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

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ABSTRACT

Aim

In many cases, human colonization drastically modified the ecosystems of remote oceanic islands before scientists arrived to document the changes. Palaeoecological records before and after human colonization provide insights into the original ecosystems and an assessment of subsequent human impact. We used pollen analysis to compare the impact of 15th century colonization of the Azores to that of natural disturbances such as volcanic eruptions and climate changes.

Location

Azores archipelago, Atlantic Ocean.

Methods

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

Results

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

Main conclusions

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

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

Keywords

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

INTRODUCTION

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

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

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

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

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

MATERIALS AND METHODS

Geographical setting

The Azores are a group of oceanic islands that straddle the Mid-Atlantic Ridge, roughly 1600 km from Portugal and 1900 km from Newfoundland (Fig. 1). The nine islands are of volcanic origin, having arisen along sea-floor fracture zones as the Eurasian, African and North American tectonic plates rifted apart (Ferreira, 2005; Azevedo & Ferreira, 2006). The oldest rocks in the archipelago are found on the easternmost island, Santa Maria, and date to 8.12 million years ago (Azevedo & Ferreira, 2006). The Azores are thus the youngest archipelago in the Macaronesian region, to which the archipelagos of Madeira, Canary Islands and Cabo Verde also belong (Fernández-Palacios *et al*., 2011).

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

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

Flora and vegetation

Perhaps because of their isolation, modest age and oceanic climate, the Azores have a relatively small number of native plant species (197), of which about a third (70) are regarded as endemics (Schaefer, 2003). The majority of Azorean plants classified as endemic occur on all the islands, whereas the other archipelagos of Macaronesia are characterized by a large number of single-island endemics (Carine & Schaefer, 2010). Recent genetic studies suggest that the Azores may harbour a considerable number of cryptic endemics, and therefore have rates of endemism similar to those of other Atlantic archipelagos (Schaefer *et al*., 2011). The Azorean flora comprises species from three main biogeographical lineages (Dias, 1996): a Tertiary Mediterranean element, a Plio-Pleistocene African element, and a Quaternary Euro-Siberian or Atlantic element. Despite the possibility of seed dispersal from the Americas, the Azores flora seems to have arrived primarily from the European and African continents via wind (potentially 40% of species) or migrating birds (58%) (Schaefer, 2003).

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

Human colonization

It is likely that the Azores were already known to mariners at least 100 years before their official discovery by the Portuguese in the 15th century (Johnson, 1994), but there is no evidence for earlier colonization. The first Portuguese colony appeared on Santa Maria in 1439 and was followed by Flemish colonies on Faial in 1466 and Flores in 1472. Portugal later assumed control of the entire archipelago. According to Dias (1996), human impact on the vegetation occurred in three phases: (1) a pre-colonization phase in which a wide variety of domestic animals was released on the islands to sustain the anticipated human population; (2) an early, extractive phase in which forests were felled for construction, ship-building and charcoal production; and (3) a later, transformative phase in which the Azorean landscape was deforested and turned over to the production of exotic monocultures. As a consequence of these drastic human interventions, little native vegetation survives on the islands today and introduced plant species outnumber native species by a factor of three to one (Schaefer, 2003, 2005).

Study sites

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

Although all the Azores islands share many geographical features, the islands of Flores and Pico differ in key aspects: Flores reaches a maximum elevation of 915 m, while Pico is the highest mountain on Portuguese territory (2351 m); Flores receives more precipitation than Pico, hence most of Flores' streams are perennial, while Pico's streams tend to be intermittent; Flores' last volcanic eruption occurred some 3000 years ago, while the last on Pico was in AD 1718–1720; and, in geological terms, Flores is around 2.15 million years old and situated entirely on the North American Plate, while Pico is the youngest member of the archipelago (0.27 million years) and rises from the Azorean microplate between the African and Eurasian Plates (Zbyszewski *et al*., 1963, 1968; Morrisseau & Traineau, 1985; Dias, 1996; Azevedo & Ferreira, 2006).

Sampling and analysis

Sediment cores were obtained from the centre of Lagoa Rasa in 1998 using a square-rod piston corer (Wright, 1967) and from the centre of Lagoa do Caveiro and Pico Bog in 2001 using a Russian corer (Björck *et al*., 2006). Coring continued until an impenetrable layer (presumably bedrock or thick tephra) was reached; each core therefore represents the sediment accumulated since a major eruption. Pre-eruption sediments were also cored from the margin of Lagoa do Caveiro. Samples of 1 cm^3 were extracted from the cores and pretreated according to standard palynological methods, including the addition of *Lycopodium* spore tablets to determine pollen concentrations (Moore *et al*., 1991). Pollen was identified at 400× magnification with reference to Reille (1992, 1995 & 1998) and reference material held at the Portuguese Institute of Archaeology (IPA). Percentage pollen diagrams were created from a sum of all terrestrial pollen taxa, including identifiable fern spores. Monolete fern spores (i.e. Polypodiales spores lacking the perine required for precise identification), Cyperaceae and aquatic taxa are excluded from the pollen sum, as are fungal spores indicative of grazing (van Geel & Aptroot, 2006). Data were plotted using Tilia programmes (Grimm, 2004).

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

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

We adopted the existing age–depth model for the Lagoa do Caveiro record (Björck *et al*., 2006) and formulated age–depth models (Fig. 2) for the other sites based on the accelerator mass spectrometry (AMS) radiocarbon dates listed in Table 3 and calibrated using CALIB 6.0.2 (Stuiver & Reimer, 1993) and CALIBOMB (Reimer & Reimer, not dated). Pre-impact and post-impact phases were identified independently through pollen zonation (binary splitting by information content), with statistical significance of the zones assessed using the 'broken stick' model (Bennett, 2008). We then calculated pollen accumulation rates for pre-impact and post-impact assemblages in order to determine pollen diversity using the method described by van der Knaap (2009). For comparison, percentage-based diversity estimates were produced in PSIMPOLL 4.26 (Bennett, 2008).

RESULTS AND INTERPRETATION

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

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

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

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

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

The pre-impact phase

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

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

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

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

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

The post-impact phase

The next phase in the vegetation history of the Azores begins around 400 cal. yr BP. Even by this time there were signs of early human interventions, probably as a consequence of the deliberate introduction of exotic mammals. Grasses (Poaceae) and bracken (*Pteridium aquilinum*) seem to have increased the earliest, followed by *Erica azorica*, an endemic that appears to have benefited from the decline of *Juniperus brevifolia* communities, and *Morella faya*, a native tree that probably replaced *Laurus azorica* at lower elevations (Figs 3–5). Previously abundant herbs (represented by *Angelica lignescens*, Asteraceae subfamily Cichorioideae, *Euphorbia* and *Ranunculus cortusifolius*-type) diminished and a suite of introduced taxa appeared (e.g. *Castanea sativa, Ligustrum*, *Vitis*, *Plantago lanceolata*, *P. major*-type, *Cerealia*-type and *Zea mays*; *Hydrangea macrophylla* and *Cryptomeria japonica* appeared later). As the replacement of native Azorean vegetation by agriculture and invasive introduced species such as *Pittosporum undulatum* has been less at higher elevations compared to the lowlands, the full extent of post-colonization plant invasion is probably not represented in the pollen diagrams. Pastoralism on the islands is attested by the appearance of spores produced by dung-inhabiting fungi (*Podospora* and *Sporormiella*) and the historically documented conflagrations that were used to open these pastures are recorded clearly in the charcoal record from Lagoa Rasa (Fig. 3). Fire does not seem to have been prevalent at any time around the high-elevation sites on Pico, perhaps because of low plant biomass.

Has human impact homogenized the vegetation across different islands?

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

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

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

Are endemic species more susceptible to human impact?

In theory, human colonization could have a stronger impact on plants endemic to oceanic islands, because in pristine ecosystems the plants have evolved or persisted in the absence of novel or exotic disturbances. Hence the proportion of non-endemic native species may increase relative to endemics in the post-colonization period. Comparison of pollen from exclusively endemic and native taxa (Fig. 6) shows that human impact caused a crash in the ratio of endemics to natives, consistent with this hypothesis. However, our pollen data are clearly dominated by *Juniperus brevifolia*, which is both an abundant pollen producer and one of the species worst affected by colonization. If *Juniperus* is excluded from the calculations, a very different pattern is observed – a slow and gradual decline in the representation of endemic taxa in the pollen records, evident even before human contact. The pattern is less pronounced for the Pico Bog record where responses to local eruptions are also evident, but the rate of decline at all sites is quite similar (Fig. 6).

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

How has biodiversity been affected by human impact?

One way of assessing changes in biodiversity from island colonization is through estimates of palynological diversity. Such estimates are only indirectly related to floristic diversity, being biased by pollen taxonomy, pollen representation and vegetation structure (Odgaard, 1999). Percentage-based diversity estimates are strongly influenced by evenness (Odgaard, 1999) and in our dataset 72% of the variance in such estimates is explained by evenness (measured by the 'probability of interspecific encounter'; see van der Knaap, 2009). We attempted to reduce bias in diversity estimates by ensuring taxonomic consistency between the two analysts and adopting an estimation method based on pollen accumulation rates (PAR) instead of percentages.

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

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

Plant extinctions are a feature common to many oceanic islands following human colonization (Table 4). *Ophioglossum lusitanicum* spores appear in the Lagoa do Caveiro and Pico Bog records, but this species is not to be found in the recent flora of Pico (Silva *et al*., 2010). *Ophioglossum azoricum* is likewise recorded in the Lagoa do Caveiro sediments, but not in the flora. These ferns produce large, morphologically distinct spores, so significant long-distance dispersal is unlikely and identification is assured. Unless these plants have been overlooked by botanists, it is probable that they have become locally extinct on Pico at some time since human colonization. Another species that has become extinct from several Azorean islands is *Taxus baccata* (Schirone *et al*., 2010). We were unable to find any *Taxus* pollen in the three pollen records, so it is unlikely that *T. baccata* trees grew around these study sites during the late Holocene.

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

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

What was the scale of human impact?

Some idea of the scale of human impact, in ecological terms, can be gauged from the ordination results (Fig. 7), as the axes are scaled to represent turnover (Gauch, 1982). Consistent with the islands' colonization histories and distribution of remnant vegetation, human impact on the westernmost island of Flores seems to have been somewhat less than on Pico, which is part of the more populous central group of the archipelago. The two Pico sites record human impact somewhat differently as one would expect of sites with different pollen source-areas (Lawson *et al*., 2008). Pre-impact variability also seems to have been higher at the high-elevation sites on Pico, which therefore may also have been more vulnerable to anthropogenic disturbances than middle-elevation vegetation on Flores, remnants of which grow around Lagoa Rasa.

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

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

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

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

CONCLUSIONS

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

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

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

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

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SUPPORTING INFORMATION

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

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

BIOSKETCH

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

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TABLES

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	39º 24.50' N, 31º 13.50' W	325 × 425 m (16 m)	Crater lake formed by Strombolian eruption	Moorland with scattered *Juniperus brevifolia*, *Erica azorica* and *Calluna vulgaris*; *Sphagnum* around lake shores
Lagoa do Caveiro, Pico	903 m	38º 26.10' N, 28º 11.79' W	30 × 40 m (3.5 m)	Crater lake with *Potamogeton polygonifolius*	Grassland of *Festuca francoi*; scattered remnants of *Juniperus* forest and laurisilva
Pico Bog, Pico	873 m	38º 26.16' N, 28º 10.30' W	20 × 25 m (1.5 m)	*Sphagnum* bog	Grassland of *Festuca francoi*; scattered remnants of *Juniperus* forest and laurisilva

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

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

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

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

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

Site and depth	^{14}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 ± 133	1500–2200	Hd-21645
Pico 559 cm	2405 ± 50	2340–2710	LuS-6105
Pico 571–572 cm	2550 ± 50	2460–2770	LuS-5871

Table 4 Comparison of some palynological studies that record the impact of human colonization of oceanic islands of the Atlantic. Sites are 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 *et al*., 2007)	*c*. 1080	*Betula* *Juniperus*	Poaceae Cyperaceae	*Hordeum*	Increased charcoal; grazing inferred	Soil acidification; expansion of *Sphagnum*
Faroe Islands (Hannon & Bradshaw, 2000)	*c*. 1400	*Juniperus* Cyperaceae	Poaceae *Cerealia*	Recorded in macrofossils	Charcoal peak; grazing inferred	Change in wetland taxa
Flores & Pico, Azores (this paper)	*c*. 400	*Juniperus*	Poaceae *Pteridium*	*Hydrangea* *Cryptomeria* *Cerealia* etc.	Charcoal and *Sporor-miella* increase	Expansion of *Sphagnum*
Bermuda (Rueger & von Wallmenich, 1996)	*c*. 350	*Juniperus* *Sabal*	*Morella* Poaceae Cyperaceae	Not shown on pollen diagram	Historical records cited	Transition from swamp forest to marsh
Tenerife (de Nascimento *et al*., 2010)	*c*. 2000	*Quercus*† *Carpinus*†	*Morella* Poaceae Asteraceae	No mention	Charcoal increase	Lowered lake level
Tristan da Cunha (Ljung & Bjorck, 2011)	*c*. 300	*Phylica arborea*	*Plantago* *Rumex* Cyperaceae	*Plantago lanceolata* *Rumex acetosa*	Increased charcoal; grazing inferred	Erosion; change to Cyperaceae dominance

FIGURE CAPTIONS

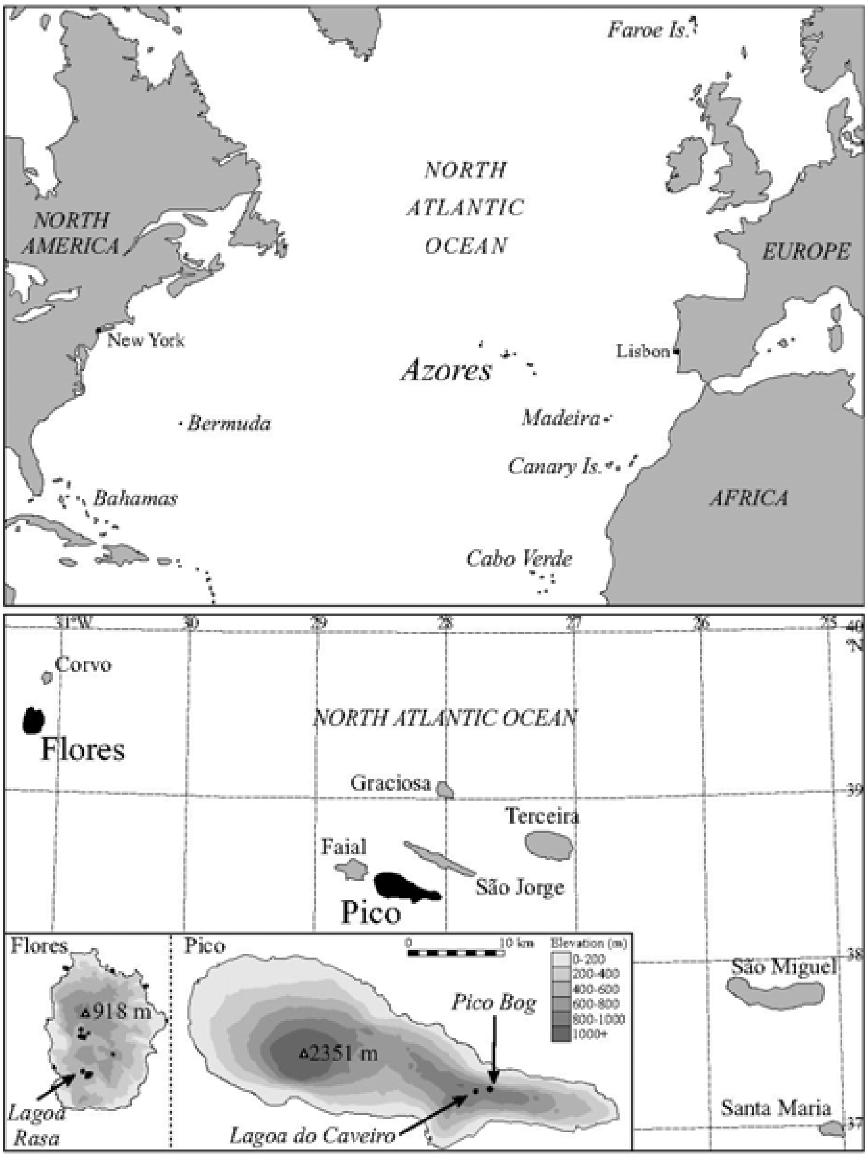

Figure 1 Map of the North Atlantic region, showing the location of the Azores archipelago and other islands (above). Map of the Azores (below) and the study sites (inset).

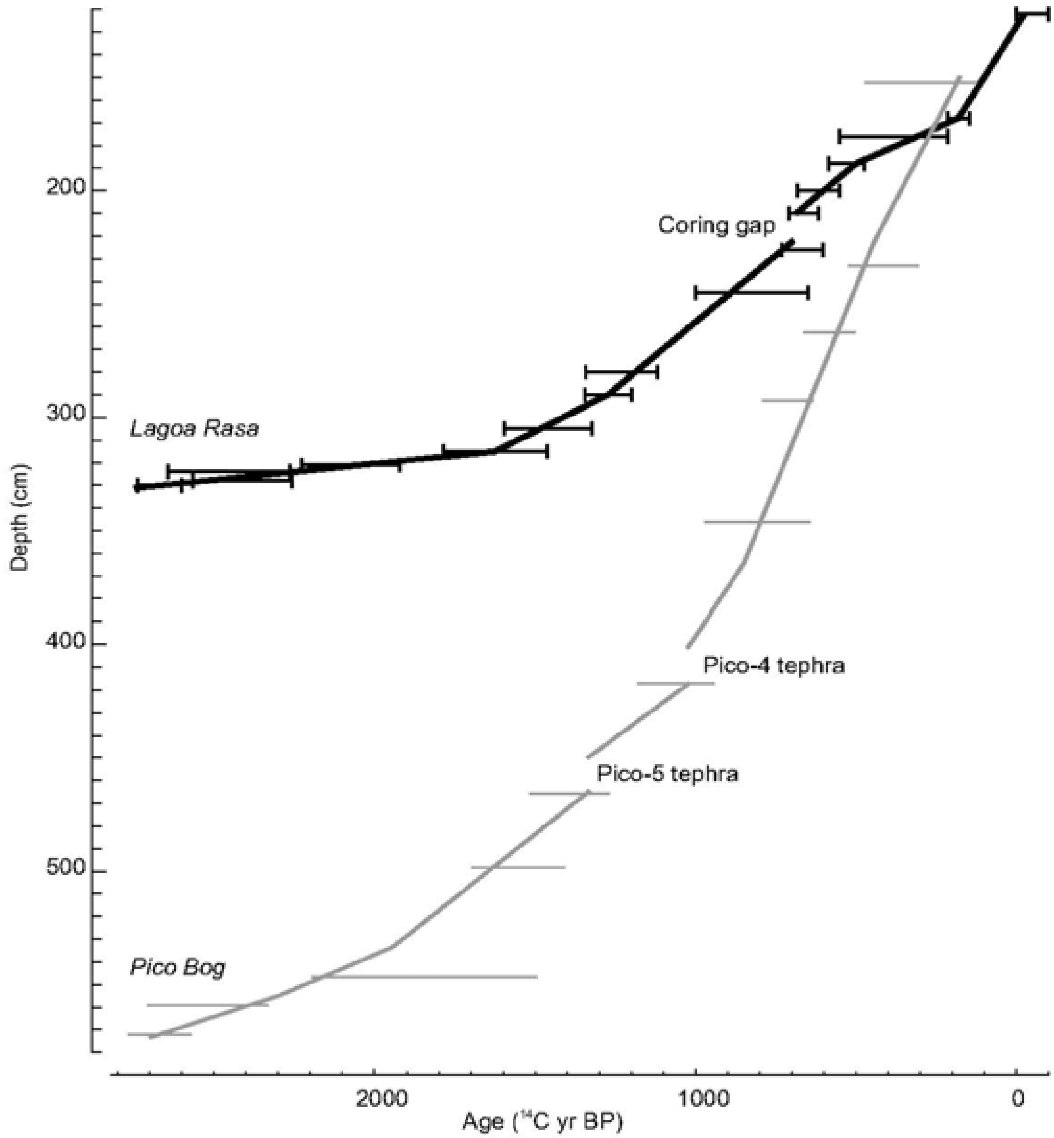

Figure 2 Age–depth profiles, for sediment records from Lagoa Rasa on the island of Flores (black line) and Pico Bog on the island of Pico (grey line), based on the radiocarbon ages in Table 3. An age–depth curve for the Lagoa do Caveiro record (Pico Island) appears in Björck *et al*. (2006).

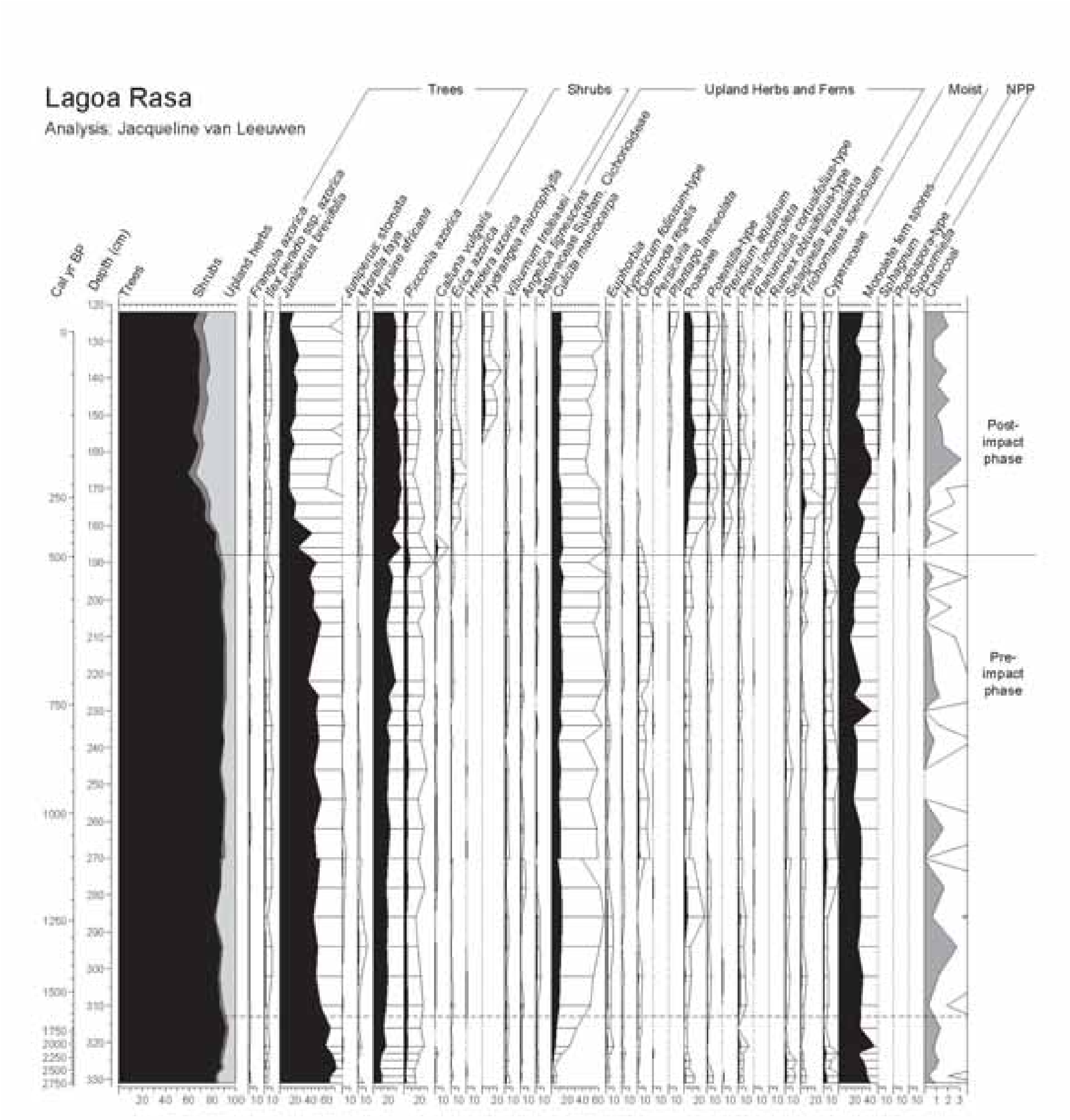

Figure 3 Pollen diagram from Lagoa Rasa on the island of Flores, showing (left to right) sample ages, depths, pollen assemblage summary, trees, shrubs, herbs, ferns and aquatic/wetland pollen types. Non-pollen palynomorphs (NPP) and charcoal are shown on the right. Open curves are 5× exaggerations of the black percentage curves. The solid horizontal line is the zone boundary between pre-impact (below) and post-impact samples (above); dotted lines indicate other significant zone boundaries. See Appendix S1 for the complete pollen diagram.

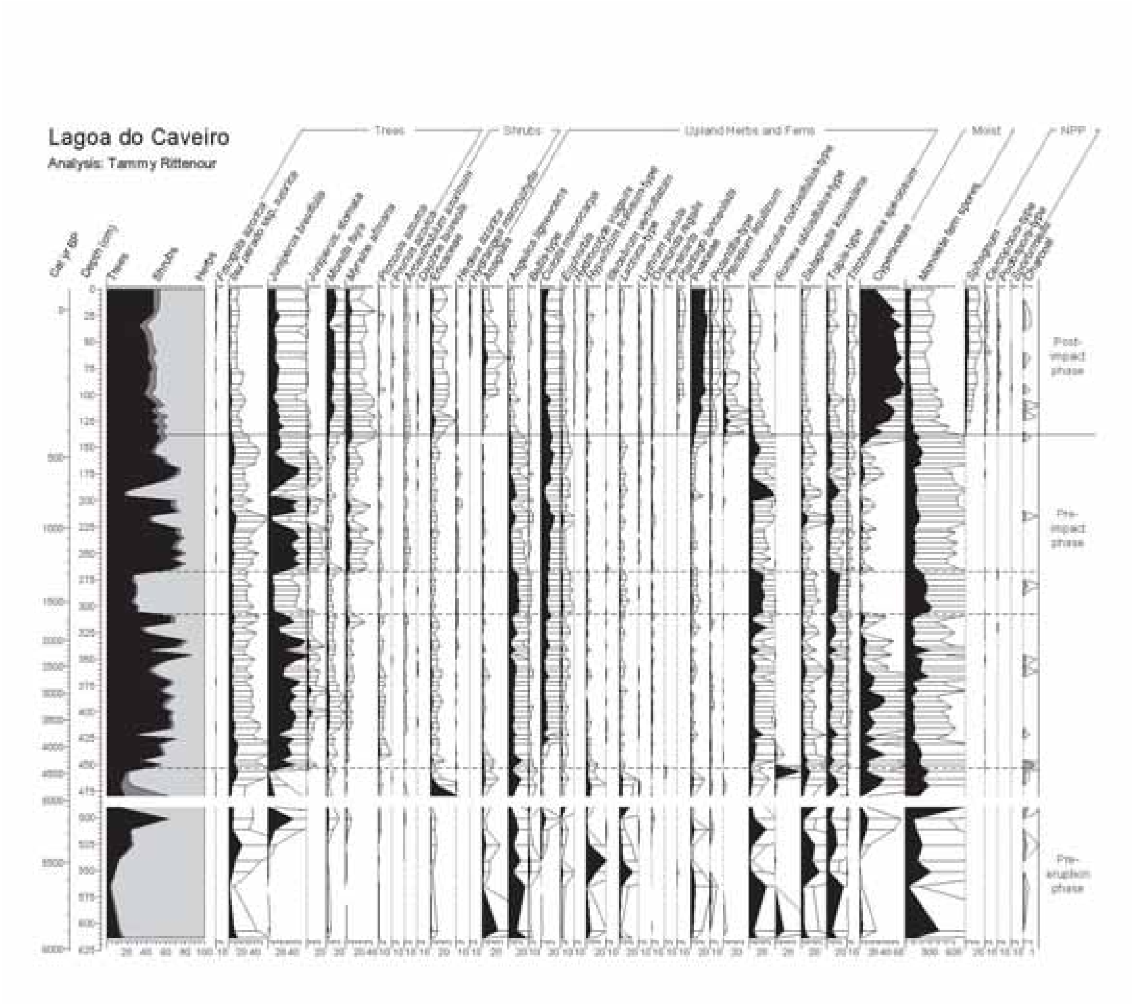

Figure 4 Pollen diagram from Lagoa do Caveiro on the island of Pico. See caption of Fig. 3 for explanation. The horizontal band represents the division between the central lake core and the marginal core (see Björck *et al*., 2006). See Appendix S1 for the complete pollen diagram.

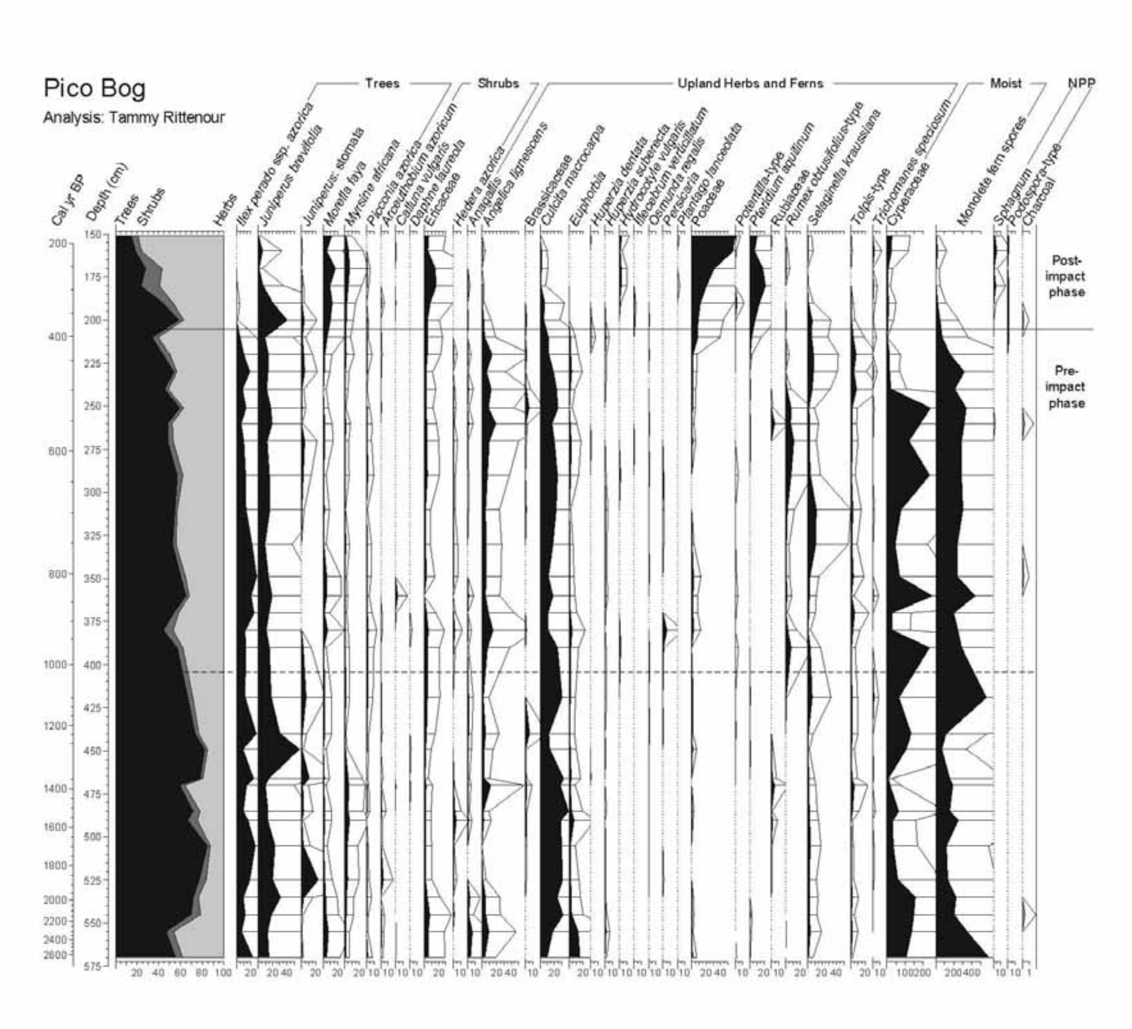

Figure 5 Pollen diagram from Pico Bog on the island of Pico. See caption of Fig. 3 for explanation and Appendix S1 for the complete pollen diagram.

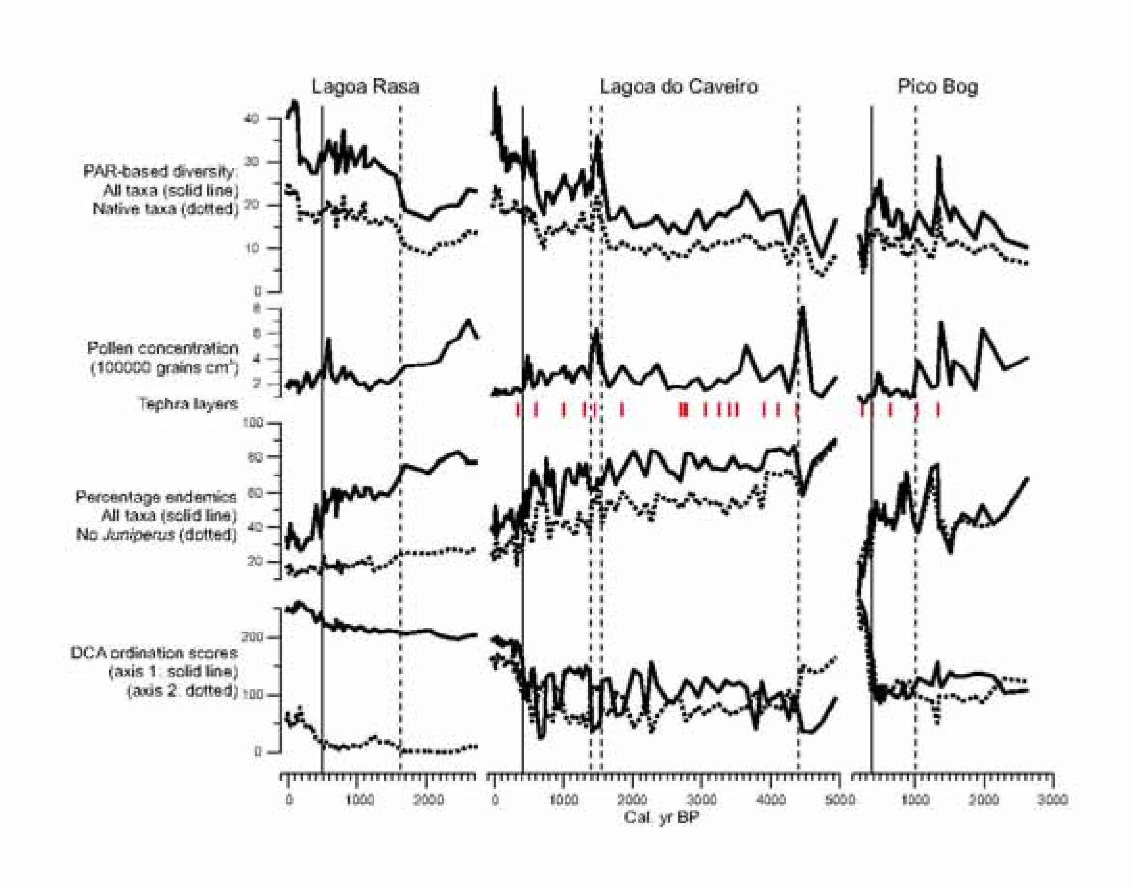

Figure 6 Temporal changes in palynological diversity and endemic species representation in the Lagoa Rasa, Lagoa do Caveiro and Pico Bog records from the Azores. Trends are shown in relation to changes in pollen concentrations, tephra layers and ordination scores (detrended correspondence analysis, DCA;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

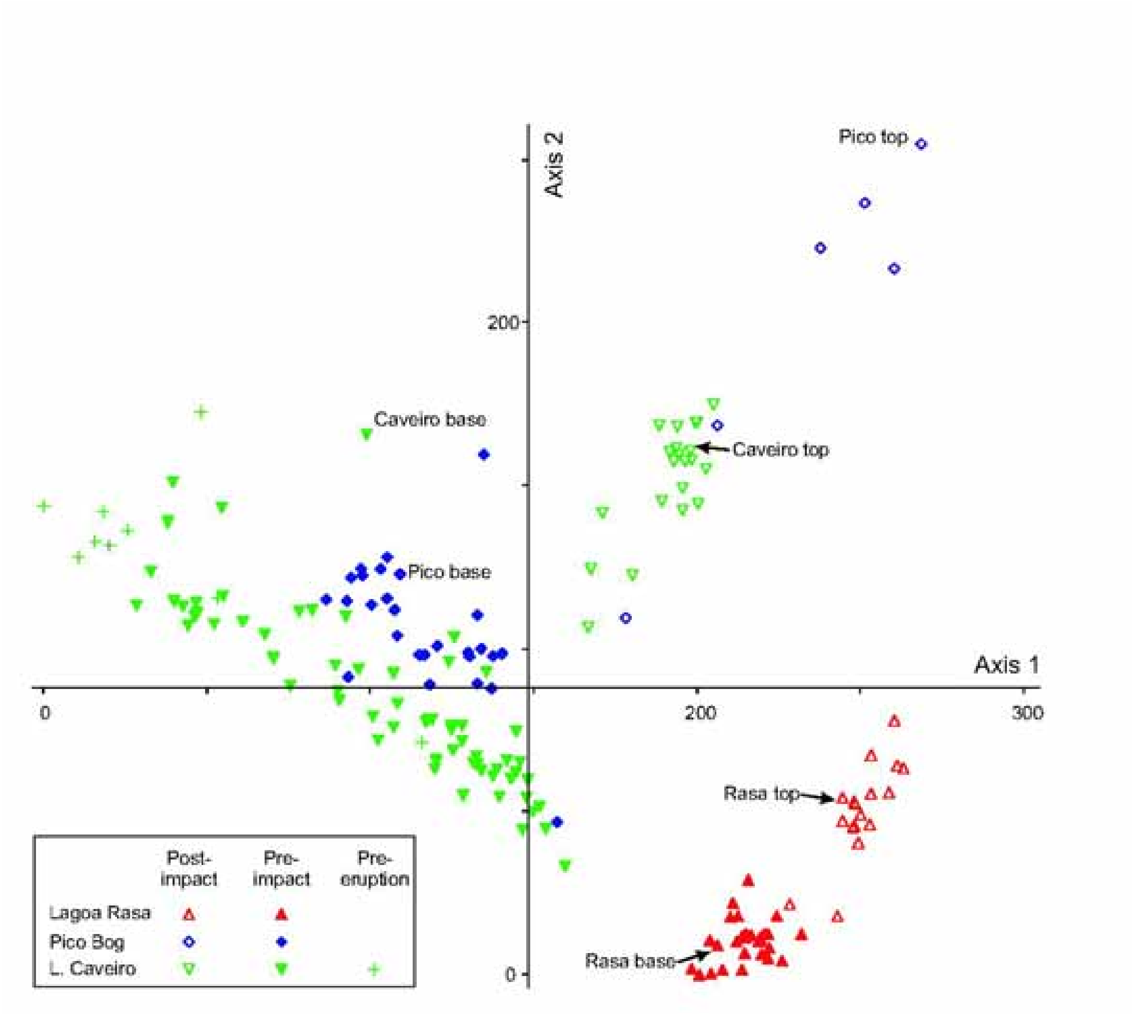

Figure 7 Detrended correspondence analysis (DCA) result for the Lagoa Rasa, Lagoa do Caveiro and Pico Bog pollen records (Figs 3–5), showing the transition from pre-impact (filled shapes) to post-colonization impacted palaeovegetation (open shapes). The lowermost and topmost samples from each record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