

1 **Holocene palaeoclimate and palaeovegetation on the islands of Flores**
2 **and Pico**

3

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7 This is a draft version of a manuscript published in *Climate Change*
8 *Perspectives from the Atlantic: Past, Present and Future* (edited by Fernández-
9 Palacios JM, de Nascimento L, Hernández JC, Clemente S, González A, Díaz-
10 González JP., 2013, Universidad de La Laguna, Tenerife, pp. 149-162). Please
11 note that there may be differences between this version and the final published
12 version. The authors will be happy to provide copies on request.

13

14 **Title**

15 Holocene palaeoclimate and palaeovegetation on the islands of Flores and Pico

16

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29

30 **Abstract**

31 Palaeoclimatic stability is regarded as an important factor in explaining patterns of
32 endemism in the Azorean flora. However, modelling simulations and quantitative
33 reconstructions for the last 6000 years suggest considerable palaeoclimatic variability.
34 Here we explore the link between Holocene palaeoclimate and palaeovegetation on the
35 islands of Flores and Pico. Modern pollen assemblages indicate that most major plant
36 communities can be detected using pollen analysis and that, in some cases, the pre-

37 colonisation vegetation was quite similar to present-day relict vegetation. A 200–500-
38 year pollen record from Alagoinha, a low-elevation mire in western Flores, shows that
39 *Juniperus brevifolia*-dominated communities were widespread at lower elevations prior
40 to large-scale deforestation. Today these communities are generally restricted to higher
41 elevations. While our results are preliminary, there appears to be a weak link between
42 palaeovegetation (which was primarily influenced by volcanism, soil formation and
43 human impact) and palaeoclimatic changes detected through geochemical proxies.
44 Even if the Azorean palaeoclimate varied substantially, its impact on the pristine
45 vegetation, at least in terms of pollen production, was relatively small.

46 **Keywords**

47 Azores, Holocene, Macaronesia, palaeoclimate, palaeovegetation, Portugal.

48

49 **Introduction**

50 Globally, most archipelagos harbour a large number of single-island endemic species
51 relative to the number of all-island endemics, but on the Azores the pattern for vascular
52 plants seems quite different (Carine & Schaefer, 2010). Several theories have been
53 developed to explain why Azorean endemic plants are few and widespread – a climatic
54 stability hypothesis, which states that long-term stability in the climate of the Azores
55 has limited diversification (Carine & Schaefer, 2010); a geographical hypothesis, which
56 links low rates of single-island endemism to the youth, size and homogeneity of the
57 Azores (Triantis *et al.*, 2011); and a cryptic diversity hypothesis, which proposes that
58 the apparent lack of endemism is only ‘skin deep’ and does not reflect real genetic
59 diversity (Schaefer *et al.*, 2012).

60 Climatic modelling simulations suggest that the Azores were less climatically stable
61 during the Holocene and Last Glacial Maximum than the Canary Islands and Madeira,
62 archipelagos which harbour many single-island endemic plants (Triantis *et al.*, 2011).
63 Palaeoclimatic reconstructions from geochemical proxies on the Azorean island of Pico
64 provide a clear North Atlantic Oscillation (NAO) signal (Björck *et al.*, 2006). However,
65 this NAO signal is not clearly detected in palynological data from the same sediment
66 records and complementary pollen data from the island of Flores point to remarkable
67 palaeovegetational stability (Connor *et al.*, 2012a; Carine *et al.*, 2012). There may be a
68 weak link between climatic changes and vegetation changes on these islands, which
69 could be one factor contributing to the lack of morphological diversification amongst
70 Azorean endemic plants.

71 According to Dias (1996), historical reports from the Azores suggest that there was no
72 vegetation zonation with respect to altitude. If this is true, there are two important
73 implications: firstly, the lack of elevational zones means that Azorean native plant
74 communities may not exhibit a clear response to changes in temperature, both now and
75 in the past; and secondly, the current distribution of native plants in relation to altitude
76 may be a consequence of human activities since European colonisation, rather than a
77 reflection of bioclimatic factors. We gathered pollen data on the present and past
78 vegetation of the Ilha das Flores to explore these issues.

79 **Materials and methods**

80 Surface samples were collected from 16 locations on the island of Flores to better
81 interpret previous palaeoecological records from the highlands of Flores (Lagoa Rasa,
82 530 m above sea level) and Pico (Lagoa do Caveiro, 903 m a.s.l., and Pico Bog, 873 m
83 a.s.l.; Björck *et al.*, 2006; Connor *et al.*, 2012a). Each sample was an agglomeration of
84 moss subsamples gathered from a 1 m² area. Plant cover-abundance was measured in

85 five 5 × 5 m quadrats, one at the sampling site and four others spaced 15 m in each
86 direction from the sample.

87 To complement previous palaeoecological records from the highland sites, a sediment
88 core was obtained from a low-elevation mire on the western side of Flores, Alagoinha
89 (39°25'37"N, 31°14'30"W, approx. 270 m a.s.l.). The site is a *Cladium mariscus*-
90 dominated mire at the base of a 200-m-high cliff, 1.3 km ESE of Fajãzinha township.
91 *Persicaria hydropiperoides*, *Carex pendula* and *Equisetum telmateia* are prevalent
92 around the margins. The mire is fed by cascades and surrounded by forests of the
93 introduced Australian tree, *Pittosporum undulatum*, along with *Acacia melanoxylon*,
94 *Cryptomeria japonica*, a few relict patches of Laurisilva (*Laurus azorica*-dominated
95 forest) and *Festuca* communities on the cliffs. The invasive *Hedychium gardnerianum*
96 dominates the understorey. The slopes below the site are abandoned agricultural
97 terraces that have been overgrown by *Pittosporum*.

98 The sediment core was collected from the centre of the mire in June 2012 using a
99 square-rod piston corer (Wright, 1967). Cores were extruded, sectioned, wrapped in
100 plastic film and stored in a refrigerator. Sediment samples of 1 cm³ and bulk samples of
101 surface moss were treated with 10% HCl, 10% KOH, 48% HF and acetolysis to isolate
102 the pollen and spores (Moore *et al.*, 1991) and mounted in glycerol for identification at
103 400× magnification. A minimum of 200 (average 1100) terrestrial pollen and spores
104 were identified in each sample. Taxonomy follows Silva *et al.* (2010) and Connor *et al.*
105 (2012a).

106 The new pollen data were combined with earlier data from Flores and Pico (Connor *et al.*
107 *et al.*, 2012a) and analysed using Detrended Correspondence Analysis and hierarchical
108 clustering (Ward's method) with PC-Ord software (McCune & Mefford, 1999).

109 A single radiocarbon date was obtained from the sediment core at a depth of 493–497
110 cm. Age determination was made on plant macrofossils, which were isolated from the
111 sediment by filtering over a tea strainer and then hand sorted using a dissecting
112 microscope. Several *Erica* seeds, two *Juniperus* scales, an unidentified flower and
113 some twigs were dated using Accelerator Mass Spectrometry (AMS).

114 **Results**

115 Modern pollen assemblages on the island of Flores clearly reflect the local vegetation at
116 each of the sampling points (Fig. 1). Samples from the extensive peatbogs of the central
117 plateau have a prevalence of *Calluna vulgaris* pollen; areas of relict *Juniperus brevifolia*
118 forest have high *Juniperus* values; *Erica azorica* pollen is dominant in some coastal and
119 heavily grazed areas; *Morella* is most abundant at low elevations; Poaceae prevails in
120 the higher elevation grasslands; *Cryptomeria* pollen reflects proximity to plantations;
121 and *Picconia* and *Pittosporum* exhibit high percentages where the trees are dominant in
122 the surrounding vegetation. *Calluna*, *Erica* and *Juniperus* are well represented
123 palynologically, whereas *Morella* tends to be over-represented and *Ilex* tends to be
124 under-represented in pollen assemblages compared to the surrounding vegetation
125 (Connor *et al.*, 2012b).

126 Coring at Alagoinha penetrated to a depth of 5 m. The uppermost 3 m of sediment was
127 unconsolidated organic material and was not recovered. From 3–4 m, the sediment
128 consisted of clayey gyttja mixed with varying quantities of volcanic sand and gravel. A
129 layer of eroded material (mostly scoria) was encountered between 4–4.5 m. From 4.5–5
130 m, the sediment consisted of organic gyttja with black sand and abundant diatoms. The
131 core terminated in impenetrable gravel at 5 m. The single AMS date from 493–497 cm
132 (Beta-330609) yielded a radiocarbon age of 270 ± 30 before 1950 AD (BP). This
133 corresponds to calendar years between 1515–1598 AD (44% probability at 2σ), 1617–

134 1678 (49%) and 1782–1797 (6%), thus post-dating the Flemish colonisation of Flores in
135 1472 AD.

136 Results of preliminary pollen analysis of the Alagoinha core are shown in Fig. 2. Pollen
137 assemblages in the lower section of the core, prior to the erosion event, are dominated
138 by *Juniperus* and *Myrsine*. Poaceae and *Dryopteris filix-mas*-type are also relatively
139 abundant. The presence of *Datura* pollen confirms that *D. stramonium* was an early
140 introduction to the flora (Schaefer, 2003). Following the erosion event, *Morella*
141 (*Myrica*) exhibits a large peak and *Juniperus* declines. *Pteridium* is more abundant after
142 the erosion event, whereas *Picconia* and *Solidago*-type are less frequent. These
143 preliminary observations suggest that *Juniperus brevifolia*-dominated vegetation
144 prevailed around Alagoinha during the 14th–15th centuries, prior to more recent
145 deforestation. A moss sample (AZ13) collected from the margins of the mire contained
146 large amounts of *Pittosporum* (51%), *Morella* (21%) and *Cryptomeria* (15%) pollen,
147 reflecting the present-day vegetation of the area, with the notable exception of *Laurus*
148 *azorica*. Two moss samples from under a large *Laurus azorica* tree near Alagoinha
149 were processed with and without acetolysis, showing that *Laurus azorica* pollen does
150 not survive this treatment (as in most Lauraceae: van der Merwe *et al.*, 1990). Even
151 when acetolysis is avoided, *Laurus azorica* appears to be a poor pollen producer,
152 assemblages under this tree having less than 10% *Laurus azorica* pollen and much
153 greater amounts of *Morella* (~40%), *Pittosporum* (~20%) and *Cryptomeria* (~15%).

154 The DCA result is very similar to the previous result for Pico Bog, Lagoa do Caveiro
155 and Lagoa Rasa (Connor *et al.*, 2012a), with the first axis interpreted as a moisture-
156 availability gradient and the second axis as a forest-cover gradient (Fig. 3). Pollen taxa
157 most correlated with the ordination axes are given in Table 1. Surface samples from the
158 most intact forest stands (e.g. AZ04, AZ05 and AZ06) are found in the top right of the

159 ordination plot near the pre-colonisation samples from Lagoa Rasa. Samples from
160 partly deforested, but still intact, areas in the northern part of the island (i.e. AZ03 and
161 AZ15) have similar pollen composition to early post-colonisation samples from Lagoa
162 Rasa and Alagoinha. Samples from forest areas in the dry SE part of Flores (AZ02 and
163 AZ12) appear to be similar to post-colonisation samples from the island of Pico.
164 However, the majority of the surface samples cluster in the lower right of the ordination
165 plot with the most recent samples from Pico Bog and Alagoinha. The Alagoinha record
166 exhibits the same temporal trend seen in all pollen records from Pico and Flores –
167 toward higher moisture availability and lower forest cover (see Connor *et al.*, 2012a).
168 These trends have no clear relationship to palaeoclimatic oscillations reconstructed
169 using other proxies (Fig. 4).

170 Ward's minimum-variance clustering produced comparable results to the DCA, clearly
171 displaying the affinity of modern *Juniperus brevifolia* forests with the pre-colonisation
172 vegetation surrounding Lagoa Rasa and Lagoa do Caveiro (group B, Fig. 3). The three
173 *Calluna*-dominated samples are separated from the remaining samples (group F, Fig. 3).
174 Lagoa do Caveiro samples associated with volcanic eruptions form a distinct group (E),
175 as do pre-colonisation samples from Pico Bog (D) and post-colonisation samples from
176 Lagoa Rasa (A). The remaining samples, including those from Alagoinha, form a large
177 group (C), indicative of the post-colonisation vegetation.

178 **Discussion**

179 Modern pollen assemblages are a useful tools for interpreting past vegetation changes
180 recorded in fossil pollen. On the island of Flores, our data suggest that the vegetation
181 around Lagoa Rasa prior to European colonisation was very similar to today's extensive
182 *Juniperus brevifolia* forests to the N and NW of Morro Alto, the highest mountain on

183 Flores. This area therefore appears to preserve a truly relict vegetation type and its
184 protection status should be carefully maintained.

185 Colonisation of the islands in the 15th century led to changes in vegetation structure and
186 composition, particularly clearance of juniper forests and the spread of *Sphagnum*
187 mosses (Connor *et al.*, 2012a). The Alagoinha record indicates that *Juniperus*
188 *brevifolia*-dominated communities extended to relatively low elevations on Flores in the
189 early period of colonisation. There is a possibility that the streams that flow into
190 Alagoinha carried some pollen down from higher altitudes, though the presence of well
191 preserved macrofossils and stomata suggest that *Juniperus brevifolia* trees were present
192 locally (see Birks & Birks, 2000). Indigenous trees that are widespread in lowland and
193 coastal areas today, such as *Morella faya* and *Picconia azorica*, are also poorly
194 represented in the early part of the Alagoinha pollen record. This leads us to the
195 conclusion that *Juniperus brevifolia* forests, which today are mainly preserved in the
196 highest parts of Flores, were the prevailing vegetation type over a much larger area of
197 the island in the past, possibly extending down to the coast in some places (compare
198 Fig. 41a in Schaefer, 2003). Human activities since colonisation, such as deforestation
199 and grazing, have led to the expansion of *Morella faya*, which was historically less
200 favoured for timber than *Juniperus* and can survive on degraded soils because of its
201 nitrogen-fixing capacity. It must be emphasised that juniper's wide elevational
202 amplitude in the past may only apply to the island of Flores, which is the wettest island
203 of the Azores Archipelago.

204 The mild, wet climate of the Azores is thought to have been an important factor in
205 limiting both endemism and altitudinal zonation (Schirone *et al.*, 2010; Carine &
206 Schaefer, 2010). Most endemic plants occur over the entire elevational range of the
207 archipelago, with few endemic or native species occupying particular altitudinal zones

208 (Schaefer, 2003). The lack of altitudinal zonation in Azorean indigenous vegetation
209 means that past changes in temperature are unlikely to leave a strong signal in pollen
210 records. Precipitation changes may register in palaeoecological records from the
211 Azores, although in some records it is difficult to distinguish real palaeovegetation
212 changes from taphonomic alterations caused by lake-level changes and volcanism (e.g.
213 Lagoa do Caveiro: Connor *et al.*, 2012a).

214 Triantis *et al.* (2011) used palaeoclimatic modelling results to challenge Carine and
215 Schaefer's (2010) assertion that the Late Quaternary climate of the Azores was far more
216 stable than on the Canary Islands. A recent pollen study from a high elevation crater on
217 La Gomera, Canary Islands, demonstrates that mid-Holocene precipitation changes had
218 a significant impact on the palaeovegetation, causing a steep decline in hygrophilous
219 taxa (Nogué *et al.*, accepted). The change coincides with the end of the African Humid
220 Period (deMenocal *et al.*, 2000) and a phase of dune instability and aridification in the
221 eastern Canary Islands around 5500 cal. yr BP (Ortiz *et al.*, 2006). In the coastal
222 lowlands of Tenerife, however, the palaeovegetation appears to have remained quite
223 stable from approx. 22,000 years ago until the arrival of humans (de Nascimento *et al.*,
224 2009, 2012). Hence vegetation response to climatic changes on the Canaries may be
225 altitude-dependent. On the Azores, palaeovegetation stability is also observed in the
226 Lagoa Rasa pollen record from Flores prior to human arrival (Connor *et al.*, 2012a).

227 Holocene pollen records from high elevations on Pico are more changeable, largely due
228 to the frequent occurrence of volcanic eruptions and lake-level changes on this island
229 (Björck *et al.*, 2006). As yet there is no clear evidence for climate-induced
230 palaeovegetation change from the Azores during the Holocene; volcanic eruptions, soil
231 formation and human impacts being the most important factors (Connor *et al.*, 2012a).

232 The available pollen data lend support to the Azorean climatic stability hypothesis put
233 forward by several authors (Avila *et al.*, 2008; Carine & Schaefer, 2010; Schirone *et al.*,
234 2010; Carine *et al.*, 2012). Even if the Azorean palaeoclimate was generally more
235 variable than that of the Canary Islands (Triantis *et al.*, 2011), its impact on the
236 vegetation, as gauged through pollen production, was minor. We wonder if high levels
237 of cryptic endemism in the Azorean flora (Schaefer *et al.*, 2011) are related to the broad
238 altitudinal range of most endemic plants. The combination of low morphological
239 diversity and high molecular diversity amongst endemic plants could stem from
240 adaptation to non-climatic factors, such as competition, periodic disturbances, soil
241 texture, geological age and nutrient availability.

242 Pollen analysis is unlikely to shed much light on this question due to taxonomic
243 constraints at the species level (Birks & Birks, 2000). However, it can reconstruct
244 distribution patterns for many Azorean plant species before human colonisation and
245 thereby determine the original altitudinal range of Azorean plants. More detailed
246 studies, from a variety of islands and altitudes, are required to fully explore the link
247 between Azorean palaeoclimate and palaeovegetation.

248 **Conclusions**

249 Modern pollen data from the Azores show that the major vegetation types are clearly
250 represented in pollen assemblages, the exception being vegetation dominated by *Laurus*
251 *azorica*. Fossil data from Alagoinha show that forests of *Juniperus brevifolia*, which
252 today occur mainly at higher elevations on Flores, extended to much lower elevations in
253 the early period of colonisation. Our results add support to the idea that Azorean
254 vegetation was not arranged in strict altitudinal zones prior to human arrival. The
255 implication of this is that Holocene vegetation changes on Flores are likely to be

256 predominantly a reflection of non-climatic factors. More data from various islands and
257 settings are required to confirm this hypothesis for the Azores generally.

258 **Acknowledgements**

259 Thanks to João Araújo (University of the Algarve) for preparing samples from
260 Alagoinha.

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332

333 **Tables and Figures for “Holocene palaeoclimate and palaeovegetation on the**
 334 **islands of Flores and Pico”**

335

336 Table 1. Pollen taxa most correlated with the first two DCA axes and their correlation
 337 coefficients (*r*). The first axis explains 39% of variance and the second 25%.

338 Abbreviations: *O. azoric.* – *Ophioglossum azoricum*; *O. lusitan.* – *Ophioglossum*

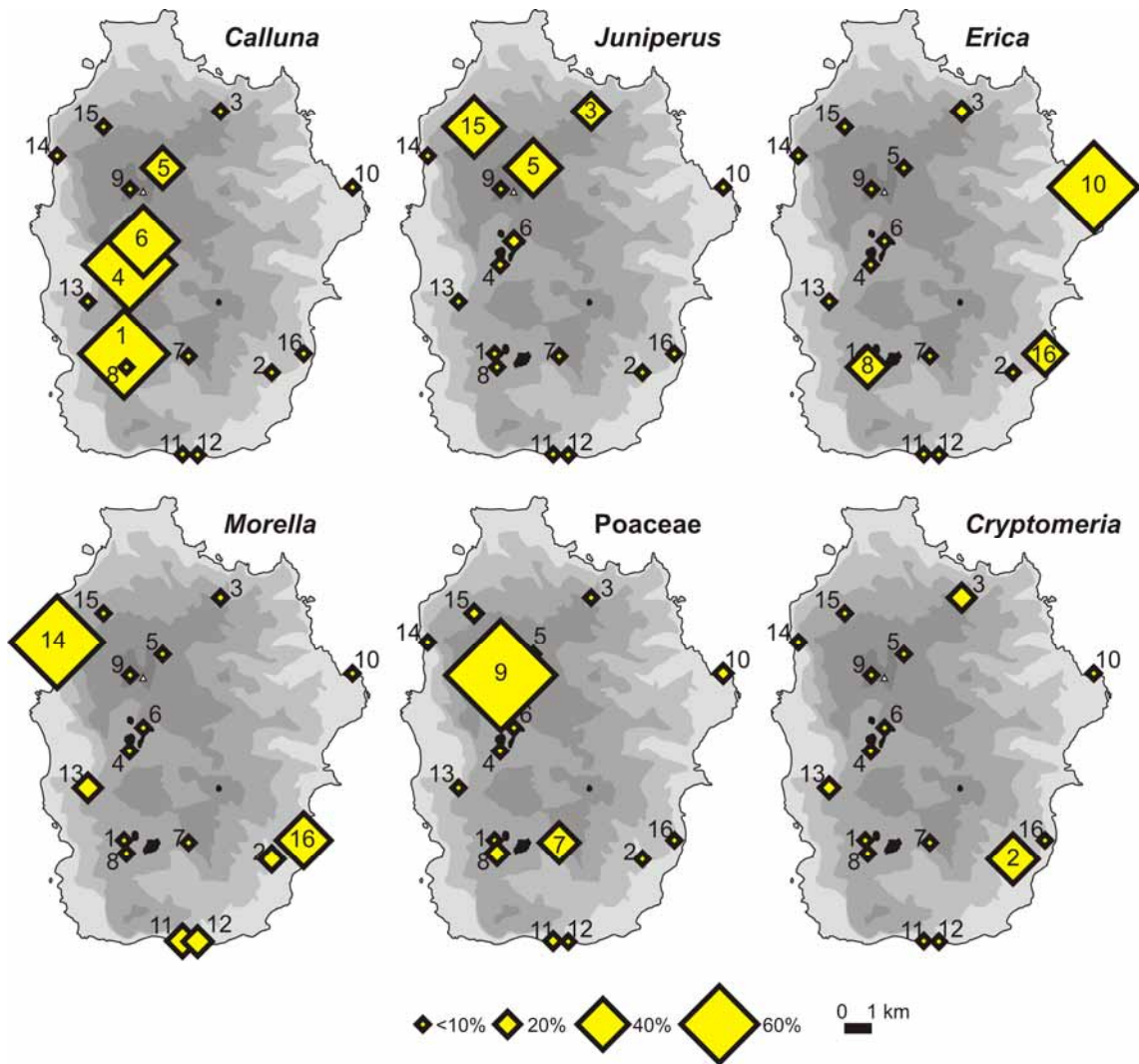
339 *lusitanicum*; *P. coronop.* – *Plantago coronopus*; *P. lanceol.* – *Plantago lanceolata*-

340 type; *R. cortusif.* – *Ranunculus cortusifolius*-type.

	DCA axis 1				DCA axis 2			
	Positive	<i>r</i>	Negative	<i>r</i>	Positive	<i>r</i>	Negative	<i>r</i>
Poaceae	0.63		<i>Angelica</i>	-0.78	<i>Juniperus</i>	0.78	<i>Morella</i>	-0.60
<i>Pteridium</i>	0.53		Cichoriodeae	-0.72	<i>Osmunda</i>	0.44	<i>Pteridium</i>	-0.59
<i>Morella</i>	0.45		<i>R. cortusif.</i>	-0.65	<i>O. lusitan.</i>	0.41	Poaceae	-0.56
<i>Myrsine</i>	0.41		<i>Ilex</i>	-0.61	<i>Viburnum</i>	0.38	<i>Hydrocotyle</i>	-0.47
<i>Potentilla</i>	0.39		<i>Bellis</i>	-0.53	<i>Myrsine</i>	0.37	<i>Erica</i>	-0.47
<i>Hydrocotyle</i>	0.39		<i>Euphorbia</i>	-0.51	<i>Umbillicus</i>	0.35	<i>P. coronop.</i>	-0.41
<i>P. coronop.</i>	0.37		<i>Huperzia</i>	-0.40	<i>Frangula</i>	0.33	<i>Lysimachia</i>	-0.33
<i>Viburnum</i>	0.34		Apiaceae	-0.39	<i>O. azoric.</i>	0.30	<i>Pinus</i>	-0.29
<i>P. lanceol.</i>	0.33		<i>Selaginella</i>	-0.33	<i>Culcita</i>	0.26	<i>P. lanceol.</i>	-0.28
<i>Trichomanes</i>	0.31		<i>Culcita</i>	-0.29	<i>Betula</i>	0.24	<i>Selaginella</i>	-0.27

341

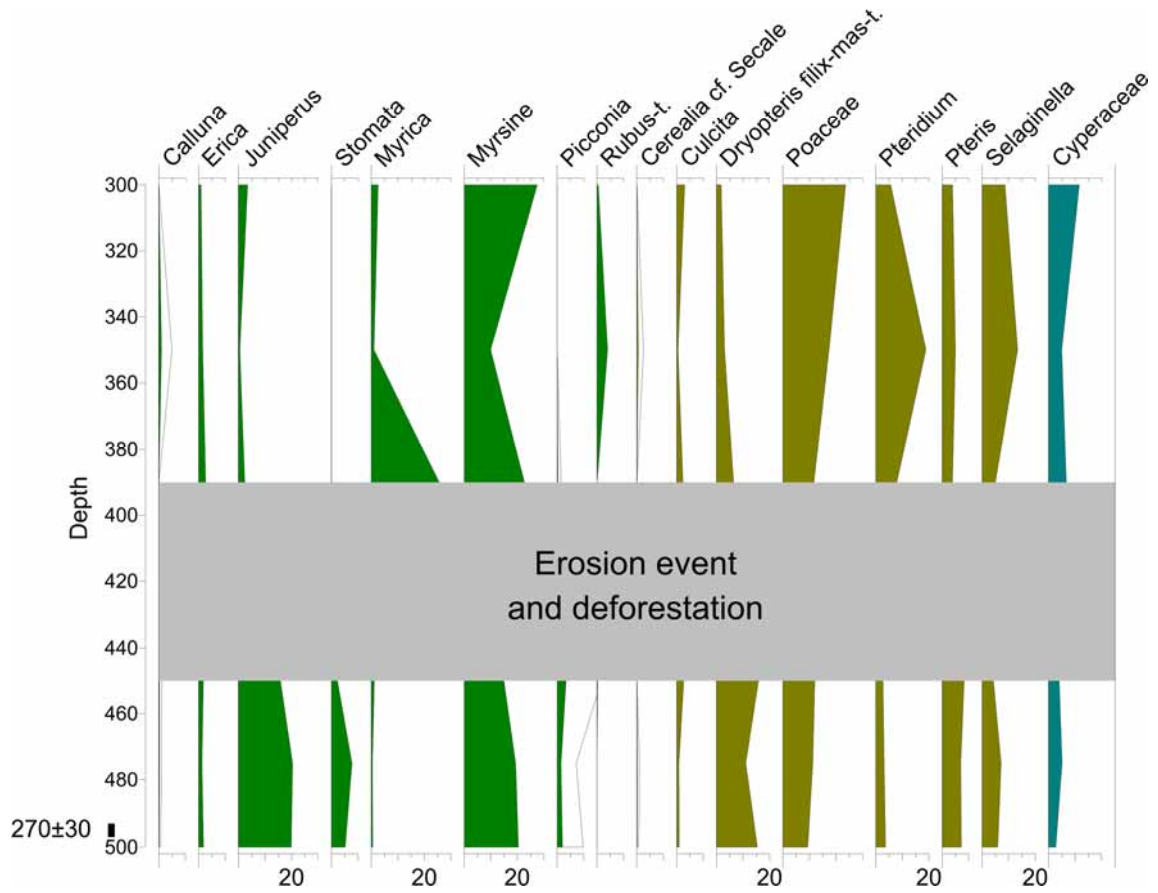
343 Figure 1. Locations of surface sediment samples on the island of Flores, Azores, with
 344 symbols scaled to represent the quantity of major pollen types in each sample.



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346

347 Figure 2. Preliminary pollen diagram from Alagoinha, Flores.



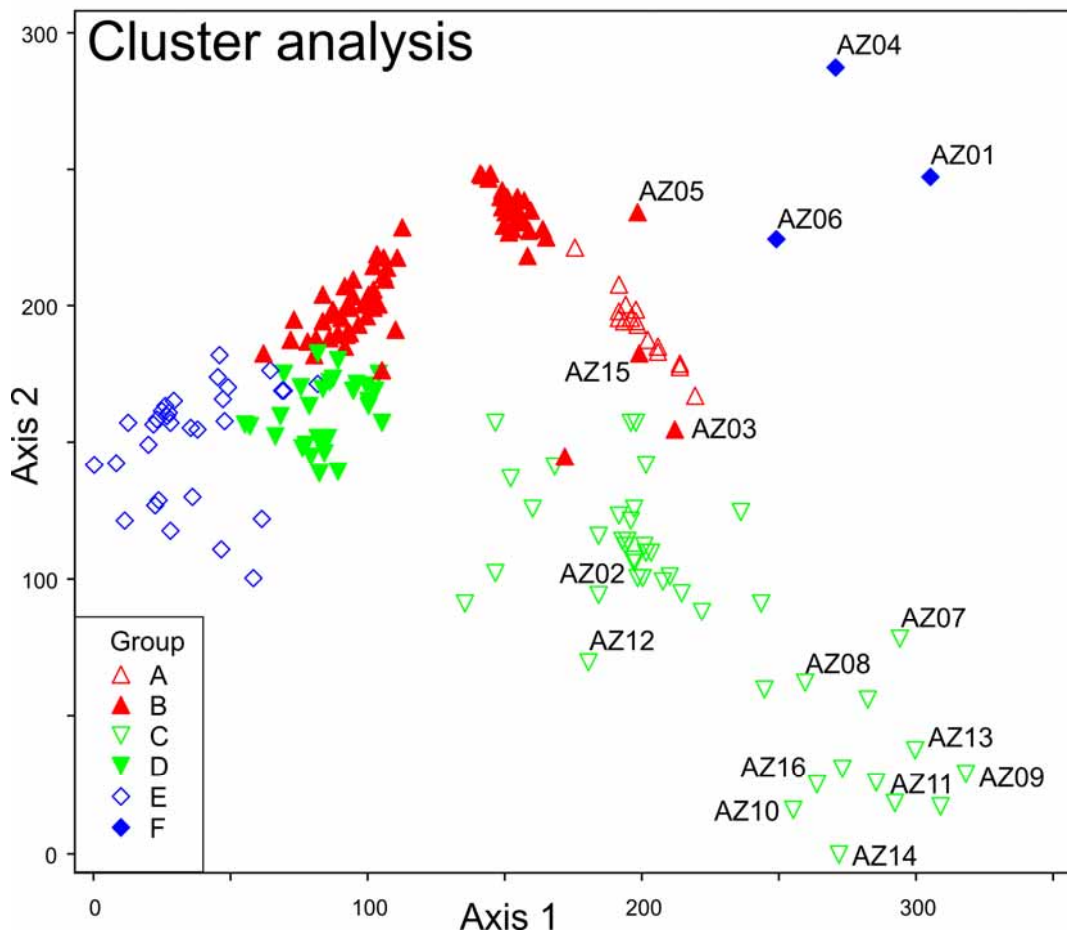
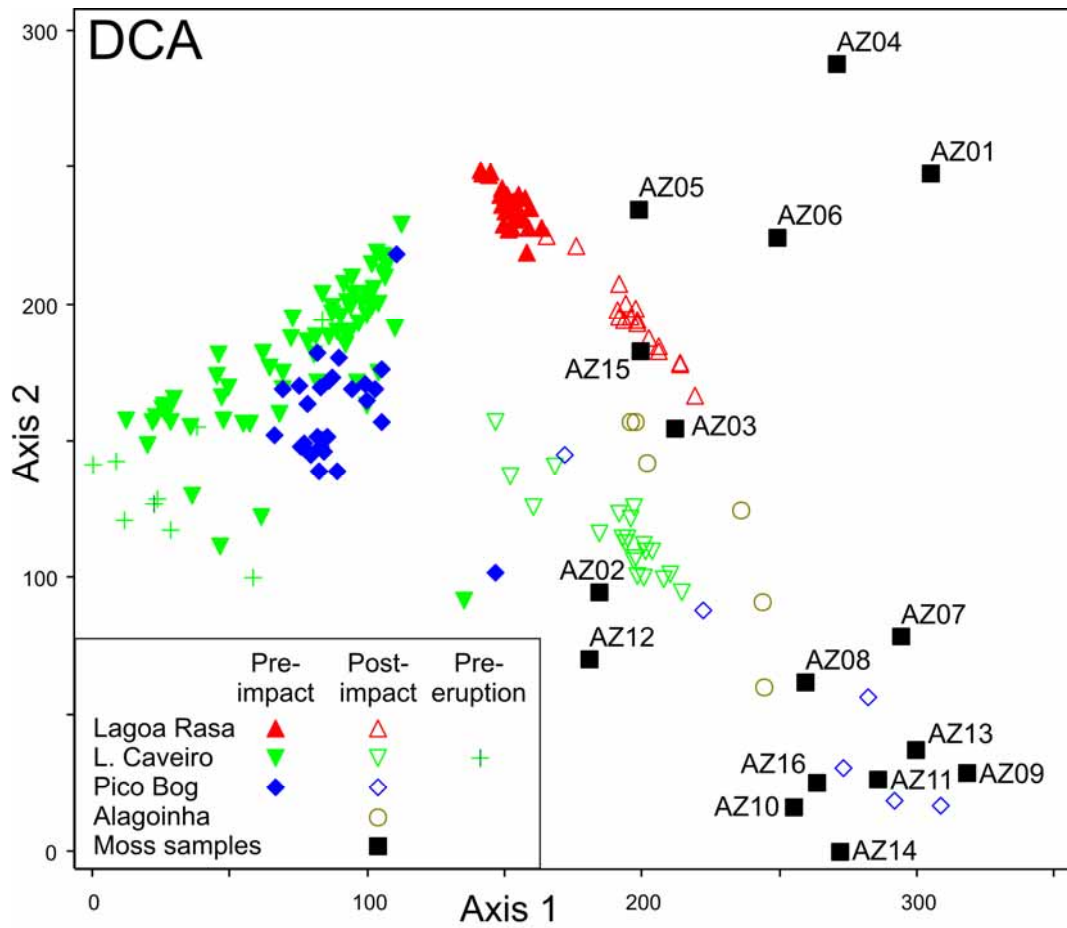
348

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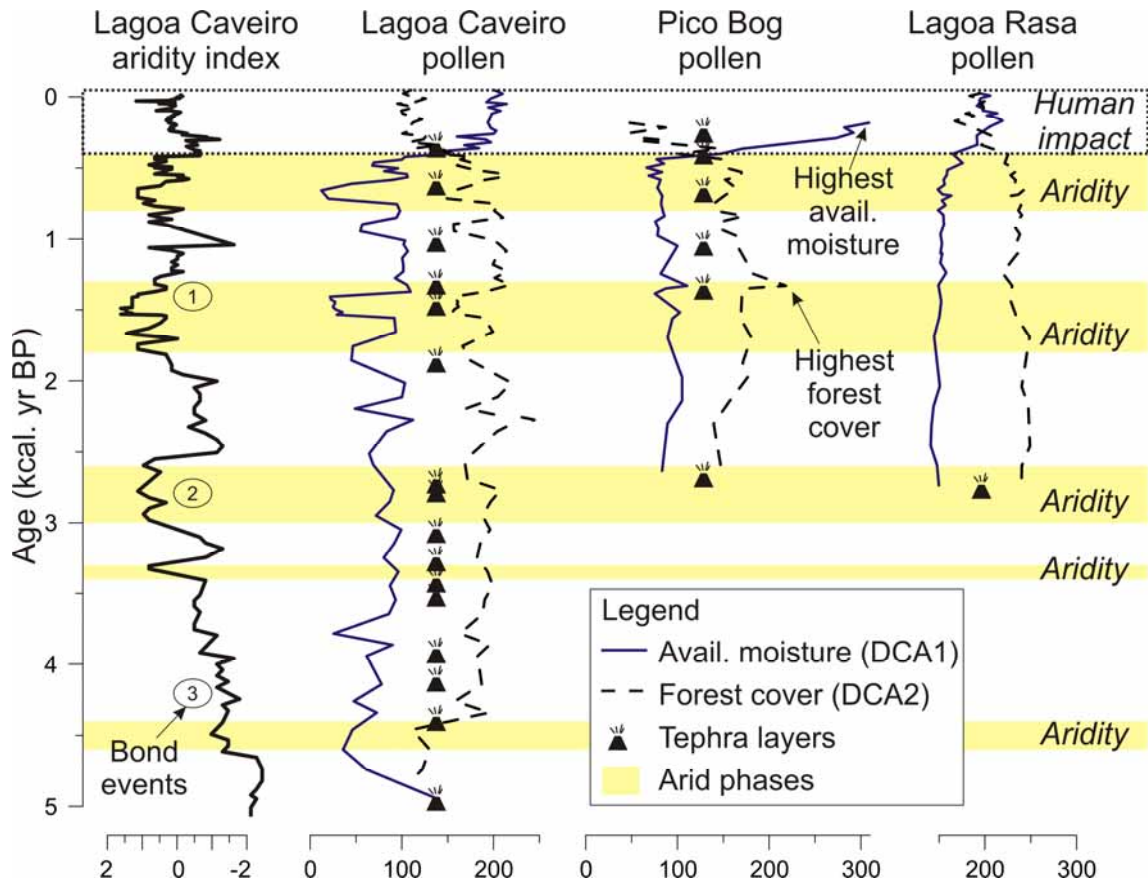
350 Figure 3. Detrended Correspondence Analysis (DCA) result for the surface samples and
351 pollen records from Alagoinha, Lagoa Rasa (Flores), Lagoa do Caveiro and Pico Bog
352 (Pico). Cluster analysis results are shown below in the same ordination space. Taxa
353 most correlated with the ordination axes are given in Table 1.

354

355 (Fig. 3 on next page...)



357 Figure 4. Comparison of ordination results from Azorean pollen records (Fig. 3) with
 358 the palaeoclimatic aridity index from Lagoa do Caveiro, Pico Island (from Björck *et al.*,
 359 2006).



360

361



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Title:

Holocene palaeoclimate and palaeovegetation on the islands of Flores and Pico

Date:

2013

Citation:

Connor, SE; van der Knaap, WO; van Leeuwen, JFN; Kuneš, P, Holocene palaeoclimate and palaeovegetation on the islands of Flores and Pico, *Climate Change Perspectives from the Atlantic: Past, Present and Future*, *Climate Change Perspectives from the Atlantic: Past, Present and Future*, 2013, 1, pp. 149 - 162

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