Fire and climate: contrasting pressures on tropical Andean timberline species

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ABSTRACT

Aim The aim was to test competing hypotheses regarding migration of the Andean timberline within the last 2000 years.
Location  The upper forest limit in Manu National Park, Peru.

Methods  A randomized stratified design provided 21 samples from forested sites just below the timberline, 15 from puna grassland sites just above the timberline and 15 from the transitional habitat at the puna–forest boundary. From each sample location a surface sample and a sample from the base of the organic horizon of the soil profile (hereafter historical) was collected. Pollen and charcoal were analysed from the surface and historical layers in the 51 soil profiles. A chronological framework was provided by 24 $^{14}$C dates. Data were ordinated as ‘modern’ and ‘historical’ groups and the temporal trends illustrated by Procrustes rotation.

Results  The organic layer in the soil pits represented the last 600–2000 years. Fire was much more abundant in all habitat types (puna, transitional, and forested) in the modern compared with the historical groups. Samples that had historically been in puna just above the timberline showed encroachment by woody species. Samples that had been forested were still classified as forest but their composition had become more transitional. Sites that were transitional appeared to represent a new or expanded class of sites that was far less abundant historically.

Main conclusions  Our results are consistent with ongoing warming causing an upslope migration of species, although not necessarily of the timberline. Weedy fire-tolerant species are spreading upslope, creating a transitional forest, softening the boundary between forest and puna. Simultaneously, fire introduced to improve grazing outside the park has increasingly penetrated the forest and is causing the upper timberline to shift towards more fire-tolerant and weedy species. Consequently, both the form of the ecotone between forest and grassland and the species
composition of these forests is changing and is expected to continue to change,
represent a shifting baseline for what is considered to be natural.

Keywords
Andes, fire, fossil pollen, landuse, migration, shifted baseline, timberline,
warming.

INTRODUCTION
The biological divide between the forested flanks of the Andes and high Andean
grasslands are of cultural, climatic, biogeographical and economic significance
(Sarmiento & Frolich, 2002). In general, montane cloud forests give way to
grasslands, locally termed puna, at elevations between c. 3400 and 3700 m a.s.l.
(Körner, 1998, 2012). The timberline, the upper limit of closed-canopy forest, in the
Peruvian Andes is a biologically rich zone that encompasses a transition from true
interior forest species, through an edge rich in scandent plants and species that are
generalists occurring in disturbed settings (Young, 1993; Young & León, 2007; Lutz
et al., 2013), to puna. The transitional habitat between forest and puna can vary in
width but is usually a blend of puna and forest edge species rather than having a
distinctive species set of its own (Young & León, 2007). The woody species in this
transitional habitat may exhibit considerable phenotypic plasticity, as they are
dwarfed or stunted by local conditions. Biologically, the disjunction between the
forest and the puna is profound, with an almost complete turnover of life-forms and
species. The boundary between puna and Andean forest is characterized by a rapid
upslope loss of biodiversity and simplification of habitat structure in the space of a
few metres (Young, 1993; Young & León, 2007).
The underlying cause of the boundary between these habitats is actively debated but appears to be strongly influenced by a combination of temperature and fire regime (Körner, 1998; Young & León, 2007). While the forests do not burn naturally, and even a lightning strike will seldom start a fire, puna grasslands are fire-adapted systems (Troll, 1968; Román-Cuesta et al., 2011). Although lightning can start fires in the puna, the majority are started deliberately by humans to increase pasture quality (Aragão et al., 2007; Malhi et al., 2010), limit the spread of woody species and trigger new growth. Generally the downslope extent of these fires is limited by the moist boundary of cloud forest. In dry years, however, fires can spread downslope, particularly along ridges, burning down to elevations of 2700 m (M.R.S., pers. obs.).

The punas have long been modified by human activity (Shepard et al., 2010), forming important agricultural regions with high-elevation crops such as quinoa and potato, and small-scale herding of livestock ranging from llama and alpaca to horse and cattle (Aldenderfer, 2008; Isbell, 2008). Pre-Incan and Incan land use in the Manu region of Peru may have been especially intense because of the trade route between the mountains and the Amazonian lowlands (Zimmerer, 2006). The population collapse associated with the European conquest may then have allowed forests to regrow before a more recent wave of intensive land use exploitation. The upper portion of the Manu National Park is a mixed-use landscape with cattle and horses grazing the grassland, and fires are regularly set by the local pastoralists (Oliveras et al., 2014). European-style deforestation, grazing of introduced livestock and fire management of the puna may have led to fires penetrating the upper montane forest more frequently than before. The fire history of this region has not been documented, but during our fieldwork we walked the 40 km from Qurqupampa to Ajcanaco and found that much of the area showed obvious signs of recent fire, such as blackening, areas in early
stages of regeneration with a charred surface, and charring on tree trunks. As many of the tree species are fire-intolerant, repeated burning is predicted to lead to a net downslope movement of the forest–puna ecotone (Sarmiento & Frolich, 2002).

Degradation of habitats can be obvious and abrupt, but it can also be a long steady process. When changes are slow, there is a risk that each generation accepts a progressively degraded version of the wild to be ‘natural’ (Pauly, 1995). Pauly termed this inter-generational unwitting acceptance of falling populations and altered communities the ‘shifted baseline’ syndrome. Here, we introduce the concept of shifting baselines in the context of a palaeoecological study to investigate the position and form of the puna–forest ecotone in the Manu National Park, Peru.

The potential for climate change to cause an accelerated migration of species and altered land use is evident in models that predict that the tropical Andes is the conservation hotspot with the highest probable rate of biome change (Malcolm et al., 2006). As temperatures warm, tree species are expected to migrate upslope (Bush, 2002; Feeley & Silman, 2010; Feeley et al., 2011). Studies in southern Peru have demonstrated that tree distributions are already responding to warming, with average upslope migration rates of 2.5–3.5 m year\(^{-1}\), although a migration of c. 9 m year\(^{-1}\) would be required for the habitat to remain in equilibrium with the observed warming (Feeley et al., 2011; Lutz et al., 2013).

Palaeoecologists have had mixed success in tracking the timberline using fossil pollen from lake- and bog-based records in Colombia and Ecuador (Wille et al., 2002; Bakker et al., 2008; Di Pasquale et al., 2008; Moscol Olivera & Hooghiemstra, 2010; Rodríguez & Behling, 2012). These records can provide a wealth of information about the system within a catchment, but if that catchment supports more than one
vegetation type the record will not allow precise reconstruction of the past timberline.

In a study in the Ecuadorian Andes, Wille et al. (2002) showed that timberline changes around a bog had moved as much as 300 m upslope between c. AD 1290 and the present, reaching an elevation of 3650–3700 m, while Moscol Oliveira and Hooghiemstra (2010) suggested that the timberline in a similar section of the Andes had not risen above c. 3650 m. In a study within the Manu reserve of southern Peru, Polylepis woodlands occupied the area above c. 3400 m in the early Holocene; by 4000 cal. yr BP, Polylepis pollen had been lost from the record and those elevations were dominated by fire-prone grasslands, a change attributed to human activity (Urrego et al., 2011). A bog at an elevation of 3495 m in southern Ecuador produced similar results, showing relatively stable conditions after 4300 cal. yr BP but degradation of the forest, and puna expansion, post-1000 cal. yr BP (Rodríguez & Behling, 2012).

We tested four hypotheses relating to the migration and composition of the Andean timberline using pollen and charcoal from soils. The hypotheses were as follows.

1. Pre-Incan and Incan land use depressed the timberline, and depopulation following contact led to upslope forest movement.

2. The timberline was not strongly influenced by human activity before modern times, but is migrating upslope in response to recent warming.

3. The ecotonal transition from closed forest to puna has been sharpened by increased fire activity eliminating outlying individuals and tree islands, thereby creating a clearly defined boundary.
The timberline has moved downslope as a result of modern land-management practices.

**MATERIALS AND METHODS**

**Site description**

The 15,000 km² Manu National Park (MNP) in southern Peru (71°10′ –72°22′ W and 11°17′ –13°11′ S) ranges from c. 350 m a.s.l. to 4500 m a.s.l., with the timberline occurring between elevations of 3400 and 3600 m. In the region where our samples were taken (Fig. 1), fires that were started outside the protected area regularly escaped into the park. In areas with regular anthropogenic fire, the timberline was usually at c. 3450 m a.s.l. (Román-Cuesta et al., 2011).

The nearest weather station is at Acjanaco, which is at 3450 m a.s.l. and a distance of 5 km from MNP. The mean annual temperature (January 2001-March 2008) for Acjanaco is 11 °C, with regular night-time frosts, and the mean annual precipitation is c. 2000 mm, with a wet season from October to April (Zimmerman et al., 2010).

Additional moisture input derives from regular cloud immersion, which maintains high levels of relative humidity even in the dry season.

This research was part of a larger consortium study (Andes Biodiversity and Ecosystem Research Group) on the ecology and biogeography of an Andes to Amazon transect centred on the eastern Andean flank in Manu. Ten years of studies have provided data on timberline ecology, species migration, palaeoecology, fire and puna–timberline ecotone composition (e.g. Gibbon et al., 2010; Malhi et al., 2010; Zimmermann et al., 2010; Román-Cuesta et al., 2011; Lutz et al., 2013).
The vegetation was divided into three zones. The forest zones had structurally complex vegetation rich in arboreal ferns and epiphytes. Common trees of the forest included members of the following genera and families: *Alnus* (Betulaceae), *Ericaceae*, *Hedyosmum* (Chloranthaceae), *Podocarpus* (Podocarpaceae), *Ocotea* (Lauraceae), *Rubiaceae*, *Solanaceae*, *Symplocos* (Symplocaceae), *Urticaceae* and *Vallea* (Elaeocarpaceae). In the transitional zone, which was generally 1–50 m in width, shrubland elements were interspersed with grasses, herbs and ferns. Common taxa included *Ericaceae*, *Melastomataceae* (especially *Miconia*), *Hedyosmum* and saplings of forest trees. In the puna, *Poaceae* and *Cyperaceae* dominated, but important herbaceous components included *Alchemilla* (Rosaceae) and *Asteraceae*, and *Schinus* (Anacardiaceae) was a common shrub.

Although lake muds provide a better archive for palynology than soils, because of their lack of bioturbation and oxidation, the scarcity of suitable deposits hampers detailed spatial reconstructions. Saturated organic-rich soils and peats in the high Andes, however, are rich in pollen and offer workable archives of historical information (Bosman et al., 1994; Wille et al., 2002). Neotropical soils have been used previously for isotope (Pessenda et al., 1998; Pessenda et al., 2001), pollen and spore (Salomons, 1986; Ruiz Pessenda et al., 2010; Groot et al., 2011; Jansen et al., 2013), phytolith (Piperno, 2006; McMichael et al., 2013) and charcoal (Di Pasquale et al., 2008) studies. While the mobility of pollen within soil profiles is a concern because of bioturbation, soil creep and other disturbances (Davidson et al., 1999), our field assessment of the soils near the timberline in Manu revealed clear subhorizons from which we inferred that, at least at a relatively coarse temporal scale, these soils had not been homogenized.
While we do not advocate attempting a fine temporal reconstruction based on this archive, sampling the uppermost and lowermost organic units within the soil profile was deemed worthwhile. We also conducted a preliminary blind study to determine whether the pollen in the surface soil horizon would lead to the correct prediction of forest, puna or transition vegetation type. That analysis yielded an accuracy of 95% correct attribution, with the only error being a transitional sample that was attributed to forest.

**Sampling**

The three categories of vegetation, closed canopy forest (forest), shrubby forest–puna transition (transition) and puna (grassland), were sampled based on random coordinates (Zimmermann et al., 2010). At each location a soil pit was dug and samples were collected from the surface organic material and from the lowest organic-rich horizon visible. In practice, this lowest sample was generally taken from a depth of 150–250 mm. Large pieces of charcoal and wood in the profile were collected for $^{14}$C dating when available, otherwise bulk samples were used. Fifteen pits were dug and sampled in both the puna and the transitional zone, and 21 pits were sampled in the forest (see Appendix S1 in Supporting Information).

Samples were returned to the palaeoecology laboratory at the Florida Institute of Technology for preparation and standard protocols were followed for fossil pollen (Stockmarr, 1972; Faegri & Iversen, 1989) and charcoal (Clark & Hussey, 1996) analyses. Fossil pollen was counted to a total of 200 grains under a Zeiss Axioskop photomicroscope at 400–1000×. Pollen identification was conducted using published texts (Heusser, 1971; Hooghiemstra, 1984) and the Florida Institute of Technology pollen reference collection and its downloadable database (Bush & Weng, 2007).
<http://research.fit.edu/paleolab/pollen.php>. Percentages relative to summed pollen data for the modern and fossil pollen were ordinated using detrended correspondence analysis (DCA; Hill, 1979). A Procrustes rotation (Peres-Neto & Jackson, 2001) was applied to allow comparison of modern and fossil pairs. Charcoal (> 180 µm) was identified under an Olympus Photomacroscope at 20× and area calculations were performed using Image-J software <http://imagej.nih.gov/ij/>. Pollen and charcoal data were plotted in C2 (Juggins, 2003).

RESULTS

Radiocarbon dating of charcoal in soils

Soils are not sedimentary units and generally do not show steady or precise accumulation through time. In this study, 24 samples dated using $^{14}$C accelerator mass spectrometry (AMS) yielded ages that were mostly in the range of 600–2500 cal. yr BP (Table 1). We sampled some macroscopic charcoal pieces from the same level as bulk charcoal samples, i.e sieved at 180 µm and grouped for dating, to determine whether there was uneven mixing of large and small fractions. Twice, two samples were taken from different heights in the same profile to determine whether the upper sample consistently dated younger than the lower sample. Our results showed that different fractions from the same soil level produced similar ages, suggesting no significant size bias in vertical movement. Similarly, our pairs of samples from high and low in the soil profiles were consistently younger above and older below.

The majority of dates were based on wood and charcoal fragments, but roots were avoided. Wood dates can be biased by the age of the tree or by deadfall (Gavin, 2006).

The types of forests studied here have relatively rapid nutrient cycling and do not
accumulate dead wood, but all ages should be taken as a maximum for the probable age of the soil (Gavin et al., 2006).

Of the 19 dates that were taken from below a soil depth of 15 cm, only one was younger than 680 cal. yr BP. This apparently errant date of 80 cal. yr BP from a depth of 40 cm was excluded as an outlier.

Modern pollen data

Pollen recovered from the uppermost organic horizon showed a strong coherence with modern vegetation (Fig. 2), with distinct pollen spectra associated with each of the major habitat types. Arboreal pollen types and Asteraceae (many of which can be shrubs or small trees) accounted for > 35% of the pollen from forested settings. Similarly, Poaceae, Cyperaceae, Apiaceae and other open-ground species accounted for 30–40% of pollen from puna settings. As would be expected, the transitional settings had intermediate values.

Some pollen types were found almost exclusively in forested settings, e.g. Clethra, Vallea, Myricaceae, Dodonaea and Solanaceae (Fig. 3). Others, such as Anacardiaceae (cf. Schinus), were only found above the timberline. Arboreal taxa that are anemophilous and known to produce large quantities of pollen were found above the timberline, e.g. Acalypha, Alchornea, Alnus, Cecropia, Hedyosmum and Urticaceae/Moraceae. This finding was consistent with prior studies showing the potential for upslope transport (Grabandt, 1985; Rodgers & Horn, 1996; Weng et al., 2004). A finding that did stand out was that Urticaceae/Moraceae were much more abundant in the near-surface samples in the transitional zone compared with samples from the base of each pit. Similarly, it was noticeable that most of the types strongly
associated with forest were slightly more abundant in the lower rather than the uppermost sample from a given pit.

**Statistical analyses**

DCA (Hill, 1979) of the combined matrix of top and bottom samples from all soil pits produced a strong pattern that segregated puna species to the negative side of axis 1 and forest taxa to the positive side. On axis 1, Poaceae, Apiaceae and Rosaceae lay at the negative extreme, while the positive extreme was characterized by Rubiaceae, *Symplocos* and Euphorbiaceae (see Appendix S2). On axis 2, the forest types that had high values on axis 1 were spread out, so that Myricaceae, *Dodonaea* and *Bocconia* characterized forests that lay at the positive extreme, while Campanulaceae, Euphorbiaceae and Solanaceae belonged to forests with strongly negative values. The upper soil samples showed more overlap between the three vegetation types (Fig. 4a) than the samples from the lower horizon of each soil pit (Fig. 4b). Samples from the transitional habitats between puna and forest also had an intermediate location on the DCA plot.

Forest samples that appeared to be misplaced into puna were collected from a very steep valley where samples were taken from just within the forest. This may also have been forest more disturbed by landslips than at other locations. Axis 2 of the DCA polarized ‘ancient’ (in the sense of not contemporary) forest types with samples rich in Euphorbiaceae and Campanulaceae at the positive extreme from those rich in Brassicaceae, *Vallea* and *Clethra* at the negative extreme.

A Procrustes rotation of the ordination data (Fig. 5) allowed the relative movement of each pollen assemblage couplet (modern and basal) for each site. The vector plot for
the first three axes of the DCA for these sites produced very similar results (see Appendix S3). Forests showed a tendency to become more transitional in their character, while puna samples either appeared to become transitional or remained as puna. The majority of sites that in modern samples were transitional forest clearly plotted as puna in the older samples.

**Charcoal data**

Charcoal was more abundant in the modern samples than in the historical counterparts (Fig. 6). Seventy per cent of pairs showed this pattern of increase, with forest sites (75%) showing the most marked increase and transition sites (64%) the least. When forests burn they produce far more charcoal than grasslands, consequently the highest absolute amounts of charcoal were consistently in the forested settings, even though the more flammable grasslands may support fire more often.

**DISCUSSION**

Using soil samples was one of the earliest applications of palynology in archaeological contexts and has been shown to provide interpretable data (Dimbleby, 1957). Nevertheless, our montane sample site posed challenges for this technique. That the pollen reflected the local vegetation is to be expected, as soils from densely vegetated settings will contain a very low proportion of pollen transported long distances and their pollen spectra will be dominated by pollen derived from within a few metres (Jackson & Lyford, 1999; Collins & Bush, 2011). That our pollen and charcoal samples were not homogeneous at the top and bottom of the soil profile supported our hypothesis that a non-modern signal could be retrieved from the base of the organic-rich horizon. Similarly, that species were represented in the bottom of
many profiles that were rare or absent in the uppermost samples (and vice versa)
indicated that the pollen was most unlikely to represent reworking from the existing
habitat type.

**Timberline migration in the late Holocene**

Hypothesis 1 was that Pre-Incan and Incan land use depressed the timberline, and that
depopulation following contact led to upslope forest movement, which would predict
that puna or very disturbed forests would exist downslope of the modern timberline,
and that these forests matured during post-abandonment succession. The data from
our sites were inconsistent with this view, as 14 out of 15 sites in modern forest
settings showed that they were forested throughout the study time period (Fig. 5).
Even the one forest sample that was grouped with puna samples may still have been
forested. The complex topography of this region may have allowed grasslands to form
on ridges closer to the site and contribute grass pollen, while the canopy above the
sample location was maintained. Hypothesis 1 is rejected.

Hypothesis 2 was that the timberline has only recently migrated upslope in response
to ongoing global warming. This hypothesis predicts that upslope migration of taxa
would lead to habitats that had been puna in the basal sample becoming transitional or
forested in the surface sample. Similarly, near-timberline forested sites would
progressively lose any sign of transitional status as the boundary moved further
upslope. In our dataset, 66% of the modern transitional sites showed a trajectory
towards being more woody, with about 40% of them clearly changing from puna to a
transitional status within the last 600–2000 years; all but one of the modern puna sites
had a more transitional status than in the basal sample of each pit. These data are
consistent with upslope migration of woody taxa. The forest settings, however, do not
fit this pattern because they too showed a tendency towards becoming more transitional. Consequently, hypothesis 2 is rejected as a complete explanation of the observed patterns.

Hypothesis 3 was that increasing fire activity causes a sharpened transition from timberline to puna. The prediction from this hypothesis is that some of the modern puna or forests would have been transitional forests earlier, and that the vertical range of the transition would have been broader in the past than now. In almost all cases, this prediction was refuted by the data as forests and puna both became more, rather than less, transitional through time.

Hypothesis 4 was that the timberline moves downslope as a result of modern land-management practices. Consequently, areas that were transitional before would now be puna, and forests would become more transitional. This pattern was supported by the forest samples but not by the transitional samples, which implied an upslope movement of species. Like the others, this hypothesis was therefore rejected.

The data appeared to support elements of hypotheses 2 and 4, and led us to propose a new, fifth hypothesis: modern climate change is causing an overall upslope migration of species, but increased fire penetration into the upper forest zone is degrading the upper forests. This hypothesis predicts that: the transitional region is expanding; weedy woody species are the most likely to withstand fire and therefore to be the colonists of the transitional forest; and the upper edge of the forest will lose fire-sensitive species.

The ordination showed that, at some time in the last few hundreds of years, habitats that were puna have become transitional (Fig. 5). Although we cannot state definitively that the upslope expansion of forest into the puna is the result of modern
A key realization from our study is that, while the tree line may be migrating, the habitat quality of the forest is changing. In addition to the overall characterization that the forests are becoming more transitional, Melastomataceae, Urticaceae, Cyperaceae and *Alnus* are among the taxa that appear to be increasing in abundance. All of these taxa are favoured by disturbance. Among the taxa that are decreasing in abundance are Myricaceae, *Clethra* and *Vallea*, which are generally associated with more mature forests. These observations of winners and losers in response to fire is supported by empirical plot data from the same region of the Andes (Oliveras *et al.*, 2013). The prediction of increasing ‘weediness’ of the forest appears to be supported.

That the upper forest edge is losing fire-sensitive species needs to be tested, although the above categorization of weedy versus mature species also reflects aspects of fire tolerance. Oliveras *et al.* (2013) found a wide variability in fire tolerance among the modern timelime vegetation. A landscape survey of forests along the timelime of Manu National Park showed that about 45% of species were fire tolerant or fire thrivers (Oliveras *et al.*, 2013). These observations support the conclusions of the palaeoecological data, that tree communities near the puna–forest ecotone collapse to a subset of fire-tolerant species in the face of repeated burning.

**Shifting baselines and timberlines**

The change in structure and composition of forests at the tree line and their collapse to more fire-tolerant species in the broader transitional regions are significant changes in this ecosystem compared with those of the past. If the modern state is accepted as
being natural, it would clearly be acceptance of a shifted baseline (sensu Pauly 1995).

The ecological effects of these changes in tree species composition are likely to ripple down through local trophic interactions. For example, colonist species thriving in disturbed forests tend to have smaller seeds than those of more mature forest (Fleming et al., 1987; Mabberley, 1992). The smaller seeds may be wind or water dispersed, or suitable for small- to medium-sized birds such as tanagers. However, if the species that produce larger fruits, e.g. Lauraceae, Rubiaceae and Elaeocarpaceae, decline in abundance, reduced availability of large lipid-rich fruits would disproportionately impact populations of larger animals and birds (Moermond & Denslow, 1985; Fleming et al., 1987). A positive feedback mechanism is then instigated as large fruits cannot disperse upslope without a vector. Consequently, as the large frugivores are lost from the forest, and the potential for seed dispersal is lost, any losses of individuals from the upper edge of the forest are not replaced. Although the forest is still present, and may even migrate upwards in response to climate change, the ecosystem services offered by the new community are downgraded compared with the former state, thus presenting a shifted baseline.

As timberline migration driven by climate change is known to have occurred throughout the Quaternary, why should this current migration be seen to be different? Palaeoecological records indicate that the migration of Andean forest ranges between c. 0.1 and 3 m year\(^{-1}\) (Bush et al., 2004; Urrego et al., 2005, 2010; González-Carranza et al., 2012). The present rate of migration required to keep pace with an ongoing climate change of 0.03–0.04 °C year\(^{-1}\) since 1975 (Vuille & Bradley, 2000) is about 9 m vertically year\(^{-1}\). A study conducted by Feeley et al. (2011) was based on data from 14 1-ha tree plots located between 650 and 3400 m a.s.l. immediately downslope of our study sites. Trees appear to be responding to this warming, although their
migratory rate of $c. \ 2.5$–$3.5 \text{ m vertically year}^{-1}$ (note the similarity with the palaeoecological data) is not keeping pace with the $c. \ 9\text{-m vertical migration rate required to keep pace with temperature. Whether temperature alone induces the upslope migration or whether it results from a synergy with the increased partial pressure of CO$_2$ as a result of greenhouse emissions (Mayle et al., 2004; Groot et al., 2011), has yet to be resolved.

In a study of a timberline impacted by grazing and fire versus a more natural state, tree migration was found to be stalled by the disturbance (Lutz et al., 2013). Thus trees are migrating but the ecotone is not, causing the rate of migration to fall further and further behind the rate of climate change. Novel assemblages would be expected to form, as selection against fire sensitivity might favour one set of species while selection against stenothermy might favour others. Overall, the baseline will continue to shift towards a set of generalist taxa that form a forest with lower carbon storage and a more depleted suite of plants and animals.

This pattern will be augmented by extreme events, such as Amazonian once-in-a-century droughts, two of which have occurred in the last decade (Lewis et al., 2011), that increase flammability in both lowland Amazonia and the adjacent Andes (Román-Cuesta et al., 2011). When human land use in areas adjacent to the reserve, or illegally within the reserve, rely heavily on fire as a management tool, the probability that wildfire escapes and burns down into the forest is greatly increased (Aragão et al., 2007; Bush et al., 2008). Thus the prediction becomes one of a slowing upslope movement of weedy species that are fire tolerant or at least rapid colonizers, replacing mature forest species that are not adapted to fire, causing a downslope erosion of habitat quality.
As fire in this setting largely results from human activities (Román-Cuesta et al., 2011), management that disincentivizes the use of fire could be a strategy that will have a substantial positive benefit for these forests (Gibbon et al., 2010; Malmer et al., 2010). Indeed, in a study that spans nearly a half century, Lutz et al. (in press) have shown that protected-area status increases ecotone migration rates by 5× through reduction in disturbance. Carbon sequestered as a result of reducing emissions from deforestation and forest degradation (REDD) offers a source of potential income for Andean landowners. Carbon sequestration above and below ground can be both quantified and monetarized (e.g. Gibbon et al., 2010). The degradation of the upper timberline by fire, however, has an impact on the value of the setting for its above-ground biomass. In a series of studies using the same soil pits and vegetation plots as in our study, carbon storage in plant material declined markedly from $63.4 \pm 5.2$ Mg C ha$^{-1}$ in the forest, to $16.9 \pm 2.2$ Mg C ha$^{-1}$ in the transition and $7.5 \pm 0.7$ Mg C ha$^{-1}$ in the puna (Gibbon et al., 2010). Soil carbon showed a different pattern, with equal amounts of carbon stored in soils above and below the tree line, but its distribution was more heavily biased to the surface in the puna (Zimmermann et al., 2010). The net result was that the above-ground : below-ground ratios of C storage were 15.8 in the puna, 8.6 in the transition zone and 2.1 in the forest (Gibbon et al., 2010).

Calculations of future carbon storage will need to include the erosion of biomass from the upper timberline and the recognition that, should the timberline move upslope, it will not have the same capacity for carbon storage as the highest biomass forest settings. Our study site within the Manu National Park may reflect a best-case scenario, in the sense that overt human pressures through logging and deliberate burning are prohibited. In other areas, where fire is more frequent, the downslope loss
of forest may be more profound, and the overall loss of woody taxa may make the
climatically driven upslope expansion even more species-poor.

CONCLUSIONS

A palaeoecological analysis of fossil pollen and charcoal from the forest–puna
transition in MNP, Peru, has revealed landscape changes in the late Holocene. Four
initial hypotheses relating to fire history and tree migration were rejected in favour of
a synthetic hypothesis that included upslope migration because of ongoing warming
and downslope degradation of forests as a result of increased fire activity.

Perhaps the most surprising outcome of this study was that forests, even those as
much as 100 m downslope of the timberline, showed a clear tendency towards being
more transitional in nature and losing some of the qualities or compositional
components that defined them as forests in the past. The most characteristic species of
mature Andean forest, e.g. *Vallea, Myricaceae, Clethra, and Polylepis*, are being
replaced by weedy species that are gap-fillers following disturbance, e.g. *Alnus,*
*Asteraceae* and *Melastomataceae*. The change in forest structure and composition, and
the increasing encroachment of fire, leads to degraded ecosystem services and less
opportunity for long-term carbon storage. The opportunity for new streams of income
to be generated through REDD initiatives could be used to offset some of the worst
effects of fire, as this could become an incentive to reduce fire frequency. The
acceptance of modern timberline forests as being relatively natural constitutes a
shifted baseline.
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line reconstruction in a deforested area in northern Ecuador based on pollen


**SUPPORTING INFORMATION**

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Site details for soil pits sampled in the Manu National Park, Peru.

**Appendix S2** Species plot of axis 1 versus axis 2 detrended correspondence analysis outputs for pollen from soil pits sampled in the Manu National Park, Peru.

**Appendix S3** Trends through time of the pollen data derived from soil pits sampled in Manu National Park, Peru.
Mark B. Bush is a professor at the Florida Institute of Technology and a palaeoecologist investigating Central- and South American ecosystem responses to past climate change. His research focuses on fossil pollen analysis of Neotropical settings, environmental reconstructions of past climates and vegetation communities, and palaeoecological evidence of human responses to climate change. The authors form part of the Andean Biodiversity and Ecology Research Group (ABERG), which has studied intensively the ecology of Manu and the Andean flank of Peru.


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Table 1: Samples analysed for \(^{14}\)C dating from soil pits dug at randomized locations between Qurqupampa and Acjanaco within the Manu National Park, Peru. All samples were dated at the radiocarbon laboratory of the Woods Hole Oceanographic Institute. Dating was based on bulk samples of soil with the exception of samples marked with M.

<table>
<thead>
<tr>
<th>Laboratory code</th>
<th>Vegetation type</th>
<th>Sample ID</th>
<th>Depth (cm)</th>
<th>(^{14})C age</th>
<th>Mean calibrated age (yr BP)</th>
<th>Sigma range 1σ</th>
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<td>OS-78042</td>
<td>Puna</td>
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</table>

*Samples from which a date was taken but which were not counted for pollen; †outliers; ‡ a sample that returned a modern age.
**Figure 1** Location and topography of the field study region and sampled sites, within the Manu National Park, Peru. Black circles, forest samples; grey circles, transitional samples; white circles, puna samples. Source of map: [http://www.USGS.gov](http://www.USGS.gov).
Figure 2 The modern pollen spectra from surface soil samples collected from sites in the Manu National Park, Peru. Puna, transition and forest categories were determined by modern vegetation. F : P, the ratio of forest : puna taxa.
Figure 3  Soil pollen percentage diagram showing modern and historical sample pairs collected from sites within the Manu National Park, Peru. Grey, modern samples; black, historical samples. Where available, dates are shown for the historical sample.
Figure 4 Detrended correspondence analysis (DCA) of pollen from modern and historical soil samples collected from sites within the Manu National Park, Peru: (a) surface samples; (b) samples from the historical soil horizon. Site numbers correspond to the puna, transition and forest numbers in Fig. 3.
Figure 5 Procrustes rotation to contrast the difference between modern and historical site ordinations for soil samples collected within the Manu National Park, Peru. Arrows indicate changes from historical samples/sites to modern ones. The sites are colour coded for modern vegetation: black, forest; blue, transition; red, puna. Site numbers correspond to the puna, transition and forest numbers in Fig. 3.
Figure 6 Charcoal concentrations from the top and bottom soil samples collected from pits within the Manu National Park, Peru. The difference in concentration between modern and historical) between the top and bottom samples is also shown. Bold plus signs and values in parentheses represent values that do not fit the scale of the diagram.