

1 Original Article

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3 RRH Fire and climate

4 **Fire and climate: contrasting pressures on tropical Andean timberline species**

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18 **ABSTRACT**

19 **Aim** The aim was to test competing hypotheses regarding migration of the Andean

20 timberline within the last 2000 years.

21 **Location** The upper forest limit in Manu National Park, Peru.

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

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

37 **Main conclusions** Our results are consistent with ongoing warming causing an
38 upslope migration of species, although not necessarily of the timberline. Weedy fire-
39 tolerant species are spreading upslope, creating a transitional forest, softening the
40 boundary between forest and puna. Simultaneously, fire introduced to improve
41 grazing outside the park has increasingly penetrated the forest and is causing the
42 upper timberline to shift towards more fire-tolerant and weedy species. Consequently,
43 both the form of the ecotone between forest and grassland and the species

44 composition of these forests is changing and is expected to continue to change,
45 represent a shifting baseline for what is considered to be natural.

46 **Keywords**

47 **Andes, fire, fossil pollen, landuse, migration, shifted baseline, timberline,**
48 **warming.**

49 **INTRODUCTION**

50 The biological divide between the forested flanks of the Andes and high Andean
51 grasslands are of cultural, climatic, biogeographical and economic significance
52 (Sarmiento & Frolich, 2002). In general, montane cloud forests give way to
53 grasslands, locally termed puna, at elevations between *c.* 3400 and 3700 m a.s.l.
54 (Körner, 1998, 2012). The timberline, the upper limit of closed-canopy forest, in the
55 Peruvian Andes is a biologically rich zone that encompasses a transition from true
56 interior forest species, through an edge rich in scandent plants and species that are
57 generalists occurring in disturbed settings (Young, 1993; Young & León, 2007; Lutz
58 *et al.*, 2013), to puna. The transitional habitat between forest and puna can vary in
59 width but is usually a blend of puna and forest edge species rather than having a
60 distinctive species set of its own (Young & León, 2007). The woody species in this
61 transitional habitat may exhibit considerable phenotypic plasticity, as they are
62 dwarfed or stunted by local conditions. Biologically, the disjunction between the
63 forest and the puna is profound, with an almost complete turnover of life-forms and
64 species. The boundary between puna and Andean forest is characterized by a rapid
65 upslope loss of biodiversity and simplification of habitat structure in the space of a
66 few metres (Young, 1993; Young & León, 2007).

67 The underlying cause of the boundary between these habitats is actively debated but
68 appears to be strongly influenced by a combination of temperature and fire regime
69 (Körner, 1998; Young & León, 2007). While the forests do not burn naturally, and
70 even a lightning strike will seldom start a fire, puna grasslands are fire-adapted
71 systems (Troll, 1968; Román-Cuesta *et al.*, 2011). Although lightning can start fires in
72 the puna, the majority are started deliberately by humans to increase pasture quality
73 (Aragão *et al.*, 2007; Malhi *et al.*, 2010), limit the spread of woody species and trigger
74 new growth. Generally the downslope extent of these fires is limited by the moist
75 boundary of cloud forest. In dry years, however, fires can spread downslope,
76 particularly along ridges, burning down to elevations of 2700 m (M.R.S., pers. obs.).

77 The punas have long been modified by human activity (Shepard *et al.*, 2010), forming
78 important agricultural regions with high-elevation crops such as quinoa and potato,
79 and small-scale herding of livestock ranging from llama and alpaca to horse and cattle
80 (Aldenderfer, 2008; Isbell, 2008). Pre-Incan and Incan land use in the Manu region of
81 Peru may have been especially intense because of the trade route between the
82 mountains and the Amazonian lowlands (Zimmerer, 2006). The population collapse
83 associated with the European conquest may then have allowed forests to regrow
84 before a more recent wave of intensive land use exploitation. The upper portion of the
85 Manu National Park is a mixed-use landscape with cattle and horses grazing the
86 grassland, and fires are regularly set by the local pastoralists (Oliveras *et al.*, 2014).
87 European-style deforestation, grazing of introduced livestock and fire management of
88 the puna may have led to fires penetrating the upper montane forest more frequently
89 than before. The fire history of this region has not been documented, but during our
90 fieldwork we walked the 40 km from Qurqupampa to Ajcanaco and found that much
91 of the area showed obvious signs of recent fire, such as blackening, areas in early

92 stages of regeneration with a charred surface, and charring on tree trunks. As many of
93 the tree species are fire-intolerant, repeated burning is predicted to lead to a net
94 downslope movement of the forest–puna ecotone (Sarmiento & Frolich, 2002).

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

102 The potential for climate change to cause an accelerated migration of species and
103 altered land use is evident in models that predict that the tropical Andes is the
104 conservation hotspot with the highest probable rate of biome change (Malcolm *et al.*,
105 2006). As temperatures warm, tree species are expected to migrate upslope (Bush,
106 2002; Feeley & Silman, 2010; Feeley *et al.*, 2011). Studies in southern Peru have
107 demonstrated that tree distributions are already responding to warming, with average
108 upslope migration rates of 2.5–3.5 m year⁻¹, although a migration of *c.* 9 m year⁻¹
109 would be required for the habitat to remain in equilibrium with the observed warming
110 (Feeley *et al.*, 2011; Lutz *et al.*, 2013).

111 Palaeoecologists have had mixed success in tracking the timberline using fossil pollen
112 from lake- and bog-based records in Colombia and Ecuador (Wille *et al.*, 2002;
113 Bakker *et al.*, 2008; Di Pasquale *et al.*, 2008; Moscol Olivera & Hooghiemstra, 2010;
114 Rodríguez & Behling, 2012). These records can provide a wealth of information about
115 the system within a catchment, but if that catchment supports more than one

116 vegetation type the record will not allow precise reconstruction of the past timberline.
117 In a study in the Ecuadorian Andes, Wille *et al.* (2002) showed that timberline
118 changes around a bog had moved as much as 300 m upslope between *c.* AD 1290 and
119 the present, reaching an elevation of 3650–3700 m, while Moscol Oliveira and
120 Hooghiemstra (2010) suggested that the timberline in a similar section of the Andes
121 had not risen above *c.* 3650 m. In a study within the Manu reserve of southern Peru,
122 *Polylepis* woodlands occupied the area above *c.* 3400 m in the early Holocene; by
123 4000 cal. yr BP, *Polylepis* pollen had been lost from the record and those elevations
124 were dominated by fire-prone grasslands, a change attributed to human activity
125 (Urrego *et al.*, 2011). A bog at an elevation of 3495 m in southern Ecuador produced
126 similar results, showing relatively stable conditions after 4300 cal. yr BP but
127 degradation of the forest, and puna expansion, post-1000 cal. yr BP (Rodríguez &
128 Behling, 2012).

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

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

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

135 **3.** The ecotonal transition from closed forest to puna has been sharpened by increased
136 fire activity eliminating outlying individuals and tree islands, thereby creating a
137 clearly defined boundary.

138 4. The timberline has moved downslope as a result of modern land-management
139 practices.

140 **MATERIALS AND METHODS**

141 **Site description**

142 The 15,000 km² Manu National Park (MNP) in southern Peru (71°10' –72°22' W and
143 11°17' –13°11' S) ranges from *c.* 350 m a.s.l. to 4500 m a.s.l., with the timberline
144 occurring between elevations of 3400 and 3600 m. In the region where our samples
145 were taken (Fig. 1), fires that were started outside the protected area regularly escaped
146 into the park. In areas with regular anthropogenic fire, the timberline was usually at
147 *c.* 3450 m a.s.l. (Román-Cuesta *et al.*, 2011).

148 The nearest weather station is at Acjanaco, which is at 3450 m a.s.l. and a distance of
149 5 km from MNP. The mean annual temperature (January 2001-March 2008) for
150 Acjanaco is 11 °C , with regular night-time frosts, and the mean annual precipitation
151 is *c.* 2000 mm, with a wet season from October to April (Zimmerman *et al.*, 2010).
152 Additional moisture input derives from regular cloud immersion, which maintains
153 high levels of relative humidity even in the dry season.

154 This research was part of a larger consortium study (Andes Biodiversity and
155 Ecosystem Research Group) on the ecology and biogeography of an Andes to
156 Amazon transect centred on the eastern Andean flank in Manu. Ten years of studies
157 have provided data on timberline ecology, species migration, palaeoecology, fire and
158 puna–timberline ecotone composition (e.g. Gibbon *et al.*, 2010; Malhi *et al.*, 2010;
159 Zimmermann *et al.*, 2010; Román-Cuesta *et al.*, 2011; Lutz *et al.*, 2013).

160 The vegetation was divided into three zones. The forest zones had structurally
161 complex vegetation rich in arboreal ferns and epiphytes. Common trees of the forest
162 included members of the following genera and families: *Alnus* (Betulaceae),
163 Ericaceae, *Hedyosmum* (Chloranthaceae), *Podocarpus* (Podocarpaceae), *Ocotea*
164 (Lauraceae), Rubiaceae, Solanaceae, *Symplocos* (Symplocaceae), Urticaceae and
165 *Vallea* (Elaeocarpaceae). In the transitional zone, which was generally 1–50 m in
166 width, shrubland elements were interspersed with grasses, herbs and ferns. Common
167 taxa included Ericaceae, Melastomataceae (especially *Miconia*), *Hedyosmum* and
168 saplings of forest trees. In the puna, Poaceae and Cyperaceae dominated, but
169 important herbaceous components included *Alchemilla* (Rosaceae) and Asteraceae,
170 and *Schinus* (Anacardiaceae) was a common shrub.

171 Although lake muds provide a better archive for palynology than soils, because of
172 their lack of bioturbation and oxidation, the scarcity of suitable deposits hampers
173 detailed spatial reconstructions. Saturated organic-rich soils and peats in the high
174 Andes, however, are rich in pollen and offer workable archives of historical
175 information (Bosman *et al.*, 1994; Wille *et al.*, 2002).

176 Neotropical soils have been used previously for isotope (Pessenda *et al.*, 1998;
177 Pessenda *et al.*, 2001), pollen and spore (Salomons, 1986; Ruiz Pessenda *et al.*, 2010;
178 Groot *et al.*, 2011; Jansen *et al.*, 2013), phytolith (Piperno, 2006; McMichael *et al.*,
179 2013) and charcoal (Di Pasquale *et al.*, 2008) studies. While the mobility of pollen
180 within soil profiles is a concern because of bioturbation, soil creep and other
181 disturbances (Davidson *et al.*, 1999), our field assessment of the soils near the
182 timberline in Manu revealed clear subhorizons from which we inferred that, at least at
183 a relatively coarse temporal scale, these soils had not been homogenized

184 (Zimmermann *et al.*, 2010). While we do not advocate attempting a fine temporal
185 reconstruction based on this archive, sampling the uppermost and lowermost organic
186 units within the soil profile was deemed worthwhile. We also conducted a preliminary
187 blind study to determine whether the pollen in the surface soil horizon would lead to
188 the correct prediction of forest, puna or transition vegetation type. That analysis
189 yielded an accuracy of 95% correct attribution, with the only error being a transitional
190 sample that was attributed to forest.

191 **Sampling**

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

201 Samples were returned to the palaeoecology laboratory at the Florida Institute of
202 Technology for preparation and standard protocols were followed for fossil pollen
203 (Stockmarr, 1972; Faegri & Iversen, 1989) and charcoal (Clark & Hussey, 1996)
204 analyses. Fossil pollen was counted to a total of 200 grains under a Zeiss Axioskop
205 photomicroscope at 400–1000 \times . Pollen identification was conducted using published
206 texts (Heusser, 1971; Hooghiemstra, 1984) and the Florida Institute of Technology
207 pollen reference collection and its downloadable database (Bush & Weng, 2007)

208 <<http://research.fit.edu/paleolab/pollen.php>>. Percentages relative to summed pollen
209 data for the modern and fossil pollen were ordinated using detrended correspondence
210 analysis (DCA; Hill, 1979). A Procrustes rotation (Peres-Neto & Jackson, 2001) was
211 applied to allow comparison of modern and fossil pairs. Charcoal (> 180 µm) was
212 identified under an Olympus Photomicroscope at 20× and area calculations were
213 performed using Image-J software <<http://imagej.nih.gov/ij/>>. Pollen and charcoal
214 data were plotted in C2 (Juggins, 2003).

215 **RESULTS**

216 **Radiocarbon dating of charcoal in soils**

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

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

230 The types of forests studied here have relatively rapid nutrient cycling and do not

231 accumulate dead wood, but all ages should be taken as a maximum for the probable
232 age of the soil (Gavin *et al.*, 2006).

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

236 **Modern pollen data**

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

244 Some pollen types were found almost exclusively in forested settings, e.g. *Clethra*,
245 *Vallea*, Myricaceae, *Dodonaea* and Solanaceae (Fig. 3). Others, such as
246 Anacardiaceae (cf. *Schinus*), were only found above the timberline. Arboreal taxa that
247 are anemophilous and known to produce large quantities of pollen were found above
248 the timberline, e.g. *Acalypha*, *Alchornea*, *Alnus*, *Cecropia*, *Hedyosmum* and
249 Urticaceae/Moraceae. This finding was consistent with prior studies showing the
250 potential for upslope transport (Grabandt, 1985; Rodgers & Horn, 1996; Weng *et al.*,
251 2004). A finding that did stand out was that Urticaceae/Moraceae were much more
252 abundant in the near-surface samples in the transitional zone compared with samples
253 from the base of each pit. Similarly, it was noticeable that most of the types strongly

254 associated with forest were slightly more abundant in the lower rather than the
255 uppermost sample from a given pit.

256 **Statistical analyses**

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

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

275 A Procrustes rotation of the ordination data (Fig. 5) allowed the relative movement of
276 each pollen assemblage couplet (modern and basal) for each site. The vector plot for

277 the first three axes of the DCA for these sites produced very similar results (see
278 Appendix S3). Forests showed a tendency to become more transitional in their
279 character, while puna samples either appeared to become transitional or remained as
280 puna. The majority of sites that in modern samples were transitional forest clearly
281 plotted as puna in the older samples.

282 **Charcoal data**

283 Charcoal was more abundant in the modern samples than in the historical counterparts
284 (Fig. 6). Seventy per cent of pairs showed this pattern of increase, with forest sites
285 (75%) showing the most marked increase and transition sites (64%) the least. When
286 forests burn they produce far more charcoal than grasslands, consequently the highest
287 absolute amounts of charcoal were consistently in the forested settings, even though
288 the more flammable grasslands may support fire more often.

289 **DISCUSSION**

290 Using soil samples was one of the earliest applications of palynology in
291 archaeological contexts and has been shown to provide interpretable data (Dimbleby,
292 1957). Nevertheless, our montane sample site posed challenges for this technique.
293 That the pollen reflected the local vegetation is to be expected, as soils from densely
294 vegetated settings will contain a very low proportion of pollen transported long
295 distances and their pollen spectra will be dominated by pollen derived from within a
296 few metres (Jackson & Lyford, 1999; Collins & Bush, 2011). That our pollen and
297 charcoal samples were not homogeneous at the top and bottom of the soil profile
298 supported our hypothesis that a non-modern signal could be retrieved from the base of
299 the organic-rich horizon. Similarly, that species were represented in the bottom of

300 many profiles that were rare or absent in the uppermost samples (and vice versa)
301 indicated that the pollen was most unlikely to represent reworking from the existing
302 habitat type.

303 **Timberline migration in the late Holocene**

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

314 Hypothesis 2 was that the timberline has only recently migrated upslope in response
315 to ongoing global warming. This hypothesis predicts that upslope migration of taxa
316 would lead to habitats that had been puna in the basal sample becoming transitional or
317 forested in the surface sample. Similarly, near-timberline forested sites would
318 progressively lose any sign of transitional status as the boundary moved further
319 upslope. In our dataset, 66% of the modern transitional sites showed a trajectory
320 towards being more woody, with about 40% of them clearly changing from puna to a
321 transitional status within the last 600–2000 years; all but one of the modern puna sites
322 had a more transitional status than in the basal sample of each pit. These data are
323 consistent with upslope migration of woody taxa. The forest settings, however, do not

324 fit this pattern because they too showed a tendency towards becoming more
325 transitional. Consequently, hypothesis 2 is rejected as a complete explanation of the
326 observed patterns.

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

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

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

345 The ordination showed that, at some time in the last few hundreds of years, habitats
346 that were puna have become transitional (Fig. 5). Although we cannot state
347 definitively that the upslope expansion of forest into the puna is the result of modern

348 climatic change, the palaeoecological data are certainly consistent with upslope
349 migrations.

350 A key realization from our study is that, while the tree line may be migrating, the
351 habitat quality of the forest is changing. In addition to the overall characterization that
352 the forests are becoming more transitional, Melastomataceae, Urticaceae, Cyperaceae
353 and *Alnus* are among the taxa that appear to be increasing in abundance. All of these
354 taxa are favoured by disturbance. Among the taxa that are decreasing in abundance
355 are Myricaceae, *Clethra* and *Vallea*, which are generally associated with more mature
356 forests. These observations of winners and losers in response to fire is supported by
357 empirical plot data from the same region of the Andes (Oliveras *et al.*, 2013). The
358 prediction of increasing ‘weediness’ of the forest appears to be supported.

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

367 **Shifting baselines and timberlines**

368 The change in structure and composition of forests at the tree line and their collapse to
369 more fire-tolerant species in the broader transitional regions are significant changes in
370 this ecosystem compared with those of the past. If the modern state is accepted as

371 being natural, it would clearly be acceptance of a shifted baseline (*sensu* Pauly 1995).
372 The ecological effects of these changes in tree species composition are likely to ripple
373 down through local trophic interactions. For example, colonist species thriving in
374 disturbed forests tend to have smaller seeds than those of more mature forest (Fleming
375 *et al.*, 1987; Mabberley, 1992). The smaller seeds may be wind or water dispersed, or
376 suitable for small- to medium-sized birds such as tanagers. However, if the species
377 that produce larger fruits, e.g. Lauraceae, Rubiaceae and Elaeocarpaceae, decline in
378 abundance, reduced availability of large lipid-rich fruits would disproportionately
379 impact populations of larger animals and birds (Moermond & Denslow, 1985;
380 Fleming *et al.*, 1987). A positive feedback mechanism is then instigated as large fruits
381 cannot disperse upslope without a vector. Consequently, as the large frugivores are
382 lost from the forest, and the potential for seed dispersal is lost, any losses of
383 individuals from the upper edge of the forest are not replaced. Although the forest is
384 still present, and may even migrate upwards in response to climate change, the
385 ecosystem services offered by the new community are downgraded compared with the
386 former state, thus presenting a shifted baseline.

387 As timberline migration driven by climate change is known to have occurred
388 throughout the Quaternary, why should this current migration be seen to be different?
389 Palaeoecological records indicate that the migration of Andean forest ranges between
390 *c.* 0.1 and 3 m year⁻¹ (Bush *et al.*, 2004; Urrego *et al.*, 2005, 2010; González-Carranza
391 *et al.*, 2012). The present rate of migration required to keep pace with an ongoing
392 climate change of 0.03–0.04 °C year⁻¹ since 1975 (Vuille & Bradley, 2000) is about 9
393 m vertically year⁻¹. A study conducted by Feeley *et al.* (2011) was based on data from
394 14 1-ha tree plots located between 650 and 3400 m a.s.l. immediately downslope of
395 our study sites. Trees appear to be responding to this warming, although their

396 migratory rate of *c.* 2.5–3.5 m vertically year⁻¹ (note the similarity with the
397 palaeoecological data) is not keeping pace with the *c.* 9-m vertical migration rate
398 required to keep pace with temperature. Whether temperature alone induces the
399 upslope migration or whether it results from a synergy with the increased partial
400 pressure of CO₂ as a result of greenhouse emissions (Mayle *et al.*, 2004; Groot *et al.*,
401 2011), has yet to be resolved.

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

410 This pattern will be augmented by extreme events, such as Amazonian once-in-a-
411 century droughts, two of which have occurred in the last decade (Lewis *et al.*, 2011),
412 that increase flammability in both lowland Amazonia and the adjacent Andes
413 (Román-Cuesta *et al.*, 2011). When human land use in areas adjacent to the reserve,
414 or illegally within the reserve, rely heavily on fire as a management tool, the
415 probability that wildfire escapes and burns down into the forest is greatly increased
416 (Aragão *et al.*, 2007; Bush *et al.*, 2008). Thus the prediction becomes one of a slowing
417 upslope movement of weedy species that are fire tolerant or at least rapid colonizers,
418 replacing mature forest species that are not adapted to fire, causing a downslope
419 erosion of habitat quality.

420 As fire in this setting largely results from human activities (Román-Cuesta *et al.*,
421 2011), management that disincentivizes the use of fire could be a strategy that will
422 have a substantial positive benefit for these forests (Gibbon *et al.*, 2010; Malmer *et al.*,
423 2010). Indeed, in a study that spans nearly a half century, Lutz *et al.* (in press) have
424 shown that protected-area status increases ecotone migration rates by 5× through
425 reduction in disturbance. Carbon sequestered as a result of reducing emissions from
426 deforestation and forest degradation (REDD) offers a source of potential income for
427 Andean landowners. Carbon sequestration above and below ground can be both
428 quantified and monetarized (e.g. Gibbon *et al.* 2010). The degradation of the upper
429 timberline by fire, however, has an impact on the value of the setting for its above-
430 ground biomass. In a series of studies using the same soil pits and vegetation plots as
431 in our study, carbon storage in plant material declined markedly from $63.4 \pm 5.2 \text{ mg C}$
432 ha^{-1} in the forest, to $16.9 \pm 2.2 \text{ Mg C ha}^{-1}$ in the transition and $7.5 \pm 0.7 \text{ Mg C ha}^{-1}$ in
433 the puna (Gibbon *et al.*, 2010). Soil carbon showed a different pattern, with equal
434 amounts of carbon stored in soils above and below the tree line, but its distribution
435 was more heavily biased to the surface in the puna (Zimmermann *et al.*, 2010). The
436 net result was that the above-ground : below-ground ratios of C storage were 15.8 in
437 the puna, 8.6 in the transition zone and 2.1 in the forest (Gibbon *et al.*, 2010).
438 Calculations of future carbon storage will need to include the erosion of biomass from
439 the upper timberline and the recognition that, should the timberline move upslope, it
440 will not have the same capacity for carbon storage as the highest biomass forest
441 settings. Our study site within the Manu National Park may reflect a best-case
442 scenario, in the sense that overt human pressures through logging and deliberate
443 burning are prohibited. In other areas, where fire is more frequent, the downslope loss

444 of forest may be more profound, and the overall loss of woody taxa may make the
445 climatically driven upslope expansion even more species-poor.

446 **CONCLUSIONS**

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

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

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473

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678

679 **SUPPORTING INFORMATION**

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

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

682 **Appendix S2** Species plot of axis 1 versus axis 2 detrended correspondence analysis

683 outputs for pollen from soil pits sampled in the Manu National Park, Peru.

684 **Appendix S3** Trends through time of the pollen data derived from soil pits sampled in

685 Manu National Park, Peru.

686

687 **BIOSKETCH**

688 **Mark B. Bush** is a professor at the Florida Institute of Technology and a
689 palaeoecologist investigating Central- and South American ecosystem responses to
690 past climate change. His research focuses on fossil pollen analysis of Neotropical
691 settings, environmental reconstructions of past climates and vegetation communities,
692 and palaeoecological evidence of human responses to climate change. The authors
693 form part of the Andean Biodiversity and Ecology Research Group (ABERG), which
694 has studied intensively the ecology of Manu and the Andean flank of Peru.

695 Author contributions: M.B.B., A.M.A.-R., D.H.U. and M.R.S. conceived the ideas;
696 M.B.B. and D.H.U. collected the data; A.M.A.-R. and B.G.V. analysed the data;
697 A.M.A-R, B.G.V., A.C.-M., D.H.U. and M.Z. contributed to data analysis; and M.B.B.
698 led the manuscript writing.

699 Editor: Jens-Christian Svenning

700

701 **TABLE**

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

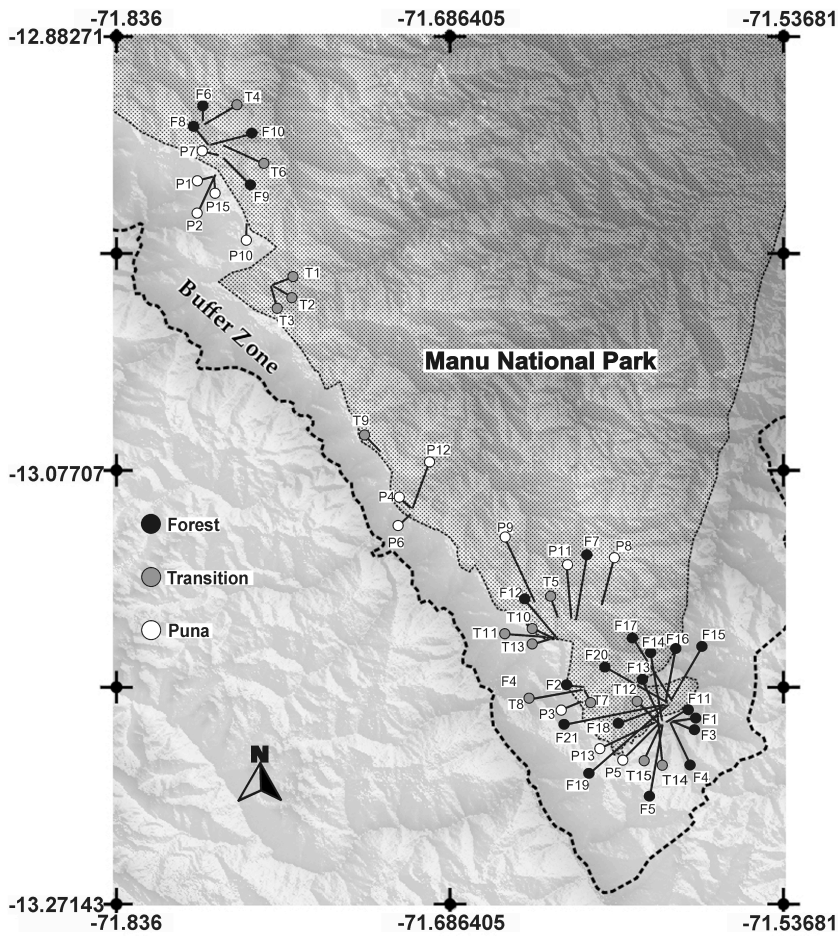
Laboratory code	Vegetation type	Sample ID	Depth (cm)	^{14}C age	Mean calibrated age (yr BP)	Sigma range 1σ
OS-78042	Puna	P6t M	14	260 ± 35	304	57
OS-78043	Puna	P6t	14	205 ± 25	221	80
OS-78044	Puna	P4b M	20	1820 ± 35	1750	48
OS-78045	Puna	P4b	20	1630 ± 25	1525	28
OS-78046	Puna	P16b*	20	1260 ± 25	1205	39
OS-78047	Puna	P16b*M	20	1620 ± 30	1513	37
OS-77912	Puna	P11b	22	1350 ± 25	1283	11
OS-77927	Puna	P11bM	22	1490 ± 25	1367	23
OS-77931	Puna	P11b†	22	8060 ± 45	8991	50
OS-77954	Puna	P6b	40	2400 ± 25	2391	54
OS-77955	Puna	P6b	40	2440 ± 30	2489	104
OS-77923	Transition	T2b	5	730 ± 25	672	9
OS-78048	Transition	T16b*	9	1320 ± 25	1268	21
OS-78049	Transition	T16b*M	9	1380 ± 30	1295	13
OS-77664	Transition	T3b	17	3550 ± 35	3841	47
OS-77665	Transition	T3bM	17	2760 ± 30	2845	35
OS-77921	Transition	T2bM	19	2860 ± 30	2966	45
OS-77922	Transition	T2b†	19	680 ± 25	652	25
OS-77666	Transition	T1bM	20	1660 ± 25	1551	25
OS-77920	Transition	T1b	20	1710 ± 35	1611	50
OS-77399	Forest	F19b*	26	1570 ± 25	1452	42
OS-77926	Forest	F1b†	30	675 ± 25	648	27
OS-77925	Forest	F17t*	40	80 ± 30	‡	‡
OS-77924	Forest	F18b*	66	2210 ± 30	2229	60

707 *Samples from which a date was taken but which were not counted for pollen;

708 †outliers; ‡ a sample that returned a modern age.

709

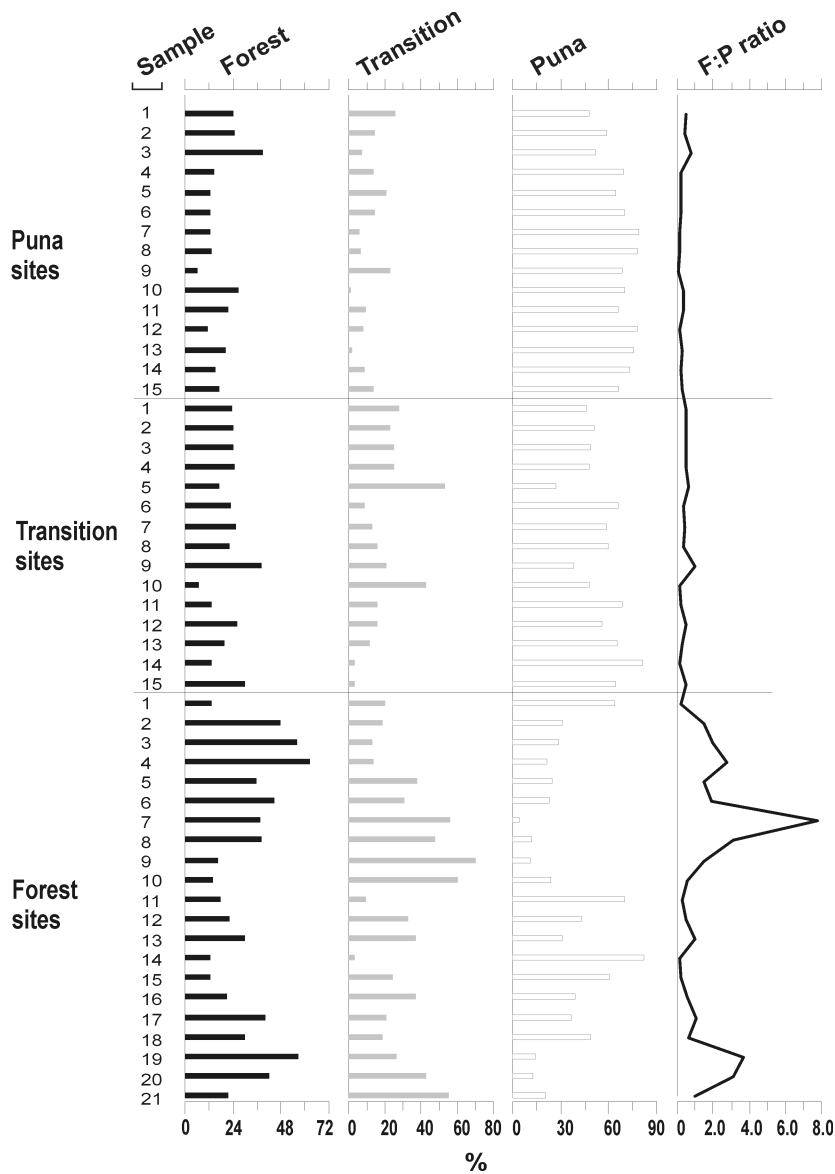
710 **FIGURE LEGENDS**



711

712 **Figure 1** Location and topography of the field study region and sampled sites, within
713 the Manu National Park, Peru. Black circles, forest samples; grey circles, transitional
714 samples; white circles, puna samples. Source of map: <http://www.USGS.gov>.

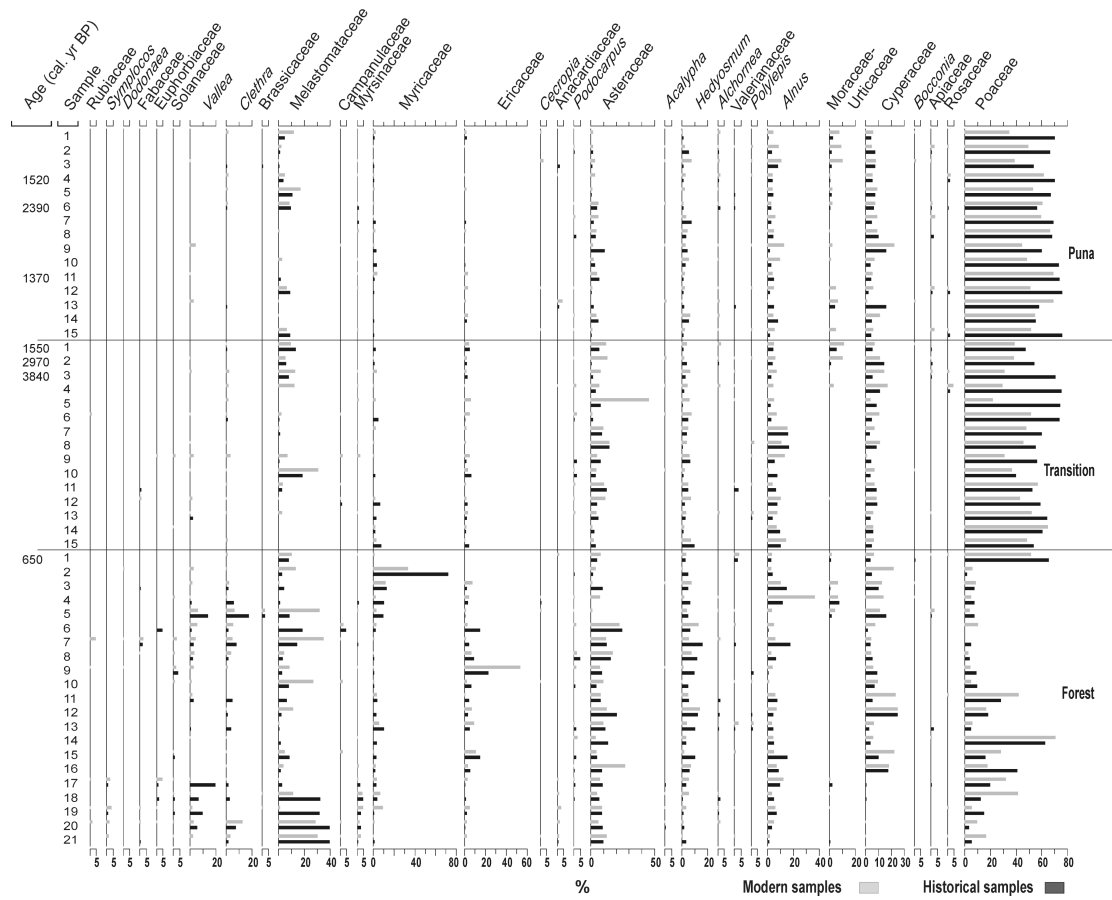
715



716

717 **Figure 2** The modern pollen spectra from surface soil samples collected from sites in
 718 the Manu National Park, Peru. Puna, transition and forest categories were determined
 719 by modern vegetation. F : P, the ratio of forest : puna taxa.

720



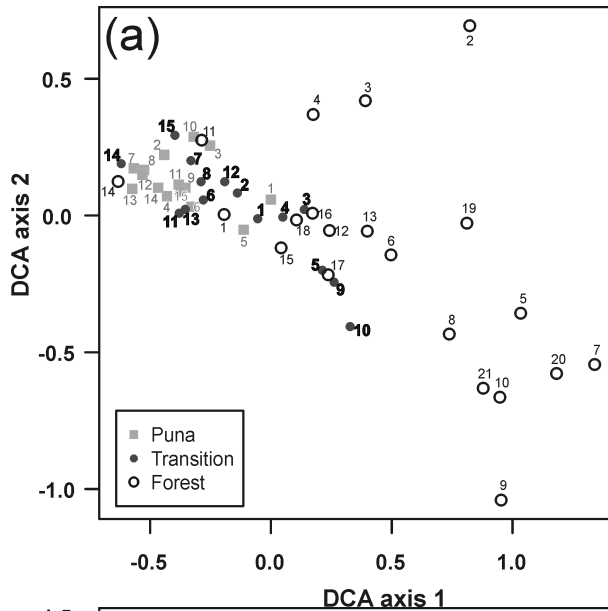
721

722 **Figure 3** Soil pollen percentage diagram showing modern and historical sample pairs

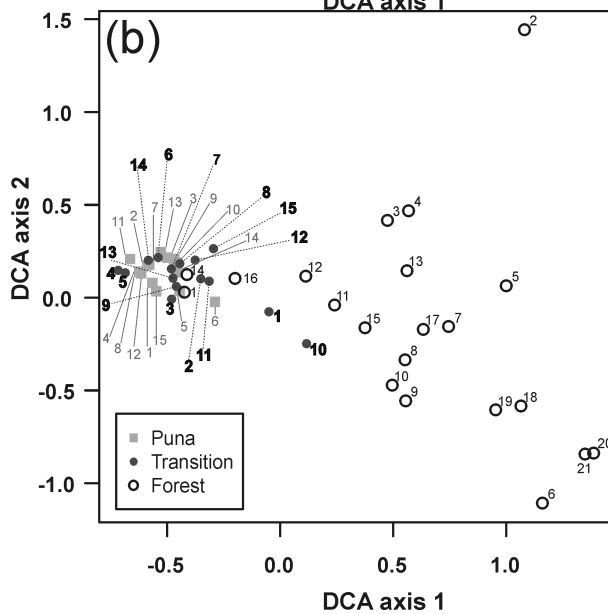
723 collected from sites within the Manu National Park, Peru. Grey, modern samples;

724 black, historical samples. Where available, dates are shown for the historical sample.

725



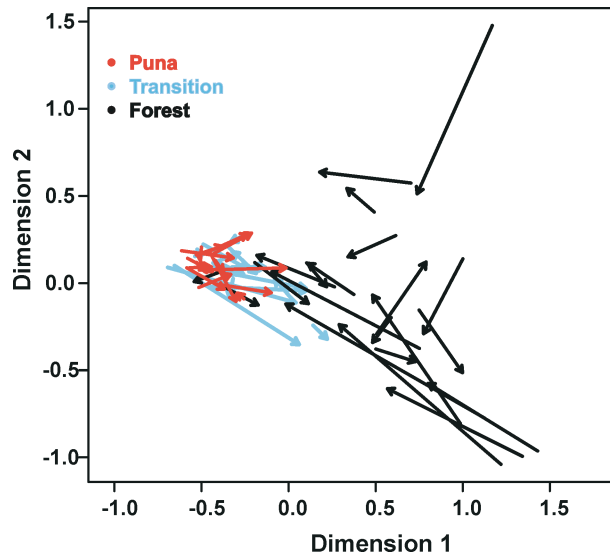
726



727

728 **Figure 4** Detrended correspondence analysis (DCA) of pollen from modern and
 729 historical soil samples collected from sites within the Manu National Park, Peru: (a)
 730 surface samples; (b) samples from the historical soil horizon. Site numbers correspond
 731 to the puna, transition and forest numbers in Fig. 3.

732



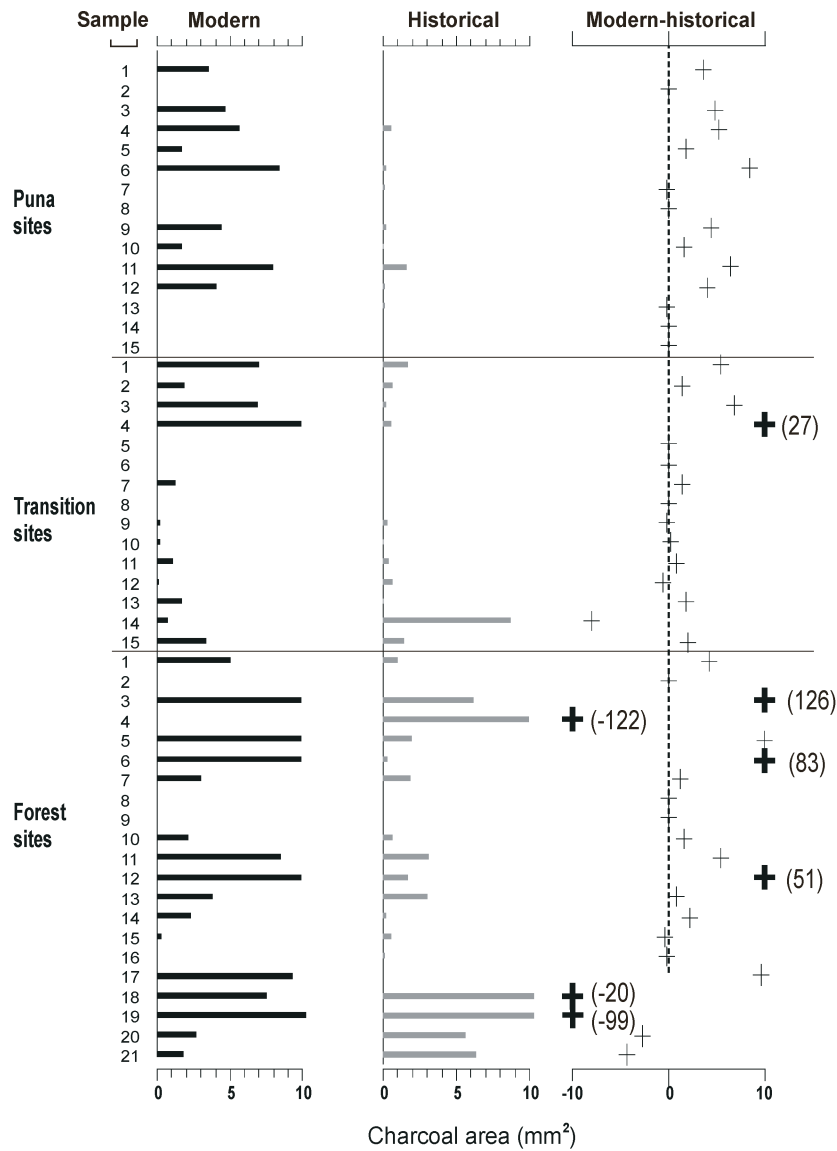
733

734 **Figure 5** Procrustes rotation to contrast the difference between modern and historical
 735 site ordinations for soil samples collected within the Manu National Park, Peru.

736 Arrows indicate changes from historical samples/sites to modern ones. The sites are

737 colour coded for modern vegetation: black, forest; blue, transition; red, puna. Site

738 numbers correspond to the puna, transition and forest numbers in Fig. 3.



739

740 **Figure 6** Charcoal concentrations from the top and bottom soil samples collected
 741 from pits within the Manu National Park, Peru. The difference in concentration
 742 between modern and historical) between the top and bottom samples is also shown.
 743 Bold plus signs and values in parentheses represent values that do not fit the scale of
 744 the diagram.