

1 **The ecological impact of oceanic island colonization – a palaeoecological**  
2 **perspective from the Azores**

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15 **The ecological impact of oceanic island colonization – a palaeoecological**  
16 **perspective from the Azores**

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27

28 **ABSTRACT**

29 **Aim**

30 In many cases, human colonization drastically modified the ecosystems of remote

31 oceanic islands before scientists arrived to document the changes. Palaeoecological

32 records before and after human colonization provide insights into the original

33 ecosystems and an assessment of subsequent human impact. We used pollen analysis to

34 compare the impact of 15th century colonization of the Azores to that of natural

35 disturbances such as volcanic eruptions and climate changes.

36 **Location**

37 Azores archipelago, Atlantic Ocean.

## 38 **Methods**

39 Sediment records from three highland sites in the Azores (on the islands of Pico and  
40 Flores) were dated radiometrically and analysed palynologically. Pollen taxa were  
41 classified as native, endemic or introduced based on comparison with flora lists. Data  
42 were statistically zoned and temporal trends identified using detrended correspondence  
43 analysis.

## 44 **Results**

45 Human colonization of the Azores resulted in rapid, widespread, persistent vegetation  
46 changes on a scale unprecedented in the last 2700 years, detectable through the decline  
47 of dominant trees, spread of grasses and fire-tolerant species, introduction of exotic  
48 plants, evidence for grazing and fire, and changes to soils and moisture availability.  
49 During the same period, volcanic eruptions appear to have had more localized impacts  
50 on the vegetation, lasting 500–1000 years and favouring endemic taxa. The effect of  
51 late Holocene climatic changes on the highland vegetation of the Azores seems to have  
52 been minor. Palaeoecological data indicate that at least two plant species went extinct  
53 on Pico after human colonization and that some plants regarded as introduced were  
54 almost certainly part of the original flora of the islands. Despite a consistent signal of  
55 human impact, compositional differences between *Juniperus brevifolia* communities on  
56 Pico and Flores remained after colonization.

## 57 **Main conclusions**

58 Human colonization had a greater impact on the pristine vegetation of Pico and Flores  
59 than climatic changes and volcanic activity during recent millennia. The similarity  
60 between post-colonization changes on the Azores and other oceanic islands suggests a  
61 consistent pattern and scale to historical-era human impact on otherwise pristine  
62 ecosystems. These characteristics could be used to further elaborate biogeographical

63 theory and direct conservation efforts towards species that appear most susceptible to  
64 human activity.

65

## 66 **Keywords**

67 Atlantic Ocean, conservation, Flores Island, human impact, island biogeography,  
68 palaeoecology, palynology, Pico Island, Portugal.

69

## 70 **INTRODUCTION**

71 Oceanic islands have provided the basis for much of our theoretical understanding of  
72 ecological processes (Whittaker *et al.*, 2008). One of the first to recognize the  
73 significance of island biotas was Joseph Hooker (1867), who presented concepts of  
74 endemism, impoverishment and dispersal, which remain major themes for  
75 biogeographical research (Williamson, 1984; Berry, 1992). The relevance of Hooker's  
76 ideas today is attested by the recent formal incorporation of island age into the theory of  
77 island biogeography (Whittaker *et al.*, 2008), the use of Quaternary climatic changes to  
78 explain patterns of diversity and endemism (Carine & Schaefer, 2010), and the  
79 confirmation that some island plants went extinct through the "catastrophes" of human  
80 impact even before botanists arrived to document them (Hooker, 1867, p. 7; de  
81 Nascimento *et al.*, 2009). Here we address the issue of historical human impact on  
82 oceanic island ecosystems, a theme of special importance in developing ecological  
83 theory (Whittaker *et al.*, 2008) and sound conservation strategies (Fernández-Palacios *et*  
84 *al.*, 2011).

85 Palaeoecological evidence has been used to recognize the first signs of human  
86 colonization and to evaluate human impact on islands from many corners of the globe  
87 (e.g. Flenley *et al.*, 1991; Lawson *et al.*, 2007, 2008; Prebble & Wilmshurst, 2009;

88 Ljung & Björck, 2011). Just as the peculiar biotas of oceanic islands have led to a  
89 greater understanding of dispersal, invasion, endemism, extinction and evolution (to  
90 name a few), the effect of human colonization on previously pristine ecosystems may  
91 help us better differentiate human impacts from other kinds of disturbance (Prebble &  
92 Wilmshurst, 2009). On the continents, such a differentiation is crucial for interpreting  
93 past ecological changes, as human impact remains a vague concept incorporating many  
94 scales, rates, processes, interactions and outcomes (Head, 2008; Connor, 2009).  
95 Oceanic islands, because of their isolation, limited area and often recent colonization,  
96 provide distinctive opportunities to examine the ecological changes that accompanied  
97 human arrival, and in so doing shed light on human impacts in general.

98 Here we present new palaeoecological data from two islands in the Azores  
99 archipelago to address the following questions.

- 100 1. Has human impact homogenized Azorean vegetation across different islands?
- 101 2. Were endemic plant species more susceptible to human impact than other native  
102 species?
- 103 3. How did human colonization affect the biodiversity of the islands?
- 104 4. What was the scale of human impact in comparison to volcanic eruptions and  
105 climate changes?

106

## 107 **MATERIALS AND METHODS**

### 108 **Geographical setting**

109 The Azores are a group of oceanic islands that straddle the Mid-Atlantic Ridge, roughly  
110 1600 km from Portugal and 1900 km from Newfoundland (Fig. 1). The nine islands are  
111 of volcanic origin, having arisen along sea-floor fracture zones as the Eurasian, African  
112 and North American tectonic plates rifted apart (Ferreira, 2005; Azevedo & Ferreira,

113 2006). The oldest rocks in the archipelago are found on the easternmost island, Santa  
114 Maria, and date to 8.12 million years ago (Azevedo & Ferreira, 2006). The Azores are  
115 thus the youngest archipelago in the Macaronesian region, to which the archipelagos of  
116 Madeira, Canary Islands and Cabo Verde also belong (Fernández-Palacios *et al.*, 2011).

117 Owing to their volcanic origin, the islands of the Azores are pock-marked with  
118 craters and calderas. Soils are generally young andisols, formed under the humid  
119 climate on relatively recent lava flows and pyroclastic deposits (Dias, 1996). Peat  
120 deposits occur in depressions, around crater lakes and in vegetation communities where  
121 *Sphagnum* mosses play a prominent role (Dias, 1996).

122 The Azores experience an oceanic climate, with high humidity and cloud cover  
123 throughout the year, and an average temperature of 17.5 °C at sea level. The main  
124 climatic controls over the Azores are the strength and position of the Azores Current, a  
125 branch of the Gulf Stream, and the Azores Anticyclone, a high-pressure cell that moves  
126 seasonally, bringing relatively dry and sunny conditions when it is positioned over the  
127 islands in summer (Schaefer, 2003). The western islands receive the highest average  
128 annual rainfall (e.g. Flores: 1716 mm at sea level), whilst the eastern islands have lower  
129 precipitation (e.g. Santa Maria: 775 mm) and a more pronounced dry season  
130 (CLIMAAT Project, 2007). Rainfall increases dramatically with elevation, such that  
131 the highest parts of Flores and Pico may receive up to 5000 mm annually.

132

### 133 **Flora and vegetation**

134 Perhaps because of their isolation, modest age and oceanic climate, the Azores have a  
135 relatively small number of native plant species (197), of which about a third (70) are  
136 regarded as endemics (Schaefer, 2003). The majority of Azorean plants classified as  
137 endemic occur on all the islands, whereas the other archipelagos of Macaronesia are

138 characterized by a large number of single-island endemics (Carine & Schaefer, 2010).  
139 Recent genetic studies suggest that the Azores may harbour a considerable number of  
140 cryptic endemics, and therefore have rates of endemism similar to those of other  
141 Atlantic archipelagos (Schaefer *et al.*, 2011). The Azorean flora comprises species from  
142 three main biogeographical lineages (Dias, 1996): a Tertiary Mediterranean element, a  
143 Plio-Pleistocene African element, and a Quaternary Euro-Siberian or Atlantic element.  
144 Despite the possibility of seed dispersal from the Americas, the Azores flora seems to  
145 have arrived primarily from the European and African continents via wind (potentially  
146 40% of species) or migrating birds (58%) (Schaefer, 2003).

147       When Portuguese mariners first encountered the Azores, they observed islands  
148 covered in impenetrable forests of *Laurus azorica*, *Juniperus brevifolia*, *Prunus azorica*  
149 and *Morella faya* (Costa, 1950), species which also feature prominently as  
150 macrobotanical fossils from the archipelago (Fries, 1968; Forjaz *et al.*, 1970).  
151 Historical descriptions indicate that each of these species, as well as *Frangula azorica*,  
152 *Taxus baccata* and *Picconia azorica*, dominated in different forests across the  
153 archipelago and suggest that there was no distinct zonation in relation to elevation  
154 (Dias, 1996; Schirone *et al.*, 2010). Only the chronicles of Gaspar Frutuoso, published  
155 in 1589, bear witness to herbaceous vegetation on the high plains of Flores (Dias, 1996).  
156 By the 16th century, however, these herbaceous communities could have been affected  
157 by introduced grazing animals (the Azores have no native land mammals apart from  
158 bats).

159

## 160 **Human colonization**

161 It is likely that the Azores were already known to mariners at least 100 years before  
162 their official discovery by the Portuguese in the 15th century (Johnson, 1994), but there

163 is no evidence for earlier colonization. The first Portuguese colony appeared on Santa  
164 Maria in 1439 and was followed by Flemish colonies on Faial in 1466 and Flores in  
165 1472. Portugal later assumed control of the entire archipelago. According to Dias  
166 (1996), human impact on the vegetation occurred in three phases: (1) a pre-colonization  
167 phase in which a wide variety of domestic animals was released on the islands to sustain  
168 the anticipated human population; (2) an early, extractive phase in which forests were  
169 felled for construction, ship-building and charcoal production; and (3) a later,  
170 transformative phase in which the Azorean landscape was deforested and turned over to  
171 the production of exotic monocultures. As a consequence of these drastic human  
172 interventions, little native vegetation survives on the islands today and introduced plant  
173 species outnumber native species by a factor of three to one (Schaefer, 2003, 2005).

174

### 175 **Study sites**

176 Three sites were sampled after extensive reconnaissance on all the islands of the  
177 archipelago – Lagoa Rasa on the island of Flores, and Lagoa do Caveiro and ‘Pico Bog’  
178 (field appellation for a mire north-east of Lagoa do Peixinho) on the island of Pico  
179 (Table 1; see also Fries, 1968; Azevedo & Ferreira, 1998; Pugin & Girardclos, 1998;  
180 Björck *et al.*, 2006). The lakes of Rasa and Caveiro were selected to represent past  
181 vegetation changes on a relatively large scale, whilst Pico Bog was chosen to reflect  
182 changes on a more local scale (larger basins receive a greater component of regional  
183 pollen relative to smaller sites: see Moore *et al.*, 1991). All three sites are craters  
184 situated in the highland vegetation zone in which *Juniperus brevifolia* and *Erica azorica*  
185 are the most important trees (Tutin, 1953).

186         Although all the Azores islands share many geographical features, the islands of  
187 Flores and Pico differ in key aspects: Flores reaches a maximum elevation of 915 m,



188 while Pico is the highest mountain on Portuguese territory (2351 m); Flores receives  
189 more precipitation than Pico, hence most of Flores' streams are perennial, while Pico's  
190 streams tend to be intermittent; Flores' last volcanic eruption occurred some 3000 years  
191 ago, while the last on Pico was in AD 1718–1720; and, in geological terms, Flores is  
192 around 2.15 million years old and situated entirely on the North American Plate, while  
193 Pico is the youngest member of the archipelago (0.27 million years) and rises from the  
194 Azorean microplate between the African and Eurasian Plates (Zbyszewski *et al.*, 1963,  
195 1968; Morrissette & Traineau, 1985; Dias, 1996; Azevedo & Ferreira, 2006).

196

### 197 **Sampling and analysis**

198 Sediment cores were obtained from the centre of Lagoa Rasa in 1998 using a square-rod  
199 piston corer (Wright, 1967) and from the centre of Lagoa do Caveiro and Pico Bog in  
200 2001 using a Russian corer (Björck *et al.*, 2006). Coring continued until an  
201 impenetrable layer (presumably bedrock or thick tephra) was reached; each core  
202 therefore represents the sediment accumulated since a major eruption. Pre-eruption  
203 sediments were also cored from the margin of Lagoa do Caveiro. Samples of 1 cm<sup>3</sup>  
204 were extracted from the cores and pretreated according to standard palynological  
205 methods, including the addition of *Lycopodium* spore tablets to determine pollen  
206 concentrations (Moore *et al.*, 1991). Pollen was identified at 400× magnification with  
207 reference to Reille (1992, 1995 & 1998) and reference material held at the Portuguese  
208 Institute of Archaeology (IPA). Percentage pollen diagrams were created from a sum of  
209 all terrestrial pollen taxa, including identifiable fern spores. Monolete fern spores (i.e.  
210 Polypodiales spores lacking the perine required for precise identification), Cyperaceae  
211 and aquatic taxa are excluded from the pollen sum, as are fungal spores indicative of

212 grazing (van Geel & Aptroot, 2006). Data were plotted using Tilia programmes  
213 (Grimm, 2004).

214 To determine whether human colonization caused the vegetation of the two  
215 islands to become more similar, we analysed percentage pollen data using detrended  
216 correspondence analysis (DCA) in the program PC-ORD 4.25 (McCune & Mefford,  
217 1999). Because DCA axes can be interpreted in terms of species turnover (Gauch,  
218 1982), the analysis forms a basis for assessing ecological responses to both human  
219 impact and other ‘natural’ disturbances, such as volcanic eruptions indicated by tephra  
220 layers or climate changes recorded in other proxies (Björck *et al.*, 2006).

221 To assess the effect of human impact on endemics in relation to other species,  
222 we classified the identified pollen taxa into ‘endemics’, ‘native’ and ‘introduced’ taxa  
223 (Table 2) with reference to their pollen morphology and the flora checklist of Silva *et al.*  
224 (2010 – plant taxonomy in this paper follows this checklist). Prior to analysis, taxa  
225 listed as ‘introduced’ occurring frequently prior to colonization were added to the  
226 ‘native’ category where their pollen representation suggested it was valid to do so (van  
227 Leeuwen *et al.*, 2005). Any taxa that represented plant species that fell into more than  
228 one category were removed from the analysis, along with long-distance transported  
229 pollen produced by wind-pollinating species widespread on neighbouring continents.  
230 We then calculated two pollen sums based on the remaining taxa, one including the  
231 dominant taxon, *Juniperus brevifolia*, and one without.

232 We adopted the existing age–depth model for the Lagoa do Caveiro record  
233 (Björck *et al.*, 2006) and formulated age–depth models (Fig. 2) for the other sites based  
234 on the accelerator mass spectrometry (AMS) radiocarbon dates listed in Table 3 and  
235 calibrated using CALIB 6.0.2 (Stuiver & Reimer, 1993) and CALIBOMB (Reimer &  
236 Reimer, not dated). Pre-impact and post-impact phases were identified independently

237 through pollen zonation (binary splitting by information content), with statistical  
238 significance of the zones assessed using the ‘broken stick’ model (Bennett, 2008). We  
239 then calculated pollen accumulation rates for pre-impact and post-impact assemblages  
240 in order to determine pollen diversity using the method described by van der Knaap  
241 (2009). For comparison, percentage-based diversity estimates were produced in  
242 PSIMPOLL 4.26 (Bennett, 2008).

243

## 244 **RESULTS AND INTERPRETATION**

245 According to the multiproxy study of Lagoa do Caveiro (Björck *et al.*, 2006), the central  
246 core (0–488 cm) covers approximately the last 4900 cal. yr BP (calendar years before AD  
247 1950). The marginal core of pre-eruption sediments (to 614 cm) extends this record  
248 back to approximately 6000 cal. yr BP (Björck *et al.*, 2006). Both the Pico Bog (570  
249 cm) and Lagoa Rasa (331 cm) records commence at approximately 2700 cal. yr BP (Fig.  
250 2), corresponding to the most recent volcanic activity on Flores (Morriseau & Traineau,  
251 1985) and the inferred timing of the Caveiro-1076 volcanic eruption on Pico Island  
252 (Björck *et al.*, 2006).

253         As our primary objective is to analyse the changes wrought by island  
254 colonization, each of the pollen diagrams has been subdivided into two statistically  
255 significant assemblage zones, termed ‘pre-impact’ and ‘post-impact’ phases (Figs 3–5).  
256 Other statistically significant zone boundaries are indicated on the diagrams, although  
257 the reduction in variance associated with these additional zones is lower. The boundary  
258 between pre-impact and post-impact phases, according to the age–depth models, falls at  
259 approximately 490 cal. yr BP for Lagoa Rasa (188 cm), 410 cal. yr BP for Lagoa do  
260 Caveiro (137.5 cm) and 385 cal. yr BP for Pico Bog (205 cm). These ages agree with  
261 the colonization history of the islands, given the uncertainties in age modelling and the

262 fact that zone boundaries record statistically significant changes rather than the first  
263 signs of change.

264 In interpreting pollen records, it is important to bear in mind a number of  
265 inherent limitations. Pollen data are biased by production (different plant species  
266 release different quantities of pollen), taphonomy (some pollen taxa preserve poorly in  
267 sediments) and taxonomic resolution (pollen types usually represent several plant  
268 species), amongst others (Moore *et al.*, 1991). The pollen production of native  
269 angiosperms on oceanic islands may be quite low (Collins & Bush, 2011), perhaps due  
270 to the prevalence of animal-mediated pollination. Some taxa may only be detected  
271 where source plants occur very close to the site of deposition, especially those with  
272 specialized pollination mechanisms (e.g. Orchidaceae, *Viola*). In the case of the Azores,  
273 pollen taphonomy is a special problem. *Laurus azorica*, formerly the dominant tree at  
274 low to middle elevations, and *Hedychium gardnerianum*, a widespread invasive species,  
275 produce pollen that preserve poorly in sediments and tend to disintegrate during  
276 laboratory treatment (S. Connor, unpublished data). *Laurus azorica* pollen also lacks  
277 the surface ornamentation characteristic of other Lauraceae pollen (see Reille, 1992,  
278 1995 & 1998), complicating its identification in fossil sediments.

279 Problems of pollen-taxonomic resolution are limited on the Azores because of  
280 the relatively low number of plant species present on the islands. The likelihood of  
281 pollen arriving from the continents is also low, although wind-dispersed pollen types  
282 such as *Alnus* may travel long distances (Collins & Bush, 2011). The level of  
283 taxonomic precision is indicated by the taxon names adopted in the text and figures.  
284 For example, *Juniperus brevifolia* represents only that plant species as it is the only  
285 Azorean plant to produce *Juniperus* pollen, *Rumex obtusifolius*-type includes all species  
286 that produce the same pollen type as *R. obtusifolius* (i.e. *R. obtusifolius* subsp.

287 *obtusifolius* and *R. crispus* on the Azores), and Asteraceae subfamily Asteroideae  
288 represents Azorean species within that group except for those with morphologically  
289 distinct pollen, such as *Bellis*-type (representing *Bellis azorica* on Pico and Flores) and  
290 *Pericallis*-type (representing *Pericallis*, *Senecio* and *Solidago* species).

291

## 292 **The pre-impact phase**

293 The most obvious feature of pre-impact assemblages is the prevalence of pollen from  
294 the endemic *Juniperus brevifolia* at all sites (Figs 3–5). Juniper pollen is more abundant  
295 in the Lagoa Rasa record than the Lagoa do Caveiro record, while Pico Bog records the  
296 lowest proportions. The Lagoa do Caveiro juniper curve stands out for its high degree  
297 of variability. Episodic reductions in *Juniperus brevifolia* pollen are accompanied by  
298 increases in certain herbaceous taxa (e.g. *Angelica lignescens*, *Ranunculus cortusifolius*-  
299 type, Asteraceae subfamily Cichorioideae, and monolete fern spores) and geochemical  
300 indicators of lowered lake levels (Björck *et al.*, 2006). We assume that these reductions  
301 reflect changes in pollen source-area controlled by water level in this shallow basin,  
302 rather than major vegetation changes. This interpretation is supported by the presence  
303 of juniper stomata during these phases and the absence of variations of similar  
304 magnitude in the Pico Bog record collected nearby.

305 Lagoa Rasa on Flores records a greater proportion of *Myrsine africana*, *Picconia*  
306 *azorica* and *Viburnum treleasei* in pre-impact assemblages compared to the two Pico  
307 records, which contain more *Hedera azorica*, *Ilex perado* ssp. *azorica*, *Morella faya*,  
308 Ericaceae and various herbaceous taxa. This may suggest that an open vegetation  
309 structure prevailed around the high-elevation sites on Pico, while Lagoa Rasa, situated  
310 at a lower elevation, was probably surrounded by denser *Juniperus brevifolia*-  
311 dominated vegetation. The importance of *Euphorbia stygiana* in this vegetation zone

312 (Tutin, 1953) is indicated by the frequent occurrence of *Euphorbia* pollen. Laurisilva  
313 (*Laurus azorica*-dominated forest) may have also been present, but is not directly  
314 recorded palynologically. Certain plant distribution patterns on the Azores today  
315 apparently existed in the pre-impact phase, including the presence of *Arceuthobium*  
316 *azoricum* and *Daphne laureola* on Pico but not on Flores (see Silva *et al.*, 2010).

317         Each of the pollen records represents vegetation changes since a major eruption  
318 or series of eruptions. This makes it possible to infer some characteristics of post-  
319 disturbance ecological succession in these presumed pristine ecosystems. On Flores, a  
320 pioneer community with *Juniperus brevifolia*, Ericaceae, Poaceae, Asteraceae and  
321 *Selaginella kraussiana* appeared around Lagoa Rasa after the eruption; *Culcita*  
322 *macrocarpa* and *Myrsine africana* gradually replaced some of these taxa over a period  
323 of 500–1000 years. The indication of juniper as a pioneer agrees with vegetation  
324 studies of recent lava flows on Terceira (Elias & Dias, 2004). On Pico, the earliest  
325 pollen assemblages from Lagoa do Caveiro are dominated by herbs, especially *Angelica*  
326 *lignescens*, *Anagallis*, *Hypericum foliosum*-type and various Asteraceae, with *Ilex*  
327 *perado* ssp. *azorica* and *Juniperus brevifolia* peaking prior to a series of major eruptions  
328 around 5150–5200 cal. yr BP (Björck *et al.*, 2006). After this event, the record shows a  
329 distinct peak in Ericaceae (*Erica azorica*), *Hypericum* and Poaceae, succeeded by  
330 assemblages like those recorded before the eruptions, and followed by *Juniperus*  
331 *brevifolia* dominance. A very similar succession appears at the beginning of the Pico  
332 Bog record (albeit with more *Euphorbia* and less Poaceae), indicating a consistent post-  
333 eruption shift from herb- and shrub-dominated communities to greater forest cover. All  
334 three pollen records suggest that *Myrsine africana* and *Culcita macrocarpa* are late-  
335 successional species.

336 Similar vegetation successions might be expected following each of the  
337 eruptions that deposited subsequent tephra layers in the sediments of Lagoa do Caveiro  
338 and Pico Bog. However, a consistent relationship between these tephra layers and vegetation  
339 change is hardly evident. Vegetation succession following major eruptions at the base  
340 of each core is clearly picked out by DCA axis 2 (Figs 6 & 7), but nothing similar is  
341 observed following each of the tephra layers. Apart from a dilution effect on pollen  
342 concentrations, the only observable impact of these tephra layers is a localized spike in  
343 endemic taxa at Pico Bog (Fig. 6). There is no indication that the pyroclastic material  
344 ejected during these smaller eruptions was sufficient to reset the successional clock.

345

#### 346 **The post-impact phase**

347 The next phase in the vegetation history of the Azores begins around 400 cal. yr BP.  
348 Even by this time there were signs of early human interventions, probably as a  
349 consequence of the deliberate introduction of exotic mammals. Grasses (Poaceae) and  
350 bracken (*Pteridium aquilinum*) seem to have increased the earliest, followed by *Erica*  
351 *azorica*, an endemic that appears to have benefited from the decline of *Juniperus*  
352 *brevifolia* communities, and *Morella faya*, a native tree that probably replaced *Laurus*  
353 *azorica* at lower elevations (Figs 3–5). Previously abundant herbs (represented by  
354 *Angelica lignescens*, Asteraceae subfamily Cichorioideae, *Euphorbia* and *Ranunculus*  
355 *cortusifolius*-type) diminished and a suite of introduced taxa appeared (e.g. *Castanea*  
356 *sativa*, *Ligustrum*, *Vitis*, *Plantago lanceolata*, *P. major*-type, *Cerealia*-type and *Zea*  
357 *mays*; *Hydrangea macrophylla* and *Cryptomeria japonica* appeared later). As the  
358 replacement of native Azorean vegetation by agriculture and invasive introduced  
359 species such as *Pittosporum undulatum* has been less at higher elevations compared to  
360 the lowlands, the full extent of post-colonization plant invasion is probably not

361 represented in the pollen diagrams. Pastoralism on the islands is attested by the  
362 appearance of spores produced by dung-inhabiting fungi (*Podospora* and *Sporormiella*)  
363 and the historically documented conflagrations that were used to open these pastures are  
364 recorded clearly in the charcoal record from Lagoa Rasa (Fig. 3). Fire does not seem to  
365 have been prevalent at any time around the high-elevation sites on Pico, perhaps  
366 because of low plant biomass.

367

### 368 **Has human impact homogenized the vegetation across different islands?**

369 The transition from pristine to human-impacted ecosystems is most vividly expressed in  
370 Fig. 7. DCA axis 1 is interpreted as representing moisture availability: strong negative  
371 correlates include Asteraceae, Apiaceae and *Euphorbia*; strong positive correlates are  
372 moisture-loving taxa such as *Trichomanes*, *Viburnum* and *Frangula*. DCA axis 2 is  
373 related to forest cover: strong negative correlates include forest taxa such as *Juniperus*,  
374 *Picconia* and *Viburnum*, while positive correlates are light-demanding herb taxa, for  
375 example Poaceae, *Anagallis* and *Pteridium*.

376         Pre-colonization variations probably relate to available soil moisture (axis 1),  
377 which is a limiting factor on the young, high porosity soils of volcanic islands (Mueller-  
378 Dombois, 1975). In the post-impact phase, however, the pattern is distinctly different,  
379 indicating a trajectory towards lower forest cover (axis 2) and more available moisture  
380 (axis 1). A separate DCA of the pre-impact samples from all sites (not shown) proved  
381 that the pattern expressed by the DCA axis 1 is robust (correlation between the two sets  
382 of results is  $r = 0.99$ ,  $P < 0.001$ ). At least as far as these pollen data are concerned, the  
383 hypothesis that human impact has homogenized the vegetation on Pico and Flores is not  
384 supported. We hasten to add that this conclusion applies only to the highland vegetation



385 of these islands and a very different result could be expected in the coastal lowlands or  
386 on the more densely populated parts of the archipelago.

387 One striking feature of the pollen diagrams is the post-impact explosion of  
388 *Sphagnum* spores, which are scarcely recorded before human impact. Sjögren (1973)  
389 remarked on how widespread burning and deforestation on the islands has led to the  
390 rapid expansion of *Sphagnum* blanket peat, causing edaphic changes that effectively  
391 prevent regeneration in remnant plant communities. Blanket mire formation can be  
392 initiated when burning forms a layer of fine hydrophobic particles on the soil surface,  
393 reducing percolation, and/or when deforestation decreases the leaf-area index, reducing  
394 evapotranspiration (Moore, 1975). The palaeoecological data provide support for  
395 Sjögren's argument in the post-impact abundance of *Sphagnum* spores, higher charcoal  
396 concentrations and the suggestion of higher available moisture and lower tree cover.  
397 There is a possibility that the role of *Sphagnum* in Azorean plant communities has  
398 increased markedly since human colonization or that human activities have somehow  
399 promoted sporulation. Similar post-colonization *Sphagnum* expansions are also  
400 recorded on other oceanic islands (e.g. Faroe and Galápagos) and may constitute a  
401 general trend initiated by hydrological changes, fire, deforestation, grazing and loss of  
402 soil fertility (Lawson *et al.*, 2007).

403

#### 404 **Are endemic species more susceptible to human impact?**

405 In theory, human colonization could have a stronger impact on plants endemic to  
406 oceanic islands, because in pristine ecosystems the plants have evolved or persisted in  
407 the absence of novel or exotic disturbances. Hence the proportion of non-endemic  
408 native species may increase relative to endemics in the post-colonization period.

409 Comparison of pollen from exclusively endemic and native taxa (Fig. 6) shows that

410 human impact caused a crash in the ratio of endemics to natives, consistent with this  
411 hypothesis. However, our pollen data are clearly dominated by *Juniperus brevifolia*,  
412 which is both an abundant pollen producer and one of the species worst affected by  
413 colonization. If *Juniperus* is excluded from the calculations, a very different pattern is  
414 observed – a slow and gradual decline in the representation of endemic taxa in the  
415 pollen records, evident even before human contact. The pattern is less pronounced for  
416 the Pico Bog record where responses to local eruptions are also evident, but the rate of  
417 decline at all sites is quite similar (Fig. 6).

418         While human impact changed the relative proportions of taxa within the  
419 endemics group, the relatively constant rate of decline and its representation at all three  
420 sites suggests that a long-term process is at work. Endemics may be better than other  
421 species at colonizing bare rock in the aftermath of a major volcanic eruption. In other  
422 words, “volcanism resulted in superior adaptation of many native species to extreme  
423 edaphic conditions existing on volcanic rockland” (Mueller-Dombois, 1975, p. 364).  
424 Thus endemics gain the upper hand on skeletal soils formed directly after a major  
425 eruption, but subsequent ecological succession and soil formation lead to their gradual  
426 replacement by other native species. The slow rate of change and high degree of recent  
427 landscape modification on the Azores mean that it may be difficult to detect this process  
428 today.

429

#### 430 **How has biodiversity been affected by human impact?**

431 One way of assessing changes in biodiversity from island colonization is through  
432 estimates of palynological diversity. Such estimates are only indirectly related to  
433 floristic diversity, being biased by pollen taxonomy, pollen representation and  
434 vegetation structure (Odgaard, 1999). Percentage-based diversity estimates are strongly

435 influenced by evenness (Odgaard, 1999) and in our dataset 72% of the variance in such  
436 estimates is explained by evenness (measured by the ‘probability of interspecific  
437 encounter’; see van der Knaap, 2009). We attempted to reduce bias in diversity  
438 estimates by ensuring taxonomic consistency between the two analysts and adopting an  
439 estimation method based on pollen accumulation rates (PAR) instead of percentages.

440 PAR-derived diversity estimates (Fig. 6) are not influenced by palynological  
441 evenness, but are susceptible to the adopted age–depth models and variations in pollen  
442 concentrations. For example, diversity peaks around 1700–1350 cal. yr BP at Lagoa do  
443 Caveiro are probably artefacts related to high sedimentation rates and sediment  
444 reworking, which clearly occurred in the Caveiro record (Björck *et al.*, 2006). Despite  
445 this, the clear and recent increase in pollen diversity at the two lake sites is likely to  
446 represent the introductions of exotic plants to the archipelago since colonization – the  
447 ‘transformative phase’ of Dias (1996). Diversity estimates for native taxa alone also  
448 exhibit a small post-impact increase, which could be attributed to changes in vegetation  
449 structure (deforestation), permitting more pollen from longer distances to enter the  
450 lakes. Diversity around Pico Bog, which has a smaller pollen source-area, appears to  
451 have crashed since island colonization.

452 One conclusion that could be drawn from these estimates is that human impact  
453 on the Azores caused diversity to decline in local settings, while on the regional scale  
454 represented by the lake records, exotic introductions and deforestation increased the  
455 number of taxa detectable palynologically.

456 Plant extinctions are a feature common to many oceanic islands following  
457 human colonization (Table 4). *Ophioglossum lusitanicum* spores appear in the Lagoa  
458 do Caveiro and Pico Bog records, but this species is not to be found in the recent flora  
459 of Pico (Silva *et al.*, 2010). *Ophioglossum azoricum* is likewise recorded in the Lagoa

460 do Caveiro sediments, but not in the flora. These ferns produce large, morphologically  
461 distinct spores, so significant long-distance dispersal is unlikely and identification is  
462 assured. Unless these plants have been overlooked by botanists, it is probable that they  
463 have become locally extinct on Pico at some time since human colonization. Another  
464 species that has become extinct from several Azorean islands is *Taxus baccata*  
465 (Schirone *et al.*, 2010). We were unable to find any *Taxus* pollen in the three pollen  
466 records, so it is unlikely that *T. baccata* trees grew around these study sites during the  
467 late Holocene.

468         An important consideration for the study of island biodiversity and conservation  
469 is the accurate determination of whether species are introduced or native (van Leeuwen  
470 *et al.*, 2008; Kueffer *et al.*, 2010). Fossil evidence is one of the main criteria for  
471 assigning native status (Webb, 1985). Palaeoecological evidence for *Selaginella*  
472 *kraussiana*, a plant previously listed as introduced, demonstrated the species to be  
473 native to Flores and Pico (van Leeuwen *et al.*, 2005). The plant is now considered  
474 native to all the Azorean islands (Schaefer, 2005; Silva *et al.*, 2010).

475         Using the same approach, we can add *Illecebrum verticillatum* and at least one  
476 *Persicaria* species to the taxa likely to be native to Flores and Pico. Just as some native  
477 species went extinct from island floras before being recorded (Hooker, 1867; de  
478 Nascimento *et al.*, 2009), other native species were incorrectly recorded as introduced,  
479 perhaps because of their occurrence in disturbed areas or their introduced status on  
480 islands in other parts of the world (Schaefer, 2003; van Leeuwen *et al.*, 2008). Three  
481 other pollen taxa require further study. *Rumex obtusifolius*-type pollen in the pre-  
482 impact sediments from Pico probably indicates that *R. azoricus* has gone extinct from  
483 that island, but could indicate that either *Rumex obtusifolius* or *R. crispus* is native.  
484 *Pericallis*-type probably suggests that a species of *Solidago* is native, but could indicate

485 that *Pericallis malvifolia* went extinct on Flores. *Myriophyllum alterniflorum* pollen  
486 could indicate that plant's extinction on Pico.

487

#### 488 **What was the scale of human impact?**

489 Some idea of the scale of human impact, in ecological terms, can be gauged from the  
490 ordination results (Fig. 7), as the axes are scaled to represent turnover (Gauch, 1982).

491 Consistent with the islands' colonization histories and distribution of remnant  
492 vegetation, human impact on the westernmost island of Flores seems to have been  
493 somewhat less than on Pico, which is part of the more populous central group of the  
494 archipelago. The two Pico sites record human impact somewhat differently as one  
495 would expect of sites with different pollen source-areas (Lawson *et al.*, 2008). Pre-  
496 impact variability also seems to have been higher at the high-elevation sites on Pico,  
497 which therefore may also have been more vulnerable to anthropogenic disturbances than  
498 middle-elevation vegetation on Flores, remnants of which grow around Lagoa Rasa.

499       The effect of major volcanic eruptions on palaeovegetation succession around  
500 the three study sites was significant, as indicated by the earliest pollen assemblage zone  
501 in each record (Figs 3–5). In the Lagoa do Caveiro record, this zone encompasses  
502 samples from before and after the series of major eruptions around 5150–5200 cal. yr  
503 BP. Hence there is no statistical difference between the pre- and post-eruption pollen  
504 assemblages until the successional change around 4500 cal. yr BP. The most significant  
505 change in the pollen records is associated with human colonization, which, in contrast to  
506 the recorded volcanic eruptions, introduced new species, caused local extinctions and  
507 resulted in long-term changes in vegetation composition. Although larger eruptions in  
508 the distant past probably had a catastrophic ecological impact, human colonization  
509 seems to have had the most significant impact on the highland vegetation of Flores and

510 Pico during the period encompassed by the three palaeoecological records considered  
511 here.

512           While it is difficult to directly compare the scale of human impact on the  
513 Azorean vegetation with that of other islands, Table 4 provides a few details on some  
514 previous pollen-based studies of Atlantic oceanic islands before and after human  
515 colonization. The list is not intended to be complete, but nevertheless a striking  
516 similarity can be seen in the taxa that increased following human colonization and that  
517 many of the major declines were of *Juniperus*. The palaeoecological signal of human  
518 colonization of islands globally is generally rapid and widespread, accompanied by  
519 forest decline, loss of ‘keystone’ arboreal species, proliferation of grasses and fire-  
520 tolerant species, appearance of cultivated and ruderal plants, evidence for fire and  
521 grazing, and changes to soils and effective moisture availability (Table 4; Flenley *et al.*,  
522 1991; Kirch, 1996; McGlone & Wilmshurst, 1999; Mann *et al.*, 2008; McWethy *et al.*,  
523 2009; Prebble & Wilmshurst, 2009). This footprint of island colonization is vividly  
524 expressed in the vegetation history of the Azores, providing further indication that it  
525 may act as a template for human impacts on terrestrial ecosystems in general.

526           Island vegetation in equatorial regions appears to be more susceptible to plant  
527 extinctions and invasions than in higher latitudes, a pattern first alluded to by Hooker  
528 (1867; see also Sadler, 1999). Our palaeoecological data from the Azores show that the  
529 level of human impact on the vegetation, at least in the highlands, falls somewhere  
530 between the drastic modifications evidenced on Tenerife, for example, and the subtle  
531 changes recorded on the Faroe Islands (Lawson *et al.*, 2008; de Nascimento *et al.*,  
532 2010). More palaeoecological data from different elevations, islands and latitudes are  
533 required to better understand this pattern of susceptibility to human impact, which is of

534 obvious value in developing ecological theory and identifying species most at risk of  
535 extinction.

536

## 537 **CONCLUSIONS**

538 On the Azores, the local impact of major (or localized) volcanic eruptions is detectable  
539 palaeoecologically as a 500- to 1000-year succession from open pioneer communities to  
540 greater forest cover. Human impact, on the other hand, took the form of a sudden shift  
541 (often over < 100 years) to open vegetation, which was then maintained over centuries  
542 through burning, grazing and edaphic changes. Even so, some differences in the  
543 composition of highland vegetation on Flores and Pico persisted after colonization.

544 Human impact on endemic species was generally negative and, in some cases,  
545 catastrophic. Some taxa, such as *Morella faya*, appear to have increased following  
546 colonization, while *Juniperus brevifolia* communities apparently collapsed and at least  
547 two species went extinct on Pico. Over the longer term, pollen of Azorean endemic  
548 plants were more prevalent immediately following volcanic eruptions, hinting at a  
549 prominent role of certain endemic species within primary succession on skeletal soils.

550 The scale of human impact, at least in terms of its palaeoecological effects, was  
551 greater than ‘natural’ impacts such as volcanic eruptions, climatic changes and  
552 landslides during recent millennia. Pre-impact palaeoclimatic variations detected using  
553 geochemical proxies (Björck *et al.*, 2006) were not clearly reflected as changes in past  
554 forest composition or structure, perhaps because of the intensely maritime climate of the  
555 archipelago. This observation supports the conclusion that the late Quaternary climate  
556 of the Azores was relatively stable in comparison to archipelagos such as the Canary  
557 Islands (Ávila *et al.*, 2008; Carine & Schaefer, 2010).

558 Our demonstration that several ‘introduced’ plants are in fact native to the  
559 Azores shows the extent to which our picture of the pristine, pre-colonization  
560 ecosystems of oceanic islands like the Azores is incomplete. While palaeoecology  
561 cannot provide all the missing pieces, it can broaden understanding of the island  
562 ecosystems that preceded major human interventions, helping to elaborate  
563 biogeographical theory and inform conservation efforts.

564

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575

## 576 **REFERENCES**

577 Ávila, S.P.A., Madeira, P., Mendes, N., Rebelo, A., Medeiros, A., Gomes, C., García-  
578 Talavera, F., Silva, C.M., Cachão, M., Hilaire-Marcel, C., Martins, A.M.F.  
579 (2008) Mass extinctions in the Azores during the last glaciation: fact or myth?  
580 *Journal of Biogeography*, **35**, 1123–1129.



- 581 Azevedo, J.M.M. & Ferreira, M.R.P. (1998) Condições da ocorrência e funções  
582 hidrogeológicas das lagoas em pequenas ilhas vulcânicas: o exemplo da ilha das  
583 Flores – Açores. *4º Congresso da Água*, Lisbon, 23–27 March 1998.
- 584 Azevedo, J.M.M. & Ferreira, M.R.P. (2006) The volcanotectonic evolution of Flores  
585 Island, Azores (Portugal). *Journal of Volcanology and Geothermal Research*,  
586 **156**, 90–102.
- 587 Bennett, K.D. (2008) *Psimpoll 4.26*. Department of Earth Sciences, Uppsala University,  
588 Uppsala.
- 589 Berry, R.J. (1992) The significance of island biotas. *Biological Journal of the Linnean*  
590 *Society*, **46**, 3–12.
- 591 Björck, S., Rittenour, T., Rosén, P., França, Z., Möller, P., Snowball, I., Wastegård, S.,  
592 Bennike, O. & Kromer, B. (2006) A Holocene lacustrine record in the central  
593 North Atlantic: proxies for volcanic activity, short-term NAO mode variability,  
594 and long-term precipitation changes. *Quaternary Science Reviews*, **25**, 9–32.
- 595 Carine, M.A. & Schaefer, H. (2010) The Azores diversity enigma: why are there so few  
596 Azorean endemic flowering plants and why are they so widespread? *Journal of*  
597 *Biogeography*, **37**, 77–89.
- 598 CLIMAAT Project (2007) *Clima e meteorología dos arquipélagos atlânticos (Climate*  
599 *and meteorology of the Atlantic archipelagos)*. Universidade dos Açores, Angra  
600 de Heroísmo. URL: <http://www.climaat.angra.uac.pt/>.
- 601 Collins, A. & Bush, M.B. (2011) An analysis of modern pollen representation and  
602 climatic conditions on the Galápagos Islands. *The Holocene*, **21**, 237–250.
- 603 Connor, S.E. (2009) Human impact – the last nail in the coffin for ancient plants?  
604 *Journal of Biogeography*, **36**, 485–486.

- 605 Costa, C. (1950) Arvoredos dos Açores: algumas achegas para a sua história. *Comissão*  
606 *Reguladora dos Cereais do Arquipélago dos Açores*, **11**, 45–60.
- 607 Dias, E. (1996) *Vegetação natural dos Açores: ecologia e sintaxonomia das florestas*  
608 *naturais*. Unpublished PhD Thesis, Universidade dos Açores, Angra de  
609 Heroísmo.
- 610 Elias R. B. & Dias E. (2004) Primary succession on lava domes on Terceira (Azores).  
611 *Journal of Vegetation Science*, **15**, 331–338.
- 612 Fernández-Palacios, J.M., de Nascimento, L., Otto, R., Delgado, J.D., García-del-Rey,  
613 E., Arévalo, J.R. & Whittaker, R.J. (2011) A reconstruction of Palaeo-  
614 Macaronesia, with particular reference to the long-term biogeography of the  
615 Atlantic island laurel forests. *Journal of Biogeography*, **38**, 226–246.
- 616 Ferreira, A.B. (2005) Geodinâmica e perigosidade natural nas ilhas dos Açores.  
617 *Finisterra*, **40**, 103–120.
- 618 Flenley, J.R., King, A.S.M., Jackson, J., Chew, C., Teller, J.T. & Prentice, M.E. (1991)  
619 The Late Quaternary vegetational and climatic history of Easter Island. *Journal*  
620 *of Quaternary Science*, **6**, 85–115.
- 621 Forjaz, V.H, Monjardino, J.L. & Fernandes, N. (1970) Contribuição para o estudo das  
622 jazidas fossilíferas das ilhas do Faial, Pico, S. Jorge e Terceira (Açores).  
623 *Comunicações dos Serviços Geológicos de Portugal*, **54**, 27–37.
- 624 Fries, M. (1968) Organic sediment and radiocarbon dates from crater lakes on the  
625 Azores. *Geologiska Föreningens i Stockholm Förhandlingar*, **90**, 360–368.
- 626 Gauch, H.G. (1982) *Multivariate analysis in community ecology*. Cambridge University  
627 Press, Cambridge.
- 628 van Geel, B. & Aptroot, A. (2006) Fossil ascomycetes in Quaternary deposits. *Nova*  
629 *Hedwigia*, **82**, 313–329.

- 630 Grimm, E.C. (2004) *TILIA and TGView software, version 2.0.2*. Illinois State Museum,  
631 Research and Collections Center, Springfield, IL.
- 632 Hannon, G.E. & Bradshaw, R.H.W. (2000) Impacts and timing of the first human  
633 settlement on vegetation of the Faroe Islands. *Quaternary Research*, **54**, 404–  
634 413.
- 635 Head, L. (2008) Is the concept of human impacts past its use-by date? *The Holocene*,  
636 **18**, 373–377.
- 637 Hooker, J.D. (1867) Insular floras. *Gardener's Chronicle and Agricultural Gazette*,  
638 **January**, 6–7, 27, 50–51, 75–76.
- 639 Johnson, D.S. (1994) *Phantom islands of the Atlantic: the legends of seven lands that*  
640 *never were*. Souvenir Press, London.
- 641 Kirch, P.V. (1996) Late Holocene human-induced modifications to a central Polynesian  
642 island ecosystem. *Proceedings of the National Academy of Sciences, USA*, **93**,  
643 5296–5300.
- 644 van der Knaap, W.O. (2009) Estimating pollen diversity from pollen accumulation  
645 rates: a method to assess taxonomic richness in the landscape. *The Holocene*, **19**,  
646 159–163.
- 647 Kueffer, C., Daehler, C.C., Torres-Santana, C.W., Lavergne, C., Meyer, J.-Y., Otto, R.  
648 & Silva, L. (2010) A global comparison of plant invasions on oceanic islands.  
649 *Perspectives in Plant Ecology, Evolution & Systematics*, **12**, 145–161.
- 650 Lawson, I.T., Gathorne-Hardy, F.J., Church, M.J., Newton, A.J., Edwards, K.J.,  
651 Dugmore, A.J. & Einarsson, Á. (2007) Environmental impacts of the Norse  
652 settlement: palaeoenvironmental data from Mývatnssveit, northern Iceland.  
653 *Boreas*, **36**, 1–19.

- 654 Lawson, I.T., Edwards, K.J., Church, M.J., Newton, A.J., Cook, G.T., Gathorne-Hardy,  
655 F.J. & Dugmore, A.J. (2008) Human impact on an island ecosystem: pollen data  
656 from Sandoy, Faroe Islands. *Journal of Biogeography*, **35**, 1130–1152.
- 657 van Leeuwen, J.F.N., Schaefer, H., van der Knaap, W.O., Rittenour, T., Björck, S. &  
658 Ammann, B. (2005) Native or introduced? Fossil pollen and spores may say – an  
659 example from the Azores Islands. *Neobiota*, **6**, 27–34.
- 660 van Leeuwen, J.F.N., Froyd, C.A., van der Knaap, W.O., Coffey, E.E., Tye, A. &  
661 Willis, K.J. (2008) Fossil pollen as a guide to conservation in the Galápagos.  
662 *Science*, **322**, 1206.
- 663 Ljung, K. & Björck, S. (2011) A pollen record of the last 450 years from a lowland peat  
664 bog on Tristan da Cunha, South Atlantic, implying early anthropogenic  
665 influence. *Journal of Quaternary Science*, **26**, 688–693.
- 666 Mann, D., Edwards, J., Chase, J, Beck, W., Reanier, R., Mass, M., Finney, B. & Loret,  
667 J. (2008) Drought, vegetation change, and human history on Rapa Nui (Isla de  
668 Pascua, Easter Island). *Quaternary Research*, **69**, 16–28.
- 669 McCune, B. & Mefford, M. J. (1999) *PC-ORD: multivariate analysis of ecological*  
670 *data*. MjM Software Design, Gleneden Beach, OR.
- 671 McGlone, M.S. & Wilmshurst, J.M. (1999) Dating initial Maori environmental impact  
672 in New Zealand. *Quaternary International*, **59**, 5–16.
- 673 McWethy, D.B., Whitlock, C., Wilmshurst, J.M., McGlone, M.S. & Li, X. (2009) Rapid  
674 deforestation of South Island, New Zealand, by early Polynesian fires. *The*  
675 *Holocene*, **19**, 883–897.
- 676 Moore, P.D. (1975) Origin of blanket mires. *Nature*, **256**, 267–269.
- 677 Moore, P.D., Webb, J.A. & Collinson, M.E. (1991) *Pollen analysis*. Blackwell Science  
678 Publishers, Oxford.

- 679 Morriseau, M. & Traineau, H. (1985) Mise en évidence d'une activité hydromagmatique  
680 Holocène sur l'Île de Flores (Açores). *Comptes Rendus de l'Académie des*  
681 *Sciences Paris*, **301**, 1309–1314.
- 682 Mueller-Dombois, D. (1975) Some aspects of island ecosystem analysis. *Tropical*  
683 *ecological systems: trends in aquatic and terrestrial research* (ed. by F.B.  
684 Golley and E. Medina), pp. 353–366. Springer-Verlag, New York.
- 685 de Nascimento, L., Willis, K.J., Fernández-Palacios, J.M., Criado, C. & Whittaker, R.J.  
686 (2009) The long-term ecology of the lost forests of La Laguna, Tenerife (Canary  
687 Islands). *Journal of Biogeography*, **36**, 499–514.
- 688 Odgaard, B.V. (1999) Fossil pollen as a record of past biodiversity. *Journal of*  
689 *Biogeography*, **26**, 7–17.
- 690 Prebble, M. & Wilmshurst, J.M. (2009) Detecting the initial impact of humans and  
691 introduced species on island environments in Remote Oceania using  
692 palaeoecology. *Biological Invasions*, **11**, 1529–1556.
- 693 Pugin, A. & Girardclos, S. (1998) *Shallow seismic reflection on two Azores volcanic*  
694 *lakes*. Unpublished report, University of Geneva, Department of Geology and  
695 Paleontology, Geneva.
- 696 Reille, M. (1992, 1995 & 1998) *Pollen et spores d'Europe et d'Afrique du Nord* (3  
697 vols). Laboratoire de Botanique historique et Palynologie, Marseille.
- 698 Reimer, P.J. & Reimer, R. (not dated) *CALIBomb radiocarbon calibration*. Queen's  
699 University Belfast, Belfast. URL: <http://calib.qub.ac.uk/CALIBomb/> (accessed  
700 15/8/2011).
- 701 Rueger, B.F. & von Wallmenich, T.N. (1996) Human impact on the forests of Bermuda:  
702 the decline of endemic cedar and palmetto since 1609, recorded in the Holocene  
703 pollen record of Devonshire Marsh. *Journal of Paleolimnology*, **16**, 59–66.

- 704 Sadler, J.P. (1999) Biodiversity on oceanic islands: a palaeoecological assessment.  
705 *Journal of Biogeography*, **26**, 75–87.
- 706 Schaefer, H. (2003) *Chorology and diversity of the Azorean flora*. Dissertationes  
707 Botanicae, Vol. 374. J. Cramer, Stuttgart.
- 708 Schaefer, H. (2005) *Flora of the Azores: a field guide*, 2<sup>nd</sup> edn. Margraf Publishers,  
709 Weikersheim.
- 710 Schaefer, H., Moura, M., Belo Maciel, M.G., Silva, L., Rumsey, F.J. & Carine, M.A.  
711 (2011) The Linnean shortfall in oceanic island biogeography: a case study in the  
712 Azores. *Journal of Biogeography*, **38**, 1345–1355.
- 713 Schirone, B., Ferreira, R.C., Vessela, F., Schirone, A., Piredda, R. & Simeone, M.C.  
714 (2010) *Taxus baccata* in the Azores: a relict form at risk of imminent extinction.  
715 *Biodiversity and Conservation*, **19**, 1547–1565.
- 716 Silva, L., Moura, M., Schaefer, H., Rumsey, F. & Dias, E.F. (2010) Vascular plants  
717 (Tracheobionta). *A list of the terrestrial and marine biota from the Azores* (ed.  
718 by P.A.V. Borges, A. Costa, R. Cunha, R. Gabriel, V. Gonçalves, A.F. Martins,  
719 I. Melo, M. Parente, P. Raposeiro, P. Rodrigues, R.S. Santos, L. Silva, P. Vieira  
720 and V. Vieira), pp. 117–146. Princípia, Cascais.
- 721 Sjögren, E. (1973) Conservation of natural plant communities on Madeira and in the  
722 Azores. *Monographiae Biologicae Canarienses*, **4**, 148–153.
- 723 Stuiver, M. & Reimer, P.J. (1993) Extended <sup>14</sup>C database and revised CALIB  
724 radiocarbon calibration program. *Radiocarbon*, **35**, 215–230.
- 725 Tutin, T.G. (1953) Vegetation of the Azores. *Journal of Ecology*, **41**, 53–61.
- 726 Webb, D.A. (1985) What are the criteria for presuming native status? *Watsonia*, **15**,  
727 231–236.

- 728 Whittaker, R.J., Triantis, K.A. & Ladle, R.J. (2008) A general dynamic theory of  
729 oceanic island biogeography. *Journal of Biogeography*, **35**, 977–994.
- 730 Williamson, M. (1984) Sir Joseph Hooker’s lecture on insular floras. *Biological Journal*  
731 *of the Linnean Society*, **22**, 55–77.
- 732 Wright, H.E. (1967) A square-rod piston sampler for lake sediments. *Journal of*  
733 *Sedimentary Petrology*, **37**, 975–976.
- 734 Zbyszewski, G., Ferreira, C.R., Ferreira, O.V. & Assunção, C.T. (1963) *Carta*  
735 *Geológica de Portugal 1/50000: notícia explicativa da folha ‘B’ da Ilha do Pico*  
736 *(Açores)*. Serviços Geológicos de Portugal, Lisbon.
- 737 Zbyszewski, G., Medeiros, A.C., Ferreira, O.V. & Assunção, C.T. (1968) *Carta*  
738 *Geológica de Portugal 1/25000: notícia explicativa da folha da Ilha das Flores*  
739 *(Açores)*. Serviços Geológicos de Portugal, Lisbon.
- 740
- 741

742 **SUPPORTING INFORMATION**

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

744

745 **Appendix S1** Complete pollen diagrams from Lagoa Rasa, Lagoa do Caveiro and Pico  
746 Bog.

747

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755 **BIOSKETCH**

756 **Simon Connor** is a researcher in environmental dynamics at the University of the  
757 Algarve. His research interests include human–environment interactions and the  
758 biogeography of Tertiary relict species.

759

760 Author contributions: S.E.C., J.F.N.L., W.O.K. and B.A. developed the ideas; J.F.N.L.  
761 and T.M.R. analysed the pollen data; B.A. and S.B. initiated the project; S.E.C. and  
762 W.O.K. made the numerical analyses; and S.E.C. wrote the paper with the help of all  
763 co-authors.

764

765 Editor: José María Fernández-Palacios

766

767 **TABLES**

768

769 **Table 1** Site details for the three coring locations on the Azores.

Site name, island	Elevation a.s.l.	Coordinates	Dimensions (max. water depth)	Site description	Surrounding vegetation
Lagoa Rasa, Flores	530 m	39° 24.50' N, 31° 13.50' W	325 × 425 m (16 m)	Crater lake formed by Strombolian eruption	Moorland with scattered <i>Juniperus brevifolia</i> , <i>Erica azorica</i> and <i>Calluna vulgaris</i> ; <i>Sphagnum</i> around lake shores
Lagoa do Caveiro, Pico	903 m	38° 26.10' N, 28° 11.79' W	30 × 40 m (3.5 m)	Crater lake with <i>Potamogeton polygonifolius</i>	Grassland of <i>Festuca francoi</i> ; scattered remnants of <i>Juniperus</i> forest and laurisilva
Pico Bog, Pico	873 m	38° 26.16' N, 28° 10.30' W	20 × 25 m (1.5 m)	<i>Sphagnum</i> bog	Grassland of <i>Festuca francoi</i> ; scattered remnants of <i>Juniperus</i> forest and laurisilva

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771

772 **Table 2** Azorean pollen taxa that could be confidently classified as having endemic, native or introduced status and their occurrence (x) in the  
 773 three records, both before (B) and after (A) significant human impact. Status based on Silva *et al.* (2010), except where the pollen evidence  
 774 demonstrates native status (taxa in boldface). The † symbol denotes taxa now extinct on Pico. The endemic category also includes  
 775 Macaronesian endemics. Single pollen-grain occurrences are indicated by a dot (•) and 49 taxa that could not be categorized for pollen-  
 776 taxonomic reasons are omitted (see Appendix S1).

Status	Taxon	Rasa		Caveiro		Pico	
		A	B	A	B	A	B
Endemic	<i>Angelica lignescens</i>	x	x	x	x	x	x
	<i>Arceuthobium azoricum</i>			x	x	x	x
	<i>Bellis</i> -type	x	x	x	x	x	x
	<i>Chaerophyllum azoricum</i>	x		x	x	•	x
	<i>Daucus carota</i> ssp. <i>azorica</i>	•		x	x		•
	<i>Diphasiastrum madeirense</i>	x	x	x	x	x	x
	<i>Erica azorica</i>	x	x				
	Ericaceae	x	x	x	x	x	x
	<i>Euphrasia</i>	•	x	•	x		
	<i>Frangula azorica</i>	x	x	x	x	•	•
	<i>Hedera azorica</i>	•	x	x	x		x
	<i>Huperzia dentata</i>	x	x	x	x	x	x
	<i>Huperzia suberecta</i>			x	x	•	x
	<i>Ilex perado</i> ssp. <i>azorica</i>	x	x	x	x	x	x
	<i>Juniperus brevifolia</i>	x	x	x	x	x	x
	<i>Lysimachia azorica</i>	x	x	x	x	x	x
	<i>Picconia azorica</i>	x	x	x	x	x	x
	<i>Polypodium azoricum</i>	x	x	x	x	x	x
	<i>Prunus azorica</i>			x	x	x	•

	<i>Vaccinium cylindraceum</i>	x	x	x	x	x	x
	<i>Viburnum treleasei</i>	x	x				
Native	<i>Apium</i>			•	x		x
	<i>Athyrium filix-femina</i>	•					
	<i>Blechnum</i>	x					
	<i>Botrychium lunaria</i>			x	x		
	<i>Calluna vulgaris</i>	x	x	x	x	x	x
	cf. <i>Umbilicus</i>	x	x				
	<i>Cheilanthes</i> -type	x	x	x	x	•	x
	<i>Culcita macrocarpa</i>	x	x	x	x	x	x
	<i>Daphne laureola</i>			x	x		x
	<i>Hydrocotyle vulgaris</i>			x		x	x
	<i>Hymenophyllum tunbrigense</i> -type	x	x	x	x		x
	<b><i>Illecebrum verticillatum</i></b>		x	x	x	x	•
	<i>Lycopodiella inundata</i>		x		x		
	<i>Lythrum portula</i>			x	x		x
	<i>Morella faya</i>	x	x	x	x	x	x
	<i>Myrsine africana</i>	x	x	x	x	x	x
	<i>Ophioglossum azoricum</i> †	x	x	x	x		
	<i>Ophioglossum lusitanicum</i> †	x	x	x	x		•
	<i>Osmunda regalis</i>	x	x	x	x	x	x
	<b><i>Persicaria</i></b>		x		x		x
	<i>Plantago coronopus</i>			x		•	
	<i>Potentilla</i> -type	x	x	x	x	x	x
	<i>Pteridium aquilinum</i>	x	x	x	x	x	x
	<i>Pteris incompleta</i>	x	x	x	x	x	x
	<i>Selaginella kraussiana</i>	x	x	x	x	x	x
	<i>Trichomanes speciosum</i>	x	x	x	x	x	x
Introduced	<i>Castanea sativa</i>		•	x			•
	Cerealia	x					
	<i>Cryptomeria japonica</i>	x		x		•	
	<i>Hydrangea macrophylla</i>	x		x			

<i>Ligustrum</i>	x		x		
<i>Pinus</i>	x	•	x	•	
<i>Plantago lanceolata</i>	x	•	x	•	x
<i>Plantago major</i>			x		
<i>Prunella vulgaris</i>					x
<i>Secale</i>	x				
<i>Ulex-type</i>	•				
<i>Verbena officinalis</i>	•				
<i>Vitis</i>			x		•
<i>Zea mays</i>	•				

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779 **Table 3** Radiocarbon ages from dated gyttja (Lagoa Rasa) and peat (Pico Bog) sediments, with calendar ages (calibrated with 2-sigma  
 780 probability). The first age post-dates AD 1950 and is therefore expressed as percentage modern carbon (pMC).

Site and depth	<sup>14</sup> C age (yr BP) and error	Calendar age (cal. yr BP)	Lab code
Rasa 124 cm	109.8 ± 0.3 pMC	-5 or -45--50	Poz-2095
Rasa 168 cm	220 ± 30	-1–308	Poz-2210
Rasa 176 cm	335 ± 30	309–477	Poz-9890
Rasa 188 cm	505 ± 35	501–625	Poz-2098
Rasa 200 cm	580 ± 30	553–649	Poz-11260
Rasa 210 cm	695 ± 30	563–686	Poz-11261
Rasa 226 cm	705 ± 35	561–699	Poz-2099
Rasa 245 cm	895 ± 35	735–911	Poz-2100
Rasa 280 cm	1290 ± 30	1175–1287	Poz-9926
Rasa 290 cm	1345 ± 30	1182–1309	Poz-11263
Rasa 305 cm	1565 ± 30	1390–1527	Poz-11264
Rasa 315 cm	1710 ± 35	1541–1702	Poz-11467
Rasa 321 cm	2105 ± 30	1996–2149	Poz-9927
Rasa 324 cm	2450 ± 35	2358–2703	Poz-11221
Rasa 328 cm	2370 ± 35	2335–2672	Poz-1222
Rasa 330 cm	2435 ± 41	2353–2702	UtC-8340
Pico 152–153 cm	240 ± 50	-11–470	LuS-5872
Pico 232–233 cm	410 ± 50	310–530	LuS-5870
Pico 262 cm	570 ± 50	510–660	LuS-6103
Pico 292–293 cm	750 ± 50	560–780	LuS-5869
Pico 346–347 cm	860 ± 100	650–970	LuS-5868
Pico 417–418 cm	1140 ± 50	930–1180	LuS-5867
Pico 465–466 cm	1460 ± 50	1280–1520	LuS-5866
Pico 498 cm	1645 ± 50	1410–1700	LuS-6104

Pico 546–548 cm	$1892 \pm 133$	1500–2200	Hd-21645
Pico 559 cm	$2405 \pm 50$	2340–2710	LuS-6105
Pico 571–572 cm	$2550 \pm 50$	2460–2770	LuS-5871

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784 **Table 4** Comparison of some palynological studies that record the impact of human colonization of oceanic islands of the Atlantic. Sites are  
 785 listed in north–south order. † = extinction. Further details can be found in the studies themselves.

Site and reference	Timing (cal. BP)	Major pollen declines	Major pollen increases	Introduced pollen taxa	Fire and grazing	Soils and moisture
Iceland (Lawson <i>et al.</i> , 2007)	c. 1080	<i>Betula</i> <i>Juniperus</i>	Poaceae Cyperaceae	<i>Hordeum</i>	Increased charcoal; grazing inferred	Soil acidification; expansion of <i>Sphagnum</i>
Faroe Islands (Hannon & Bradshaw, 2000)	c. 1400	<i>Juniperus</i> Cyperaceae	Poaceae <i>Cerealia</i>	Recorded in macrofossils	Charcoal peak; grazing inferred	Change in wetland taxa
Flores & Pico, Azores (this paper)	c. 400	<i>Juniperus</i>	Poaceae <i>Pteridium</i>	<i>Hydrangea</i> <i>Cryptomeria</i> <i>Cerealia</i> etc.	Charcoal and <i>Sporormiella</i> increase	Expansion of <i>Sphagnum</i>
Bermuda (Rueger & von Wallmenich, 1996)	c. 350	<i>Juniperus</i> <i>Sabal</i>	<i>Morella</i> Poaceae Cyperaceae	Not shown on pollen diagram	Historical records cited	Transition from swamp forest to marsh
Tenerife (de Nascimento <i>et al.</i> , 2010)	c. 2000	<i>Quercus</i> † <i>Carpinus</i> †	<i>Morella</i> Poaceae Asteraceae	No mention	Charcoal increase	Lowered lake level
Tristan da Cunha (Ljung & Bjorck, 2011)	c. 300	<i>Phyllica arborea</i>	<i>Plantago</i> <i>Rumex</i> Cyperaceae	<i>Plantago lanceolata</i> <i>Rumex acetosa</i>	Increased charcoal; grazing inferred	Erosion; change to Cyperaceae dominance

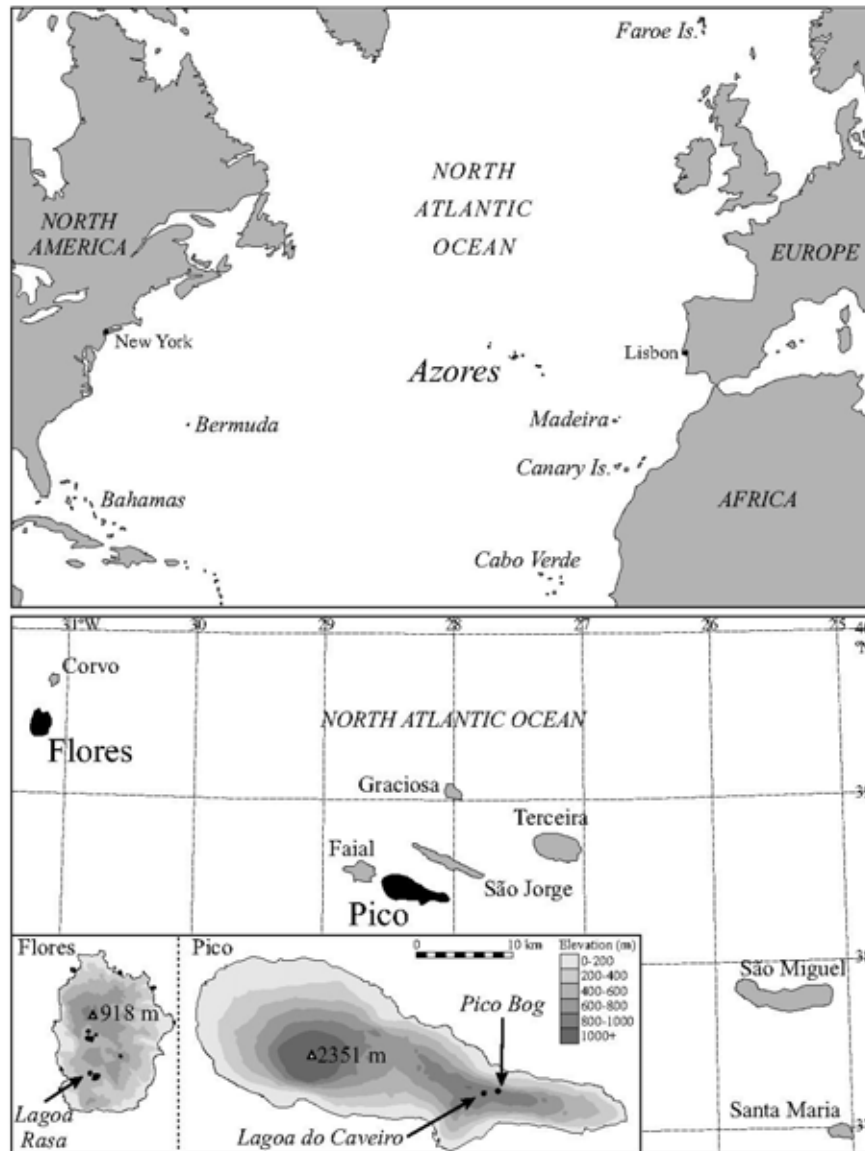
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788 **FIGURE CAPTIONS**

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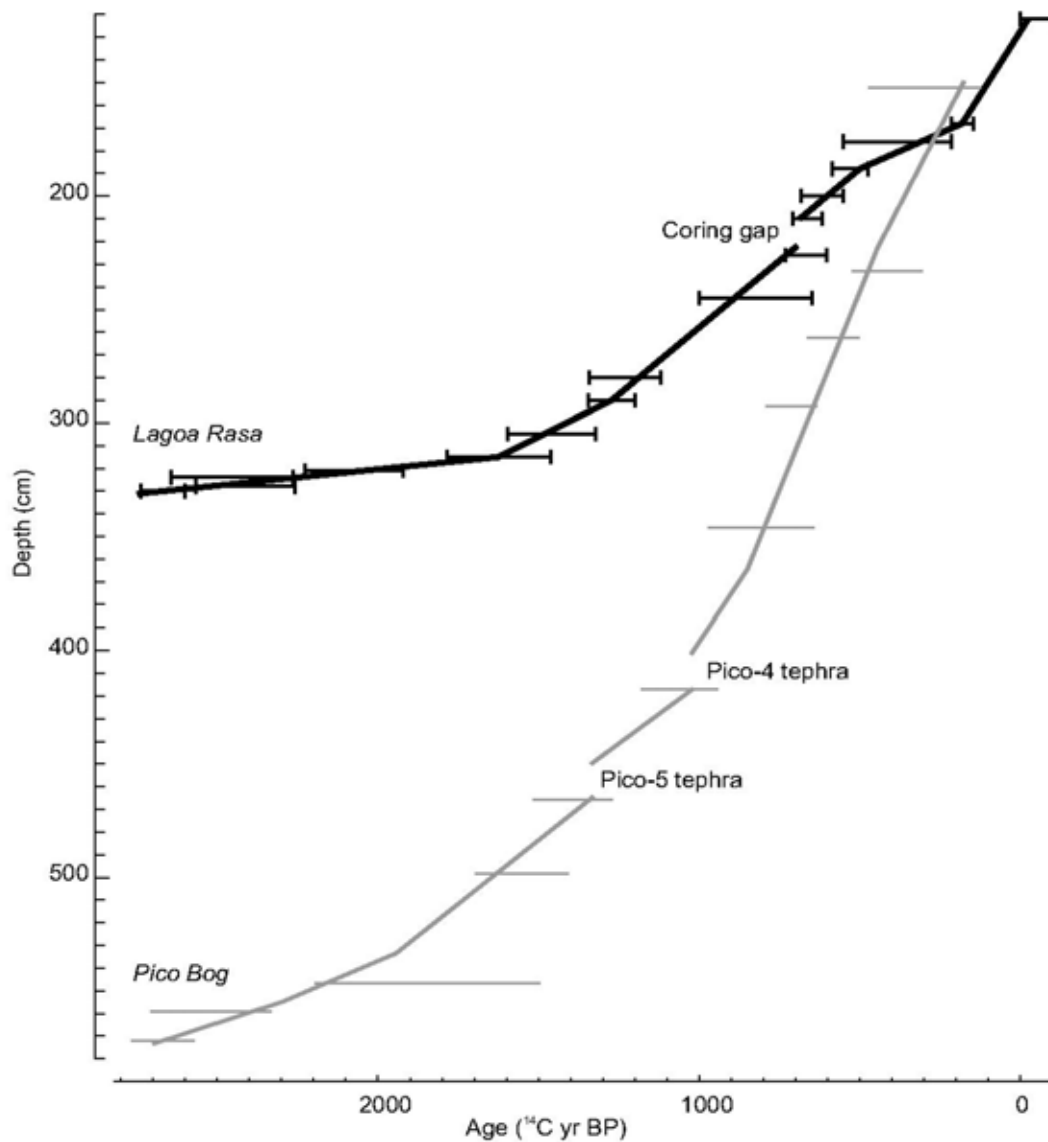
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791 **Figure 1** Map of the North Atlantic region, showing the location of the Azores

792 archipelago and other islands (above). Map of the Azores (below) and the study sites

793 (inset).

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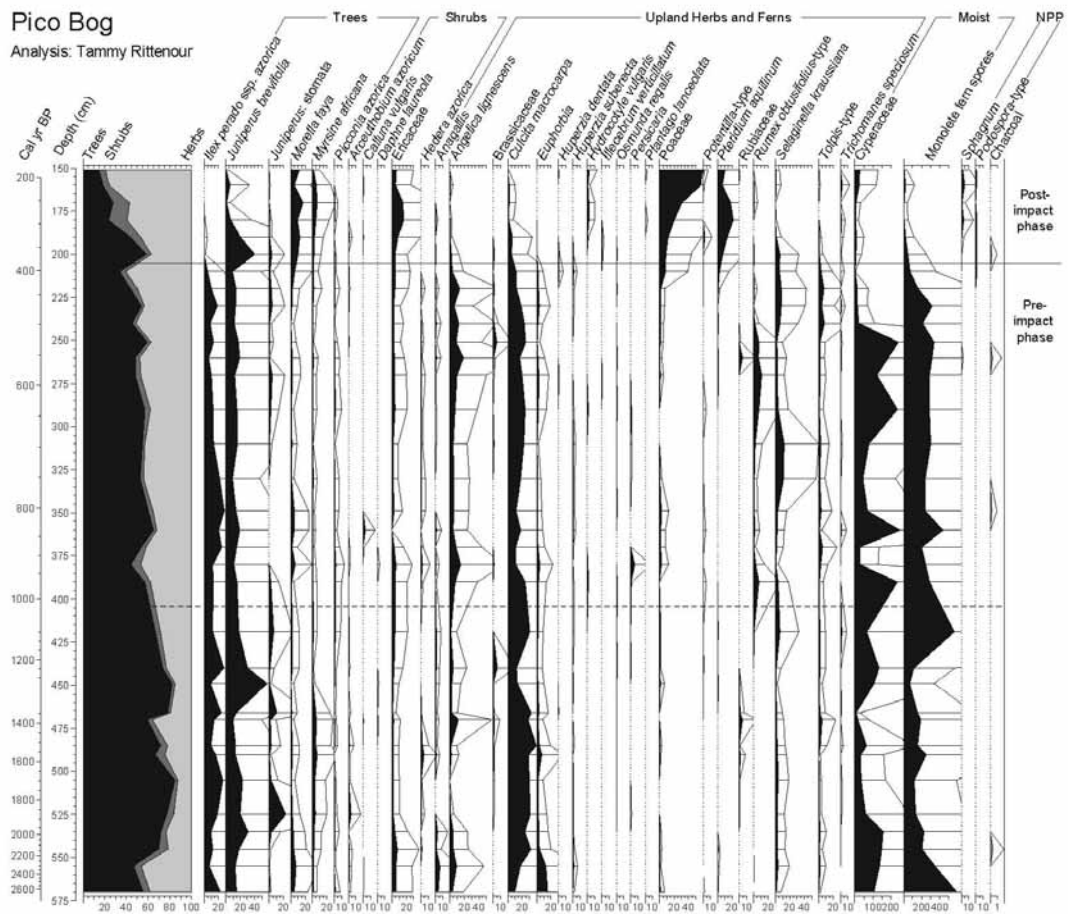
796 **Figure 2** Age–depth profiles, for sediment records from Lagoa Rasa on the island of  
 797 Flores (black line) and Pico Bog on the island of Pico (grey line), based on the  
 798 radiocarbon ages in Table 3. An age–depth curve for the Lagoa do Caveiro record (Pico  
 799 Island) appears in Björck *et al.* (2006).

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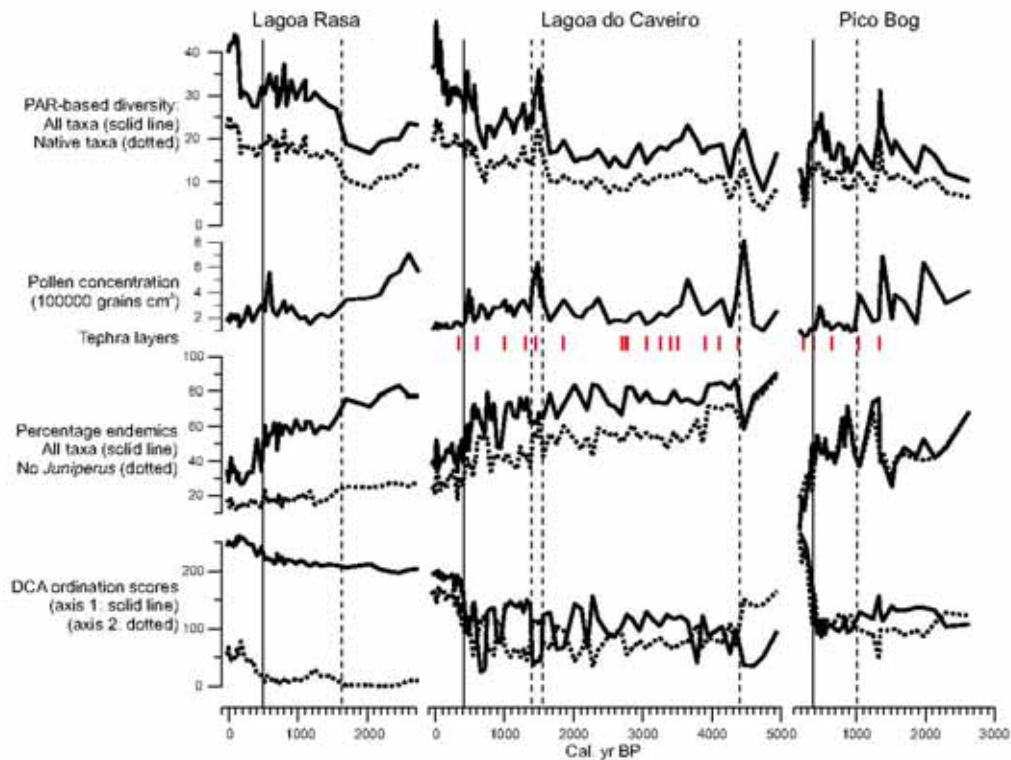




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818 **Figure 5** Pollen diagram from Pico Bog on the island of Pico. See caption of Fig. 3 for  
 819 explanation and Appendix S1 for the complete pollen diagram.

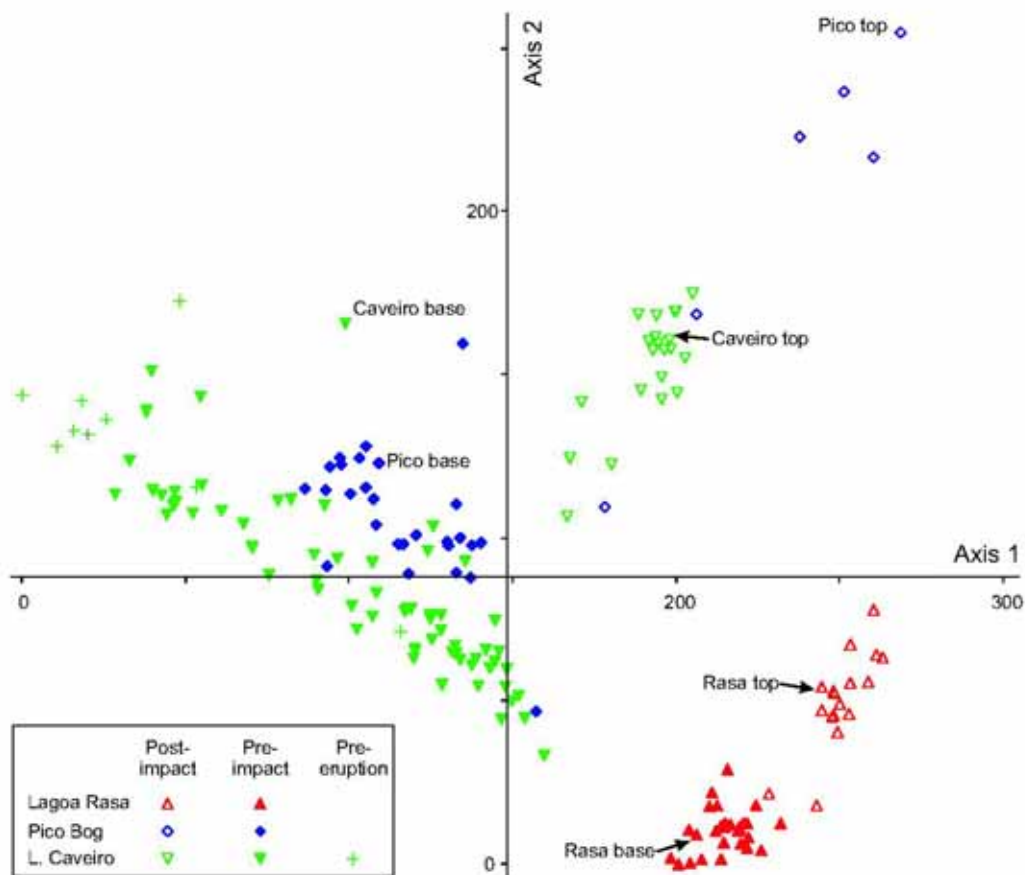
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822 **Figure 6** Temporal changes in palynological diversity and endemic species  
 823 representation in the Lagoa Rasa, Lagoa do Caveiro and Pico Bog records from the  
 824 Azores. Trends are shown in relation to changes in pollen concentrations, tephra layers  
 825 and ordination scores (detrended correspondence analysis, DCA; Fig. 7). The solid  
 826 vertical line represents the transition from pre-impact to post-impact (pollen zone  
 827 boundary) in each record; the dashed vertical lines are other significant zone  
 828 boundaries. Samples from the marginal core from Lagoa do Caveiro were not graphed  
 829 due to dating uncertainties in the earliest part of the record (Björck *et al.*, 2006). PAR,  
 830 pollen accumulation rates.

831



832

833 **Figure 7** Detrended correspondence analysis (DCA) result for the Lagoa Rasa, Lagoa  
 834 do Caveiro and Pico Bog pollen records (Figs 3–5), showing the transition from pre-  
 835 impact (filled shapes) to post-colonization impacted palaeovegetation (open shapes).  
 836 The lowermost and topmost samples from each record are indicated and samples from  
 837 Lagoa do Caveiro prior to a major series of eruptions are also shown. Total inertia  
 838 value 1.52; axis 1 eigenvalue = 0.36 (gradient length 2.69); axis 2 eigenvalue = 0.20  
 839 (gradient length 2.55).