, A., and Watson, F. (2003). Sufficiency to scarcity: Medieval Scotland, 500 1600. *In* "People and woods in Scotland." (T. C. Smout, Ed.), pp. 60 82. Edinburgh University Press, Edinburgh.
- Cundill, P. R. (1991). Comparisons of moss polster and pollen trap data: a pilot study. *Grana* **30**, 301
- Cushing, E. J. (1967). Evidence for differential pollen preservation in late Quaternary sediments in Minnesota. *Review of Palaeobotany & Palynology* **4,** 87 101.
- Dalton, C., Birks, H. J. B., Brooks, S. J., Cameron, N. G., Evershed, R. P., Pelgar, S. M., Scott, J. A., and Thompson, R. (2005). A multi-proxy study of lake-development in response to catchment changes during the Holocene at Lochnagar, north-east Scotland. *Palaeogeography, Palaeoclimatology, Palaeoecology* **221,** 175 201.
- Dark, P. (2006). Climate deterioration and land-use change in the first millennium BC: perspectives from the British palynological record. *Journal of Archaeological Science* **33**, 1381.
- Davies, A. L. (2007). Upland agriculture and environmental risk: a new model of upland land-use based on high spatial resolution palynological data from West Affric, North West Scotland. *Journal of Archaeological Science* **34**, 1 11.
- Davies, A. L., and Tipping, R. (2004). Sensing small-scale human activity in the palaeoecological record: Fine spatial resolution pollen analyses from Glen Affric, northern Scotland. *The Holocene* **14**, 233-245.
- Davies, A. L., Tisdall, E., and Tipping, R. (2004). Holocene climatic ability and human settlement in the Scottish Highlands: fragility and robustness. *In* "Atlantic connections and adaptions." (R. A. Housley, and G. M. Coles, Eds.), pp. 2 11. Oxbow, Oxford.
- Davis, J. C. (2002). "Statistics and data analysis in geology." John Wiley and Sons, New York.
- Davis, M. B. (1963). On Theory Of Pollen Analysis. American Journal Of Science 261, 897-&.
- Davis, M. B. (1968). Pollen Grains in Lake Sediments: Redeposition Caused by Seasonal Water Circulation. *Science* **162**, 796.
- Davis, M. B. (1969). Climatic changes in Southern Connecticut recorded by pollen deposition at Rogers Lake. *Ecology* **50**, 409 422.
- Davis, M. B. (1973). Redeposition of Pollen Grains in Lake Sediment. *Limnology and Oceanography* **18**, 44. 52
- Davis, M. B. (2000). Palynology after Y2K Understanding the source area of pollen in sediments. *Annual Review of Earth and Planetary Sciences* **28**, 1.
- Davis, M. B., and Brubaker, L. B. (1973). Differential Sedimentation of Pollen Grains in Lakes. *Limnology and Oceanography* **18**, 635.
- Davis, M. B., Brubaker, L. B., and Webb, T. I. (1973). Calibration of absolute pollen influx. *In* "Quaternary Plant Ecology." (H. J. B. Birks, and R. G. West, Eds.), pp. 9 226. Blackwell Scientific Publications, Oxford.
- Davis, M. B., and Deevey, E. S. (1964). Pollen Accumulation Rates: Estimates from Late-Glacial sediment of Rogers Lake. *Science* **145**, 1293 1295.
- Davis, M. B. and Ford, M. S. (1982) Sediment focussing in Mirror Lake, New Hampshire. Limnology and Oceanography, 27, 137 - 150
- Davis, M. B., Moeller, R. E., and Ford, J. (1984). Sediment focusing and pollen influx. *In* "Lake sediments and environmental history." (E. Y. Haworth, and J. W. G. Lund, Eds.), pp. 261 293. Leicester University Press, Leicester.
- Dearing, J. (1999). Magnetic susceptibility. *In* "Environmental magnetism: a practical guide." (J. Walden, F. Oldfield, and J. T. Smith, Eds.), pp. 243. Quaternary Research Association, London.
- Dearing, J., Battarbee, R., Dikau, R., Larocque, I., and Oldfield, F. (2006a). Human–environment interactions: learning from the past. *Regional Environmental Change* **6**, 1 16.

- Dearing, J., Battarbee, R., Dikau, R., Larocque, I., and Oldfield, F. (2006b). Human–environment interactions: towards synthesis and simulation. *Regional Environmental Change* **6**, 115 123.
- Delcourt, H. R., Delcourt, P. A., and Webb III, T. (1983). Dynamic plant ecology: The spectrum of vegetational change in space and time. *Quaternary Science Reviews* **1**, 153 175.
- Dennis, R. (2002). Birds and Mammals. *In* "The ecology, land use and conservation in the Cairngorms." (C. H. Gimmingham, Ed.), pp. 43 53. Packard Publishing Limited, Chichester.
- Duffin, K.I. and Bunting, M.J (2008). Relative pollen productivity and fall speed estimates for southern Arican savanna taxa, *Vegetation History and Archaeobotany* **17**, 507 526.
- Dungan, J. L., Perry, J. N., Dale, M. R. T., Legendre, P., Citron-Pousty, S., Fortin, M. J., Jakomulska, A., Miriti, M., and Rosenburg, M. S. (2002). A balanced view of scale in spatial statistical analysis. *Ecography* **25**, 626 640.
- Dumayne-Peaty, L. (1998). Human impact on the environment during the Iron Age and Romano-British times: palynological evidence from three sites near the Antonine Wall, Great Britain. *Journal of Archaeological Science* **25**, 203 241.
- Dumayne-Peaty, L. (1999). Late Holocene human impact on the vegetation of southeastern Scotland: a pollen diagram from Dogden Moss, Berwickshire. *Review of Palaeobotany and Palynology* **105**, 121 141.
- Dunlop, B. M. S. (1994). The native woodlands of Strathspey. *In* "Scottish Natural Heritage Research, Survey and Monitoring report 33." pp. 128. SNH, Perth.
- Dunlop, B. M. S. (1997). The woods of Strathspey. *In* "Scottish Woodland History." (T. C. Smout, Ed.), pp. 175 189. Scottish Cultural Press, Dalkeith.
- Durham, O. C. (1946). The volumetric incidence of atmospheric allergens III. The rate of fall of pollen grains in still air. *Journal of Allergy* **17**, 70 78.
- Edwards, K. J. (1990). Fire and the Scottish Mesolithic: evidence from microscopic charcoal. *In* "Contributions to the Mesolithic in Europe." (P. M. Vermeersch, and P. Van Peer, Eds.), pp. 71 79. Leuven University Press, Leuven.
- Edwards, K. J. (1999). Palynology and people: Observations on the British record. *Quaternary Proceedings* **7**, 531 544.
- Edwards, K. J., and MacDonald, G. M. (1991). Holocene palynology: II human influence and vegetation change. *Progress In Physical Geography* **15**, 364 391.
- Edwards, K. J., and Ralston, I. B. M. (1997). "Scotland environment and archaeology, 8000BC 1000AD." Wiley.
- Edwards, K. J., and Whittington, G. (2000). Multiple charcoal profiles in a Scottish lake: Taphonomy, fire ecology, human impact and inference. *Palaeogeography, Palaeoclimatology, Palaeoecology* **164,** 67.
- Edwards, K. J., and Whittington, G. (2001). Lake sediments, erosion and landscape change during the Holocene in Britain and Ireland. *Catena* **42**, 143-173.
- Edwards, K. J., Whittington, G., and Hirons, K. R. (1995). The relationship between fires and long-term wet heath development in South Uist, Outer Hebrides, Scotland. *In* "Heaths and Moorland: cultural landscapes." (D. B. A. Thompson, A. J. Hestor, and M. B. Usher, Eds.), pp. 240 248. Her Majesty's Stationary Office, Edinburgh.
- Eisenhut, G. (1961). Untersuchungen über die Morphologie Ökologie der pollenkörner heimischer und fremdländischer Waldbäume. *forstwiss. Forsch* **15,** 1 68.
- Eklöf, M., Broström, A., Gaillard, M. J., and Pilesjo, P. (2004). OPENLAND3: A computer program to estimate plant abundance around pollen sampling sites from vegetation maps: A necessary step for calculation of pollen productivity estimates. *Review of Palaeobotany and Palynology* **132**, 67-77.
- El-Daoushy, F. (1988). A summary on the Lead-210 cycle in nature and related applications in Scandinavia. *Environment International* **14**, 305 319.
- Ettema, C. H., and Wardle, D. A. (2002). Spatial soil ecology. *TRENDS in Ecology and Evolution* **17,** 177 183.

- EU Life Project. (2002). Capercaillie LIFE project: Urgent conservation management for Scottish Capercaillie.
- EU Life Project. (2007). Urgent conservation management for Scottish Capercaillie: Layman's report, pp. 6.
- Ewing, H. A. (2002). The Influence of Substrate on Vegetation History and Ecosystem Development. *Ecology* **83**, 27-66.
- Faegri, K. (1966). Some problems of representativity in pollen analysis. *The Palaeobotanist* **15**, 135 140.
- Faegri, K., and Iversen, J. (1989). "Textbook of Pollen Analysis." John Wiley and Sons, London.
- Fagerlind, F. (1952). The real signification of pollen diagrams. *Botaniska Notiser* **105**, 185 224.
- Falck, R. (1927). Über die Grössen, fallgeschwindigkut und Schwebewarte der Pilzsporopenund inhre Gruppierung mit Bezug auf zu ihrer Verbritung nötigen Temperaturströmungs-Geschwindigkeit. *Ber. Dtsch. Bot. Ges* **45**, 262 281.
- Finnlayson, B., and Edwards, K. J. (1997). The Mesolithic. *In* "Scotland: Environment and archaeology 8000BC AD1000." (K. J. Edwards, and I. B. M. Ralston, Eds.), pp. 109 125. John Wiley and Sons, Chichester.
- Finsinger, W., and Tinner, W. (2005). Minimum count sums for charcoal-concentration estimates in pollen slides: accuracy and potential errors. *The Holocene* **15**, 293 297.
- Foot, D. (2002). The twentieth century: forestry takes off. *In* "People and woods in Scotland: A history." (T. C. Smout, Ed.). Edinburgh University Press, Edinburgh.
- Forestry Commission. (1981). "Yield models for forest management." Edinburgh.
- Forestry Commission. (2002). Scotland's trees, woods and forests, pp. 1 41. Forestry Commission Scotland, Edinburgh.
- Forestry Commission. (2003). "Realising a vision: Native woodlands on the Forestry Commission estate in Scotland." Forestry Commission, Edinburgh.
- Forestry Commission. (2004). The UK Forestry Standard: The Government's approach to sustainable forestry., pp. 74, Edinburgh.
- Forestry Commission. (2006a). Scottish Forestry Strategy, pp. 1 84. Forestry Commission Scotland, Edinburgh.
- Forestry Commission. (2006b). The Scottish Forestry Strategy: Implementation Plan 2007 2008, pp. 1 31. Forestry Commission Scotland, Edinburgh.
- Fortin, M. J. (1999). Effects of sampling unit resolution on the estimation of spatial autocorrelation. *Ecoscience* **6**, 636 641.
- Fortin, M. J., Drapeau, P., and Legendre, P. (1989). Spatial autocorrelation and sampling design in plant ecology. *Vegetatio* **83**, 209 222.
- Foster, D. R., and Motzkin, G. (2003). Interpreting and conserving the openland habitats of coastal New England: insights from landscape history. *Forest Ecology and Management* **185**, 127.
- Froyd, C. A. (2002). "Holocene pine (*Pinus sylvestris*) forest dynamics in the Scottish Highlands Ph.D. thesis, University of Cambridge." University of Cambridge.
- Froyd, C. A. (2005). Fossil stomata reveal early pine presence in Scotland: implications for postglacial colonization analysis. *Ecology* **86**, 579 586.
- Froyd, C. A. (2006). Holocene fire in the Scottish highlands: Evidence from macroscopic charcoal records. *Holocene* **16**, 235 249.
- Froyd, C. A., and Bennett, K. D. (2006). Long-term ecology of native pinewood communities in East Glen Affric, Scotland. *Forestry* **79**, 279 291.
- Froyd, C. A., and Willis, K. J. (2008). Emerging issues in biodiversity & conservation management: The need for a palaeoecological perspective. *Quaternary Science Reviews* **27**, 1723-1732.
- Fuller, R. M., Cox, R., Clarke, R. T., Rothery, P., Hill, R. A., Smith, G. M., Thomson, A. G., Brown, N. J., Howard, D. C., and Stott, A. P. (2005). The UK Land Cover Map 2000: Planning, construction and calibration of a remotely sensed, user-oriented map of broad habitats. *International Journal of Applied Earth Observation and Geoinformation* 7, 202.

- Fuller, R. M., Smith, G. M., Sanderson, J. M., Hill, R. A., Thomson, A. G., Cox, R., Brown, N. J., Clarke, R. T., Rothery, P., and Gerard, F. F. (2002). Land Cover Map 2000 Final Report, pp. 69. Centre for Ecology and Hydrology, Dorchester.
- Fyfe, R. (2006). GIS and the application of a model of pollen deposition and dispersal: A new approach to testing landscape hypotheses using the POLLANDCAL models. *Journal of Archaeological Science* **33**, 483 493.
- Fyfe, R., de Beaulieu, J.-L., Binney, H., Bradshaw, R., Brewer, S., Le Flao, A., Finsinger, W., Gaillard, M.-J., Giesecke, T., Gil-Romera, G., Grimm, E., Huntley, B., Kunes, P., Kühl, N., Leydet, M., Lotter, A., Tarasov, P., and Tonkov, S. (2009). The European Pollen Database: past efforts and current activities. *Vegetation History and Archaeobotany* **18**, 417 424.
- Gaillard, M. J., Birks, H. J. B., Emanuelsson, U., and Berglund, B. E. (1992). Modern pollen/land-use relationships as an aid in the reconstruction of past land-uses and cultural landscapes: an example from south Sweden. *Vegetation History and Archaeobotany* 1, 3 17.
- Gaillard, M. J., Birks, H. J. B., Emanuelsson, U., Karlsson, S., Lageras, P., and Olausson, D. (1994). Application of modern pollen/land-use relationships to the interpretation of pollen diagrams reconstructions of land-use history in south Sweden, 3000-0 BP. Review of Palaeobotany & Palynology 82, 47-73.
- Gaillard, M. J., Sugita, S., Bunting, M. J., Middleton, R., Broström, A., Caseldine, C., Giesecke, T., Hellman, S. E. V., Hicks, S., Hjelle, K., Langdon, C., Nielsen, A. B., Poska, A., von Stedingk, H., and Veski, S. (2008). The use of modelling and simulation approach in reconstructing past landscapes from fossil pollen data: a review and results from the POLLANDCAL network. *Vegetation History And Archaeobotany* 17, 419-443.
- Gavin, D. G., Oswald, W. W., Wahl, E. R., and Williams, J. W. (2003). A statistical approach to evaluating distance metrics and analog assignments for pollen records. *Quaternary Research* **60**, 356 367.
- Geiger, R. (1950). "The climate near the ground." Harvard University Press, Cambridge, U.S.A.
- Gervais, B. R., and MacDonald, G. M. (2001). Modern pollen and stomate deposition in lake surface sediments from across the treeline on the Kola Peninsula, Russia. *Review of Palaeobotany and Palynology* **114**, 223 237.
- Gething, P. W., Atkinson, P. M., Noor, A. M., Gikandi, P. W., Hay, S. I., and Nixon, M. S. (2007). A local space-time kriging approach applied to a national outpatient malaria data set. *Computers & Geosciences* **33**, 1337 1357.
- Gibbard, P. L., Head, M. J., and Walker, M. J. C. (2010). Formal ratification of the Quaternary System/Period and the Pleistocene Series/Epoch with a base at 2.58 Ma. *Journal of Quaternary Science* **25,** 96 102.
- Giesecke, T., and Fontana, S. L. (2008). Revisiting pollen accumulation rates from Swedish lake sediments. *The Holocene* **18**, 293 305.
- Gifford, F. A. J. (1968). An outline of theories of diffusion in the lower layers of the atmosphere. *In* "Meteorology and atomic energy." (D. H. Slade, Ed.), pp. 65 116. Atomic Energy Commission, Tennessee.
- Gillson, L. (2009). Landscapes in Time and Space. Landscape Ecology 24, 149-155.
- Gillson, L., and Duffin, K. I. (2007). Thresholds of potential concern as benchmarks in the management of African savannahs. *Philosophical Transactions Of The Royal Society B-Biological Sciences* **362**, 309 319.
- Gillson, L., and Willis, K. J. (2004). 'As Earth's testimonies tell': wilderness conservation in a changing world. *Ecology Letters* **7**, 990-998.
- Gimmingham, C. H. (1960). Biological flora of the British Isle *Calluna vulgaris* (L.) Hull. *Journal Of Ecology* **48**.
- Gimmingham, C. H. (2002). Vegetation. *In* "The ecology, land use and conservation of the Cairngorms." (C. H. Gimmingham, Ed.), pp. 23 42. Packard Publishing Limited, Chichester.
- Gordon, J. E. (1993). The Cairngorms. *In* "Quaternary of Scotland." (J. E. Gordon, and D. G. Sutherland, Eds.). Chapman and Hall, London.

- Gordon, J., Wignall, R. Brazier, N. and Bruneau, P. (2006). Cairngorms: A landscape fashioned by geology, Scottish Natural Heritage, Perth, pp. 41
- Gorham, E., and Boyce, F. M. (1989). Influence of lake surface area and depth upon thermal stratification and the depth of the summer thermocline. *Journal of Great Lakes Research* **15,** 233 245.
- Gould. (1970). Is statistix interens the geographical name for wild goose. *Economic Geography* **46**, 439 448.
- Green, F. H. W. (1974). Climate and Weather. *In* "The Cairngorms: Their natural history and scenery." (D. Nethersole-Thompson, and A. Watson, Eds.), pp. 22 8 -236. Collins, London.
- Gregory, P. H. (1973). "The Microbiology of the Atmosphere." Leonard Hill.
- Grime, J. P., Hodgson, J. G., and Hunt, R. (1988). "Comparative plant ecology: a functional approach to common British species." Unwin Hyman, London.
- Grimm, E. C. (1987). CONISS: a FORTRAN 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. *Computers & Geosciences* **13**, 13 35.
- Grimm, E. C. (1991). TILLIA and TILLIA GRAPH, Illinois State Museum, Springfield.
- Groenman-van Waateringe, W. (1993). The effects of grazing on the pollen production of grasses. *Vegetation History and Archaeobotany* **2**, 157 162.
- Grove, J. M. (2004). "The little ice ages; ancient and modern." Routledge, London.
- Guiot, J. (1990). Methodology of the last climatic cycle reconstruction in France from pollen data. *Palaeogeography, Palaeoclimatology, Palaeoecology* **80,** 49 69.
- Haines-Young, R. H., and Petch, J. R. (1983). Multiple Working Hypotheses: Equifinality and the Study of Landforms. *Transactions of the Institute of British Geographers* **8**, 458 466.
- Halliday, S. P. (1993). Marginal agriculture in Scotland. *In* "Scotland since Prehistory: Natural change and human impact." (T. C. Smout, Ed.), pp. 64 78.
- Hampson, A. M., and Peterken, G. F. (1998). Enhancing the biodiversity of Scotland's forest resource through the development of a network of forest habitats. *Biodiversity and Conservation* **7**, 179 192.
- Hansen, B.C.S., MacDonald, G. M. and Koser, K.A. (1996). Identifying the tundra-forest border in the stomatae record. *Canadian Journal of Botany* **74**, 796 800.
- Hansen, B. C. S. (1995). Conifer stomate analysis as a palaeoecological tool: an example from the Hudson Bay Lowlands. *Canadian Journal of Botany* **73,** 244 252.
- Hanson, W. S. (2004). Scotland and the northern frontier: second and forth centuries A.D. *In* "A companion to Roman Britain." (M. Todd, Ed.), pp. 136 161. Blackwell Publishing Limited, Oxford.
- Harding, D. W. (2004). "The Iron Age in northern Britain: Celts and Romans, natives and invaders." Routledge, London.
- Harrison, S. J. (1997). Changes in Scottish climate. *Botanical Journal of Scotland* 49, 287 300.
- Hättestrand, M., Jensen, C., Hallsdóttir, M., and Vorren, K.-D. (2008). Modern pollen accumulation rates at the north-western fringe of the European boreal forest. *Review of Palaeobotany and Palynology* **151**, 90 104.
- Havinga, A. J. (1984). A 20 year experimental investigation into the differential corrosion susceptibility of pollen and spores in various soil types. *Pollen et Spores* **26**, 541 558.
- Heiri, O., Lotter, A. F., and Lemcke, G. (2001) Loss on ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results. *Journal of Palaeolimnology* **25**, 101 110.
- Hellman, S., Gaillard, M.-J., Broström, A., and Sugita, S. (2007). The REVEALS model, a new tool to estimate past regional plant abundance from pollen data in large lakes: validation in southern Sweden. *Journal of Quaternary Science*, **23**, 21 41.
- Hellman, S., Gaillard, M. J., Broström, A., and Sugita, S. (2008). Effects of the sampling design and selection of parameter values on pollen-based quantitative reconstruction of regional vegetation: a case study in southern Sweden using the REVEALS model. *Vegetation History and Archaeobotany.* 17, 445 459

- Hellman, S., Bunting, M. J., and Gaillard, M. J. (2009a). Relevant Source Area of Pollen in patchy cultural landscapes and signals of anthropogenic landscape disturbance in the pollen record: A simulation approach. *Review Of Palaeobotany And Palynology* **153**, 245-258.
- Hellman, S., Gaillard, M.-J., Bunting, J. M., and Mazier, F. (2009b). Estimating the Relevant Source Area of Pollen in the past cultural landscapes of southern Sweden -- A forward modelling approach. *Review of Palaeobotany and Palynology* **153**, 259 271.
- Hendon, D. D., Charman, D. D., and Kent, M. M. (2001). Palaeohydrological records derived from testate amoebae analysis from peatlands in northern England: within-site variability, between-site comparability and palaeoclimatic implications. *The Holocene* **11**, 127.
- Henshall, H. S. (1963). "The Chambered tombs of Scotland. Volume 1." Edinburgh University Press, Edinburgh.
- Heslop-Harrision, J. (1979). An interpretation of the hydrodynamics of pollen. *American Journal of Botany* **66**, 737 743.
- Hibbard, A. (1999) High resolution modelling of the advance of the Younger Dryas ice sheet and its climate in Scotland. *Quaternary Research*, **52**, 27 43
- Hibberd, B. G. (1986) "Forestry Practice" Forestry Commission Bulletin 14, Her Majesty's Stationary Office, London
- Hibberd, B. G. (1991). "Management Handbook." Her Majesty's Stationary Office, London.
- Hicks, S. (1999). The relationship between climate and annual pollen deposition at northern tree-lines. *Chemosphere Global Change Science* **1,** 403.
- Hicks, S. (2001). The use of annual arboreal pollen deposition values for delimiting tree-lines in the landscape and exploring models of pollen dispersal. *Review of Palaeobotany and Palynology* **117,** 1 29.
- Hicks, S. (2006). When no pollen does not mean no trees? *Vegetation History and Archaeobotany* **15**, 253-261.
- Hicks, S. and Birks, H.J.B (1996) Numerical analysis of modern and fossil pollen spectra as a tool for elucidating the nature of fine-scale human activities in boreal areas. *Vegetation History and Archaeobotany*, **5**, 257 272
- Hicks, S., and Hyvärinen, H. (1999). Pollen influx values measured in different sedimentary environments and their palaeoecological implications. *Grana* **38**, 228 242.
- Hicks, S., and Sunnari, A. (2005). Adding precision to the spatial factor of vegetation reconstructed from pollen assemblages. *Plant Biosystems* **139**, 127 134.
- Hilton, J. (1985). A conceptual framework for predicting the occurrence of sediment focusing and sediment redistribution in small lakes. *Limnology and Oceanography* **30**, 1131 1143.
- Hingley, R. (1992) Society in Scotland 700 BC A.D. 200. Proceedings of the Society of Antiquities Scotland, 122, 7 55
- Hirst, J. M. (1953). Changes in the atmospheric spore content: Diurnal periodicity and the effects of weather. *Transactions of the British Mycological Society* **36**, 375 393.
- Hjelle, K. L. (1998). Herb pollen representation in surface moss samples from mown meadows and pastures in western Norway. *Vegetation History And Archaeobotany* **7**, 79-96.
- Hjelle, K. L. (1999). Modern pollen assemblages from mown and grazed vegetation types in western Norway. *Review Of Palaeobotany And Palynology* **107**, 55-81.
- Hobbs, R. J., and Gimingham, C. H. (1984). Studies on Fire in Scottish Heathland Communities II. Post-Fire Vegetation Development. *Journal of Ecology* **72**, 585 610.
- Holl, K., and Smith, M. (2002). Ancient wood pasture in Scotland: classification and management principles. Scottish Natural Heritage, Edinburgh.
- Holl, K., and Smith, M. (2007). Scottish upland forests: History and lessons for the future. *Forest Ecology and Management* **249**, 45 53.
- House, S., and Dingwell, C. (2002). 'A nation of planters': Introducing new trees, 1650 1900. *In* "People and woods in Scotland: A history." (T. C. Smout, Ed.), pp. 128 158. Edinburgh University Press, Edinburgh.
- Humphrey, J. W., Quine, C., and Watts, K. (2006). The influence of forest and woodland management on biodiversity in Scotland: recent ideas and future prospects. *In* "Farming,

- forestry and the natural heritage: towards a more integrated approach." (R. Davidson, and C. A. Galbraith, Eds.), pp. 59 75. Scottish Natural Heritage, Edinburgh.
- Huntley, B. (1981). The past and present vegetation of the Caenlochan National Nature Reserve, Scotland II. Palaeoecological investigations. *New Phytologist* **87**, 189 222.
- Huntley, B. (1990). Dissimilarity mapping between fossil and contemporary pollen spectra in Europe for the past 13,000 years. *Quaternary Research* **33**, 360 376.
- Huntley, B., and Birks, H. J. B. (1983). "An atlas of past and present pollen for Europe: 0 13000 years ago." Cambridge University Press, Cambridge.
- Huusko, A., and Hicks, S. (2009). Conifer pollen abundance provides a proxy for summer temperature: evidence from the latitudinal forest limit in Finland. *Journal of Quaternary Science*.
- Hyvärinen, H. (1975). Absolute and relative pollen diagrams from northernmost Fennoscandia. *Fennia* **142**, 1 23.
- Innes, J. B., and Simmons, I. G. (2000). Mid-Holocene charcoal stratigraphy, fire history and palaeoecology at North Gill, North York Moors, UK. *Palaeogeography, Palaeoclimatology, Palaeoecology* **164,** 151.
- Institute, T. M. L. U. R. (1988). Land Cover of Scotland 1988 Final Report. The Macaulay land use research institute, Aberdeen.
- IPCC. (2007). Climate change 2007: Physical and Science basis. *In* "Contribution of Working Group 1 to the fourth assessment report of the Intergovernmental Panel on Climate Change." (S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, and H. L. Miller, Eds.). Cambridge University Press, Cambridge.
- Jackson, S. T. (1990). Pollen Source Area and representation in small lakes of the Northeastern United States. *Review of Palaeobotany & Palynology* **63**, 53 76.
- Jackson, S. T. (1994). Pollen and spores in Quaternary lake sediments as sensors of vegetation composition: theoretical models and empirical evidence. *In* "Sedimentation of Organic Particles." (A. Traverse, Ed.), pp. 253 286. Cambridge University Press.
- Jackson, S. T., and Hobbs, R. J. (2009). Ecological Restoration in the Light of Ecological History. *Science* **325**, 567-569.
- Jackson, S. T., and Kearsley, J. B. (1998). Quantitative representation of local forest composition in forest-floor pollen assemblages. *Journal of Ecology* **86**, 474 490.
- Jackson, S. T., and Lyford, M. E. (1999). Pollen dispersal models in Quaternary plant ecology: assumptions, parameters and prescriptions. *Botanical Review* **65**, 39 75.
- Jackson, S. T., and Overpeck, J. T. (2000). Responses of plant populations and communities to environmental changes of the late Quaternary. *Palaeobiology* **26**, 194 220.
- Jackson, S. T., and Smith, S. J. (1994). Pollen dispersal and representation on an isolated, forested plateau. *New Phytologist* **128**, 181 193.
- Jackson, S. T., Webb, R. S., Anderson, K. H., Overpeck, J. T., Webb Iii, T., Williams, J. W., and Hansen, B. C. S. (2000). Vegetation and environment in Eastern North America during the Last Glacial Maximum. *Quaternary Science Reviews* **19**, 489 508.
- Jackson, S. T., and Williams, J. W. (2004). Modern analogs in Quaternary palaeoecology: Here today, gone yesterday, gone tomorrow? *Annual Review Of Earth And Planetary Sciences* **32**, 495-537.
- Jacobson, G. L., and Bradshaw, R. (1981). The selection of sites for palaeoenvironmental studies. *Quaternary Research* **16**, 80 96.
- Janssen, C. R. (1970). Problems in the recognition of plant communities in pollen diagrams. *Vegetatio* **20**, 187 198.
- Janssen, C. R. (1972). local and regional pollen deposition. *In* "Quaternary Plant Ecology." (H. J. B. Birks, and R. G. West, Eds.), pp. 31 43. Blackwell Scientific, Oxford.
- Joint Nature Conservation Committee (2009). Special areas of conservation Insh Marshes.
- Jones, V. J., Flower, R. J., Appleby, P. G., Natkanski, J., Richardson, N., Rippey, B., Stevenson, A. C., and Battarbee, R. W. (1993). Palaeolimnological Evidence For The Acidification And

- Atmospheric Contamination Of Lochs In The Cairngorm And Lochnagar Areas Of Scotland. *Journal Of Ecology* **81,** 3-24.
- Kabailiene, M. V. (1969). On formation of pollen spectra and restoration of vegetation. *Ministry of Geology of the USSR, Institute of Geology (Vilnius) Transactions* **11,** 1 146.
- Kangur, M. (2009). Spatio-temporal distribution of pollen in Lake Väike-Juusa (South Estonia) sediments. *Review of Palaeobotany and Palynology* **153**, 354 369.
- Kinloch, B. B., Westfall, R. D., and Forrest, G. I. (1986). Caledonian Scots pine: origins and genetic structure. *New Phytologist* **104**, 703 729.
- Koff, T., Punning, J. M., and Kangur, M. (2000). Impact of forest disturbance on the pollen influx in lake sediments during the last century. *Review of Palaeobotany and Palynology* **111**, 19.
- Kortland, K. (2006). "Forest Management for Capercaillie." Nevisprint, Fort William.
- Kuoppamaa, M., Huusko, A., and Hicks, S. (2009). *Pinus* and *Betula* pollen accumulation rates from the northern boreal forest as a record of interannual variation in July temperature. *Journal of Quaternary Science*.
- Kuuluvainen, T., Jarvinen, E., Hokkanen, T. J., Rouvinen, S., and Heikkinen, K. (1998). Structural heterogeneity and spatial autocorrelation in a natural mature *Pinus sylvestris* dominated Forest. *Ecography* **21**, 159.
- Lamb, H. H. (1964). Trees and climate history in Scotland. *Quarterly Journal of the Royal Meteorological Society* **90,** 382 394.
- Lamb, H. H. (1966). Britain's climate in the past. *In* "The Changing Climate." (H. H. Lamb, Ed.), pp. 170 196. Methuen and Co Ltd, London.
- Lambert, R. A. (2004). In search of wilderness, nature and sport: The visitor to Rothiemurchus, 1780 2000. *In* "Rothiemurchus: Nature and people on a highland estate, 1500 2000." (T. C. Smout, and R. A. Lambert, Eds.), pp. 32 59. Scottish Cultural Press, Dalkeith.
- Langdon, P. G., and Barber, K. E. (2005). The climate of Scotland over the last 5000 years inferred from multiproxy peatland records: Inter-site correlations and regional variability. *Journal of Quaternary Science* **20**, 549.
- Larsen, C. P. S., and MacDonald, G. M. (1993). Lake morphometry, sediment mixing and the selection of sites for fine resolution palaeoecological studies. *Quaternary Science Reviews* **12**, 781 792.
- Lee, J. A., and Tallis, J. H. (1973). Regional and historical aspects of lead pollution in Britain. *Nature* **245**, 216 218.
- Legendre, P. (1993). Spatial Autocorrelation: Trouble or New Paradigm? *Ecology* **74**, 1659.
- Legendre, P., and Fortin, M.-J. e. (1989). Spatial Pattern and Ecological Analysis. *Vegetatio* **80**, 107 137.
- Lehman, J. T. (1975). Reconstructing the rate of accumulation of lake sediments: The effects of sediment focusing. *Quaternary Research* **5**, 541 550.
- Leps, J., and Smilauer, p. (2003). "Multivariate analysis of ecological data using CANOCO." Cambridge University Press, Cambridge.
- Likens, G. E., and Davis, M. B. (1975). Post-glacial history of Mirror lake and its watershed in New Hampshire, USA: An initial report. *Verhandlungen Internationale Vereinigung Limnologie* **19**, 982 993.
- Lillesand, T. M., and Kiefer, R. W. (1994). "Remote sensing and image interpretation." John Wiley and Sons, USA.
- Lindbladh, M., Brunet, J., Hannon, G., Niklasson, M., Eliasson, P., Eriksson, G. R., and Ekstrand, A. (2007). Forest history as a basis for ecosystem restoration- A multidisciplinary case study in a south Swedish temperate landscape. *Restoration Ecology* **15**, 284-295.
- Lindsay, J. M. (1977). Forestry and agriculture in the Scottish Highlands 1700-1850: A problem in estate management. *Agricultural History Review* **25**, 23 37.
- Livingstone, D. A. (1968). Some Interstadial and Postglacial pollen diagrams from Eastern Canada. *Ecological Monographs* **38,** 87 125.
- Longman, K. A. (1984). Physiological studies in Birch. *Proceedings of the Royal Society of Edinburgh* **85**, 97 113.

- Lowe, J. J. (1994). Isolating the climatic factors in early- and mid-Holocene palaeobotanical records from Scotland. *In* "Climate change and human impact on the landscape: studies in palaeoecology and environmental archaeology." (F. C. Chambers, Ed.), pp. 67 82. Chapman and Hall, London.
- Lowe, J. J., Lowe, S., Fowler, A. J., Hedges, R. E. M., and Austin, T. J. F. (1988). Comparison of accelerator and radiometric radiocarbon measurements obtained from Late Devensian Late glacial lake sediments from Llyn Gwernan, North Wales, UK. *Boreas* 17, 355-369.
- Lowe, J. J., and Walker, M. J. C. (1997). "Reconstructing Quaternary Environments." Pearson Education Limited, Essex.
- Lytle, D. E. L., and Wahl, E. R. W. (2005). Palaeoenvironmental reconstructions using the modern analogue technique: the effects of sample size and decision rules. *The Holocene* **15**, 554 569.
- MacDonald, G. M. (2001). Conifer stomata. *In* "Tracking environmental change using lake sediments. Volume 3: Terrestrial, algal and siliceous indicators." (J. P. Smol, H. J. B. Birks, and W. M. Last, Eds.), pp. 33 47. Kluwer Academic Publishers, Dordrecht.
- MacDonald, G. M., Larsen, C. P. S., Szeicz, J. M., and Moser, K. A. (1991). The reconstruction of boreal forest fire history from lake sediments: A comparison of charcoal, pollen, sedimentological and geochemical indices. *Quaternary Science Reviews* **10**, 53 71.
- Mackay, E. E. F. (1999). Wet woods LIFE project hydrological survey of Inshriach, pp. 45. Scottish Natural Heritage Commissioned Report, Dingwall.
- Mackenzie, N. A. (2002). The native woodlands History, decline and present status. *In* "The ecology, land use and conservation of the cairngorms." (C. H. Gimmingham, Ed.), pp. 107 119. Packard Publishing Limited, Chichester.
- Manning, A. D., Fischer, J., Felton, A., Newell, B., Steffen, W., and Lindenmayer, D. B. (2009). Landscape fluidity a unifying perspective for understanding and adapting to global change. *Journal Of Biogeography* **36**, 193-199.
- Mason, W. L., Connolly, T., Pommerening, A., and Edwards, C. (2007). spatial structure of seminatural and plantation stands of Scots pine (*Pinus sylvestris* L.) in northern Scotland. *Forestry* **80**, 567 586.
- Mason, W. L., Hampson, A., and Edwards, C. (2004). "Managing the Pinewoods of Scotland." Forestry Commission, Edinburgh.
- Maxwell, G. (2004). The Roman penetration of he north in the late first century A.D. *In* "A companion to Roman Britain." (M. Todd, Ed.), pp. 75 90. Blackwell Publishing Limited, Oxford.
- Mayer, A. L., and Rietkerk, M. (2004). The dynamic regime concept for ecosystem management and restoration. *Bioscience* **54**, 1013-1020.
- Mazier, F., Broström, A., Gaillard, M. J., Sugita, S., Vittoz, P., and Buttler, A. (2008). Pollen productivity estimates and relevant source area of pollen for selected plant taxa in a pasture woodland landscape of the Jura Mountains (Switzerland). *Vegetation History and Archaeobotany* **17**, 479 495
- Mazier, F., Galop, D., Brun, C., and Buttler, A. (2006). Modern pollen assemblages from grazed vegetation in the western Pyrenees, France: a numerical tool for more precise reconstruction of past cultural landscapes. *The Holocene* **16**, 91-103.
- Mazier, F., Galop, D., Gaillard, M. J., Rendu, C., Cugny, C., Legaz, A., Peyron, O., and Buttler, A. (2009). Multidisciplinary approach to reconstructing local pastoral activities: an example from the Pyrenean Mountains (Pays Basque). *The Holocene* **19**, 171 188.
- McCarroll, D., Jalkanen, R., Hicks, S., Tuovinen, M., Gagen, M., Pawellek, F., Eckstein, D., Schmitt, U., Autio, J., and Heikkinen, O. (2003). Multiproxy dendroclimatology: A pilot study in northern Finland. *Holocene* **13**, 829.
- McLauchlan, K. K., Elmore, A. J., Oswald, W. W., and Sugita, S. (2007). Detecting open vegetation in a forested landscape: pollen and remote sensing data from New England, USA. *Holocene* 17, 1233-1243.

- McVean, D. N. (1953). Biological flora of the British Isle: *Alnus glutinosa* (L.) Gaertn. *Journal Of Ecology* **41**, 447 466.
- McVean, D. N., and Ratcliffe, D. A. (1962). "Plant communities of the Scottish Highlands." Her Majesty's Stationary Office, London.
- Meisel, J. E., and Turner, M. G. (1998). Scale detection in real and artificial landscapes using semi-variance analysis. *Landscape Ecology* **13**, 347 362.
- Messerli, B., Grosjean, M., Hofer, T., Núñez, L., and Pfister, C. (2000). From nature-dominated to human-dominated environmental changes. *Quaternary Science Reviews* **19**, 459.
- Middleton, R., and Bunting, M. J. (2004). Mosaic v1.1: Landscape scenario creation software for simulation of pollen dispersal and deposition. *Review of Palaeobotany and Palynology* **132**, 61-66.
- Mieszczankin, T., and Noryskiewicz, B. (2000). Processes that can disturb the chronostratigraphy of laminated sediments and pollen deposition. *Journal Of Paleolimnology* **23**, 129 140.
- Mitchell, F. J. G. (2005). How open were European primeval forests? Hypothesis testing using palaeoecological data. *Journal of Ecology* **93,** 168.
- Moore, J. (2000). Forest fire and human interaction in the early Holocene woodlands of Britain. *Palaeogeography, Palaeoclimatology, Palaeoecology* **164,** 125.
- Moore, P. D., Webb, J. A., and Collinson, M. E. (1991). "Pollen Analysis." Blackwell Scientific, Oxford.
- Nakagawa, T., Tarasov, P. E., Nishida, K., Gotanda, K., and Yasunda, Y. (2002). Quantitative pollen-based climate reconstruction in central Japan: application to surface and Late Quaternary spectra. *Quaternary Science Reviews* **21**, 2099 2113.
- Nielsen, A. B. (2004). Modelling pollen sedimentation in Danish lakes at c. AD 1800: An attempt to validate the POLLSCAPE model. *Journal of Biogeography* **31,** 1693.
- Nielsen, A. B., and Odgaard, B. V. (2005). Reconstructing land cover from pollen assemblages from small lakes in Denmark. *Review of Palaeobotany and Palynology* **133**, 1.
- Nielsen, A. B., and Sugita, S. (2005). Estimating relevant source area of pollen for small Danish lakes around AD 1800. *Holocene* **15**, 1006-1020.
- Nilsson, M. M. N., Klarqvist, M. M. K., Bohlin, E. E. B., and Possnert, G. G. P. (2001). Variation in ¹⁴C age of macrofossils and different fractions of minute peat samples dated by AMS. *The Holocene* **11**, 579.
- O'Sullivan, P. E. (1970). "The ecological history of the Forest of Abernethy, Inverness-shire." New University of Ulster.
- O'Sullivan, P. E. (1973). Pollen analysis of Mor humus layers from a native Scots pine ecosystem, interpreted with surface samples. *Oikos* **24**, 259 272.
- O'Sullivan, P. E. (1973b). Contemporary pollen studies in a native Scots pine ecosystem. *Oikos* **24**, 143 150.
- O'Sullivan, P. E. (1974). Two Flandrian pollen diagrams from the East-Central highlands of Scotland. *Pollen et Spores* **16**, 3 57.
- O'Sullivan, P. E. (1975). Vegetation and the native pinewoods. *In* "Native pinewoods of Scotland: Proceedings of the Aviemore Symposium." (R. G. H. Bunce, and J. N. R. Jeffers, Eds.), pp. 60 69. NERC, Cambridge.
- O'Sullivan, P. E. (1976). Pollen analysis and radiocarbon dating of a core from Loch Pityoulish. *Journal of Biogeography* **3,** 293 302.
- Odgaard, B. V. (1993). Wind-determined sediment distribution and Holocene sediment yield in a small, Danish, kettle lake. *Journal Of Paleolimnology* **8,** 3 13.
- Oldfield, F., and Appleby, P. (1984). Empirical testing of ²¹⁰Pb-dating models of lake sediments. *In* "Lake sediments and environmental history: studies in palaeolimnology and palaeoecology in honour of Winifred Tutin." (E. Y. Haworth, and J. W. G. Lund, Eds.). Leicester University Press, Leicester.
- Oldfield, F., Appleby, P. G., Cambray, R. S., Eakins, J. D., Barber, K. E., Battarbee, R. W., Pearson, G. R., and Williams, J. M. (1979). ²¹⁰Pb, ¹³⁷Cs and ²³⁹Pu Profiles in Ombrotrophic Peat. *Oikos* **33**, 40.

- Oliver, M. A., and Webster, R. (1987). The elucidation of soil pattern in the Wyre Forest of the West Midlands England, II. Spatial distribution. *Journal of Soil Science* **38**, 293 307.
- Oliver, M. A., Webster, R., Edwards, K. J., and Whittington, G. (1997). Multivariate, autocorrelation and spectral analyses of a pollen profile from Scotland and evidence of periodicity. *Review of Palaeobotany and Palynology* **96,** 121 144.
- Olsson, F., Gaillard, M.-J., Lemdahl, G., Greisman, A., Lanos, P., Marguerie, D., Marcoux, N., Skoglund, P., and Wäglind, J. A continuous record of fire covering the last 10,500 calendar years from southern Sweden -- The role of climate and human activities. *Palaeogeography, Palaeoclimatology, Palaeoecology* **In Press, Corrected Proof**.
- Oram, R. (1997). "Scottish Prehistory." Edinburgh, Birlinn.
- Ortu, E., Peyron, O., Bordon, A., De Beaulieu, J.-L., Siniscalco, C., and Caramiello, R. (2008). Lateglacial and Holocene climate oscillations in the South-western Alps: An attempt at quantitative reconstruction. *Quaternary International* **190**, 71 88.
- Oswald, W. W., Anderson, P. M., Brown, T. A., Brubaker, L. B., Hu, F. S., Lozhkin, A. V., Tinner, W., and Kaltenrieder, P. (2005). Effects of sample mass and macrofossil type on radiocarbon dating of arctic and boreal lake sediments. *The Holocene* **15**, 758-767.
- Overpeck, J. T., Webb III, J. A., and Prentice, I. C. (1985). Quantitative interpretation of fossil pollen spectra: Dissimilarity coefficients and the method of modern analogues. *Quaternary Research* 23, 87 109.
- Ozesmi, S. L., and Bauer, M. E. (2002). Satellite remote sensing of wetlands. *Wetlands ecology and management* **10,** 381 402.
- Pardoe, H. S. (2008). Surface pollen deposition in oak woodlands: the Pollen Monitoring Programme in Britain. *In* "12th International Palynological Congress." Bonn.
- Parry, M. L. (1978). "Climate change, agriculture and settlement." Dawson and Sons, Folkestone.
- Parshall, T. (1999). Documenting forest and stand invasion: fossil stomata and pollen in forest hollows. *Canadian Journal of Botany* **77**, 129 1538.
- Parshall, T., and Calcote, R. (2001). Effect of pollen from regional vegetation on stand-scale forest reconstruction. *Holocene* **11**, 81-87.
- Parsons, R. W., Gordon, A. D., and Prentice, I. C. (1983). Statistical Uncertainty In Forest Composition Estimates Obtained From Fossil Pollen Spectra Via The R-Value Model. *Review Of Palaeobotany And Palynology* **40**, 177-189.
- Parsons, R. W., and Prentice, I. C. (1981). Statistical Approaches To R-Values And The Pollen-Vegetation Relationship. *Review Of Palaeobotany And Palynology* **32**, 127-152.
- Patterson, W. A., Edwards, K. J., and Maguire, D. J. (1987). Microscopic Charcoal As A Fossil Indicator Of Fire. *Quaternary Science Reviews* **6,** 3-23.
- Payne, W.W. (1981) Structure and function in angiosperm pollen wall evolution. *Review of Palaeobotany and Palynology*, **35**, 39 59
- Pebesma, E. J. (2004). Multivariable geostatistics in S: the gstat package. *Computers & Geosciences* **30**, 683.
- Pebesma, E. J., and Wesseling, C. G. (1999). Gstat, a program for geostatistical modelling, prediction and simulation. *Computers & Geosciences* **24**, 17 31.
- Peck, R. M. (1973). Pollen budget studies in a small Yorkshire catchment. *In* "Quaternary Plant Ecology." (H. J. B. Birks, and R. G. West, Eds.), pp. 43 60. Blackwell Scientific Publications, Oxford.
- Pelánková, B., and Chytrý, M. (2009). Surface pollen-vegetation relationships in the forest-steppe, taiga and tundra landscapes of the Russian Altai Mountains. *Review of Palaeobotany and Palynology* **157,** 253.
- Pelankova, B., Kunes, P., Chytry, M., Jankovska, V., Ermakov, N., and Svobodova-Svitavska, H. (2008). The relationships of modern pollen spectra to vegetation and climate along a steppe-forest-tundra transition in southern Siberia, explored by decision trees. *The Holocene* **18**, 1259-1271.
- Pennington, W. (1974). Seston and sediment formation in five Lake District lakes. *Journal Of Ecology* **61**, 215 51.

- Pennington, W., Haworth, E. Y., Bonnay, A. P., and Lishman, J. P. (1972). Lake sediments in northern Scotland. *Philosophical Transactions of the Royal Society of London Series B* **264**, 191 294.
- Peterken, G. F. (1981). "Woodland Conservation and Management." Chapman and Hall, London.
- Peterken, G. F. (1999). Applying natural forestry concepts in an intensively managed landscape. *Global Ecology and Biogeography* **8,** 321 328.
- Peterken, G. F., and Stevenson, A. W. (2004). "A new dawn for native woodland restoration on the Forestry Commission estate in Scotland." Forestry Commission Scotland, Edinburgh.
- Peters, and Higuera. (2007). Quantifying the source area of macroscopic charcoal with a particle dispersal model. *Quaternary Research* **67**, 304 310.
- Pickles, A. (1985). "An introduction to likelihood analysis." Geo Books, Norwich.
- Pielou, E. C. (1984). "The interpretation of ecological data." John Wiley and Sons, New York.
- Pilcher, J. R., and Hall, V. A. (1992). Towards a tephrochronology for the Holocene of the north of Ireland. *Holocene* **2**, 255.
- Pilcher, J. R. and Hall, V.A (1996) A tephrachronology for the Holocene of Northern England. *The Holocene*, **6**, 485 494
- Pilcher, J. R., Hall, V. A. and McCormac, F. G. (1996) An outline tephrochronology for the Holocene of the north of Ireland, *Journal of Quaternary Science*, 11, 485 494
- Pohl, F. (1933). Untersuchungen über Bestäubungsverhältnisse der Traubereiche. *Beihefte zum botanischen Zentralblatt* **51,** 693 6.
- Poska, A., Sepp, E., Veski, S., and Koppel, K (2008) Using quantitative pollen-based land-cover estimations and a spatial CA_Markov model to reconstruct the development of cultural landscape at Rouge, South Estonia, *Vegetation History and Archaeobotany*, **17**(5), 527 541
- Pratt, S. (2007). Long term landscape dynamics in Caledonian pine forest. University of Edinburgh, Unpublished PhD thesis,.
- Prentice, I. C. (1980). Multidimensional scaling as a research tool in Quaternary palynology: a review of theory and methods. *Review of Palaeobotany & Palynology* **31,** 71.
- Prentice, I. C. (1985). Pollen Representation, Source Area, and Basin Size Toward A Unified Theory Of Pollen Analysis. *Quaternary Research* **23**, 76-86.
- Prentice, I. C., Berglund, B. E., and Olsson, T. (1987). Quantitative Forest-Composition Sensing Characteristics Of Pollen Samples From Swedish Lakes. *Boreas* **16**, 43-54.
- Prentice, I. C., Cramer, W., Harrison, S. P., Leemans, R., Monserud, R. A., and Solomon, A. M. (1992). Special Paper: A Global Biome Model Based on Plant Physiology and Dominance, Soil Properties and Climate. *Journal of Biogeography* **19**, 117.
- Prentice, I. C., Guiot, J., Huntley, B., Jolly, D., and Cheddadi, R. (1996). Reconstructing biomes from palaeoecological data: A general method and its application to European pollen data at 0 and 6 ka. *Climate Dynamics* **12**, 185.
- Prentice, I. C., and Parsons, R. W. (1983). Maximum-Likelihood Linear Calibration Of Pollen Spectra In Terms Of Forest Composition. *Biometrics* **39**, 1051-1057.
- Prentice, I. C., and Webb III, T. (1986). Pollen percentages, tree abundances and the Fagerlind Effect. *Journal of Quaternary Science* **1**, 35 43.
- Pringle, D. (1994). "The Forestry Commission: The First 75 years."
- Pryor, S. N., Curtis, T. A., and Peterken, G. F. (2002). Restoring plantations on ancient woodland sites. The Woodland Trust.
- Punning, J. M., Terasmaa, J., Koff, T., and Alliksaar, T. (2003). Seasonal fluxes of particulate matter in a small closed lake in Northern Estonia. *Water Air And Soil Pollution* **149**, 77 92.
- Qi, Y., and Wu, J. (1996). Effects of changing spatial resolution on the results of landscape pattern analysis using spatial autocorrelation indices. *Landscape Ecology* **11**, 39.
- Quelch, P. R. (1997). Ancient trees in Scotland. *In* "Scottish Woodland History." (T. C. Smout, Ed.), pp. 23 38. Scottish Cultural Press, Dalkeith.
- Quelch, P. R. (2001). Ancient wood pasture in Scotland. Forestry Commission.

- Quine, C., and Humphrey, J. W. (2003). The future management of plantation forests for biodiversity. *In* "Biodiversity in Britain's planted forests." (J. W. Humphrey, R. Ferris, and C. Quine, Eds.), pp. 103 - 114. Forestry Commission, Edinburgh.
- Quine, C., and Humphrey, J. W. (In press). Plantations of exotic tree species in Britain: irrelevant for biodiversity or novel habitat for native species? *Biodiversity and Conservation*.
- R Core Development Team (2009). R: A language and environment for statistical computing.
- Rackham, O. (1980). "Ancient Woodland, its History, Vegetation and Uses in England." Edward Arnold, London.
- Rackham, O. (1990). "Trees and woodlands in the British landscape." Phoenix Press, London.
- Rackham, O. (2006). "Woodlands." Collins.
- Ralston, I., and Armit, I. (1997). The early historic period: an archaeological perspective. *In* "Scotland: Environment and archaeology, 8000 BC AD 1000." (K. J. Edwards, and I. Ralston, Eds.), pp. 217 240. John Wiley and Sons, Chichester.
- Randall, R. E., Andrew, R., and West, R. G. (1986). Pollen catchment in relation to local vegetation: Ceann Ear, Monarch Isles, Outer Hebrides. *New Phytologist* **104**, 271 310.
- Räsänen, S., Hicks, S., and Odgaard, B. V. (2004). Pollen deposition in mosses and in a modified 'Tauber trap' from Hailuoto, Finland: What exactly do the mosses record? *Review of Palaeobotany and Palynology* **129**, 103-116.
- Räsänen, S., Suutari, H., and Nielsen, A. (2007). A step further towards quantitative reconstruction of past vegetation in Fennoscandian boreal forests: Pollen productivity estimates for six dominant taxa. *Review of Palaeobotany and Palynology* **146**, 208 220.
- Ratcliffe, D. A. (1974). The Vegetation. *In* "The Cairngorms: Their natural history and scenery." (D. Nethersole-Thompson, and A. Watson, Eds.), pp. 42 77. Collins, London.
- Ratcliffe, P. R., Peterken, G. F., and Hampson, A. M. (1998). A Forest Habitat Network for the Cairngorms. *In* "Scottish Natural Heritage Research, Survey and Monitoring Report Number 114." Scottish Natural Heritage, Edinburgh.
- Raynor, G. S., Hayes, J. V., and Ogden, E. C. (1974). Particulate dispersion into and within a forest. *Boundary-Layer Meteorology* **7**.
- Raynor, G. S., Hayes, J. V., and Ogden, E. C. (1975). Particulate dispersion from sources within a forest. *Boundary-Layer Meteorology* **9**.
- Reimer, P. J., Ballie, M. G. L., Bard, E., Bayliss, A., Beck, J. W., Bertrand, C. J. H., Blackwell, P. G., Buck, C. E., Burr, G. S., Cutler, K. B., Damon, P. E., Edwards, R. L., Fairbanks, R. G., Friedrich, M., Guilderson, T. P., Hogg, A. G., Hughen, K. A., Kromer, B., McCormac, G., Manning, S., Bronk Ramsey, C., Reimer, R. W., Remmele, S., Southon, J. R., Stuiver, M., Talamo, S., Taylor, F. W., Van der Plicht, J., and Weyhenmeyer, C. E. (2004). IntCal 04 terrestrial radiocarbon age calibration, 0-26 cal kyr BP. *Radiocarbon* 46, 1029 1058.
- Rempe, H. (1937). Untersuchungen über die Verbreitung des Blütenstaubes durch die Luftstromungen. *Planta* **27,** 93 147.
- Renberg, I., and Wik, M. (1985). Carbonaceous particles in lake sediments Pollutants from fossil fuel combustion. *Ambio* **14**, 161 163.
- Richards, E. (2002). "The Highland Clearances." Birlinn Limited, Edinburgh.
- Ritchie, J. C. (1969). Absolute pollen frequencies and carbon-14 age of Holocene lake sediment from the Riding mountain area of Manitoba. *Canadian Journal of Botany* **47**, 1345 1349.
- Roberts, A. J., Russell, C., Walker, G. J., and Kirby, K. J. (1992). Regional variation in the origin, extent and composition of Scottish woodland. *Botanical Journal of Scotland* **46**, 167 189.
- Roberts, N. (1998). "The Holocene: An environmental history." Blackwell Publishers Limited, Oxford.
- Robinove, C. J. (1981). The logic of multispectral classification and mapping of land. *Remote Sensing and the Environment* **11,** 231 244.
- Rodwell, J. S. (1991a). "British plant communities. Volume 2: Mires and heath." Cambridge University Press, Cambridge.
- Rodwell, J. S. (1991b). "British plant communities: Volume 1 Woodland and scrub." Cambridge University Press, Cambridge.

- Romshoo, S. (2004). Geostatistical analysis of soil moisture measurements and remotely sensed data at different spatial scales. *Environmental Geology* **45**, 339.
- Rose, N. L. (1990). A method for the extraction of carbonaceous particles from lake sediment. *Journal of Paleolimnology* **3,** 45 53.
- Rose, N. L. (1994). A note on further refinements to a procedure for the extraction of carbonaceous fly-ash particles from sediments. *Journal of Paleolimnology* **11**, 201.
- Rose, N. L. (1995). Carbonaceous particle record in lake sediments from the Arctic and other remote areas of the Northern Hemisphere. *Science of The Total Environment*, **487**, 160-161
- Rose, N. L. (2001). Fly-Ash particles. *In* "Tracking Environmental Change using Lake Sediments, Volume 2: Physical and geochemical methods." (W. M. Last, and J. P. Smol, Eds.), pp. 319 349. Kluwer Academic Publishers, Dordrecht.
- Rose, N. L. (2008). Quality control in the analysis of lake sediments for spheroidal carbonaceous particles. *Limnology and Oceanography: Methods* **6,** 162 171.
- Rose, N. L., and Appleby, P. G. (2005). Regional applications of lake sediment dating by spheroidal carbonaceous particle analysis I: United Kingdom. *Journal of Paleolimnology* **34**, 349 358.
- Rose, N. L., Harlock, P. G., Appleby, P. G., and Battarbee, R. W. (1995). Dating of recent lake sediments in the United Kingdom and Ireland using spheroidal carbonaceous particle (SCP) concentration profiles. *The Holocene* **5**, 328 335.
- Rose, N. L., and Harlock, S. (1998). The spatial distribution of characterised fly-ash particles and trace metals in lake sediments and catchment mosses in the United Kingdom. *Water, Air and Soil pollution* **106,** 287 308.
- Rose, N. L., Harlock, S., and Appleby, P. G. (1999). The spatial and temporal distributions of Spheroidal Carbonaceous Fly-Ash Particles (SCP) in the sediment records of European mountain lakes. *Water, Air and Soil pollution* **113,** 1 32.
- Ross, A. (2004). Assessing the impact of past grazing regimes: transhumance in the forest of Stratha'an, Banffshire. *In* "Short Report 3." pp. 7. Research centre for environmental history, University of Stirling, Stirling.
- Rossi, R. E., Mulla, D. J., Journel, A., and Franz, E. H. (1992). Geostatistical tools for modelling and interpreting ecological spatial dependence. *Ecological Monographs* **62**, 277 314.
- Roy, M. (1997). The highlands and islands of Scotland. *In* "Regional climates of the British Isle." (D. Wheeler, and J. Mayes, Eds.). Routledge, London.
- Royal Commission on Ancient and Historic Monuments of Scotland (2009). Canmore. Royal Commission on the Ancient and Historic Monuments of Scotland.
- Sandgren, P., and Snowball, I. (2001). Application of mineral magnetic techniques to paleolimnology. *In* "Tracking Environmental Changes in Lake Sediments: Physical and Chemical Techniques." (W. M. Last, and J. P. Smol, Eds.), pp. 217 237. Kluwer Academic Publishers, Dordrecht.
- Schofield, J. E., Edwards, K. J., and McMullen, J. A. (2007). Modern pollen-vegetation relationships in subarctic southern Greenland and the interpretation of fossil pollen data from the Norse *landnám. Journal of Biogeography* **34**, 473 488.
- Schwartz, M. W. (1989). Predicting Tree Frequencies From Pollen Frequency An Attempt To Validate The R-Value Method. *New Phytologist* **112**, 129-143.
- Scottish Executive. (2006). The Scottish Forest Strategy, pp. 88. Forestry Commission, Edinburgh.
- Seppa, H., and Hicks, S. (2006). Integration of modern and past pollen accumulation rate (PAR) records across the arctic tree-line: a method for more precise vegetation reconstructions. *Quaternary Science Reviews* **25**, 1501 1516.
- Shaw, H., and Tipping, R. (2006). Recent pine woodland dynamics in east Glen Affric, northern Scotland, from highly resolved palaeoecological analyses. *Forestry* **79**, 331 341.
- Shore, J. S., Bartley, D. D., and Harkness, D. D. (1995). Problems encountered with the 14C dating of peat. *Quaternary Science Reviews* **14**, 373 383.
- Simpson, G. L. (2007). Analogue methods in palaeoecology: Using the analogue package. *Journal of Statistical Software* **22,** 1 25.

- Sisson, J. B. (1979) The Loch Lomond stadial in the British Isle. Nature, 280, 199 203
- Sjogren, P., van Leeuwen, J. F. N., van der Knaap, W. O., and van der Borg, K. (2006). The effect of climate variability on pollen productivity, AD 1975-2000, recorded in a Sphagnum peat hummock. *The Holocene* **16**, 277-286.
- Skøien, J. O., and Blöschl, G. (2006). Scale effects in estimating the variogram and implications for soil hydrology. *Vadose Zone Journal* **5**, 153 167.
- Smith, A. J. E. (1978) The moss flora of Britain and Ireland, Cambridge University Press, Cambridge
- Smith, A. G., and Pilcher, J. R. (1973). Radiocarbon dates and vegetational history of the British Isle. *New Phytologist* **72**, 903 914.
- Smith, S., and Gilbert, J. (2001). National Inventory of woodland and trees: Scotland, Highland region, pp. 30. Forestry Commission, Edinburgh.
- Smout, T. C. (1993). "Scotland since prehistory: Natural change and human impact."
- Smout, T. C. (1997). Cutting into the Pine: Loch Arkaig and Rothiemurchus in the 18th Century. *In* "Scottish Woodland History." (T. C. Smout, Ed.), pp. 114 125. Scottish Cultural Press, Dalkeith.
- Smout, T. C. (1997b). Highland land use before 1800: Misconceptions, evidence and realities. *In* "Scottish Woodland History." (T. C. Smout, Ed.). Scottish Cultural Press, Dalkeith.
- Smout, T. C. (1999). The history of Rothiemurchus woodlands. *In* "Rothiemurchus: Nature and people on a highland estate 1500 2000." (T. C. Smout, and R. A. Lambert, Eds.), pp. 60 79. Scottish Cultural Press, Dalkeith.
- Smout, T. C. (2006). The pinewoods and human use, 1600-1900. Forestry 79, 341.
- Smout, T. C., MacDonald, A. R., and Watson, F. (2005). "A history of the native woodlands of Scotland 1500 1920." Edinburgh University Press, Edinburgh.
- Smout, T. C., and Watson, F. (1997). Exploiting semi-natural woods 1600 1800. *In* "Scottish Woodland History." (T. C. Smout, Ed.), pp. 85 100. Scottish Cultural Press, Dalkeith.
- Soepboer, W., and Lotter, A. F. (2009). Estimating past vegetation openness using pollenvegetation relationships: A modelling approach. *Review of Palaeobotany and Palynology* **153**, 102 107.
- Soepboer, W., Sugita, S., Lotter, A., F., van Leeuwen, J., F. N., and van der Knaap, W., O. (2007). Pollen productivity estimates for quantitative reconstruction of vegetation cover on the Swiss Plateau. *The Holocene* **17**, 65.
- Soepboer, W., Vervoort, J., Sugita, S., and Lotter, A. (2008). Evaluating Swiss pollen productivity estimates using a simulation approach. *Vegetation History and Archaeobotany* **17**, 497.
- Soepboer, W., Sugita, S., and Lotter, A.F. (2010) Regional vegetation-cover changes on the Swiss Plateau during the past two millennia: A pollen-based reconstruction using the REVEALS model. *Quaternary Science Reviews*, **29**, 472 483
- Steven, H. M., and Carlisle, A. (1959). "The Native Pinewoods of Scotland." Oliver and Boyd, Edinburgh.
- Steven, H. M., and Carlisle, A. (1959). "The Native Pinewoods of Scotland." Oliver and Boyd, Edinburgh.
- Stevenson, G. B. (2007). "An historical account of the social and ecological causes of Capercaillie *Tetrao urogallus* extinction and reintroduction in Scotland." University of Stirling.
- Stewart, M. (2002). Using the Woods, 1600 1850 (2) Managing for profit. *In* "People and woods in Scotland: A history." (T. C. Smout, Ed.), pp. 105 128. Edinburgh University Press, Edinburgh.
- Sugita, S. (1993). A Model Of Pollen Source Area For An Entire Lake Surface. *Quaternary Research* **39**, 239-244.
- Sugita, S. (1994). Pollen Representation Of Vegetation In Quaternary Sediments Theory And Method In Patchy Vegetation. *Journal Of Ecology* **82**, 881-897.
- Sugita, S. (2007a). POLLSCAPE model. *In* "Encyclopaedia of Quaternary Science." (S. A. Elias, Ed.), pp. 2561 2570. Elsevier, London.

- Sugita, S. (2007b). Theory of quantitative reconstruction of vegetation I. Pollen from large lakes reveals regional vegetation. *Holocene* **17**, 229 241.
- Sugita, S. (2007c). Theory of quantitative reconstruction of vegetation II. All you need is LOVE. *Holocene* **17**, 243 257.
- Sugita, S., Gaillard, M. J., and Broström, A. (1999). Landscape openness and pollen records: A simulation approach. *Holocene* **9**, 409-421.
- Sugita, S., Hicks, S., and Sormunen, H. (in press). Absolute pollen productivity and pollen vegetation relationships in northern Finland. *Journal of Quaternary Science*.
- Sugita, S., and Walker, K. (2000). Landscape reconstruction algorithm for estimating vegetation changes from pollen records: a case study in the Upper Great Lakes region using modern and pre-settlement pollen-vegetation data sets. *In* "AGU Fall Meeting." San Francisco.
- Summers, R. W., Mavor, R. A., MacLennan, A. M., and Rebecca, G. W. (1999). The structure of ancient native pinewoods and other woodlands in the Highlands of Scotland. *Forest Ecology and Management* **119**, 231 245.
- Sutton, O. G. (1947). The problem of diffusion in the lower atmosphere. *Quarterly Journal of the Royal Meteorological Society* **73**, 257 276.
- Sutton, O. G. (1953). "Micrometeorology." McGraw-Hill, New York.
- Svenning, J.-C. (2002). A review of natural vegetation openness in north-western Europe. *Biological Conservation* **104**, 133.
- Sweeney, C. A. (2004). A key for the identification of stomata of the native conifers of Scandinavia. *Review of Palaeobotany & Palynology* **128**, 281 290.
- Swetnam, T. W., Allen, C. D., and Betancourt, J. L. (1999). Applied historical ecology: using the past to manage for the future. *Ecological Applications* **9**, 1189-1206.
- Tallantire, P. A. (2002). The early-Holocene spread of hazel (*Corylus avellana* L.) in Europe north and west of the Alps: an ecological hypothesis. *The Holocene* **12**, 81-96.
- Tallis, J. H., and Switsur, V. R. (1990). forest and moorland in the South Pennine uplands in the mid-Flandrian period: II the hillslope forests. *Journal Of Ecology* **78,** 857 883.
- Tauber, H. (1965). Differential pollen dispersal and the interpretation of pollen diagrams. *Dansmark Geologiske Undersøgelse II RÆKKE* **89**.
- Telford, R. J., and Birks, H. J. B. (2005). The secret assumption of transfer functions: problems with spatial autocorrelation in evaluating model performance. *Quaternary Science Reviews* **24**, 2173.
- Telford, R. J., Heegaard, E., and Birks, H. J. B. (2004). The intercept is a poor estimate of a calibrated radiocarbon age. *The Holocene* **14**, 296 298.
- Ter Braak, C. J. F., and Prentice, I. C. (1988). A theory of gradient analysis. *Advances in Ecological Research* **18**, 271 317.
- Ter Braak, C. J. F., and Smilauer, P. (2002). "CANOCO reference manual and CanoDraw for windows user's guide. Software for Canonical community ordination (version 4.5)." Microcomputer Power, New York.
- ter Braak, C. J. F., and Šmilauer, P. (2002). "CANOCO reference manual and CanoDraw for windows user's guide: Software for Canonical community ordination (version 4.5)." Microcomputer Power, New York.
- Thomson, K. J. (2002). Agriculture. *In* "The ecology, land use and conservation of the cairngorms." (C. H. Gimmingham, Ed.), pp. 97 106. Packard Publishing Limited, Chichester.
- Tinner, W., Conedera, M., Ammann, B., Gäggeler, N. W., Gedye, S., and Gäggeler, B. (1998). Pollen and charcoal in lake sediments compared with historically documented forest fires in southern Switzerland since AD 1920. *The Holocene* **8**, 31 42.
- Tinsley, H. (2001). Modern pollen deposition in traps on a transect across an anthropogenic treeline on Exmoor, southwest England: a note summarising the first three years of data. *Review of Palaeobotany and Palynology* **117**, 153.
- Tinsley, H. M., and Smith, R. T. (1974). Surface pollen studies across a woodland/heath transition and their application to the interpretation of pollen diagrams. *New Phytologist* **73**, 547 565.

- Tipping, R. (1994). The form and fate of Scotland's woodlands. *Proceedings of the Society of Scottish Antiquity* **124**, 1 54.
- Tipping, R. (2002). Climatic variability and 'marginal' settlement in upland British landscapes: a re-evaluation. *Landscapes* **3**, 10 28.
- Tipping, R., Davies, A., McCulloch, R., and Tisdall, E. (2008). Response to late Bronze Age climate change of farming communities in north east Scotland. *Journal of Archaeological Science* **35**, 2379.
- Tipping, R., Davies, A., and Tisdall, E. (2006). Long-term woodland dynamics in West Glen Affric, northern Scotland. *Forestry* **79**, 351 360.
- Tipping, R., and Tisdall, E. (2004). Continuity, crisis and climate change in the Neolithic and early Bronze Age periods of North West Europe. *In* "Scotland in ancient Europe." (I. A. Shepherd, and G. J. Barclay, Eds.), pp. 71 83. Society of Antiquities of Scotland, Edinburgh.
- Törnqvist, T., De Jong, A. F. M., Oosterbaan, W. A., and van der Borg, K. (1992). Accurate dating of organic deposits by AMS ¹⁴C measurement of macrofossils. *Radiocarbon* **34,** 566 577.
- Troels-Smith, J. (1955). Characterization of unconsolidated sediments. *Dansmark Geologiske Undersøgelse*, *Series IV* **3**, 38 73.
- Trumbore, S. E. (2000). Radiocarbon Geochronology. *In* "Quaternary Geochronology: Methods and applications." (J. S. Noller, J. M. Sowers, and W. R. Lettis, Eds.), pp. 41 60. AGU Reference Shelf 4.
- Trust, T. W. Woodland Biodiversity. The Woodland Trust, Grantham.
- Turner, J. (1964). Surface sample analyses from Ayrshire, Scotland. Pollen et Spores 6.
- Turney, C. S. M., Coope, G. R., Harkness, D. D., Lowe, J. J., and Walker, M. J. C. (2000). Implications for the Dating of Wisconsinan (Weichselian) Late-Glacial Events of Systematic Radiocarbon Age Differences between Terrestrial Plant Macrofossils from a Site in SW Ireland. *Quaternary Research* 53, 114.
- Urban, N. R., Eisenreich, S. J., Grigal, D. F., and Schurr, T. (1990). Mobility and diagenesis of Pb and ²¹⁰Pb in peat. *Geochimica et Cosmochimica Acta* **54**, 3329 3346.
- van der Knaap, W. O., van Leeuwen, J. F. N., and Ammann, B. (2001). Seven years of annual pollen influx at the forest limit in the Swiss Alps studied by pollen traps: relations to vegetation and climate. *Review of Palaeobotany and Palynology* **117**, 31.
- van der Knapp, W. O. (1990). Relations between present-day pollen deposition and vegetation in Spitsbergen. *Grana* **29,** 63 78.
- Van Geel, B., Buurman, J., and Waterbolk, H. T. (1996). Archaeological and palaeoecological indications of an abrupt climate change in The Netherlands and evidence for climateological teleconnections around 2650 BP. *Journal of Quaternary Science* 11, 451 460
- Vera, F. W. M. (2000). "Grazing ecology and forest history." CABI Publishing, Oxford.
- Vile, M. A., Wieder, R. K., and Novak, M. (1999). Mobility of Pb in *Sphagnum*-derived peat. *Biogeochemistry* **45**, 35 52.
- von Post, L. (1916). Skosträdpollen i Sydsvenska Tormosselagerföljder. *Forhandlingar Vid* **16**, 434 465.
- Von Stedingk, H., and Fyfe, R. (2009). The use of pollen analysis to reveal Holocene treeline dynamics: a modelling approach. *The Holocene* **19,** 273 283.
- von Stedingk, H., Fyfe, R., M., and Allard, A. (2008). Pollen productivity estimates from the forest tundra ecotone in west-central Sweden: implications for vegetation reconstruction at the limits of the boreal forest. *The Holocene* **18**, 323.
- Wahl, E. R. (2004). A general framework for determining cutoff values to select pollen analogs with dissimilarity metrics in the modern analog technique. *Review of Palaeobotany and Palynology* **128**, 263 280.
- Walker, M., Johnsen, S., Rasmussen, S. O., Popp, T., Steffensen, J.-P., Gibbard, P., Hoek, W., Lowe, J., Andrews, J., Björck, S., Cwynar, L., C., Hughen, K., Kershaw, P., Kromer, B., Litt, T., Lowe, D., J., Nakagawa, T., Newnham, R., and Schwander, J. (2009). Formal

- definition and dating of the GSSP (Global Stratotype Section and Point) for the base of the Holocene using the Greenland NGRIP ice core, and selected auxiliary records. *Journal of Quaternary Science* **24**, 3-17.
- Walker, M. J. C., Bohncke, S. J. P., Coope, G. R., Connell, M. O., Usinger, H., and Verbruggen, C. (1994). The Devensian/Weichselian Late-glacial in northwest Europe (Ireland, Britain, north Belgium, The Netherlands, northwest Germany). *Journal of Quaternary Science* 9, 109-118.
- Walker, M. J. C., Bryant, C., Coope, G. R., Harkness, D. D., Lowe, J. J., and Scott, E. M. (2001). Towards radiocarbon chronology of the late-glacial: sample selection strategies. *Radiocarbon* **43**, 1007 1019.
- Waller, M. P., Binney, H., Bunting, J., and Armitage, R. A. (2005). The interpretation of fen carr pollen diagrams: pollen-vegetation relationships within the fen carr. *Review of Palaeobotany and Palynology* **133**, 179 202.
- Wareing, P. F. (1959). Problems of juvenility and flowering in trees. *Journal of the Linnean Society of London, Botany* **56,** 282 289.
- Watts, K., Humphrey, J. W., Griffiths, M., Quine, C., and Ray, D. (2005). Evaluating biodiversity in fragmented landscapes: Principles. *In* "Information Note." pp. 8. Forestry Commission, Edinburgh.
- Webb, T., Howe, S. E., Bradshaw, R. H. W., and Heide, K. M. (1981). Estimating Plant Abundances From Pollen Percentages The Use Of Regression-Analysis. *Review Of Palaeobotany And Palynology* **34**, 269-300.
- Webster, R., and Oliver, M. A. (1992). Sample adequately to estimate variograms of soil properties. *European Journal of Soil Science* **43**, 177-192.
- Webster, R., and Oliver, M. A. (2000). "Geostatistics for environmental scientists." John Wiley and Sons, New York.
- Whitlock, C., and Larsen, C. (2001). Charcoal as a fire proxy. *In* "Tracking environmental change using lake sediments: Volume 3." (J. P. Smol, H. J. B. Birks, and W. M. Last, Eds.), pp. 75 97. Kluwer Academic Publishers, The Netherlands.
- Whittington, G., and Edwards, K. J. (1993). 'Ubi solitudinem faciunt pacem appellant': The Romans in Scotland, a Palaeoenvironmental Contribution. *Britannia* **24,** 13.
- Whyte, I., and Whyte, K. (1991). "The Changing Scottish Landscape 1500 1800." Routledge, London.
- Wik, M., and Natkanski, J. (1990). British And Scandinavian Lake Sediment Records Of Carbonaceous Particles From Fossil-Fuel Combustion. *Philosophical Transactions Of The Royal Society B-Biological Sciences* **327**, 319-323.
- Wik, M., and Renberg, I. (1991). Spheroidal carbonaceous particles as a marker for recent sediment distribution. *Hydrobiologia* **214**, 85 90.
- Williams, J. M., and Jackson, S. T. (2007). Novel climates, no-analog communities, an ecological surprises. *Frontiers in Ecology and Environment* **5**, 475 482.
- Williams, J. W., Shuman, B. N., and Thompson, W., III. (2001). Dissimilarity Analyses of Late-Quaternary Vegetation and Climate in Eastern North America. *Ecology* **82**, 3346.
- Willis, K. J., and Birks, H. J. B. (2006). What is natural? The need for a long-term perspective in biodiversity conservation. *Science* **314**, 1261-1265.
- Willis, K. J., Gillson, L., Brncic, T. M., and Figueroa-Rangel, B. L. (2005). Providing baselines for biodiversity measurement. *Trends In Ecology & Evolution* **20**, 107-108.
- Wohlfarth, B., Skog, G., Possnert, G., and Holmquist, B. (1998). Pitfalls in the AMS radiocarbondating of terrestrial macrofossils. *Journal of Quaternary Science* **13**, 137-145.
- Wolter, P. T., Townsend, P. A., and Sturtevant, B. R. (2009). Estimation of forest structural parameters using 5 and 10 meter SPOT-5 satellite data. *Remote Sensing of Environment* **113,** 2019.
- Yang, H., Rose, N. L., and Battarbee, R. W. (2001). Dating of recent catchment peats using spheriodal carbonaceous particle (SCP) concentration profiles with particular reference to Lochnagar, Scotland. *Holocene* **11**, 593.