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6 **Potential natural vegetation and pre-anthropogenic pollen records on the Azores**

7 **Islands in a Macaronesian context**

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26 **Abstract**

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28 This paper discusses the concept of potential natural vegetation (PNV) in light of the pollen records  
29 available to date for the Macaronesian biogeographical region, with emphasis on the Azores Islands. The  
30 classical debate on the convenience or not of the PNV concept has been recently revived in the Canary  
31 Islands, where pollen records of pre-anthropogenic vegetation seemed to strongly disagree with the existing  
32 PNV reconstructions. Contrastingly, more recent PNV model outputs from the Azores Islands show  
33 outstanding parallelisms with pre-anthropogenic pollen records, at least in qualitative terms. We suggest the  
34 development of more detailed quantitative studies to compare these methodologies as an opportunity  
35 for improving the performance of both. PNV modelling may benefit by incorporating empirical data on  
36 past vegetation useful for calibration and validation purposes, whereas palynology may improve past  
37 reconstructions by minimizing interpretative biases linked to differential pollen production, dispersal  
38 and preservation.

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42 **Keywords:** Azores Islands, Canary Islands, Macaronesia, paleoecology, palynology, potential natural  
43 vegetation, pre-anthropogenic vegetation

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53 The idea of potential natural vegetation (PNV) –i.e., the vegetation that would be expected to occur  
54 according to the environmental features (notably climate and geology) of a particular area, in the  
55 absence of human disturbance or major natural catastrophes- has been the object of intense debate.  
56 Critics argue that the concept of PNV has inherent methodological flaws and is rather static, as it ignores  
57 ecological dynamics in naturally changing environments (Jackson, 2013). According to these critics, the  
58 idea of PNV is based on the unwarranted Clementsian view that each set of climatic conditions has its  
59 corresponding climax vegetation and, once both have attained a perfect equilibrium, they remain  
60 unchanged in the absence of human disturbance (Chiarucci *et al.*, 2010). Paleoecological  
61 reconstructions, especially those based on palynological studies, have been instrumental in  
62 reconstructing the more relevant vegetation and landscape features before human disturbance, thus  
63 providing empirical evidence to test predictions based on PNV theoretical reconstructions (Rull, 2012).  
64 In general, paleoecological studies lend little support to the PNV concept, showing that both climate and  
65 vegetation have been constantly changing even in the absence of anthropogenic forcing. Even in cases  
66 of low or negligible environmental variability, the concept of PNV seems difficult to sustain (Rull, 2015).  
67 Jackson (2013) considers that the PNV concept is potentially useful at broad spatio-temporal scales but  
68 unrealistic at local to regional spatial scales and annual to multicentennial temporal scales.  
69 Nevertheless, new modeling methods, such as predictive vegetation modelling (PVM) may provide PNV  
70 with a new foundation (Somodi *et al.*, 2012). This paper focuses on the Azores Islands, in the  
71 Macaronesian region (Fig. 1), which has been a preferred arena for the discussion of the PNV idea in the  
72 face of paleoecological evidence.

73  
74 Debate began in the Canary Islands, where, based on bioclimatic features, Rivas-Martínez *et al.* (1993)  
75 considered that the PNV of this archipelago prior to human arrival was dominated by *Laurus-Persea*  
76 forests (laurel forests).. However, recent palynological studies developed on the Tenerife Island revealed  
77 that some areas that would be reconstructed as laurel forests using PNV were found to be covered with  
78 forests of *Quercus* and *Carpinus* (with *Pinus*), two genera that were hitherto considered allochthonous  
79 to the islands (de Nascimento *et al.*, 2009). This generated an intense debate between the defenders

80 and the detractors of the PNV concept that is still ongoing (Carrión & Fernández, 2009; Carrión, 2010;  
81 Loidi *et al.*, 2010). The defenders of the PNV argue that the critics misinterpret this concept. Another  
82 interesting observation is that the pollen of *Laurus* is poorly preserved in the sediments and tends to  
83 disintegrate during the laboratory treatment (Connor *et al.*, 2012), which could cause its  
84 underrepresentation or absence in past pollen assemblages, thus preventing realistic reconstructions of  
85 the pre-anthropogenic vegetation. This and other drawbacks of palynological reconstructions, as for example  
86 differential pollen production and dispersal among species, are mentioned by the defenders of the PNV  
87 concept to highlight that past pollen assemblages are not a straightforward record of the vegetation  
88 types that produced them and, therefore, pollen analysis is not a panacea to document past vegetation  
89 patterns and trends (Loidi *et al.*, 2010).

90  
91 New data from the Azores Islands allow PNV reconstructions to be compared to paleoecological  
92 evidence. Elias *et al.* (2016), following the concept of potential natural vegetation (PNV) of Somodi *et al.*  
93 (2012), used MAXENT modeling to produce the first distribution maps of the potential natural zonal  
94 vegetation for each island of this archipelago, one of the four archipelagos of the Macaronesian  
95 biogeographic region (Fig. 1). The model calibration set was obtained in 139 plots from the better  
96 preserved vegetation patches of the archipelago. The study identified eight vegetation types arranged in  
97 an elevational pattern, namely (from lowest to highest elevations): *Erica-Morella* coastal woodlands,  
98 *Picconia-Morella* lowland forests, *Laurus* submontane forests, *Juniperus-Ilex* montane forests, *Juniperus*  
99 montane woodlands, *Calluna-Juniperus* altimontane scrublands, *Calluna-Erica* subalpine scrublands and  
100 *Calluna* alpine scrublands. These vegetation types were mapped across the whole archipelago.

101 Assuming that the climate around the time of discovery of the islands was not significantly different  
102 from today's, these maps may be used as a reference to reconstruct the pre-human vegetation of the  
103 Azores. The model of Elias *et al.* (2016) suggests that the potential vegetation that likely dominated the  
104 archipelago under natural conditions (i.e. before human impact) were the *Picconia-Morella* lowland  
105 forests and the *Laurus* submontane forests (laurel forests). Today, the vegetation of the Azores Islands is  
106 largely anthropogenic and the most impacted vegetation type were the laurel forests. The best

107 preserved vegetation types can be found at high elevations, above 600 m, were the *Juniperus-Ilex*  
108 forests and the *Juniperus* woodlands are still present. Elias *et al.* (2016) emphasize that their  
109 reconstruction is useful for landscape management and for restoration planning, in the face of the  
110 potential effects of ongoing climate change.

111  
112 The case of the Azores Islands provides another opportunity for testing the PNV predictions with  
113 empirical palynological evidence in the Macaronesian region. To date, there is palynological information  
114 on the pre-anthropoc vegetation for the islands of Pico, Flores and São Miguel (van Leeuwen *et al.*, 2005;  
115 Connor *et al.*, 2012; Rull *et al.*, 2017), covering the entire geographical range of the archipelago (Fig. 1).  
116 On São Miguel Island, the paleoecological record available is located within the caldera of Sete Cidades,  
117 for which Elias *et al.* (2016) predict a PNV dominated by *Laurus* submontane forests with patches of  
118 *Juniperus-Ilex* montane forests on the upper part of the eastern slopes. The pollen record corresponding  
119 to the period before Portuguese occupation of the islands (AD 1449) is dominated by *Juniperus*  
120 *brevifolia*, *Morella faya* and *Myrsine africana*, followed by *Erica azorica* and *Picconia azorica*. *Ilex perado*  
121 is also present but less abundant. The pollen of *Laurus azorica* is absent –possibly due to its chemical  
122 lability and poor preservation- but *Laurus* stomata are present, which is interpreted as the evidence of  
123 the local occurrence of the species (Rull *et al.*, 2017). All these species are typical of the *Laurus* and  
124 *Juniperus-Ilex* forests, showing a very good agreement between the MAXENT results and the  
125 palynological records in terms of presence-absence. The pollen records available for Pico Island lie in an  
126 area which predicted PNV is dominated by *Juniperus-Ilex* montane forests with patches of *Calluna-*  
127 *Juniperus* altimontane scrubs (Elias *et al.*, 2016). Pre-anthropoc pollen assemblages are dominated by  
128 *Juniperus brevifolia* and *Ilex perado* subsp. *azorica*, with the common occurrence of *Morella faya*,  
129 *Myrsine africana* and *Picconia azorica* (Connor *et al.*, 2012), which is also in agreement with the  
130 MAXENT PNV predictions, in qualitative terms. On Flores Island, the available pollen record comes from  
131 a lake (Lagoa Rasa), which, according to the MAXENT PNV outputs, is potentially an area of *Laurus*  
132 submontane forests surrounded by patches of *Juniperus-Ilex* montane forests (Elias *et al.*, 2016). Similar  
133 to the Sete Cidades record, from São Miguel Island, pre-anthropoc pollen assemblages from Lagoa Rasa

134 are dominated by *Juniperus brevifolia*, with *Myrsine africana* as the subdominant species. The main  
135 difference is that *Morella faya* is less abundant at higher elevations. All these PNV reconstructions and  
136 pre-anthropogenic pollen inferences also show a close correspondence, in qualitative terms, with the  
137 vegetation descriptions available from the initial stages of Portuguese colonization (e.g., Frutuoso,  
138 1589; Moreira, 1987).

139  
140 From these preliminary observations, it can be concluded that the predictions of the MAXENT PNV  
141 modeling used by Elias *et al.* (2016) fit well with empirical observations based on the pollen analysis of  
142 pre-anthropogenic sediment samples, at least in qualitative terms. More detailed quantitative comparisons  
143 would require extra work, which is worth doing. Ideally, ecologists studying modern and past vegetation  
144 patterns and trends should develop joint research projects aimed at comparing theoretical model  
145 outputs with actual empirical data, which would benefit both sides by alleviating their respective  
146 methodological limitations. On the one hand, paleoecology could provide calibration and validation data  
147 sets hopefully leading to more realistic, empirically-tuned PNV model performance (Abraham *et al.*,  
148 2016). On the other hand, past vegetation reconstructions based on pollen data are rapidly improving as  
149 new modelling approaches overcome pollen production and dispersal biases (e.g. Hjelle *et al.*, 2015;  
150 Mariani *et al.*, 2016), but are often hindered by a lack of detailed plant abundance data mapped over  
151 large spatial areas (Bunting *et al.*, 2013). . Qualitative and quantitative relationships between current  
152 vegetation patterns and their palynological expression in lake and peat bog sediments could provide the  
153 necessary link between scholars using past and present evidence to unravel the natural (i.e., pre-  
154 anthropic) vegetation and landscape features. Such a synergistic approach seems more constructive and  
155 efficient than the continued controversy between antagonistic and often inflexible positions.

156  
157 However, it should not be forgotten that PNV reconstructions, as proxies for pre-anthropogenic vegetation  
158 patterns, are intrinsically based on the idea of climatic similarity and, therefore, they are only applicable  
159 to time periods of climate similar to present. A similar problem arises when using modern pollen analogs  
160 to interpret past vegetation if past climatic conditions were significantly different from today (Jackson &

161 Williams, 2004). Widespread human occupation of the Azorean archipelago and associated  
162 environmental impacts took place during the Little Ice Age, under climates reasonably similar to the  
163 present, though slightly cooler and probably drier (Björck *et al.*, 2006). This should be taken into account  
164 in landscape management practices, especially in evaluating potential restoration targets, in order to  
165 assure their viability under present environmental conditions. Comparisons between PNV modelling and  
166 pre-anthropogenic pollen records should also contemplate that PNV reconstructions furnish broad-scale  
167 information (i.e., for a whole island), whereas pollen inferences use to provide clues on the vegetation  
168 lying around the coring site and surrounding areas of similar elevation. Therefore, island-wide  
169 comparative surveys should be based on representative networks of pollen records, which to date are  
170 still unavailable although a number of them are already in progress.

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172 It should be stressed that the Azorean model discussed here cannot be extrapolated to the whole  
173 Macaronesian region. However, further methodological developments to compare PNV output models  
174 with pre-anthropogenic paleoecological records in the Azores could be useful to address the problem in a  
175 wider context, not only in Macaronesia but in other island complexes as well.

176

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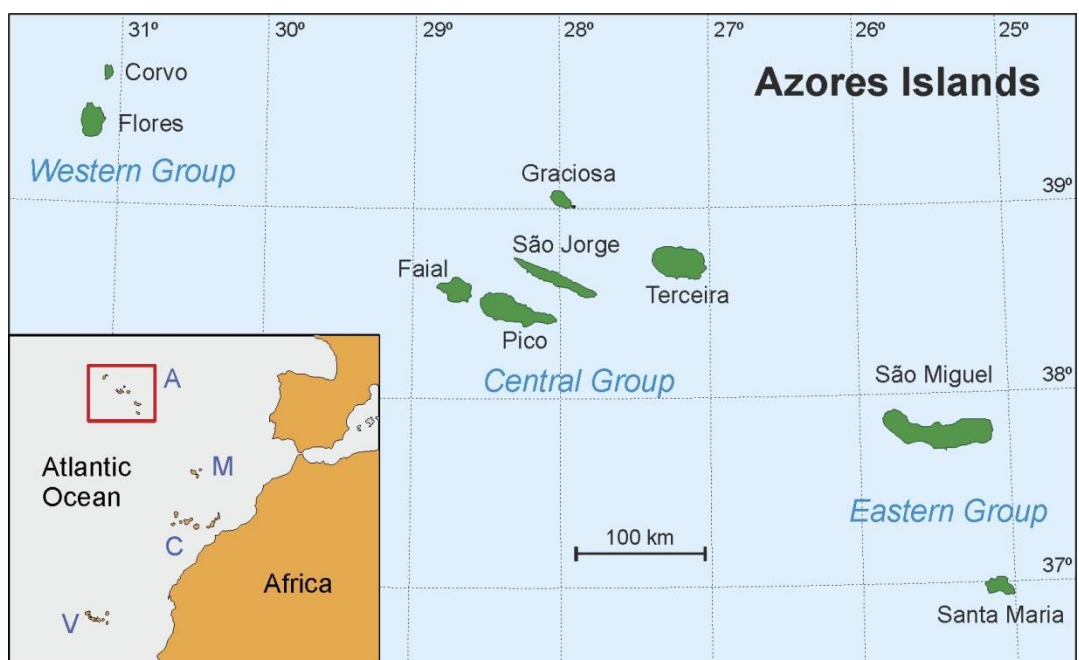
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Figure 1

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251 The Azores Islands in the Macaronesian context. A – Azores; M – Madeira; C – Canaries; V – Cape Verde.

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