

# A Last Glacial Maximum pollen record from Bodmin Moor showing a possible cryptic northern refugium in southwest England

ANN KELLY, DAN J. CHARMAN, REWI M. NEWNHAM

School of Geography, University of Plymouth, Drake Circus, Plymouth PL4 8AA UK

## Abstract

A Late Devensian palynological record is presented from Dozmary Pool (Bodmin Moor, southwest England), beyond the southern limit of the Last Glacial Maximum (LGM) British ice sheet. The pollen assemblages indicate predominantly herbaceous tundra-steppe communities but also include elevated levels (typically 10-20%) of conifer tree pollen (*Picea*, *Pinus*, *Abies*) and lower but persistent percentages of broadleaf tree pollen during the LGM. This record is seemingly at odds with the orthodox view of an entirely tree-less tundra-steppe environment for this region and elimination of tree species from the British Isles during glacial maxima. Long distance pollen transport seems an unlikely explanation for the tree pollen considering distance to the nearest known refugia, except possibly for *Pinus*. Reworking of the tree pollen, often invoked in these circumstances, remains a possible alternative, especially given the abundance of these trees in the region during early Devensian interstadials. However, this explanation has been challenged by studies reporting plant macrofossil and faunal evidence for survival of temperate biota during glacial maxima and from climate modelling work that suggests some trees could have survived the glacial extremes in areas well beyond the recorded glacial refugia. Assuming reworking was not a major factor, the Dozmary Pool pollen record is consistent with the 'cryptic northern refugia hypothesis' that invokes survival of trees in small, scattered populations under locally favourable conditions during glacial maxima.

KEYWORDS: Late Devensian; palynology; glacial tree refugia; conifer trees, Dozmary Pool, Mystery Interval

## Introduction

The palaeoecological record of environmental change in the British Isles for the last glacial (Devensian) period is surprisingly incomplete. To the south of the glaciated zone (Fig. 1) only a generalised picture of the changing landscape and biotic communities is available, due to a lack of well-dated, continuous sequences. The fragmentary records (e.g., Simpson & West, 1958; Coope *et al.*, 1961; Morgan, 1973; Hall, 1990; Maddy *et al.*, 1998) are derived mostly from fluvial deposits and are biased towards warmer intervals more likely to result in deposition and preservation of finer sediment under low energy conditions. In detail, large gaps remain for certain regions and intervals and there is limited direct evidence for the Last Glacial Maximum (LGM; ca 24 – 18 cal ka; Mix *et al.*, 2001) in particular.

Nevertheless, from these fragmentary records, a prevailing view (e.g. Godwin, 1975) has emerged of unglaciated regions of Britain characterised by tree-less tundra-steppe communities during long glacial periods, interspersed with milder intervals or interstadials, when woody vegetation temporarily expanded in less inhospitable areas. These interruptions to the treeless landscape were more prominent in the early stages of the Devensian glaciation and, by the late Devensian glacial maximum, it seems that trees had been eliminated completely from the British landscape. This view is consistent with traditional concepts of vegetation response during glacial-interglacial cycles, where tree species from the northern temperate zone of today retreated to southern glacial refugia, from which they expanded

1 during periods of climate amelioration. This conventional view has been questioned recently  
2 using various lines of evidence, including plant macrofossils (e.g., Willis & van Andel, 2004)  
3 mammalian faunas (e.g., Stewart & Lister, 2001) and pollen (e.g. Caseldine *et al.*, 2007)  
4 which point independently toward the stronger presence of thermophilous trees and  
5 persistence of woodland habitat during the last glacial period in central and northwestern  
6 Europe including the British Isles. In this context, there is an obvious need to develop  
7 continuous, well-dated palaeoecological records from unglaciated sites in Britain that extend  
8 through the LGM  
9

10  
11  
12 The southwest of England is one region with potential for more continuous deposits of  
13 Devensian age to be preserved, due to it being free of ice cover during this period (Figure 1,  
14 Campbell, 1998, Bowen *et al.*, 1999). Palynological investigations of potential pre-Holocene  
15 sediments in the mainland Southwest have so far only yielded sequences covering the  
16 Lateglacial (Brown, 1977), with the oldest dates on continuously accumulated sediments  
17 extending back to an indefinite time before c. 15,000 cal yr BP (Hill *et al.*, 2007).  
18 Additionally, some data are available on organic units interbedded with soliflucted material in  
19 coastal sections on the Isles of Scilly (Scourse, 1991, 1996). These records suggest *Betula* and  
20 *Pinus* may have been present during the Lateglacial interstadial (Brown, 1977; Hill *et al.*,  
21 2007) and there are records of *Pinus* from mid/late-Devensian sediments on the Isles of  
22 Scilly, albeit attributed to long distance pollen transport (Scourse, 1991).  
23  
24  
25

26  
27 This paper presents details of a new pollen record from limnic sediments beneath the peat of  
28 Dozmary Pool mire on Bodmin Moor, Southwest England, dated to the LGM. The pollen  
29 assemblages indicate tundra-steppe communities, but also contain significant amounts of  
30 coniferous tree pollen and some broadleaf tree pollen. We discuss the possible origins of this  
31 tree pollen in the context of the debate over glacial tree refugia in northern Europe.  
32

### 33 **Changing concepts of European glacial tree refugia**

34  
35  
36 The concept of glacial refugia developed from observations based largely on pollen records  
37 that vegetation communities tended to track their climatic optima during glacial-interglacial  
38 cycles. A simplistic view emerged of the principal vegetation biomes adjusting their  
39 geographical ranges over time, predominantly in a north-south direction, in response to  
40 marked temperature changes between cold and warm stages. For example, the unglaciated  
41 regions of northern Europe that today are characterised by temperate broadleaf forests were  
42 occupied by steppe-tundra during cold stages (West, 2000). The temperate forest trees  
43 survived these long, unfavourable periods in 'glacial refugia', from which they subsequently  
44 expanded during transitions to warm stages. In Europe, the assumption that these glacial  
45 refugia were all distantly located in southern or eastern regions is supported by long pollen  
46 records from Greece (Tzedakis, 1993; Tzedakis *et al.*, 2002) and Italy (Follieri *et al.*, 1988) in  
47 particular. The term 'bottleneck' has also been suggested instead of 'refugium' for such  
48 temporarily reduced populations (Bennett and Provan, 2008). However, for the purpose of  
49 this paper, the terms 'refugia', 'refugial' and 'refugium' will be employed.  
50  
51  
52

53  
54 Recent views suggest a more complex pattern of glacial refugia, based in part on macrofossil  
55 evidence for tree survival during the LGM beyond these southern refugial regions, for  
56 example in Hungary (Willis *et al.*, 2000; Willis & van Andel, 2004) and Slovakia (Ltyńska-  
57 Zajac, 1995). Fossil records of temperate mammals found in stratigraphic context with cold-  
58 stage faunas, particularly from cave sites, have also prompted suggestions that northern  
59 woodland refugia must have existed. For example, the remains of red deer (*Cervus elaphus*), a  
60 temperate to boreal woodland species, have been found in several late Devensian cave

1 deposits in the UK, including Kent's Cavern, Devon (Fig. 1) (Lister, 1984). Drawing on this  
2 evidence, Stewart and Lister (2001) proposed the concept of "cryptic northern refugia":  
3 isolated and scattered areas of sheltered topography that provided suitable microclimates for  
4 temperate plants and animals during cold stages and which supplemented the well known  
5 southern and eastern refugia. This hypothesis can be tested by palaeobotanical investigations  
6 of the last cold stage that target possible refugial areas in unglaciated parts of northern  
7 Europe, such as southwest England.  
8  
9

### 10 11 **Site description and previous work**

12  
13 Dozmary Pool, Bodmin Moor (SX 192744; 50° 32' 5N"; 4° 32' 9"W) is a large, shallow,  
14 fresh water pool and associated mire at a present day altitude of 265m OD (Figure 2) on the  
15 southern flanks of Bodmin Moor, one of several extensive granite batholiths that largely  
16 define the upland areas of the Devon-Cornwall peninsula of southwestern England. It is one  
17 of three sites examined by Brown (1977) to reconstruct Late Glacial and Holocene vegetation  
18 change. A date (9053 ± 120 radiocarbon years BP) was obtained for the silty detritus mud at  
19 the base of Brown's profile, and which is overlain by Holocene peats.  
20  
21  
22

23 At present the lake is less than 2m at its deepest part with a surface area of 15.7 ha (Newbold  
24 & Hazlehurst, 2000). Input is from springs along the western edge of the lake and a mire has  
25 developed on the south-west margin extending over 4.7 ha.  
26  
27

28 The lake and mire are contained within a clearly defined shoreline which is surrounded by  
29 gently sloping grassland where an acid brown earth has developed overlain by a peaty  
30 horizon. The mire supports an oligotrophic bog including *Sphagnum* mosses, *Eriophorum*  
31 spp., *Molinia caerulea*, *Calluna vulgaris*, *Erica* spp., and *Juncus* spp. Aquatic macrophytes  
32 include *Elatine hexandra*, *Isoetes echinospora*, *Littorella uniflora*, *Nitella flexilis* var. *flexilis*,  
33 *Fontinalis anitpyretica* and *Drepanocladu fluitans* (Newbold & Hazlehurst, 2000). Both for  
34 biological and geological criteria (Campbell, 1998) Dozmary Pool is a Site of Special  
35 Scientific Interest (SSSI).  
36  
37

38 The current climate at Dozmary Pool is predominantly temperate oceanic with 30-year  
39 average winter minimum temperatures ranging between 1.5°C and 1.7 °C and average summer  
40 maximum temperatures reaching values of 17.2°C to 19.0 °C. Air frost occurs on fewer than  
41 54 days per year and average annual rainfall is 1690mm., Snow may lie on the ground for up  
42 to 16 days in any year (UK Met Office, 2009).. The data provided by the Met Office are  
43 extrapolated from the nearest weather stations of St. Mawgan and Princetown, Dartmoor.  
44  
45  
46

### 47 **Methods**

#### 48 49 **Field and laboratory sub-sampling**

50  
51 Three cores were removed from Dozmary Pool mire at the sample point (Figure 2), DZ1, DZ2  
52 and DZ10, using a cobra percussion auger with 50mm diameter, lined corer head. Cores DZ1  
53 and DZ2 were removed less than two metres apart and DZ10, at a later date, fifteen metres  
54 away. The three cores reached depths between 5.90m and 6.20m and coring halted once the  
55 underlying granite surface was encountered. All cores showed near identical stratigraphy.  
56 DZ1 provided material for a pilot study and DZ2 was sub-sampled for multiple laboratory  
57 analyses; DZ10 was used to provide material for a range-finder luminescence date.  
58  
59  
60

## Palynology

Ninety-one sub-samples were removed from DZ2. Samples of 2cm<sup>3</sup> were prepared following Moore *et al.*, (1991) but were sieved at 300µm rather than 180µm after the pilot study revealed the presence of *Abies* pollen in some samples. *Abies* pollen is sufficiently large to have been impeded by sieving at 180µm. It may have been previously overlooked, therefore, in British late Quaternary investigations.

The samples were examined using an Olympus CH-2 light microscope at magnifications of x400 and oil immersion x1000. Identification was verified using pollen keys published in Moore *et al.*, (1991) and Faegri & Iversen, (1989) and the University of Plymouth pollen reference collection. Taxonomy and nomenclature followed that of Bennett (1994). A count of 300 Total Land Pollen (TLP) was made where this was possible or 1000 *Lycopodium* spores whichever total was reached first. Counts of TLP grains were below 100 between 495.5 and 508.5cm and although most grains were well preserved some of those between these depths showed signs of degradation. A further 9 samples had counts of between 150 and 300 TLP. Those samples containing low TLP counts were included in the final pollen diagram as it was considered that they were relevant to the overall pollen profile but are interpreted with a lower degree of confidence.

## Luminescence dating

One optically stimulated luminescence (OSL) date was obtained from a bulk sample of the basal sediments of core DZ10 in order to inform the subsequent radiocarbon dating programme. Particular care was taken to prevent exposure to daylight by immediately covering the retrieved end of the core with triple layers of black plastic and by sub-sampling in a darkened room. The sample was removed from the core at a depth of 570 – 575cm and further sub-sampled under light-controlled conditions at the Luminescence Dating Laboratory, University of Oxford. Laboratory preparation involved the removal of carbonates using hydrochloric acid and then wet sieving to isolate grains between 90-125µm and 180-250µm. Further treatment with concentrated hydrofluoric acid (48%) for 100 minutes dissolved feldspar grains and removed (etched) the outer surface of the quartz grains. Heavy grains were removed by centrifuging in sodium polytungstate solution at 2.68g.cm<sup>3</sup>. Final sieving removed the heavily etched grains. The remaining quartz grains were mounted on 1cm diameter aluminium disks using viscous silicon oil and analysed following methodology described by Rhodes *et al* (2003). Concurrently, a separate sample was sent for commercial analysis to determine the dose rate (mGy/a), and a measure of the water content of the sediments made. The results of the analysis are presented in Table 1.

## AMS <sup>14</sup>C dating of sediments removed from DZ2

Because of a lack of plant macrofossils, bulk sediments were dated from 1cm thick slices removed from DZ2. Care was taken to remove samples from points identified as significant in the pollen diagram. Discs of sediment were removed using a clean scalpel and the outer 1-2mm of material removed. At the NERC Radiocarbon Laboratory at East Kilbride, samples were digested in 2M HCl (80°C, 8 hours), washed free of mineral acid with deionised water and then dried and homogenised. The samples were heated with CuO in sealed quartz tubes and the resultant CO<sub>2</sub> gas was converted to graphite by Fe/Zn reduction, prior to <sup>14</sup>C analysis by Accelerator Mass Spectrometry (AMS). <sup>14</sup>C AMS results were calibrated using Radiocarbon Calibration Programme Calib5.02 (Stuiver & Reimer, 1993). The calibrated results of the analyses are shown in Table 1.

### Charcoal particle counts

Charcoal particles were counted on the prepared pollen slides and results calculated using a formula described by Clark (1982) to give  $\text{cm}^2$  of charcoal per  $\text{cm}^3$  sample, for each level. Only those particles between  $10\mu\text{m}$  and  $300\mu\text{m}$  size were counted as particles below  $10\mu\text{m}$  were difficult to identify positively as charcoal. The results are presented on the pollen diagram (Figure 4). Alternate samples throughout core DZ2 were also examined to identify macro particles of charcoal but none were observed.

### Percentage organic carbon analysis

Sub-samples from DZ2 were removed from the profile at the same depths as the pollen samples and were analysed to measure the organic carbon content throughout the profile using a Shiadzu Total Carbon Analyser. Two sieved ( $<1\text{mm}$ ) samples from each level were combusted, one at  $900^\circ\text{C}$  for total carbon measurement, and one at  $1200^\circ\text{C}$  for minerogenic carbon measurement (Figure 4).

## Results

### Description of core lithostratigraphy and organic carbon

At the base of the core, the granite substrate is overlain by ca 20 cm of coarse sand and gravel and between 600 cm and 330 cm depth by minerogenic grey-white clays with occasional coarse sand or fine gravel. The sediments contain very low levels of organic carbon, typically 0.1-0.3%. Between 329 and 330cm level, an inclusion of fine black particles within the clay matrix coincides with the start of an upwards trend in proportion of organic carbon and a change to grey clay. Isolated roots are visible in the profile, extending from 295 cm to 310 cm. The truncated upper surface of these roots at ca 295 cm coincides with a visible horizontal surface at this horizon that may indicate a possible hiatus. The change from predominantly minerogenic sediments to structure-less organic material occurs at 284cm.

### Chronology

OSL and  $^{14}\text{C}$  ages are presented in Table 1 and illustrated as an age/depth profile in Fig. 3. The  $^{14}\text{C}$  ages range from  $25,416 \pm 672$  cal. yr BP to  $17,569 \pm 523$  cal. yr BP but show two age reversals (Fig 3). Two of the  $^{14}\text{C}$  AMS ages (SUERC-9590 and SUERC-9595) were measured from samples containing very small amounts of carbon, 0.07% and 0.08%, and are thus more susceptible to contamination, in particular by younger C. Omission of these two dates from the chronology removes the age reversals evident in the age-depth profile (Fig. 3). The OSL date provides an independent check of this age model (Fig. 3). An alternative explanation that calls upon an ageing effect in other dated samples (SUERC-9589, SUERC-9591, SUERC-9592) due to inwash of older material seems less likely. In either case, it is clear that the sediments were deposited during the latter stages of the Late Devensian, broadly corresponding with the LGM (24 – 18ka BP).

The age-depth profile (Fig. 3) includes a further datapoint of ca 11,000 cal yr BP at ca 305 cm, based on comparison between the pollen assemblages presented here and Brown's (1977)  $^{14}\text{C}$ -dated early Holocene pollen diagram from the site. We include this additional age estimate to indicate a major change in sediment accumulation rates between the parts of the sequence below

324 cm (ca 31 cm. 1000 yr<sup>-1</sup>) and above 324 cm (ca 3 cm. 1000 yr<sup>-1</sup>). This marked difference in sediment accumulation between the LGM and lateglacial parts of the record is consistent with sedimentological and palynological evidence for a hiatus during the latter period, as discussed further below.

#### DZ2 Pollen Assemblage Zones

Cluster analysis (CONISS, based on total sum of squares) provided a basis for zonation of the diagram (Figure 4) into five Pollen Assemblage Zones (PAZ). The pollen record above 284cm depth is not presented here since it corresponds closely to the Holocene sequence for this site which has been comprehensively described by Brown (1977). The pollen diagram for core DZ2 (Figure 4) presents only the principle taxa observed and the full dataset is given in Appendix 1.

#### DZ2-PAZ 1 610-516cm

Through this zone, pollen assemblages are dominated by Poaceae (up to 60%) and Cyperaceae (up to 40%), these two together always contributing almost 90% TLP. There is, however, a very gradual increase in both *Pinus* and *Picea*, up to a combined maximum of 10% TLP and occasional occurrences of small numbers of broadleaf taxa such as *Betula*, *Corylus* and *Salix*. At 605cm, a small number of *Juniperus* were observed. At modest levels also, *Artemisia*, Chenopodiaceae and Saxifragaceae together contribute variably up to 10% of the overall TLP count. The aquatics *Isoetes* and *Myriophyllum* feature strongly throughout the zone with a peak of *Isoetes* at 525cm. Charcoal levels increase gradually from very low values, and some zero counts, towards a maximum of 32 cm<sup>2</sup>/cm<sup>3</sup> by the end of the zone.

#### DZ2-PAZ 2 516-492.5cm

The TLP count for the assemblages in this zone is fewer than 100 TLP grains per sample with most grains poorly preserved. All taxa (including aquatics) appear to decline during this zone except for *Picea*, which is likely to have inflated values due to the low pollen count combined with the comparatively robust, easily-recognised features of this taxon. Poaceae and Cyperaceae remain significant at values approaching 20% TLP.

#### DZ2-PAZ 3 492.5-320cm

A steep rise in Poaceae levels is observed early in this zone, whilst Cyperaceae levels decline from ca 40% to ca 15% during this zone. The zone is defined by a constant level of 10 - 15% TLP for *Picea* and about 10% TLP for *Pinus* together with isolated grains of *Abies* (450-425cm), which also occurs in small numbers in zones 1 and 2 between 525cm and 505cm. The curve for the combined coniferous species reaches peaks of 25 – 30% TLP, between 41 and 91 grains per sample, the most substantial volume seen in the diagram for these species. Small numbers of *Alnus*, *Betula* and *Corylus* are also present throughout this zone. There is an increase in *Artemisia*, Chenopodiaceae and Saxifragaceae, which is observed throughout zone 3. *Myriophyllum* levels are much lower in this zone than in the previous one, whilst *Isoetes* levels fluctuate markedly throughout.

#### DZ2-PAZ 4 320-305cm

The boundary between PAZ 3 and PAZ 4 at 320cm depth marks a considerable change. Although there is an increase in Poaceae (to ca 50%) and Cyperaceae (to ca. 20%), there is a

1 marked decline in most of the other taxa, particularly the coniferous tree curves. Of these,  
2 *Pinus* declines to much lower levels than previously, whilst *Picea* virtually disappears at the  
3 lower zone boundary. *Abies* is no longer present. There are low values for herbaceous taxa,  
4 notably *Artemisia* and Saxifragaceae whilst Chenopodiaceae and Empetraceae maintain their  
5 previous levels. There are low values recorded for *Betula*, *Ulmus* and *Corylus* and tree pollen  
6 overall is much reduced throughout the zone. The zone is further characterised by a large  
7 increase in the aquatic *Isoetes* which reaches 80% of the TLP, aquatics and spores total. Total  
8 pollen concentration and charcoal influx increases considerably in this zone, presumably a  
9 consequence of the marked reduction in sedimentation accumulation rate noted earlier.

#### 13 DZ2-PAZ 5 305-284cm

14  
15  
16 Poaceae and particularly Cyperaceae values are reduced in zone 5 but steep increases in  
17 *Corylus* and *Betula*, and the emergence of *Quercus* and *Ulmus* characterise the zone and  
18 clearly differentiates it from zone 4. Corresponding with the increase in *Corylus* there is a  
19 decrease in *Salix* and Empetraceae as well as a substantial reduction in Chenopodiaceae. The  
20 aquatics *Myriophyllum* and *Isoetes* are also reduced at this time. Charcoal levels are highly  
21 variable. Both the pollen concentration curve and the organic carbon content of the sediments  
22 remain elevated throughout this zone.

#### 25 Discussion

26  
27  
28 The pollen diagram for Dozmary Pool (Figure 4) shows significant change between the upper  
29 and lower portion of the profile. PAZ 5 is dominated by the pollen of broadleaved tree taxa  
30 and Poaceae, similar to the deepest pollen spectra recovered by Brown (1977) and can be  
31 attributed to the early Holocene. In contrast, PAZ 1 to PAZ 4 are dominated by pollen of  
32 Poaceae and Cyperaceae which together consistently make up 70-80% TLP and include  
33 numerous other herbaceous taxa such as *Artemisia*, Chenopodiaceae and Saxifragaceae.  
34 Aquatic taxa are present throughout, in particular *Isoetes*, whereas *Myriophyllum* pollen  
35 declines markedly after PAZ 2. These assemblages, within highly minerogenic sediments,  
36 indicate an open tundra-steppe environment and persistent lacustrine conditions at Dozmary  
37 Pool throughout PAZ 1-3.

38  
39  
40  
41 Zones PAZ 2 and PAZ 3 are marked by a substantial increase in coniferous tree pollen to  
42 unexpected levels. The comparatively high *Picea* percentages during PAZ 2 must be viewed  
43 with caution due to the low pollen concentrations and low pollen counts (<100 total land  
44 pollen grains per sample) during this zone. In PAZ 3, however, where total land pollen counts  
45 exceed 300 grains throughout, both *Picea* and *Pinus* are present continuously and usually at  
46 levels > 10%, along with more sporadic occurrences of *Abies*, *Alnus*, *Betula* and *Corylus*. At  
47 the same time, Cyperaceae values decrease and Poaceae values increase. The radiocarbon and  
48 OSL age estimates spanning approximately 26 to 17 ka cal yr BP constrain the sediments in  
49 PAZ 1 to PAZ 3 to the LGM. At the top of PAZ3 (c 17.5 ka), both *Picea* and *Pinus* pollen  
50 levels decline abruptly and *Picea* disappears from the record.

51  
52  
53  
54 The high levels of coniferous tree pollen at Dozmary Pool are interesting in light of the  
55 current debate over glacial tree refugia in northern Europe. Below we consider the three most  
56 likely sources for this tree pollen.

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

### (1) Long distance transport

Conifer trees are wind-pollinated and hence typically produce large volumes of pollen dispersed well above ground level, while most species have saccate pollen which is comparatively buoyant and hence more prone to long distance transport by wind and by water. This phenomenon is especially well known in the case of *Pinus* and, as a consequence, high percentages of *Pinus* pollen within cold stage assemblages otherwise dominated by herbaceous plants are not uncommon and typically interpreted as long distance transport, rather than reflecting local presence of trees.

In contrast to *Pinus*, *Picea* is not considered a strong pollen producer and is not known for long-distance transport in modern pollen rain studies. Previous work has used 5% (Huntley & Birks, 1983; Magri, 1999) 4% (Ravazzi, 2002) and 2% (Latalowa & van der Knaap, 2007) as minimum *Picea* pollen percentage levels for indicating local presence of trees and 2% in the case of *Abies* (Huntley & Birks, 1983). In their discussion of *Picea*-pollen representation, Latalowa & van der Knapp (2007) consider that  $\geq 2\%$  pollen indicates with near-certainty that *Picea* was locally present but might fail to detect small populations or those present in low density. Such thresholds should be viewed with caution if applied to cold stages, when redeposition of pollen through erosion processes was more likely (Terhürne-Berson *et al.*, 2004) and when tree pollen could travel further across a more open landscape often under stronger wind regimes. Nevertheless, the persistence of high *Picea* pollen levels (often  $>10\%$ ) during PAZ3, well above these thresholds, would seem to discount long distance transport as a factor for that taxon, especially as the nearest reported refugial sources for *Picea* are as far away as northern Italy (Ravazzi, 2002). Similar arguments may apply to *Abies*, despite lower pollen levels for this taxon at Dozmary Pool, because the large *Abies* pollen is reported to have a limited dispersal range (Godwin, 1975).

It is much harder to reject long distance transport as a primary source for the LGM *Pinus* pollen at Dozmary Pool, due to its greater capacity for long distance dispersal. The nearest analogous records to the Dozmary Pool late Devensian pollen assemblages are from Carn Morval and Watermill Cove on the Isles of Scilly, where high levels of *Pinus* pollen (up to 40-50%) were attributed to long distance travel (Scourse, 1991). Moreover, Scourse interprets increasing *Pinus* values as evidence of climatic deterioration as a result of lower local pollen productivity in the flora generally and selective preservation of sacs and intact grains for *Pinus*. This interpretation may similarly apply to the *Pinus* pollen at Dozmary Pool, where low pollen counts and concentrations may have contributed to artificially high percentages of more robust and easily recognised grains. Alternatively, the co-occurrence of elevated *Picea* and sporadic *Abies* pollen levels with elevated *Pinus* pollen levels at Dozmary Pool during the LGM raises the possibility that long distance transport of *Pinus* to that site and to the Isles of Scilly may not have been the sole factor.

### (2) Reworking

Similar arguments apply in consideration of reworking as a possible explanation for elevated LGM coniferous pollen levels at Dozmary Pool. The contiguous and consistently elevated percentages of *Pinus* and *Picea* pollen seemingly argue against this explanation. Reworking would be expected to result in a more variable pattern, with pulses of sediment flux represented by prominent peaks dominated by the more hardy coniferous pollen, separated by in situ deposition characterised by far fewer or no coniferous pollen. An exceptional situation can be envisaged for this extreme environment however, whereby pervasive reworking of older catchment sediment persisted as the dominant means of pollen delivery to the basin,



1 during an interval of sparse local vegetation cover, low pollen productivity and hence low  
2 airborne pollen input. The highly minerogenic sediments deposited at a comparatively fast  
3 rate support this scenario whilst the likely occurrence in the catchment of early Devensian  
4 (e.g. Chelford Interstadial; Simpson & West, 1958) soils or sediments rich in *Picea*, *Pinus* and  
5 *Abies* pollen provides a possible source for reworking.  
6  
7

8  
9 Another feature of the Dozmary Pool pollen diagram that may be consistent with this  
10 reworking scenario are the highly elevated percentages of *Picea* pollen during PAZ2  
11 (estimated age 22.5 – ca 24 cal ka, i.e. early LGM). During this zone *Picea* pollen percentages  
12 reach 30% TLP despite a greatly impoverished pollen flora, indicated by very low pollen  
13 concentrations, low pollen counts and comparatively poor preservation. This pattern is  
14 consistent with a major flux of older sediment or interval of increased inwash into the basin at  
15 a time when there was comparatively little aerial pollen input from *in situ* vegetation,  
16 resulting in pronounced distortion of the more resilient and identifiable *Picea* grains. Similar  
17 processes may have operated but to a lesser degree during PAZ3 where pollen counts improve  
18 and *Picea* percentages decline to 10-20%.  
19  
20  
21

### 22 (3) *Survival of trees*

23  
24 How likely is it that coniferous tree populations survived during the LGM in southwest  
25 England or the adjacent continental shelf? There are two lines of evidence that might be used  
26 to address this question; other palaeoecological data and results of climate modelling.  
27  
28

29 As discussed earlier, the strongest supporting palaeoecological evidence for the existence of  
30 northerly forest refugia comes from mammalian remains, including those from Kent's  
31 Cavern, also in southwest England (Stewart and Lister, 2001). Ecological niche modelling of  
32 potential ranges for caribou (*Rangifer tarandus*) and red deer (*Cervus elaphus*) during the  
33 LGM over Northwest Europe also suggests these species could have survived in southwest  
34 England (Banks *et al.*, 2008). Further supporting palaeoecological evidence comes from plant  
35 macrofossil evidence for northerly refugia of trees in central and eastern Europe at up to 50°N  
36 (Willis and van Andel, 2004), further north than the well established refugia in the southern  
37 peninsulas of Europe (Bennett *et al.*, 1991). Suggestions of tree refugia on the continental  
38 shelf near Scandinavia based on Lateglacial radiocarbon dates on plant macrofossils of  
39 *Betula*, *Pinus* and *Picea* (Kullman 2002) contradict all the other palaeoecological and  
40 glaciological evidence (Birks *et al.*, 2005), although the case for presence is strengthened by  
41 further recent data (Kullman, 2008; Stewart and Cooper, 2008). Closer to the study area, the  
42 only other tree macrofossil data is a Lateglacial interstadial date on *Quercus*, from Belgium  
43 (Otte, 1994 cited in Stewart and Lister, 2001). Support for this hypothesis from other  
44 palaeoecological evidence in the region is therefore present but uncertain and pollen records,  
45 unless supported by macrofossil evidence, have been equivocal (Birks and Birks, 2000). As  
46 discussed above, much depends upon the validity of the prevailing assumption that elevated  
47 tree pollen levels in cold stage assemblages must derive from reworking or long distance  
48 transport; an assumption often justified in terms of an implicit precautionary approach, but  
49 which carries an inherently circular argument.  
50  
51  
52  
53  
54

55 Turning to climate modelling results, climate during the coldest phases of Marine Isotope  
56 Stage 3 (the closest simulated analogue available at appropriate spatial resolution) shows a  
57 strengthened north-south gradient with winter temperatures up to 20°C cooler than today in  
58 the north but with mid-latitude Europe (45-50°N) only 7-10°C cooler and even less in  
59 southwesterly regions such as the Iberian peninsula (Barron and Pollard, 2002). Summer  
60 temperatures may have only been 4-7° cooler than today in this region. Although precipitation

1 was lower than present, it was higher in mid-latitudes than in southern Europe. The tree  
2 species with elevated pollen levels at Dozmary Pool occur today in regions with more severe  
3 climates. For example, *Picea abies* can tolerate frosts up to  $-38^{\circ}\text{C}$  as long as annual rainfall is  
4 at least 400 mm (Ravazzi, 2002), limits that lie well within the modelled glacial climate for  
5 southwest England. Similarly, Cheddadi *et al.*, (2006) show that the potential LGM  
6 distribution of *Pinus sylvestris*, determined by applying modern climatic limits of this species  
7 to modelled climate reconstructions, extends as far north as Cornwall. Investigations of  
8 palaeoecological evidence for the timing and provenance of postglacial tree migration in the  
9 British Isles (Birks, 1989) and genetics (Ennos *et al.*, 1997) have both concluded that a glacial  
10 refugium for *P. sylvestris* in north-central Europe is likely. The steep climate gradients  
11 modelled for cold stages have been used to explain the local presence of trees in central and  
12 eastern Europe during the LGM (Willis and van Andel, 2004). If the climate model results are  
13 correct, conditions in the far south-western peninsula of Britain and offshore areas may not  
14 have been very much different to those in regions such as southern Poland, where charcoal  
15 remains of *Pinus*, *Abies* and *Larix* have been dated to the LGM at  $26,170\pm 220$  and  $27,590$   
16  $\pm 700$  cal yr BP (Willis and van Andel, 2004, based on radiocarbon ages in Damblon *et al.*,  
17 1996 and Musil, 2003). The sites are at approximately the same latitude as each other (c.  
18  $50^{\circ}\text{N}$ ) so this does not seem unreasonable. It is feasible therefore that tree populations  
19 survived in microclimatically suitable areas of southwest England and the adjacent  
20 continental shelf. Further support is provided by recent climate modelling work showing  
21 potential LGM ranges for *Alnus incana*, *Betula pendula*, *Betula pubescens*, *Picea abies*, *Pinus*  
22 *syvestris* and *Salix caprea* as far north as the southern limits of the British ice sheet  
23 (Svenning *et al.*, 2008).  
24  
25  
26  
27  
28  
29

30 What does this tell us about likely patterns and characteristics of northern cryptic refugia? The  
31 likely species represented by the three coniferous taxa with elevated pollen levels at Dozmary  
32 Pool (*Picea abies*, *Pinus sylvestris* & *Abies alba*) share certain common ecological affinities  
33 that provide some clues. All three occur in montane-alpine regions of central and southern  
34 Europe and throughout northern Europe, with *Picea abies* & *Pinus sylvestris* extending to the  
35 northernmost limits of forest in Europe. In some respects these regions may be viewed as  
36 interglacial refugia. Severe temperature depression can occur in these regions but the key to  
37 survival of these trees is more likely to be moisture availability. *Picea*, for example, is most  
38 sensitive to extreme continental climate and in particular to winter desiccation (Ravazzi 2002)  
39 whilst *Abies alba* is drought intolerant (Terhune–Berson *et al.*, 2004). *Pinus sylvestris* can  
40 tolerate temperatures as low as  $-18^{\circ}\text{C}$  but does not survive today in areas that experience less  
41 than 400 mm annual rainfall (Cheddadi *et al.*, 2006). Moisture dependency may explain the  
42 postulated occurrence of these three conifers in the oceanic setting of southwestern England  
43 during the LGM. If so, cryptic northern refugia are more likely to be found in situations where  
44 local precipitation or moisture availability is enhanced, such as in sheltered valleys of the low  
45 hills of Bodmin Moor.  
46  
47  
48  
49

50 One further question might be asked at this point: if small remnant populations of *Picea*  
51 survived near Dozmary Pool during the LGM, why did the species disappear so completely at  
52 the end of the LGM, represented by PAZ 3, and not persist through the Lateglacial into the  
53 Holocene warm phase? This part of the Dozmary Pool pollen record is subject to greater  
54 uncertainty as just 20 cm sediment accumulation separates the horizon where *Picea* abruptly  
55 declines, dated at ca. 17 ka and the earliest Holocene sediments, by which time *Picea* has  
56 disappeared from the record. As argued above, sediment accumulation slowed dramatically or  
57 at times may have ceased during this interval. Almost certainly the lake level fell at times,  
58 exposing the lake bed; loss of sediment through winnowing accompanying desiccation of the  
59 lake may also have occurred.  
60

1  
2  
3 The marked reduction in coniferous pollen, including elimination of *Picea* and *Abies*, at  
4 Dozmary Pool thus coincides with a major change in the local depositional environment (Fig.  
5 5). The period of no or markedly reduced sediment accumulation, extending from ca 17 ka to  
6 the early Holocene, includes the so-called deglacial “mystery interval” (17.5 to 14.5 ka) of  
7 Denton *et al.*, (2006) and the subsequent Lateglacial oscillation. During the ‘mystery  
8 interval’, ice-rafted debris was discharged extensively into the North Atlantic (the Heinrich-1  
9 Event; Hemming, 2004), North Atlantic meridional overturning circulation was shut down  
10 (McManus *et al.*, 2004), sea surface temperatures in the northern Atlantic Ocean and  
11 Mediterranean Sea were significantly depressed (Bard *et al.*, 2000; Cacho *et al.*, 2001) and  
12 hypercold winters occurred in northwestern Europe (Renssen & Isarin, 2001) and in  
13 Greenland (Denton *et al.*, 2005). Paradoxically, during this interval of extreme cold in  
14 Western Europe, extensive deglaciation occurred in the European Alps (Denton *et al.*, 1999)  
15 and global atmospheric CO<sub>2</sub> levels, measured from Antarctic ice cores rose markedly  
16 (Monnin *et al.*, 2001). Denton *et al.*, (2006) explain this contradiction by suggesting the cold  
17 oceanic and terrestrial conditions reflect extensive winter sea ice cover in the northern  
18 Atlantic, perhaps as far south as 48°N, whilst the retreat of temperate mountain glaciers reflect  
19 warmer summers linked to rising atmospheric CO<sub>2</sub>.  
20  
21  
22  
23

24 The effect of these severe conditions on the climate and vegetation of southwestern England  
25 must have been marked. Hypercold winters would have posed a major threat to any woody  
26 vegetation that, having survived the LGM, was already close to its climatic limits. Extreme  
27 cold would have been exacerbated by dry and windy conditions that are likely to have  
28 accompanied expansion of sea ice and southwards displacement of the ITCZ (Lea *et al.*,  
29 2003). For survival of woody vegetation, these highly detrimental winter conditions would  
30 have outweighed the favourable conditions that accompanied warmer summers. The decline  
31 of tree pollen and disappearance of *Picea* pollen at Dozmary Pool during the ‘mystery  
32 interval’ therefore is consistent with wider scale regional changes in the North Atlantic and  
33 western Europe regions, and in particular with hypercold winters and reduced moisture  
34 availability. Similarly, the evidence for lake desiccation concurs with a scenario of warmer  
35 summers with higher rates of evaporation and hypercold winters when the lake basin is likely  
36 to have frozen.  
37  
38  
39  
40

41 A similar pattern was observed in marine sediment cores in the Gulf of Lions interpreted as  
42 indicating LGM survival of *Abies*, *Picea* and deciduous *Quercus* in the drainage basins of the  
43 Pyreneo-Languedocian rivers of southeastern France (Beaudoin *et al.*, 2007). These trees  
44 were subsequently absent from the Rhone drainage basin during the deglaciation and also  
45 disappeared from the Pyreneo-Languedocian drainage basins from ca 17 to 15 cal ka BP  
46  
47

48 Also contained within the Dozmary Pool LGM sediments are pollen grains of broadleaf trees  
49 and shrubs, *Betula*, *Alnus* and *Corylus*, and although in low numbers, they are recorded  
50 throughout PAZ 3 at a time when the coniferous tree pollen curves reach their maximum  
51 levels. As with the conifer trees, these taxa are currently presumed to have been eliminated  
52 from the British Isles during glacial maxima but the Dozmary Pool record raises the  
53 possibility that these broadleaf trees and shrubs also occurred near the site in cryptic refugia.  
54  
55

## 56 Conclusion

57  
58 Our understanding of environmental and biotic changes in the unglaciated mid-high latitude  
59 regions of the northern hemisphere during the most extreme cold stages of the Quaternary is  
60 constrained by a paucity of sedimentary and palaeocological records. In regions bordering the  
great northern ice sheets a limited array of scattered sites and fragmentary records is perhaps

1  
2  
3  
4 an inevitable legacy of a combination of harsh, changing climate and environmental  
5 instability. Often no direct archive survives of the most extreme intervals and reconstructions  
6 rely upon untested assumptions and extrapolation across broad intervals of space and time. It  
7 is not surprising therefore, that alternative views about glacial tree refugia in northern Europe  
8 have emerged.  
9

10  
11 The palaeoecological record from Bodmin Moor in southwest England near the maximum  
12 extent of Late Devensian ice provides a near-continuous pollen record through the LGM.  
13 Interpretation of this pollen record in terms of vegetation change is hampered by  
14 comparatively low pollen concentrations and the paucity of comparable, coeval records from  
15 the region. The inferred vegetation record must also be qualified by the untested assumption  
16 that alternative pollen-taphonomic sources were not a significant factor in delivering pollen to  
17 the core site. Although long distance transport of pollen seems unlikely, reworking of at least  
18 some pollen from older strata remains a strong possibility. Nevertheless recent climate  
19 modelling showing the potential for tree survival in this region during the LGM compels us to  
20 consider this more straightforward explanation for the Dozmary Pool pollen record.  
21

22  
23 Assuming the pollen assemblages reasonably reflect the contemporary vegetation around the  
24 site, two features stand out. First, the occurrence of high percentages of coniferous tree pollen  
25 and lower but persistent percentages of broadleaf tree pollen between  $25,416 \pm 672$  and  
26  $17,569 \pm 523$  cal yr BP, broadly coinciding with the LGM. This evidence is contrary to the  
27 orthodox view of tree-less steppe-tundra grasslands, but consistent with the 'northern cryptic  
28 refugia hypothesis' that invokes survival of temperate biota during glacial maxima and with  
29 climate modelling work that suggests some trees could have survived the glacial extremes in  
30 areas well beyond the recorded glacial refugia where moisture availability was not a limiting  
31 factor.  
32  
33

34  
35 Second, the decline of tree pollen (at ca 17 ka) and inferred extensive period of lake  
36 desiccation imply more severe environmental conditions were experienced in southwest  
37 England during the deglaciation than during the LGM. This apparent contradiction  
38 nevertheless is consistent with wider regional evidence for climate deterioration and strong  
39 seasonal differentiation across western Europe and the North Atlantic region during the so-  
40 called 'mystery interval', ca 17.5 – 14.5 ka. An obvious corollary is that bioclimatic  
41 conditions were more severe in southwest England (and perhaps further afield) during the  
42 deglaciation 'mystery interval' than during the LGM.  
43  
44

45  
46 The critical assumption underpinning these observations can be tested by further  
47 palaeoecological investigation at other sites in the region, including offshore. Substantial  
48 replication of the Dozmary Pool LGM record would go some way to confirming the cryptic  
49 refugia hypothesis, which has profound ramifications for biogeography and prehistory.  
50 Similarly, there is a clear need to find and investigate other sedimentary sequences  
51 representing the last deglaciation in southwest England that might provide further insight into  
52 the marked environmental changes during the so-called 'mystery interval'.  
53  
54

55  
56 *Acknowledgements* We would like to thank the Natural Environment Research Council  
57 (Scottish Universities Environmental Research Centre) for funding six AMS  $^{14}\text{C}$  dates,  
58 allocation number: 1137.1005. We also thank The Quaternary Research Association and the  
59 School of Geography, University of Plymouth for funding the range-finder OSL date and the  
60 Cartography Unit of the School of Geography, University of Plymouth for the preparation of  
Figures 1 and 2.

## References

- Bard E, Rostek F, Turon J-L, Gendreau S. 2000. Hydrological impact of Heinrich events in the Subtropical Northeast Atlantic. *Science* **289**: 1321-1324. DOI: 10.1126/science.289.5483.1321
- Barron E, Pollard D. 2002. High-Resolution Climate Simulations of Oxygen Isotope Stage 3 in Europe. *Quaternary Research* **58**: 296–309. DOI: 10.1006/qres.2002.2374
- Beaudoin C, Jouet G, Suc JP, Berné S, Escarguel G. 2007. Vegetation dynamics in southern France during the last 30ky in the light of marine palynology. *Quaternary Science Review* **26**: 1037-1054. DOI: 10.1016/j.quascirev.2006.12.009
- Bennett KD, Provan J. 2008. What do we mean by refugia? *Quaternary Science Reviews* **27**: 2449-2455. DOI: 10.1016/j.quascirev.2008.08.019
- Bennett KD. 1994. *Annotated catalogue of pollen and pteridophyte spore types of the British Isles*. Department of Plant Sciences, University of Cambridge.
- Bennett KD, Tzedakis PC, Willis KJ. 1991. Quaternary refugia of north European trees, *Journal of Biogeography* **18**: 103-115.
- Birks HJB. 1989. Holocene isochrones maps and patterns of tree-spreading in the British Isles. *Journal of Biogeography* **16**: 503-540.
- Birks HJB, Birks HH. 2000. Future use of pollen analysis must include plant macrofossils. *Journal of Biogeography* **27**: 31-35. DOI: 10.1046/j.1365-2699.2000.00375.x
- Birks HH, Larsen E, Birks HJB. 2005. Did tree-Betula, Pinus and Picea survive the last glaciation along the west coast of Norway? A review of the evidence, in light of Kullman (2002). *Journal of Biogeography* **32**: 1461-1471. DOI: 10.1111/j.1365-2699.2005.01287.x
- Bowen DQ, Lewis G, Maddy D, Gibbard PL, Preece RC, Campbell S, Hunt CO, Scourse JD, Keen DH, Croot DG, Thomas GSP, Sutherland DG, McCabe A M, Cameron TDJ & Holmes R. 1999. *A Revised Correlation of Quaternary Deposits in the British Isles*. Geological Society Special Report, 23
- Brown AP. 1977. Late-Devensian and Flandrian vegetational history of Bodmin Moor, Cornwall. *Phil. Trans. R. Soc. Lond* **B 276**: 251-320.
- Cacho I, Grimalt J O, Sierro F J, Shackleton N J, Canals M.. 2001. Evidence for enhanced Mediterranean thermohaline circulation during rapid climatic coolings. *Earth and Planetary Science Letters* **183**: 417-429. DOI: 10.1016/S0012-821X(00)00296-X
- Campbell S, Hunt CO, Scourse JD, Keen DH. 1998. *Quaternary of South-West England*. Geological Conservation Review Series, Chapman & Hall, London.
- Caseldine CJ, McGarry SF, Baker A, Hawkesworth C and Smart P. 2007. Late Quaternary speleothem pollen in the British Isles *Journal of Quaternary Science* **23**: 193-200. DOI: 10.1002/jqs.1121

- 1  
2  
3 Cheddadi R, Vendramin GG, Litt T, Francois L, Kageyama M, Lorentz S, Laurent J-M,  
4 Beaulieu J-L, Sadori L, Lost A, Lunt D. 2006. Imprints of glacial refugia in the modern  
5 genetic diversity of *Pinus sylvestris*. *Global Ecology and Biogeography* **15**: 271-282. DOI:  
6 10.1111/j.1466-8238.2006.00226.x  
7  
8  
9 Clark RL. 1982. Point count estimation of charcoal in pollen preparations and thin sections of  
10 sediments. *Pollen et Spores* **24**: 523-535.  
11  
12 Coope, GR, Shotton, FW, Strachan, I. 1961. A late Pleistocene flora and fauna from Upton  
13 Warren, Worcestershire. *Phil. Tran. R. Soc. Lond. Royal Society* **B244**: 379-421.  
14  
15  
16 Damblon, F, Haesaerts, P, Van der Plicht, J. 1996. New datings and considerations on the  
17 chronology of Upper Palaeolithic sites in the Great Eurasian Plain. *Préhistoire Européenne*  
18 **9**: 177-231.  
19  
20  
21 Denton GH, Heusser CJ, Lowell TV, Moreno PI, Andersen BG, Heusser LE, Schluchter C, &  
22 Marchant DR. 1999. 'Interhemispheric Linkage Of Paleoclimate During The Last Glaciation.  
23 *Geografiska Annaler* **81a**: 107-153.  
24  
25  
26 Denton G H, Alley R B, Comer G C, Broecker W S. 2005. The role of seasonality in abrupt  
27 climate change. *Quaternary Science Reviews* **24**: 1159-1182. DOI: 10.1016/j.quascirev.2004.12.CO2  
28  
29 Denton GH, Broecker WS, Alley R B. 2006. The Mystery Interval 17.5 to 14.5 kyrs ago.  
30 *Pages News* **14**: 14-16.  
31  
32  
33 Ennos RA, Sinclair WT, Perks MP. 1997. Genetic insights into the evolution of Scots pine,  
34 *Pinus sylvestris* L., in Scotland. *Botanical Journal of Scotland* **49**: 257-265.  
35  
36 Faegri K, Iversen J. 1989. *Textbook of Pollen Analysis* (4<sup>th</sup> Edition with K. Krzywinski) John  
37 Wiley, Chichester & New York.  
38  
39  
40 Follieri, M, Magri, D, Sadori L. 1988. 250,000-year pollen record from Valle di Castiglione  
41 (Roma). *Pollen et Spores* **30**: 329-356.  
42  
43 Godwin H. 1975. *Quaternary history of the British Flora* (2nd Edition). Cambridge  
44 University Press: Cambridge.  
45  
46  
47 Hall K. 1990. Quaternary glaciations in the southern ocean: Sector 0° long.-180° long  
48 *Quaternary Science Reviews* **9**: 217-228. DOI: 10.1016/0277-3791(90)90019-7  
49  
50  
51 Hemming SR. 2004. Heinrich events: massive late Pleistocene detritus layers of the North  
52 Atlantic and their global climate imprint. *Reviews of Geophysics* **42**: 1, RG1005.  
53  
54  
55 Hill DJ, Haywood AM, Hindmarsh RCA, Valdes PJ. 2007. Characterising ice sheets during  
56 the mid Pliocene: evidence from data and models, In: M. Williams, A.M. Haywood, J.  
57 Gregory and D. Schmidt (Ed) *Deep-time perspectives on climate change: marrying the signal*  
58 *from computer models and biological proxies*. The Micropalaeontological Society, Special  
59 Publication, The Geological Society: London, 517-538.  
60

- 1  
2 Huntley B, Birks H J B. 1983. An Atlas of Past and Present Pollen Maps for Europe 0-13,000  
3 years ago. Cambridge University Press: New York.  
4
- 5 Kullman L. 2008. Early postglacial appearance of tree species in northern Scandinavia:  
6 review and perspective. *Quaternary Science Reviews* **27**: 2467-2492. DOI:  
7 10.1016/j.quascirev.2008.09.004  
8
- 9  
10 Kullman L. 2002. Boreal tree taxa in the central Scandes during the Late-Glacial: implications  
11 for Late-Quaternary forest history. *Journal of Biogeography* **29**: 1117-1124. DOI:  
12 10.1046/j.1365-2699.2002.00743.x  
13
- 14  
15 Latalowa M, van der Knaap WO. 2007. Late Quaternary expansion of Norway spruce *Picea*  
16 *abies* (L.) Karst. In Europe according to pollen data. *Quaternary Science Reviews* **25**: 21-22,  
17 2780-2805. DOI: 10.1016/j.quascirev.2006.06.007  
18
- 19  
20 Lea DW, Pak DK, Peterson LC, Hughen KA. 2003. Synchronicity of tropical and high-latitude  
21 Atlantic temperatures over the Last Glacial termination. *Science* **301**: 1361-1364. DOI:  
22 10.1126/science.1088470  
23
- 24  
25 Lister, AM. 1984. Evolutionary and ecological origins of British deer. *Proc. R. Soc.*  
26 *Edinburgh* **82**: 205-229.  
27
- 28  
29 Ltyńska-Zajac M. 1995. Anthracological analysis. In: Hromada J, Kozłowski J, eds. *Complex*  
30 *of Upper Palaeolithic sites near Moravany, western Slovakia*. Kraków, Poland. Jagiellonian  
31 University Press: 74-79.  
32
- 33  
34 Maddy, D, Lewis SG, Scaife RG, Bowen DQ, Coope GR, Green CP, Hardaker Y, Keen DH,  
35 Rees-Jones J, Parfitt S, Scott K. 1998. The Upper Pleistocene deposits at Cassington, near  
36 Oxford, England. *Journal of Quaternary Science* **13**: 3. 205-231. DOI:  
37 10.1002/(SICI)1099.1417(199805/06)13:3<205::AID-JQS357>3.0.CO:2-N  
38
- 39  
40 Magri D.1999. Late Quaternary vegetation history at Lagacione near lago di Bolsena (central  
41 Italy). *Rev. Palaeobot. Palynol.* **106**: 171-208.  
42
- 43  
44 Mix AC, Bard E, Schneider R. 2001. Environmental processes of the ice age: land, oceans,  
45 glaciers (EPILOG). *Quaternary Science Reviews* **20**: 4. 627-657. DOI: 10.1016/SO277-  
46 3791(00)00145-1  
47
- 48  
49 McManus JF, Francois R, Gherardi J-M, Keigwin LD, Brown-Leger S. 2004. Collapse and  
50 rapid resumption of Atlantic meridional circulation linked to deglacial climate changes.  
51 *Nature* **428**: 834-837. DOI: 10.1038/nature.02494  
52
- 53  
54 Monnin E, Indermühle A, Dällenbach A, Flückiger J, Stauffer B, Stocker TS, Reynaud D,  
55 Barnola J-M. 2001. Atmospheric CO<sub>2</sub> concentrations over the Last Glacial Termination.  
56 *Science*. **291**. 112–114 DOI: 10.1126/science.291.5501.112.  
57
- 58  
59 Moore, Webb & Collinson. 1991. *Pollen Analysis*. Blackwell Sci. Pub: London  
60
- 60  
61 Morgan A. 1973. The Pleistocene geology of the area north and west of Wolverhampton,  
Staffordshire, England. *Phil. Tran. R. Soc. Lond.* **B265**: 233-297.

- 1  
2 Musil, R. 2003. *The Middle and Upper Palaeolithic game suite in central and south-eastern*  
3 *Europe*. In: van Andel, T.H., Davies, S.W. (Eds.), *Neanderthals and Modern Humans in the*  
4 *European Landscape during the Last Glaciation*. McDonald Institute for Archaeological  
5 Research, Cambridge, pp. 167–190.  
6  
7  
8 Newbold C, Hazlehurst D. 2000. *Dozmary Pool, Bodmin Moor, Cornwall: A survey of the*  
9 *aquatic macrophytes*. English Nature, Peterborough & Truro.  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60
- Otte M. Ed. 1994. *Le Magdalénien du Trou de Chaleux* ERAUL 60, Liege.
- Ravazzi C. 2002. Late Quaternary history of spruce in southern Europe. *Review of Paleobotany and Palynology* **120**: 131-177.
- Renssen H, Isarin R F B, 2001. The two major warming phases of the last deglaciation at ~14.7 and ~11.5 ka cal BP in Europe: climate reconstructions and AGCM experiments. *Global and Planetary Change* **30**: 1-2.
- Rhodes E J, Bronk Ramsey C, Outram Z, Batt C, Willis L, Dockrill S, Bond J. 2003. Bayesian methods applied to the interpretation of multiple OSL dates: high precision sediment ages from Old Scatness Broch excavations, Shetland Isles. *Quaternary Science Reviews* **22**: 10-13. 1231-1244. DOI: 10.1016/S0277-3791(03)00046-5
- Scourse JD 1991. Late Pleistocene Stratigraphy and Palaeobotany of the Isles of Scilly. *Phil. Tran. R. Soc. Lond.* **B334**: 405-448.
- Scourse JD. 1996. A Field Guide for the Isles of Scilly Excursions. In: Field Guide. Late Quaternary Coastal Change in West Cornwall, UK Ed. MG Healy
- Simpson IM, West RG. 1958. On the stratigraphy and palaeobotany of a Late-Pleistocene organic deposit at Chelford, Cheshire. *New Phytologist* **57**: 239-250.
- Stewart, J R. and Cooper, A. 2008. Introduction: Ice Age refugia and Quaternary extinctions: An issue of Quaternary evolutionary palaeoecology. *Quaternary Science Reviews* **17**: 2443-2448. DOI: 10.1016/j.quascirev.2008.10.005
- Stewart JR, Lister AM. 2001. Cryptic northern refugia and the origins of the modern biota. *Trends in Ecology & Evolution* **16**: 608-613. DOI: 10.1016/S0169-5347(01)02338-2
- Stuiver M and Reimer PJ. 1993. Radiocarbon Calibration Program CALIB Rev5.0.2 *Radiocarbon* **35**: 215-230.
- Svenning J-C, Normand S, Kageyama M. 2008. Glacial refugia of temperate trees in Europe: insights from species distribution modelling. *Journal of Ecology* **96**: 1117-1127. DOI: 10.1111/j.1365-2745.2008.01422x
- Terhürne-Berson R, Litt T, Cheddadi R. 2004. The spread of *Abies* throughout Europe since the last glacial period: combined macrofossil and pollen data. *Vegetation History and Archaeobotany* **13**: 257-268. DOI: 10.1007/s00334-004-0049-4
- Tzedakis, PC. 1993. Long-term tree populations in northwest Greece through multiple Quaternary climatic cycles. *Nature* **364**: 437-440. DOI: 10.1038/364437a0



1  
2  
3 Tzedakis, PC. Lawson IT, Frogley MR, Hewitt GM, Preece, RC. 2002. Buffered tree  
4 populations in a Quaternary refugium: evolutionary implications. *Science* **297**: 2044-2047.  
5 DOI: 10.1126/science.1073083  
6

7  
8 UK Met Office. 2009. [www.metoffice.gov.uk](http://www.metoffice.gov.uk). Accessed January 2009.  
9

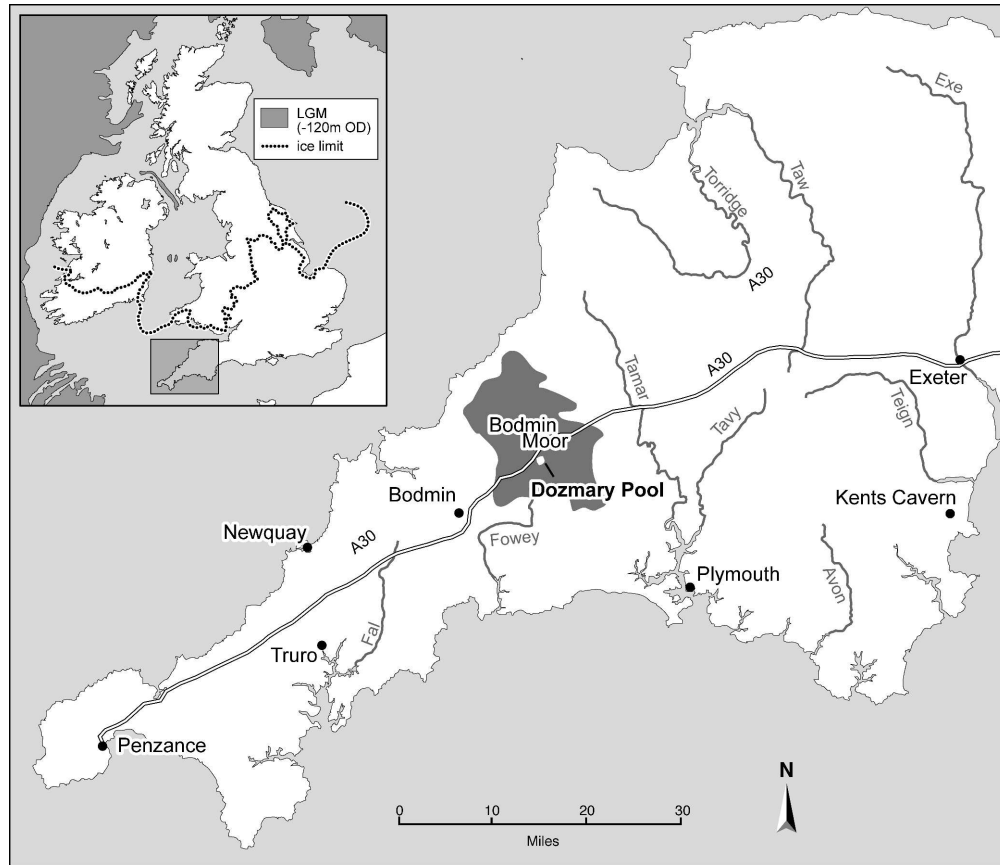
10 West R G, 2000. *Plant Life of the Quaternary*, Cambridge University Press: Cambridge, UK.  
11

12 Willis KJ, Rudner E, Sümegei, P. 2000. The full-glacial forests of Central and Southeastern  
13 Europe. *Quaternary Research* **53**: 203-213. DOI: 10.1006/qres.1999.2119  
14

15  
16 Willis KJ van Andel TH. 2004. Trees or no trees? The environments of central and eastern  
17 Europe during the Last Glaciation. *Quaternary Science Reviews* **23**: 23-24. 2369-2387. DOI:  
18 10.1016/j.quascirev.2004.06.002  
19

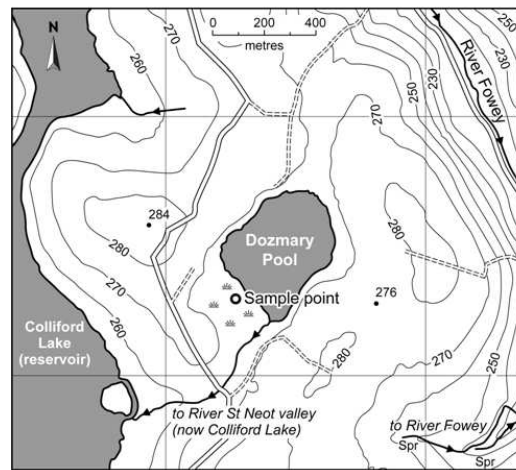
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

For Peer Review



176x151mm (600 x 600 DPI)

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60



254x190mm (96 x 96 DPI)

review

Top

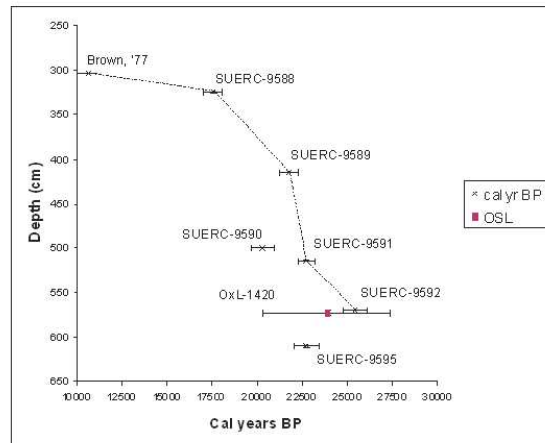


Figure 3 Ann Kelly

254x190mm (96 x 96 DPI)

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

Top

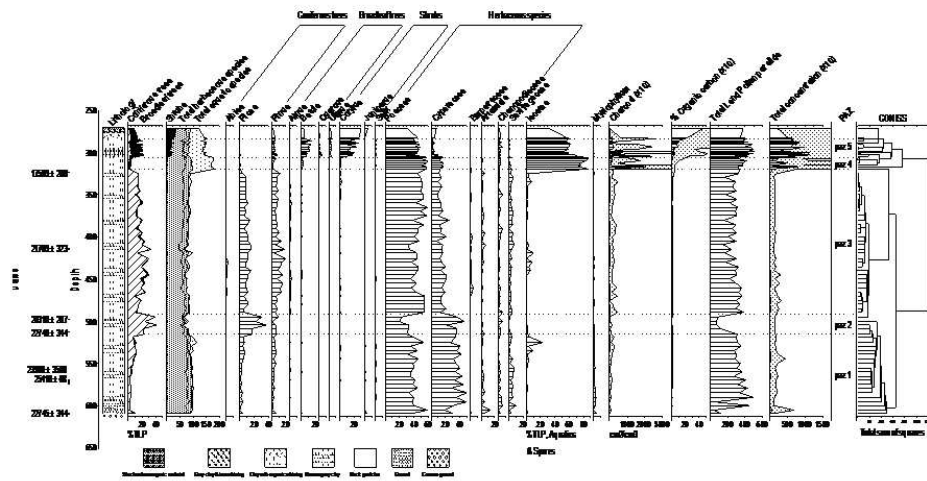
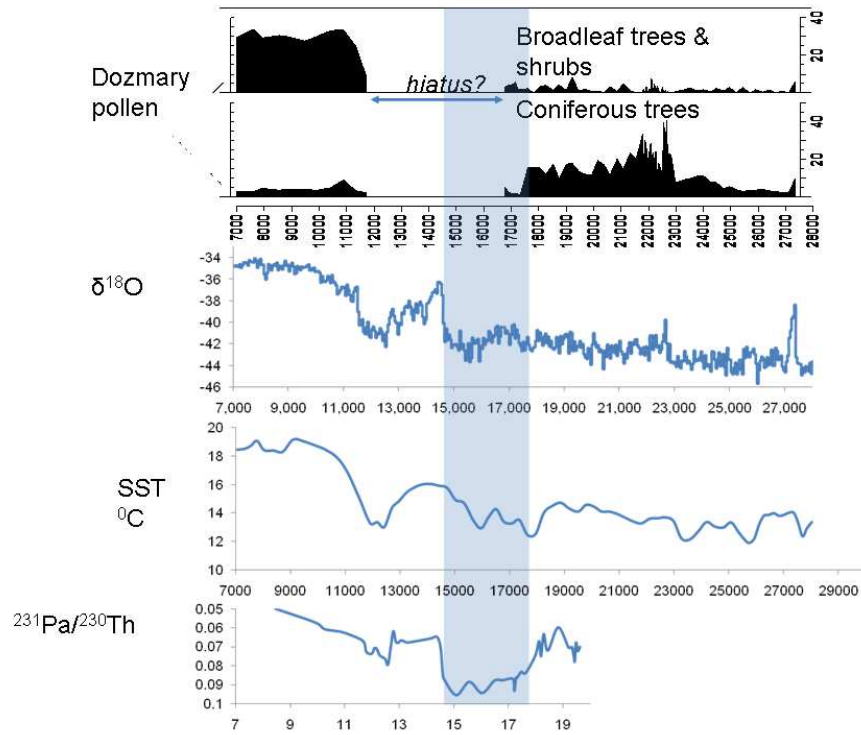


Figure 4 Ann Kelly

254x190mm (96 x 96 DPI)

Review



254x190mm (96 x 96 DPI)

Review

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29  
30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60