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Potential natural vegetation and pre-anthropic pollen records on the Azores Islands in a Macaronesian context

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Abstract

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

Keywords: Azores Islands, Canary Islands, Macaronesia, palaeoecology, palynology, potential natural vegetation, pre-anthropic vegetation

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

Debate began in the Canary Islands, where, based on bioclimatic features, Rivas-Martínez et al. (1993) considered that the PNV of this archipelago prior to human arrival was dominated by *Laurus-Persea* forests (laurel forests). However, recent palynological studies developed on the Tenerife Island revealed that some areas that would be reconstructed as laurel forests using PNV were found to be covered with forests of *Quercus* and *Carpinus* (with *Pinus*), two genera that were hitherto considered allochthonous to the islands (de Nascimento *et al.*, 2009). This generated an intense debate between the defenders and the detractors of the PNV concept that is still ongoing (Carrión & Fernández, 2009; Carrión, 2010; Loidi *et al.*, 2010). The defenders of the PNV argue that the critics misinterpret this concept. Another interesting observation is that the pollen of *Laurus* is poorly preserved in the sediments and tends to disintegrate during the laboratory treatment (Connor *et al.*, 2012), which could cause its underrepresentation or absence in past pollen assemblages, thus preventing realistic reconstructions of the pre-anthropic vegetation. This and other drawbacks of palynological reconstructions, as for example differential pollen production and dispersal among species, are mentioned by the defenders of the PNV concept to highlight that past pollen assemblages are not a straightforward record of the vegetation types that produced them and, therefore, pollen analysis is not a panacea to document past vegetation patterns and trends (Loidi *et al.*, 2010).

New data from the Azores Islands allow PNV reconstructions to be compared to palaeoecological evidence. Elias *et al.* (2016) followed the concept of potential natural vegetation (PNV) of Somodi *et al.* (2012), to produce the first distribution maps of the potential natural zonal vegetation for each island of this archipelago, one of the four archipelagos of the Macaronesian biogeographic region (Fig. 1). According to this concept, PNV may be used as a null model for comparison with past, present or future land-cover. Established stands that persist with little or no human intervention were sampled to estimate the potential distribution of the vegetation under current climate conditions. MAXENT was used to model the potential distribution of vegetation types (Predictive Vegetation Modelling- PVM). In modeling community distribution, the “assemble first predict later” strategy (Ferrier & Guisan 2006) was applied, combining data from multiple species at the community level and yielding predictive maps of community types. The model calibration set was obtained in 139 plots from the better preserved vegetation patches of the archipelago. The study identified eight vegetation types arranged in an elevational pattern, namely (from lowest to highest elevations): *Erica-Morella* coastal woodlands, *Picconia-Morella* lowland forests, *Laurus* submontane forests, *Juniperus-Ilex* montane forests, *Juniperus* montane woodlands, *Calluna-Juniperus* altimontane scrublands, *Calluna-Erica* subalpine scrublands and *Calluna* alpine scrublands. These vegetation types were mapped across the whole archipelago.

Assuming that the climate around the time of discovery of the islands was not significantly different from today's, these maps may be used as a reference to reconstruct the pre-human vegetation of the Azores. The model of Elias *et al.* (2016) suggests that the potential vegetation that likely dominated the archipelago under natural conditions (i.e. before human impact) were the *Picconia-Morella* lowland forests and the *Laurus* submontane forests (laurel forests). Today, the vegetation of the Azores Islands is largely anthropogenic and the most impacted vegetation type were the laurel forests. The best preserved vegetation types can be found at high elevations, above 600 m, were the *Juniperus-Ilex* forests and the *Juniperus* woodlands are still present. Elias *et al.* (2016) emphasize that their reconstruction is useful for landscape management and for restoration planning, in the face of the potential effects of ongoing climate change.

The case of the Azores Islands provides another opportunity for testing the PNV predictions with empirical palynological evidence in the Macaronesian region. To date, there is palynological information on the pre-anthropic vegetation for the islands of Pico, Flores and São Miguel (van Leeuwen *et al.*, 2005; Connor *et al.*, 2012; Rull *et al.*, 2017), covering the entire geographical range of the archipelago (Fig. 1). On São Miguel Island, the palaeoecological record available is located within the caldera of Sete Cidades, for which Elias *et al.* (2016) predict a PNV dominated by *Laurus* submontane forests with patches of *Juniperus-Ilex* montane forests on the upper part of the eastern slopes. The pollen record corresponding to the period before Portuguese occupation of the islands (AD 1449) is dominated by *Juniperus brevifolia*, *Morella faya* and *Myrsine africana*, followed by *Erica azorica* and *Picconia azorica*. *Ilex perado* is also present but less abundant. The pollen of *Laurus azorica* is absent –possibly due to its chemical lability and poor preservation- but *Laurus* stomata are present, which is interpreted as the evidence of the local occurrence of the species (Rull *et al.*, 2017). All these species are typical of the *Laurus* and *Juniperus-Ilex* forests, showing a very good agreement between the MAXENT results and the palynological records in terms of presence-absence. The pollen records available for Pico Island lie in an area which predicted PNV is dominated by *Juniperus-Ilex* montane forests with patches of *Calluna-Juniperus* altimontane scrubs (Elias *et al.*, 2016). Pre-anthropic pollen assemblages are dominated by

Juniperus brevifolia and *Ilex perado* subsp. *azorica*, with the common occurrence of *Morella faya*, *Myrsine africana* and *Picconia azorica* (Connor *et al.*, 2012), which is also in agreement with the MAXENT PNV predictions, in qualitative terms. On Flores Island, the available pollen record comes from a lake (Lagoa Rasa), which, according to the MAXENT PNV outputs, is potentially an area of *Laurus* submontane forests surrounded by patches of *Juniperus-Ilex* montane forests (Elias *et al.*, 2016). Similar to the Sete Cidades record, from São Miguel Island, pre-anthropic pollen assemblages from Lagoa Rasa are dominated by *Juniperus brevifolia*, with *Myrsine africana* as the subdominant species. The main difference is that *Morella faya* is less abundant at higher elevations. All these PNV reconstructions and pre-anthropic pollen inferences also show a close correspondence, in qualitative terms, with the vegetation descriptions available from the initial stages of Portuguese colonization (e.g., Fructuoso, 1589; Moreira, 1987).

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

However, it should not be forgotten that PNV reconstructions, as proxies for pre-anthropic vegetation patterns, are intrinsically based on the idea of climatic similarity and, therefore, they are only applicable to time periods of climate similar to present. The same problem arises when using modern pollen analogs to interpret past vegetation if past climatic conditions were significantly different from today (Jackson & Williams, 2004). Widespread human occupation of the Azorean archipelago and associated environmental impacts took place during the Little Ice Age, under climates reasonably similar to the present, though slightly cooler and probably drier (Björck *et al.*, 2006). This should be taken into account in landscape management practices, especially in evaluating potential restoration targets, in order to assure their viability under present environmental conditions. Furthermore, vegetation changes, especially over long time scales, may occur due to large scale disturbances (especially on volcanic islands), species migration and extinction, or biotic interactions such as competition. Comparisons between PNV modelling and pre-anthropic pollen records should also contemplate that PNV reconstructions furnish broad-scale information (i.e., for a whole island), whereas pollen inferences use to provide clues on the vegetation lying around the coring site and surrounding areas of similar elevation. Therefore, island-wide comparative surveys should be based on representative networks of pollen records, which to date are still unavailable although a number of them are already in progress.

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

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Figure 1

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