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Abstract

The Azores archipelago has provided significant clues to the ecological, biogeographic and evolutionary knowledge of oceanic islands. Palaeoecological records are comparatively scarce, but they can provide relevant information on these subjects. We report the palynological reconstruction of the vegetation and landscape dynamics of the São Miguel Island before and after human settlement using the sediments of Lake Azul. The landscape was dominated by dense laurisilvas of Juniperus brevifolia and Morella faya from ca. AD 1280 to the official European establishment (AD 1449). After this date, the original forests were replaced by a complex of Erica azorica/Myrsine africana forests/ shrublands and grassy meadows, which remained until ca. AD 1800. Extractive forestry, cereal cultivation (rye, maize, wheat) and animal husbandry progressed until another extensive deforestation (ca. AD 1774), followed by the large-scale introduction (AD 1845) of the exotic forest species Cryptomeria japonica and Pinus pinaster, which shaped the present-day landscape. Fire was a significant driver in these vegetation changes. The lake levels experienced a progressive rise during the time interval studied, reaching a maximum by ca. AD 1778-1852, followed by a hydrological decline likely due to a combination of climatic and anthropogenic drivers. Our pollen record suggests that São Miguel were already settled by humans by ca. AD 1287, approximately one century and a half prior to the official historically documented occupation of the archipelago. The results of this study are compared with the few palynological records available from other Azores islands (Pico and Flores).

Keywords: palynology; palaeoecology; palaeoclimates; last millennium; Azores; early settlement

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Suggested reviewers: Luis Silva, Sandra Nogué

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Response to reviewer.docx [Response to Reviewers]

Azul pollen 3.2 (R1).docx [Manuscript File]

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Dear Editor,

I submit the revised versión of the manuscript entitled: Vegetation and landscape dynamics under natural and anthropogenic forcing on the Azores Islands: a 700-year pollen record from the São Miguel Island (formerly “Vegetation dynamics and human impact in the caldera of Sete Cidades (Sao Miguel, Azores Islands) during the last 700 years: the Lagoa Azul pollen record”), by V. Rull, A. Lara, M.J. Rubio-Inglés, S. Giralt, Vítor Gonçalves, P. Raposeiro, A. Hernández, Guiomar Sánchez-López, D. Vázquez-Loureiro, R. Bao, P. Masqué and A. Sáez.

All the comments and corrections of the reviewers have been addressed and several parts of the manuscript have been rewritten. A figure has been added (Fig. 4) and others have been modified according to the reviewer’s observations. The detailed amendments are listed and described in an attached file called “response to reviewers”.

Thank you for your attention.

Sincerely,
Valentí Rull

Barcelona, 27 January 2017

Review of the manuscript by Rull et al., "Vegetation changes and human impact in the caldera of Sete Cidades (São Miguel, Azores Islands) during the last 700 years: the Lake Azul pollen record"

This is an important article on environmental changes on the Azores islands through the last millennium. It contains new data and novel findings in relation to historical colonisation and palaeoclimate. The authors have done a wonderful job assembling the various lines of evidence and their interpretations are generally sound. The text is well written and the structure needs only minor improvements. In my opinion it would be a suitable contribution to QSR after moderate revision. I have some general comments below, followed by specific remarks.

The introduction needs more elaboration. Although the context for the research is clear – with a very good section detailing the previous palaeoecological research in the Azores – it is unclear what broader questions are to be answered. Perhaps the authors could provide a paragraph or two reviewing the literature on oceanic island ecosystems and the relevance of long-term perspectives for answering important ecological questions. As it stands, the introduction is not sufficiently broad to generate genuine international interest. The aims should align closely with the broader questions being asked – at the moment it seems that the aims arise from the data, rather than the data being used to address the aims.

Response. We added the following paragraph at the beginning of the introduction and the corresponding references to the reference list: "Islands, in particular oceanic islands, have been considered natural microcosmic laboratories to study fundamental ecological and evolutionary issues and their biogeographical expression (Whittaker & Fernández-Palacios, 2007). Since the proposal of the dynamic equilibrium model of island biogeography by MacArthur & Wilson (1967), island biotas and their communities have been viewed as the result of the continuous interaction of ecological and evolutionary patterns and processes across spatial and temporal scales (Whittaker et al., 2008). A key aspect of island ecology is the assembly of their ecological communities and how they change through time under the influence of internal (e.g., species' autoecology, competition, predation), and external (e.g., immigration, environmental change) ecological drivers (Whittaker & Fernández-Palacios, 2007). In the last millennium, human colonization of oceanic islands has become a paramount ecological factor that has determined profound changes in the composition and ecological functioning of island's biotas and ecosystems, mainly by the introduction of exotic elements, the extinction of autochthonous species and the replacement of original communities. The role of humans in the shaping of current biotic patterns of oceanic islands has been decisive worldwide (Gillespie & Clague, 2009). Paleoecology has been successfully used to record the timing and the ecological consequences of human colonization of oceanic islands (e.g., Prebble & Dowe, 2008; Prebble & Wilmshurst, 2009; Connor et al., 2012; Rull et al., 2016). In this paper, we use paleoecological methods to reconstruct the vegetation dynamics of the last millennium in the Atlantic Azores archipelago and their main drivers of ecological change, with emphasis on climate changes and the timing of the initial human settlement and its further consequences. The main aim is to understand how present-day plant communities and landscapes have been shaped." (lines 101-123).

The authors interpret their results in terms of disturbances from human impact and lake-level change. This is fine, but they have neglected a very important disturbance – the volcanic eruption in ~1283 AD. Some discussion of post-eruption vegetation succession would be a welcome addition.

Response. The post-eruption vegetation succession corresponds to pollen zone AZ1 and is explained in the results section. To emphasize this, we have modified the first sentence of the paragraph to: "In this pollen zone, which corresponds to the post-eruption phase, *Juniperus brevifolia* experiences a significant reduction…" (lines 420-421). On the other hand, it has not been possible to attest the effects of the volcanic eruption on the original vegetation because we do not have evidence of the pre-eruption conditions (i.e., the record starts just after the eruption).

Lake levels are reconstructed on the basis of changes in lithology, Myriophyllum pollen and Botryococcus remains. As mentioned in my specific comments for lines 366, 509 and 528, these proxies need better justification and explanation.

Response. See comments in the corresponding points below.

Some very important findings rest on evidence from Laurus stomata and Secale pollen. It would be very helpful to include microphotographs of both of these fossils, both to add weight to the authors' arguments and to assist other researchers. Recent publication of Quercus and Carpinus records from Tenerife has led some Macaronesian ecologists to doubt palynological research. I would encourage the authors remove this doubt by including photographs as supplementary online information.

Response. The required microphotographs have been added as a new figure (Figure 4).

A major concern is that the authors often give precise dates given without consideration of errors involved. The authors downplay the errors inherent in calibration to the point of non-existence (see my comments below on line 604). The age-depth model does not consider the major eruption in 1283 AD as a starting point for sedimentation; instead it begins earlier. This does not seem plausible. Early human occupation is dated to the year 1287 AD, so people were farming in the crater only 5 years after the volcano erupted. Is this a likely scenario? I would encourage the authors to embrace the errors inherent in the age model. After all, their conclusion of early human occupation stands even when the errors are properly taken into account.

Response. The errors of all dates mentioned in the text derived from the application of the age-depth model have been added. The chronological difference between the eruption and the beginning of the sequence falls within the dating errors (typically ±40 years at the base of the sequence); hence, these two events cannot be precisely separated and we assume that they are more or less simultaneous. Concerning human settlement, the consideration of dating errors places this event between AD 1247 and 1327 (1287±40), that is, approximately 100-180 years before the official discovery of the island (AD 1427) and 120-200 years before the official settlement of the archipelago (AD 1449). This has been added to the text (lines 642-645). Therefore, our point of an earlier colonization than previously assumed still remains.

Overall, I think this is a very interesting and novel contribution. I hope the authors find my comments helpful in improving their manuscript for publication.

Regards,

Simon Connor

Specific comments (by line number):

55 (and 67, 260) – the authors use the term "São Miguel lowlands" to describe the surroundings of Lagoa Azul, but I find this a very confusing term, as the pollen record only pertains to the caldera of Sete Cidades and not to other lowland areas of São Miguel Island.

Response. The term "lowlands" has been removed to avoid confusion.

101 – why "relevant"? Isn't this word superfluous?

Response. Deleted.

102 – check spelling of Schäffer/Schäfer (Hanno tells me he prefers Schaefer)

Response. Schaefer has been used in all cases.

105 – spelling of Trianis/Triantis; explain why the debates are "stimulating"

Response. Trianis replaced by Triantis. The term "stimulating" has been deleted as it is not necessary.

106-110 – I don't see how the Azores are "unique" in this way… the same statement applies to all remote oceanic islands.

Response. The term "unique" has been replaced by "unprecedented".

145-163 – this is a very important section but lacks any references to relevant literature

Response. The following references have been added in the appropriate parts: Fructuoso (1589), Tutin (1953), Moreira (1987), Silva & Smith (2004), Dias et al. (2005), Dias (2007) and Connor et al. (2012).

161 – algal remains?

Response. Yes, replaced.

191 – replace "where" with "when"

Response. Done

208 – “Macaronesic” perhaps should be “Macaronesian”

Response. Replaced.

209 – the flora appears to be poor, but, as some of Hanno Schaefer and Monica Moura’s recent work has shown, this may be a problem of the ‘Linnean shortfall’ where there are high levels of unseen (cryptic) diversity

Response. The following sentence has been added “…-although some recent studies suggest that taxa richness would be significantly higher if the cryptic genetic variability was considered (Schaefer et al. (2011b)-…” (lines 234-236).

211 – please correct the spelling of “Scaeffer” and “Trianis”

Response. Done.

213 – there is emerging genetic evidence of there being more single island endemics than previously thought (e.g. Angelica lignescens is to be split into separate species).

Response. Maybe, but the degree of endemism is still low as compared with other archipelagos.

216 – isn’t this particular species of Vicia globally extinct?!

Response. The reference to this species has been deleted.

227-228 – the description of high elevation grasslands applies to the island of Flores, and not generally as your statement seems to suggest.

Response. The sentence has been modified as follows: “Some historical descriptions seem to suggest that higher elevations of the Flores Island were covered by grasslands, but this has not been confirmed (Dias, 2007).” (lines 253-254).

234 – consider “islands” rather than “island”

Response. Replaced.

242 – “a large part… is dominated”

Response. Corrected.

248 – species name is misspelled

Response. Changed to “*gardnerianum*”.

266 – Shotton & Williams reference is not provided in the reference list.

Response. Added.

309 – no age-depth model is shown in the manuscript. At a minimum, please add an age scale alongside the depth scale on the pollen diagram (Fig. 3).

Response. An age scale in years AD has been added to figures 3 and 5.

340 – the pollen counts here are quite low… how was 'saturation of diversity' assessed?

Response. These are the minimum counts required by the method. The revised version reports the actual counts: "Counting followed the criteria of Rull (1987), ranging from 306 to 1051 (average 580) pollen grains and pteridophyte spores per sample." (lines 367-368).

354 – the age model suggests the oldest sediments are from 1273 AD, but the volcano apparently erupted in 1283 AD (see line 266)… is this possible? Would it not be simpler to assume that the 1283 AD eruption marks the beginning of the sedimentation? How well is this eruption dated?

Response. As explained above, the dating error is larger than the difference between these two dates. The revised version contains these errors for more clarity.

366-368 – I think the interpretation of flood events needs better justification/explanation. I note that there are peaks of fern spores and Anthoceros in the pollen diagram, which does suggest inwash of terrestrial sediments – this could be additional evidence for the authors' interpretation of flood deposits. Is there additional information from loss-on-ignition or diatoms that could help?

Response. The facies of the sedimentary sequence represented in this core were studied and described in detail, and interpreted in terms of sedimentary environments, by Rubio-Inglés (2016), who made the interpretation using a large set of physico-chemical proxies. In our paper, only a brief summary is presented. This is stated in the manuscript: "The sedimentary sequence represented in this core was described in detail and interpreted in terms of sedimentary environments by Rubio-Inglés (2016). Here, a brief summary is presented. The section encompassed four lithological units named U1 (base) to U4 (top) (Figure 4)." (lines 380-383).

376-383 – it is hard to see the relevance of this paragraph. Consider omitting

Response. Deleted.

377 – check spelling of Poaceae

Response. This part of the paragraph has been deleted.

390 – the stomata of Laurus azorica are very interesting. How were they identified? It would be useful to include a photograph of these (perhaps as supplementary information) to help other researchers to identify them.

Response. This has been added to the methods section: "*Laurus azorica* stomata were identified by comparison with living material from the Botanical Garden of Barcelona." (lines 363-364). The photograph was also added as Figure 4B.

426 – the idea that Morella alone remained in the vegetation could be questioned – it is a very high pollen producer and the pollen disperses very well, so the presence of pollen is not a reliable indicator of local plant presence (see also interpretation on line 635).

Response. In the results section, the sentence has been modified by pointing that "…only the pollen of *Morella faya* remained…" (lines 446-447), which has no direct implications for forest composition. In the interpretation, we do not say that *Morella* forests grow *in situ*.

448-450 – the idea that Erica is indicative of forestry is questionable. While old-growth Erica plants are large enough to be used for timber, most of the Erica found on the Azores is in the form of shrubby secondary regrowth after disturbance. Erica azorica is very tolerant of grazing and seems to be abundant today because of this tolerance. Perhaps, in the case of the Lagoa Azul record, Erica is an indicator of abandoned fields?

Response. We obtained the information on *Erica/Myrsine* forests from the cited literature, where the use of *Erica* for forestry purposes is well documented. We did not find the interpretation of grazing tolerance and abandoned fields. However, we introduced the reviewer's suggestion as personal communication: "At present, *Erica azorica* is a grazing-tolerant species, which is also frequent in the form of secondary regrowth after disturbance (S. Connor, pers. comm.). It is possible that this fact has also contributed to its higher abundance in this zone" (lines 478-481).

457 – could these earthquakes also have had an impact on the lake sediments through slumping?

Response. We have no evidence on this phenomenon and we consider that it is not relevant in this context.

509-521 – while I think the idea of reconstructing lake levels is wonderful, I have some doubts about the interpretation of Myriophyllum and Botryococcus as good indicators of lake level. The authors acknowledge (lines 502-4) that "historical vegetation changes in the Lake Azul catchment have been driven mostly by humans, pollen and spores are not reliable palaeoenvironmental and palaeoclimatic proxies", so why should Myriophyllum and Botryococcus be any different? It would help to have more than one reference linking each of these taxa to lake-level variations.

Response. We have several reasons to believe that *Myriophyllum* and *Botryococcus* were not as affected by human activities as terrestrial plants. First, both genera were present since the beginning of the sequence, well before island settlement, demonstrating that they are indigenous taxa not introduced by humans. Second, the stratigraphic variations of these taxa do not follow the same patterns of terrestrial plants, whose shifts are primarily the consequence of human activities. This is well depicted in Figure 5, where it can be seen that shifts in *Myriophyllum* and *Botryococcus* do not agree with the zonation based on anthropogenic changes in terrestrial vegetation. Third, there are no historical reports of human introductions and local extinctions of aquatic plants and planktonic algae comparable to the abundant and detailed literature on the management of terrestrial plants. Given the thoroughness and accuracy of historical documents about human impact on plant ecology in the archipelago, it would be expected that, if aquatic plants had been managed in a similar fashion as terrestrial plants, this fact would have been clearly reported in historical documents. The only references available to date about the anthropogenic influence on aquatic plant communities of Lake Azul correspond to the 20th century and report the former presence of macrophytic green algae such as *Chara* and *Nitella* (Cunha, 1939), and the likely accidental introduction of exotic species (*Egeria*, *Elodea*) by aquarium enthusiasts since the 1970s (Pacheco et al., 1998). This reasoning has been added to the text (lines 533-570). Also, we have provided additional references on the use of *Botryococcus* as water-level proxy (Jankovská & Komarek, 2000; Rull et al., 2008; Niehman & Behling, 2009; Koff & Terasmaa, 2011; Cohen, 2012; Leroy et al., 2014; Zhao et al., 2015) (lines 544-546)

528-30 – "coexistence of macrophytes and diatom types of different ecological requirements may suggest the occurrence of oscillating water levels at the time"… have the authors considered that this may also occur under stable water levels where there are various depth zones within a lake? Lagoa Azul appears to have a complex bathymetry, so it is not surprising to find pollen and diatoms with various depth tolerances mixed together. The text should take account of this complexity. In general terms, this section could benefit from a better integration of the previous results of diatom analysis (Raposeiro et al. 2016) to form a stronger argument for lake level changes.

Response. The reviewer's suggestion has been incorporated as follows: "The sequence begins with the dominance of *Potamogeton* (90-113 cm; AD 1273±40 to 1289±40), minimum abundances of *Botryococcus* and the absence of *Myriophyllum*. This assemblage suggests low water levels, prior to the inundation of the platform (Figure 2). Preliminary data on diatom assemblages, however, indicate that the euplanktonic *Aulacoseira granulata*, typical of moderate to high water levels (Wollin & Stone, 2010), was one of the dominant taxa in the interval 110-114 cm (Vázquez-Loureiro et al., in prep.). This apparent discrepancy can be explained by either oscillating water levels at the time of deposition, or by the mixing of sediments with pollen and diatoms derived from littoral and pelagic environments, respectively." (lines 572-580). The study of diatoms is still in progress but the preliminary results show a good agreement with lake-level history as reconstructed here. This has been added to the text: "It is important to stress that lake-level shifts, as reconstructed in this study, significantly agree with the same trends as deduced from diatom assemblages, whose study is in progress (Vázquez-Loureiro et al., in prep.)." (lines 548-550).

581-88 – no mention is made here of dating errors, which could be a significant source of age uncertainty when comparing these records.

Response. The following sentence has been added: "Dating errors should also be taken into account, although they do not significantly affect comparisons" (lines 639-640).

604 – the authors claim that the "radiocarbon date calibrated to AD 1287 (690±30 14C BP or 663±12 cal BP)". The reported error margin of 12 years is not correct, as a 2-sigma (95% probability) calibration of a date of 690±30 BP gives a result of 1266-1312 AD (70% probability) and 1358-1387 AD (30% probability). This equates to an error of approximately ±60 years. While I appreciate the authors' excitement at finding this evidence of early occupation, I think it should be reported with correct consideration of the errors involved.

Response. We corrected these numbers as indicated by the reviewer (lines 649-650) but the dates are still before the official discovery and settlement of the island; therefore, our hypothesis or an earlier colonization still survives.

629 and 633 – there are conflicting interpretations of Juniperus pollen abundance here – on the one hand, it is supposed to be important in the forests during a period of dry climate (line 629), while on the other hand it is said to be a wetland plant (line 633). While Azorean junipers can tolerate waterlogging, I have never seen them growing in a lake, so I doubt the idea that "Juniperus brevifolia develops well in permanent aquatic habitats" (line 645).

Response. The reference to drier climates has been deleted, as a paleoclimatic study that is in progress does not support this interpretation.

691-3 – the statement about "Cryptomeria japonica and Pinus pinaster… absence in all the pollen diagrams of Pico and Flores Islands" is incorrect. These taxa are given in Table 2 in Connor et al. (2012), as well as in supplementary information. Certainly they are less abundant in the Pico and Flores records than in the Lagoa Azul record, but it is incorrect to say they were 'absent'. The statement about these species not being recorded in vegetation surveys is strange… there are certainly many Cryptomeria and Pinus trees on Pico and Flores nowadays.

Response. We have replaced "absence" by "scarcity" and deleted the reference to present-day vegetation. The sentence now reads: "Also noteworthy is the high abundance of *Cryptomeria japonica* and *Pinus pinaster* in our record during the last centuries and their scarcity in the pollen diagrams of Pico and Flores Islands" (lines 736-738).

707 – The authors incorrectly state that "In the Pico and Flores records, however, Secale cereale is absent". See Table 2 of Connor et al. (2012).

Response. The sentence has been modified to: "In the Pico and Flores records, however, *Secale cereale*, *Zea mays* and other cereals appear in very low amounts only in the Rasa diagram after human settlement (Connor et al., 2012)." (lines 750-752).

Fig 3. The "ES" on the right-hand side of the graph appears to be later (95 cm) than the first appearance of Secale pollen (98 cm) – this should be corrected. The second occurrence of Secale does not align with the other pollen samples around this depth – I think the dot is placed incorrectly.

Response. The "ES" mark has been deleted from this figure.

Fig. 4. This figure would be more helpful if the vertical axis was by age rather than by depth. It is very difficult to compare the Myriophyllum and Botryococcus curves to other late Holocene palaeoclimatic records from the Azores and the North Atlantic while they are plotted by depth.

Response. We prefer to maintain this figure (now figure 5) as is for a better comparison with the pollen diagram (but we have added the same age scale of figure 3 for more clarity). The same patterns and trends of this figure are already expressed in terms of age in Figure 6 and compared with other Holocene records.

Fig 5. Consider “wetting” instead of “wettening” (see also Fig. 4)

Response. This word does no longer appears in the figures.

Vegetation and landscape dynamics under natural and anthropogenic forcing on the Azores Islands: a 700-year pollen record from the São Miguel Island

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Abstract

The Azores archipelago has provided significant clues to the ecological, biogeographic and evolutionary knowledge of oceanic islands. Palaeoecological records are comparatively scarce, but they can provide relevant information on these subjects. We report the palynological reconstruction of the vegetation and landscape dynamics of the São Miguel Island before and after human settlement using the sediments of Lake Azul. The landscape was dominated by dense laurisilvas of *Juniperus brevifolia* and *Morella faya* from ca. AD 1280 to the official European establishment (AD 1449). After this date, the original forests were replaced by a complex of *Erica azorica/Myrsine africana* forests/shrublands and grassy meadows, which remained until ca. AD 1800. Extractive forestry, cereal cultivation (rye, maize, wheat) and animal husbandry progressed until another extensive deforestation (ca. AD 1774), followed by the large-scale introduction (AD 1845) of the exotic forest species *Cryptomeria japonica* and *Pinus pinaster*, which shaped the present-day landscape. Fire was a significant driver in these vegetation changes. The lake levels experienced a progressive rise during the time interval studied, reaching a maximum by ca. AD 1778-1852, followed by a hydrological decline likely due to a combination of climatic and anthropogenic drivers. Our pollen record suggests that São Miguel were already settled by humans by ca. AD 1287, approximately one century and a half prior to the official historically documented occupation of the archipelago. The results of this study are compared with the few palynological records available from other Azores islands (Pico and Flores).

Keywords: palynology, palaeoecology, palaeoclimates, last millennium, Azores, early settlement

Introduction

Islands, in particular oceanic islands, have been considered natural microcosmic laboratories to study fundamental ecological and evolutionary issues and their biogeographical expression (Whittaker & Fernández-Palacios, 2007). Since the proposal of the dynamic equilibrium model of island biogeography by MacArthur & Wilson (1967), island biotas and their communities have been viewed as the result of the continuous interaction of ecological and evolutionary patterns and processes across spatial and temporal scales (Whittaker et al., 2008). A key aspect of island ecology is the assembly of their ecological communities and how they change through time under the influence of internal (e.g., species' autoecology, competition, predation), and external (e.g., immigration, environmental change) ecological drivers (Whittaker & Fernández-Palacios, 2007). In the last millennium, human colonization of oceanic islands has become a paramount ecological factor that has determined profound changes in the composition and ecological functioning of island biotas and ecosystems, mainly by the introduction of exotic elements, the extinction of autochthonous species and the replacement of original communities. The role of humans in the shaping of current biotic patterns of oceanic islands has been decisive worldwide (Gillespie & Clague, 2009). Paleoecology has been successfully used to record the timing and the ecological consequences of human colonization of oceanic islands (e.g., Prebble & Dowe, 2008; Prebble & Wilmshurst, 2009; Connor et al., 2012; Rull et al., 2016). In this paper, we use paleoecological methods to reconstruct the vegetation dynamics of the last millennium in the Atlantic Azores archipelago and their main drivers of ecological change, with emphasis on climate changes and the timing of the initial human settlement and its further consequences. The main aim is to understand how present-day plant communities and landscapes have been shaped.

The Azores Islands have been the target of biogeographic, evolutionary and ecological studies (e.g., Tuya & Haroun, 2009; Schaefer et al., 2011a; Illera et al., 2012; Whittaker et al., 2014). Evolutionarily, this volcanic archipelago is of relatively recent origin, ranging from <1 to 8 million years, and the origin and further evolution of its flora have been the subject of debate (Schaefer et al., 2011b; Triantis et al., 2012). Ecologically, the Azores may be viewed as the home of a large-scale, unintentional experiment, in which plants introduced by humans from disparate geographical and ecological origins have replaced the original vegetation and have developed new communities, whose composition and ecological functioning are unprecedented (Dias, 2007; Dias et al., 2005; Schaefer et al., 2011a).

The ecological study of the Azores flora and vegetation may benefit significantly from palaeoecology, especially from palynology, but this discipline has not been thoroughly applied to the archipelago. To date, only a few records from a couple of islands of the archipelago are available, covering the last 6000 years (Björck et al., 2006; Connor et al., 2012). In spite of this paucity, these past environmental and ecological records have provided relevant and useful results. For example, van Leeuwen et al. (2005) demonstrated that *Selaginella kraussiana*, a species that had been previously considered as introduced by Europeans, was native to the Azores because its spores were present in the pollen records prior to human arrival. Björck et al. (2006) reconstructed the climatic and volcanic history of Pico Island (Figure 1) during the last 6000 years using multiproxy analysis of sediments from Lake Caveiro. Despite the dominant volcanic signal, these authors were able to unravel the palaeoclimatic trends, suggesting that precipitation changes since the mid Holocene were linked to the North Atlantic drift-ice variation, with a remarkable effect of the North Atlantic Oscillation (NAO) during the last millennia. Björck et al. (2006) identified a number of centennial-scale cooler/drier and wetter phases, of which the most significant for the time frame of this study correspond to 400-800 cal y BP (AD 1150-1550) (cooler/drier) and 300-400 cal y BP (AD 1550-1650) (wetter).

The previous palynological studies of the Azores were performed on the islands of Pico (Lake Caveiro and Pico bog) and Flores (Lake Rasa) (Connor et al., 2012). According to these studies, human colonization had a greater impact on the pristine vegetation than climatic change and volcanic activity in the last millennia. Human impact was manifested in the form of a sudden shift (<100 years) to open vegetation, which was maintained for centuries by burning, grazing and edaphic changes. Endemic species were especially affected by humans. For example, the native *Juniperus brevifolia* communities declined and at least two native fern species of *Ophioglossum* went extinct on Pico. Connor et al. (2012) also reported that a number of species previously considered as human introductions were in fact native. These authors concluded that the pre-anthropogenic palaeoclimatic variation was not clearly reflected as changes in the Holocene forest composition or structure and that major volcanic eruptions favored the establishment of endemic species as first colonizers of newly formed soils, but the vegetation did not change significantly.

The palaeoecological study of the Azores archipelago could provide important clues to the understanding of the present-day landscape and the natural or anthropogenic drivers involved, which has relevant implications for conservation management (Connor et al., 2012). An additional advantage is that many aspects of landscape development and transformation after human settlement have been reported in historical documents (e.g., Fructuoso, 1589; Tutin, 1953; Moreira, 1987; Silva & Smith, 2004; Dias et al., 2005; Dias, 2007), enabling comparison with palynological records, which can significantly improve ecological reconstructions. The comparison of the ecosystem composition and development before and after human colonization of the islands could also provide useful clues to disentangle the natural environmental and anthropogenic drivers of ecological change. In this paper, we address the palynological study of São Miguel using sediments from Lake Azul. This island is devoid of palaeoecological studies of this nature. Previous surveys using lake sediments were conducted in Lake Azul and others from the same island (Fogo, Furnas) to assess the ecological effect of recent introductions of exotic fish species (Skov et al., 2010; Buchaca et al., 2011; Raposeiro et al., 2017). We use pollen and spore analysis combined with charcoal and selected non-pollen palynomorphs (NPP) to reconstruct the development of the vegetation of the island before and after European settlement. Additionally, we use pollen from aquatic plants and algal remains to infer preliminary palaeoenvironmental trends, in terms of lake levels. Finally, we attempt an integrated reconstruction of the landscape dynamics using all these data. The record covers the last ~700 years at decadal to multidecadal resolution.

Study site

General description

The island of São Miguel is in the volcanic Azores archipelago, situated near the middle of the North Atlantic, 1400 km from Europe and 1800 km from North America (Figure 1). The Azores Islands lie at the intersection of three major tectonic structures: the Eurasiatic, the African and the American plates. Currently, there are 12 active volcanoes, five of which are submarine, and the main volcanic manifestations are fumaroles and hot springs. Due to its geographic dispersion, the archipelago has been subdivided into three groups of islands: the Western Group (Flores and Corvo), the Central Group (Terceira, São Jorge, Graciosa, Pico and Faial) and the Eastern Group (Santa Maria and São Miguel) (Gillespie & Clague, 2009). The maximum elevation is Montanha do Pico (2350 m) on Pico Island. São Miguel is the largest (745 km^2) and most populated (125,000 inhabitants) island of the archipelago and contains the capital, Ponta Delgada. The maximum elevation of this island is Pico da Vara (1100 m). There are three active volcanic calderas on the island: Furnas, Fogo and Sete Cidades, all of which contain lakes (Figure 1).

The Azorean climate is temperate oceanic with low thermal variation throughout the year but significant seasonal and interannual variability in precipitation (Cropper & Hanna, 2014; Hernández et al., 2016). In São Miguel, the average annual temperature at sea level is approximately 17 ºC, and it decrease with elevation at a rate of >0.7 ºC/100 m (Moreira, 1987). Atmospheric humidity is high (80-90%), and the formation of dense mists is frequent, especially above 300 m elevation. Precipitation is also dependent on elevation, ranging from 960 mm on the coasts to >2500 mm above 600 m elevation. The average precipitation is ~1700 mm per year with a rainy season between October and March, when ~75% of the precipitation occurs (Cruz et al., 2015; Hernández et al., 2016).

The most accepted date of human colonization of the Azores Islands is 1432, when Gonzalo Velho Cabral arrived at Santa Maria and took possession of the island in the name of the King of Portugal. The same navigator reached São Miguel in 1432. The official settlement of the islands began in 1449 (Fructuoso, 1589). Some historians believe the Azores Islands, like many other archipelagos of the North Atlantic region, were already known, although not settled, a century before the Portuguese colonization. This idea is based on maps from the 14^{th} century (AD 1339), where the islands Corvo and São Miguel were already present, though with different names: Corvinaris for Corvo and Caprara for São Miguel (Moreira, 1987).

Flora and vegetation

The Azores Islands are part of the biogeographical region known as Macaronesia (Figure 1), together with Madeira, the Canary Islands and Cape Verde (Fernández-Palacios et al., 2011). Compared with other Macaronesian islands, for example, Madeira and the Canaries, the Azorean flora is comparatively poor –although some recent studies suggest that taxa richness would be significantly higher if the cryptic genetic variability was considered (Schaefer et al. (2011b)- likely due to geographical isolation, stable climate, younger geological origin, small island size and habitat homogeneity (Carine & Scaeffer, 2010; Triantis et al., 2012). The Azorean flora consists of 811 species, of which 197 are considered native and 70 are endemic to the Azores (Schaefer, 2003, 2005; Borges et al., 2010). The number of single-island endemisms is low, which contrasts with other archipelagos, notably the Canary Islands, where local endemisms are frequent (Carine & Schaefer, 2010). A high proportion of the Azorean endemics (~75%) occur on São Miguel.

The current vegetation of the Azores Islands is largely anthropogenic. After several centuries of deforestation and the introduction of exotic species, the native vegetation has been drastically reduced to a few small sites that are now under active protection (Schaefer, 2002; Connor et al., 2012). According to historical documents, when Portuguese colonizers arrived at the Azores, the islands were covered with luxuriant and dense laurisilvas dominated by *Laurus azorica*, *Juniperus brevifolia*, *Prunus azorica* and *Morella faya* (Dias, 2007). In addition to these dominant species, the laurisilvas of São Miguel contained *Ilex perado*, *Erica azorica*, *Myrsine africana*, *Vaccinium cylindraceum*, *Viburnum tinus*, *Frangula azorica*, *Taxus baccata*, *Picconia azorica* and *Calluna vulgaris* (Moreira, 1987). Some historical descriptions seem to suggest that higher elevations of the Flores Island were covered by grasslands, but this has not been confirmed (Dias, 2007).

The Azores Islands were seen by the Portuguese crown as a new space for economic development, primarily for cereal cultivation—mainly wheat (*Triticum* spp.) but also rye (*Secale cereale*), barley (*Hordeum* spp.) and oats (*Avena* spp.)—and meat production. As a consequence, the native forests were destroyed by felling and burning. With time, the deforestation of the islands progressed and more and more exotic species were introduced for cultivation (woad, sugar, vines, pepper, pineapple, and oranges), forestry and ornamental purposes, thus shaping the present-day Azorean landscape, which Dias (2007) describes as "a botanical garden in the Atlantic". São Miguel is one of the Azorean islands with a higher proportion (~70%) of non-indigenous species (Silva & Smith, 2004, 2006).

Today, most of the Azores surface (75%) is dedicated to human activities (46% to crops, 15% to towns and 14% to other purposes), whereas forests occupy only 25% of the area (Dias, 2007). A large part of these forested areas is dominated by introduced trees. In the forests of São Miguel, the dominant trees are *Pittosporum undulatum*, *Acacia melanoxylon*, and *Eucalyptus globulus*, which were introduced from Australia, *Cryptomeria japonica* from Japan, and few representatives of the native forests, mainly *Morella faya* and *Laurus azorica*. *Pittosporum undulatum*, initially introduced as a hedgerow species, is considered one of the more successful and dangerous invaders of the island, along with *Hedychium gardnerianum*, *Gunnera tinctoria* and *Clethra arborea* (Hortal et al., 2010; Gil et al., 2013). *Cryptomeria japonica* and the Mediterranean *Pinus pinaster* were introduced for silviculture and transformed the island's landscape by establishing dense forests that replaced the former laurisilvas above 300 m elevation (Moreira, 1987). The present landscape of São Miguel is almost totally cultural, in contrast with other islands, such as Pico and Flores, where human pressure has been less intense (Dias, 2007).

Material and methods

Coring lake

The sediments analyzed in this study were obtained from Lake Azul, situated in the São Miguel Island. A ~1.5 m long sediment core (AZ11-02-01; 37º52'20" N-25º46'26" W) was taken in October 2011 using a UWITEC© gravity corer at a water depth of 25.1 m (Figure 1). Lake Azul is located within the caldera of Sete Cidades (~5 km diameter and ~400 m maximum elevation), together with three smaller lakes, named Lake Verde, Lake Santiago and Lake Rasa (Figure 1). The caldera is the result of explosive volcanic activity during the last 200,000 years. In the last 5000 years, 17 eruptions have been documented, the last (P17) ending 667 years BP (Shotton & Williams, 1971; Cole et al., 2008; Queiroz et al., 2008). Lake Azul and Lake Verde are two sedimentary basins that are hydrologically connected by a narrow passage. Sometimes the complex of the two lakes appears in the literature under the name Lake Sete Cidades, which is the most extensive lake of the Azores Islands (Cruz et al., 2006, 2015). The lakes are situated at 259 m elevation with a total surface area of 4.35 km^2. Lake Azul is 2600 m long (SW-NE) and 2100 m wide (SE-NW), with a total surface area of 3.6 km^2 and a maximum depth of 28.5 m (Cruz et al., 2015). The water level is relatively constant due to the existence of a tunnel excavated in 1937 on the northern side of the volcanic cone to drain freshwater to the sea, to prevent flooding of the Sete Cidades village. The bathymetry of Lake Azul shows an internal topography that is relevant for sedimentation history and palaeoenvironmental interpretation (Figure 2). The deepest part of the basin (28-25 m water depth) is to the NE, where the lake shore is shaped by the inner walls of the caldera. Most of the sediments accumulate in this basin plain, which is interrupted at the NW by a steep slope ranging from 25 to 12 m in depth in less than 500 m distance. Between 12 m depth and the SW lake shore, there is a gentle platform ramp that represents nearly the half of the water spill surface. The vegetation of the caldera has been totally modified, and the current main activities are agriculture (24% of the inner surface) and silviculture (>40%). Forests grow mainly on the steep slopes of the crater and are dominated by the introduced trees *Cryptomeria japonica*, *Pittosporum undulatum, Acacia melanoxylon* and *Hedychium gardnerianum*. Lake-shore macrophytic communities are composed mainly of *Egeria densa* and *Myriophyllum alterniflorum*, with *Ceratophyllum demersum*, *Potamogeton polygonifolius, Nymphaea alba* and *Chara fragilis* also present (Rubio-Inglés et al., 2013). Some of these species are believed to have been released accidentally or deliberately by aquarists in the early 1970s (Pacheco et al., 1998). At present, Lake Azul is in the process of eutrophication as a result of land fertilization for agriculture (Cruz et al., 2015).

Dating and age-depth model

The chronological model is based on both the ^{210}Pb profile and four radiocarbon AMS dates (Table 1). The concentration profile of ^{210}Pb was determined every centimeter for the uppermost 21 cm through quantification of ^{210}Po by alpha spectroscopy, following Sánchez-Cabeza et al. (1998), at the Autonomous University of Barcelona. The concentration of ^{226}Ra (via ^{214}Pb) was determined in selected samples along the core by gamma spectrometry, and the excess ^{210}Pb concentrations were calculated by subtracting ^{226}Ra from the total ^{210}Pb concentrations. $^{210}Pb_{ex}$-derived sedimentation rates were calculated by applying the CRS model (Appleby and Oldfield, 1978). The radiocarbon AMS dates were obtained from a pollen enrichment extract prepared by acid digestion (Rull et al., 2010) and three plant macroremains (Table 1) and were analyzed at Beta Analytic Lab (USA). The AMS radiocarbon dates were calibrated using Calib 7.1 software and the Intcal13 curve (Reimer et al., 2013) and selecting the median of the 95.4% distribution (2σ probability interval).

The age-depth model of the Lake Azul sequence was calculated using the dynamic age model technique (Rúbio-Inglés, 2016). This method calculates the age of the samples of a given historical sequence by redistributing the time along the profile according to the amount of terrigenous material present in samples. It derives the short- and long-term sedimentation rate changes from the chemical composition of the terrigenous sediments obtained from the XRF core scanner dataset. The main advantage of this method is that it assumes that the sedimentary environment does not have previous "memory" and, hence, abrupt sedimentation rate changes are possible. This method was applied from the top to a core depth of 86 cm, where the last radiocarbon date was found. The age of the pollen samples from 86 cm to 113 cm, i.e., the base of the pollen diagram (Figure 3), was obtained by applying a linear regression model considering that the lithology of the bottom of the core represents the latest phase of the last volcanic eruption (P17) that affected the lake (Shotton & Williams, 1971). The age-depth model obtained in this way has been successfully used in a chironomid-based paleoecological study of the same lake (Raposeiro et al., 2016).

Sample processing and analysis

A total of 57 samples were taken at regular intervals for pollen analysis (one sample every 2 cm, on average). After spiking with *Lycopodium clavatum*, these samples were submitted to KOH, HCl and HF digestion and acetolysis. The residues were suspended in glycerine, and the microscopic slides were mounted in the same medium (Bennett & Willis, 2001). Processing was carried out at the Institute of Plant Science, University of Bern (Switzerland) and the Botanic Institute of Barcelona (Spain). The identification of pollen and fern spores followed Moore et al. (1991), Reille (1992-1998), Beug (2004) and Demske et al. (2013). Non-pollen palynomorphs (NPP) were identified according to van Geel & Aptroot (2006), van Geel et al. (2011), Cugny et al. (2010), Gerolini et al. (2012) and Montoya et al. (2012). Conifer stomata were identified with the help of Sweeny (2004) and Zhang et al. (2011). *Laurus azorica* stomata were identified by comparison with living material from the Botanical Garden of Barcelona. Cerealia were separated from the rest of the Poaceae using the diameter of the pollen grain (>47 μm) and the annulus (>11 μm) (Joly et al., 2007). *Zea mays* and *Secale cereale* were identified according to Beug (2004). Counting followed the criteria of Rull (1987), ranging from 306 to 1051 (average 580) pollen grains and pteridophyte spores per sample. The pollen sum included all pollen types except those from aquatic and semi-aquatic taxa (Cyperaceae, *Myriophyllum* and *Potamogeton*). Diagrams were plotted and zoned with *psimpoll 4.27* using the method of optimal splitting by information content (OSIC) (Bennett, 1996).

Results and interpretation

Sedimentary facies

According to the obtained results, the recovered lacustrine sedimentary infill (133 cm thick) from Lake Azul records the time period between AD 1273±40 and AD 2010±1. Core AZ11-02-01 was retrieved from the deepest plain of the offshore zone of the lake. The sedimentary sequence represented in this core was described in detail and interpreted in terms of sedimentary environments by Rubio-Inglés (2016). Here, a brief summary is presented. The section encompassed four lithological units named U1 (base) to U4 (top) (Figure 3). Unit 1 (133-103 cm) was composed mainly of volcanic ash and lapilli interbedded with thin muddy lacustrine layers. These deposits indicate the occurrence of lacustrine environments with frequent input of volcaniclastic material from an active volcano inside the Sete Cidades caldera. According to the age-depth model, this interval likely corresponds to the end of the P17 eruption phase, dated to ca. AD 1280 by Shotton & Williams (1971). Unit 2 (103-85 cm) was composed mainly of light-gray laminated mud rich in volcanic particles. This unit is interpreted as the result of the reworking of volcanic ash sediments previously deposited elsewhere in the catchment. Unit 3 (85-61 cm) consists of brownish-green laminated fine to coarse silts. These fine offshore deep deposits are interbedded with dark layers rich in plant debris and terrestrial aerophilous diatoms and barren of chironomids, representing episodic terrigenous input, likely from flood events in the catchment. Unit 4 (61-0 cm) was composed of massive to poorly laminated light-brown silty clays deposited in offshore conditions similar to today (i.e., 25 m water depth). Interbedded layers corresponding to rapid flooding sedimentation are more frequent in this unit, especially in its lower half, with a relevant event of this type between ca. 40 and 46 cm (Figure 3).

Vegetation shifts and human activities

The pollen diagram was subdivided into three significant assemblage zones, which are described and discussed in the following.

Zone AZ1 (74-113 cm, 15 samples, AD 1273±40 to1358±40)

This zone is dominated by the native trees *Juniperus brevifolia* and *Morella faya*, together with the native shrub *Myrsine africana*, followed by Poaceae and another native shrub, *Erica azorica* (Figure 3). Also noteworthy is the presence of *Picconia azorica* pollen and the occurrence of stomata of *Laurus azorica* (Figure 4), whose pollen is poorly preserved in sediments and/or was lost during laboratory processing (Connor et al., 2012). This assemblage strongly suggests the dominance of the native laurisilvas that covered the island before the arrival of the first settlers (Moreira, 1987), which are preserved today as small remnants—known as "laurifolia" forests—restricted to protected sites mainly on the less disturbed islands (Dias et al., 2005). Among the ferns, *Culcita macrocarpa* reaches its maximum values in this zone. This fern is typical of the extant laurifolia forests, where it forms a dense and diverse herbaceous layer together with other ferns, such as *Dryopteris* spp. and *Pteris incompleta*, whose spores are also present in this pollen zone.

In this pollen zone, which corresponds to the post-eruption phase, *Juniperus brevifolia* experiences a significant reduction starting at 107 cm (AD 1281±40) and culminating at 87 cm (AD 1290±40), when its pollen almost disappears from the record. During the *Juniperus* decline, the pollen of *Secale cereale* (rye) (Figure 4) and other cereals began to appear (93-98 cm, AD 1286-88±40), showing a consistent occurrence pattern until the top of the zone. The *Juniperus* collapse coincided with the initiation of a decreasing trend in *Morella faya* and with increases in *Erica azorica*, *Myrsine africana*, Poaceae, psilate monoletes, *Botryococcus* and the coprophilous fungi. At the same time, there is also a slight increase in fire incidence, as shown by the charcoal curve, and a lithological change from ash-rich to ash-free lacustrine mud, indicating the cessation of the latest volcanic event (P17). The whole picture is suggestive of limited but recognizable human disturbance of the landscape, possibly in the form of local forest burning and the first attempts of cereal cultivation around the lake. The consistent occurrence of coprophilous fungi (*Sordaria*, *Sporormiella*, *Cercophora*, *Podospora*) is suggestive of animal husbandry because the only mammals living on the island before European contact were bats (Moreira, 1987). Forest burning is also supported by the increase of *Pteridium* and psilate monoletes, as representative of the secondary fern growth that is common after forest disturbance, as well as the increase of shrubs, which is possibly favored by forest clearing.

Zone AZ2 (24-69 cm, 25 samples, AD 1422±40-1845±21)

In this zone, *Juniperus brevifolia* and *Picconia azorica* disappeared from the pollen record and *Morella faya* reached its minimal values (Figure 3), indicating that the former native forests were no longer present. The continuity of *Morella faya* and the stomata of *Laurus azorica*, as well as the scattered occurrence of *Juniperus brevifolia* and *Picconia azorica*, until the middle of the zone (ca. 48 cm) suggests that these forests could have survived as remnant patches until approximately AD 1697±30; however, after this date, only the pollen

Morella faya remained. The dominance of *Erica azorica*, *Myrsine africana* and Poaceae pollen suggests that the vegetation within the caldera was more open and dominated by these native shrubs and grass meadows, possibly in the form of mixed communities or in a mosaic pattern. Today, *Erica azorica* and *Myrsine africana* coexist in some Azorean vegetation types, notably in the low *Erica* forests, that are adapted to wind exposure and dry soils and in shrublands growing on lava outcrops (Tutin, 1953; Dias et al., 2005).

Deforestation by fire was the more likely cause of the landscape shift recorded in this zone, as suggested by the occurrence of a significant charcoal peak at the base of the zone shortly after the date of the official colonization of the archipelago. According to historical documents, most of the São Miguel lowlands (<300 m elevation) were occupied by wheat (*Triticum* spp.) crops by AD 1509 (Moreira, 1987). This is not reflected in our pollen diagram, where the pollen of "other cereals", which usually includes wheat pollen, is absent from most of the zone. The same is true for other cereals, such as *Secale cereale* and *Zea mays*, which do not appear in a consistent fashion until the upper part of the zone (ca. 38 cm, AD 1774±26). A possible explanation is that the plains of the caldera of Sete Cidades were not suitable for cultivation, and the slopes were used for other purposes, such as forestry. Fructuoso (1589) mentioned the occurrence of large interannual lake level fluctuations, which would have hindered the establishment of cereal crops around the lake. The same author describes the present lake platform (Figure 2) as an extended beach of white sand, unusable for cultivation. The low values of *Plantago* and coprophilous fungi suggest that pastures could have existed but not as the main activity. Forestry is supported by the high abundance of *Erica*, of which the frequent use for wood production has been documented historically (Dias, 2007), and the decline of fire incidence. Both cereal cultivation and grazing require frequent and extensive burning to create open meadows at the expense of forest, whereas forestry practices avoid fire to preserve wood. Historical documents provide support of forestry practices, as they note that during the phase of colonization and further development of cereal cultivation, which consequently increased the population, forests were intensively used to provide charcoal and wood for housing and sheep habitat construction and repair (Moreira, 1987; Dias, 2007). During this phase, earthquakes were also frequent, and the reconstruction of human settlements was not unusual (Silveira et al., 2003; Ferreira, 2005). At present, *Erica azorica* is a grazing-tolerant species, which is also frequent in the form of secondary regrowth after disturbance (S. Connor, pers. comm.). It is possible that this fact has also contributed to its higher abundance in this zone.

The upper part of the zone (AD 1774±26 onwards) shows a different situation, with the decline of *Erica azorica* and *Myrsine africana* and the disappearance of *Picconia azorica* and *Laurus azorica*, coupled with the increase of *Morella faya*, *Rumex acetosella* and *Plantago lanceolata* and the first appearances—although still in very low quantities—of introduced trees, such as *Pinus pinaster* and *Cryptomeria japonica*. Additionally, the cereals started to appear in a consistent manner. These traits were accompanied by an increase in charcoal concentration, *Pteridium aquilinum* and psilate monoletes, indicating an increase of fire incidence. The overall picture suggests a second event of deforestation by fire, this time affecting the *Erica/Myrsine* forests/shrublands, and their partial replacement by cereal crops (rye, maize, wheat) and pastures. This phase was transitional towards the greater landscape modification that occurred in the uppermost zone.

Zone AZ3 (0-22 cm, 17 samples, AD 1848±21 to 2010±1)

This zone represents a major revolution that accounts for the shaping of present-day landscapes. The most relevant feature is the strong declines of *Erica azorica* and *Myrsine africana*, coupled with the increase of *Morella faya* and the appearance and subsequent increase of the imported trees *Pinus pinaster* and *Cryptomeria japonica* (Figure 3). Also noteworthy is the appearance of *Alnus*, *Olea europaea* and *Hydrangea macrophylla* and the disappearance of *Secale cereale*. *Plantago lanceolata* also declines significantly. Most elements outside the pollen sum also decrease—*Myriophyllum alterniflorum*, *Pteridium aquilinum*, psilate monoletes and the coprophilous fungi. The charcoal concentration indicates that fire incidence was similar to the uppermost part of the former zone. Therefore, fire was likely used to remove the *Erica/Myrsine* forests/shrublands, which were replaced by exotic forests dominated by *Cryptomeria japonica* and *Pinus pinaster*, together with the native *Morella faya*. This interpretation has strong support in the historical documents, including the use of *Morella faya* in modern reforestation (Dias, 2007). The base of the zone coincides with the well-documented, large-scale introduction of *Pinus pinaster* and *Cryptomeria japonica* for forestry purposes (AD 1845-46), whereas the increase in *Hydrangea macrophylla* is synchronous with the massive introduction of ornamental plants to São Miguel Island (AD 1853-72) (Moreira, 1987). This zone, however, is not completely homogeneous, as the dominant trees show disparate trends in time. *Pinus* experienced a significant increase shortly before its introduction by AD 1889±15 (18 cm), whereas *Cryptomeria* increased gradually and attained its acme more recently, by AD 1997±2 (4 cm). This is likely the palynological reflection of a change in forestry practices that occurred in the mid-20th century, when the local Forestry Service began to prioritize *Cryptomeria japonica* over *Pinus pinaster* due to its faster growth and higher resistance to wind (Dias, 2007). An outstanding charcoal peak occurs at 3 cm (AD 2002±1), but there is no record of a significant fire on that dates.

Lake levels

Because the historical vegetation changes in the Lake Azul catchment have been driven mostly by humans, pollen and spores are not reliable palaeoenvironmental and palaeoclimatic proxies. Therefore, we used selected aquatic palynomorphs, combined with inferences from lithology, as proxies for lake levels to derive preliminary palaeohydrologic insights. Here we concentrated on the major palaeoecological tendencies. Minor oscillations existed, but their detailed study will be addressed in the future using a high-resolution multiproxy approach (geochemistry, pollen, diatoms, and chironomids). The elements selected here, due to their indicator character and their abundance in the Lake Azul sediments, were two aquatic plants: *Myriophyllum alterniflorum* and *Potamogeton* spp. and the alga *Botryococcus* spp. *Myriophyllum alterniflorum* is a widely distributed freshwater species that lives submersed near the shoreline of oligotrophic and mesotrophic lakes (Kohler & Labus, 1983; Gacia et al., 2009). *Potamogeton* is represented in the Azores Islands by four species growing in small ponds (Tutin, 1953; Dias et al., 2005). *Botryococcus* is a cosmopolitan genus of planktonic algae that lives in a wide range of aquatic environments, which has been used in palaeolimnological studies on lake sediments as a proxy for water-level shifts (Bradbury et al., 2001). The abundance of *Botryococcus* tends to increase with water depth in a quantifiable fashion, which has been used to reconstruct past water-level fluctuations since the Last Glacial Maximum (e.g., Ybert, 1992; Jankovská & Komárek, 2000; Rull et al., 2008; Niehman & Behling, 2009; Koff & Terasmaa, 2011; Cohen, 2012; Leroy et al., 2014; Zhao et al., 2015). The stratigraphic variation of the selected indicators is depicted in a separate diagram for more clarity (Figure 5). It is important to stress that lake-level shifts, as reconstructed in this study, significantly agree with the same trends as deduced from diatom assemblages, whose study is in progress (Vázquez-Loureiro et al., in prep.).

The selected palynomorphs (*Potamogeton*, *Myriophyllum* and *Botryococcus*) represent taxa that have not as affected as terrestrial plants by human activities for several reasons. First, these taxa were present since the beginning of the sequence, well before island settlement, demonstrating that they are indigenous taxa not introduced by humans. Second, the stratigraphic variations of these taxa do not follow the same patterns of terrestrial plants, whose shifts are primarily the consequence of human activities. This is well depicted in Figure 5, where it can be seen that shifts in *Potamogeton, Myriophyllum* and *Botryococcus* do not agree with the zonation based on anthropogenic changes in terrestrial vegetation. Third, there are no historical reports of human introductions and local extinctions of aquatic plants and planktonic algae comparable to the abundant and detailed literature on the management of terrestrial plants. Given the thoroughness and accuracy of historical documents about human impact on plant ecology in the archipelago, it would be expected that, if aquatic plants had been managed in a similar fashion as terrestrial plants, this fact would have been clearly reported in historical documents. The only references available to date about the anthropogenic influence on aquatic plant communities of Lake Azul correspond to the 20th century and report the former presence of macrophytic green algae such as *Chara* and *Nitella* (Cunha, 1939), and the likely accidental introduction of exotic species (*Egeria*, *Elodea*) by aquarium enthusiasts since the 1970s (Pacheco et al., 1998).

The sequence begins with the dominance of *Potamogeton* (90-113 cm; AD 1273±40 to 1289±40), minimum abundances of *Botryococcus* and the absence of *Myriophyllum*. This assemblage suggests low water levels, prior to the inundation of the platform (Figure 2). Preliminary data on diatom assemblages, however, indicate that the euplanktonic *Aulacoseira granulata*, typical of moderate to high water levels (Wollin & Stone, 2010), was one of the dominant taxa in the interval 110-114 cm (Vázquez-Loureiro et al., in prep.). This apparent discrepancy can be explained by either oscillating water levels, or by the mixing of sediments with pollen and diatoms derived from littoral and pelagic environments, respectively. Afterwards, *Potamogeton* decreased progressively as *Botryococcus* increased, indicating that the water level was rising and the basin was being steadily filled. The first significant and consistent appearance of *Myriophyllum* occurred at 75 cm (AD 1349±40), suggesting that the platform started to be inundated and *Myriophyllum* was able to grow in the shallow and flat environment with light availability. The lake infilling progressed—likely with minor yearly oscillations, as noted by Fructuoso (1589)—with a net increasing trend until it reached a water depth and extension similar to today (~50-65 cm; AD 1447±40 to 1673±30), which is supported by the abundance of *Myriophyllum* and *Botryococcus* similar to the present. The increase in *Botryococcus* indicates lake deepening, and the increase in *Myriophyllum* suggests that the shallower parts of the platform were likely occupied by populations of this macrophyte similar to today. After this phase, a dramatic decrease in both *Botryococcus* and *Myriophyllum* occurred. At first sight, this could be interpreted as a reversal to lower water levels between ~40 and 45 cm (AD 1771±26 to 1774±26). However, this interval corresponds to an event of instantaneous flooding sedimentation, and the more likely interpretation is a palynomorph dilution effect caused by the massive input of sediments to the lake.

The *Myriophyllum* maximum occurred later, between 22 and 37 cm (AD 1778±26 to 1852±20), reaching values significantly higher than today. This could suggest expansion of the platform surface due to lake levels that were higher than today, leading to the inundation of the alluvial plain. Since those times, the lake level experienced a gradual decline until its present level. This lake lowering was due to natural (i.e., climatic) causes until AD 1937, when the drainage tunnel that maintains the lake level in its present position was built (Figure 5). However, *Myriophyllum alterniflorum* is also sensitive to changes in water quality, mainly eutrophication (Kohler & Labus, 1983). Therefore, the decline of this aquatic plant at the beginning of the 19th century could also be due to a combination of lake-level dropping and the eutrophication trend in the lake in modern times as a consequence of agricultural intensification (Cruz et al., 2015). This is supported by the presence of pollen from *Zea mays* and other cereals (Figure 3) and the historical records, which document the large-scale introduction of maize cultivation on São Miguel Island by AD 1832 (Moreira, 1987).

The lowstand phase at the base of the record (AD 1273±40 to 1289±40) coincided with the end of the Medieval Climate Anomaly (MCA), which in SW Europe, was characterized by drier climates than the present (Figure 6) (Nieto-Moreno et al., 2013, Sánchez-López et al., 2016). The extended phase of the lake-level increase, with minor oscillations, of Lake Azul (AD 1289±40 to 1771±26) was coeval with the European Little Ice Age (LIA), during which climates were equally characterized by oscillating moisture trends. The phase of the maximum lake levels (highstand) identified in Lake Azul between AD 1778±26 and AD 1852±20 corresponds to the transition between the LIA and the Industrial Period (IP) in Europe, where climates were also humid. The modern decline of water levels in Lake Azul could be interpreted in terms of drier climates (Rubio-Inglés, 2016) or the artificial draining of Lake Azul, or both. Between AD 1852±20 and the construction of the drainage tunnel (AD 1937), the roles of climate and water quality on the composition of the macrophytic community could not be resolved by the available information, and any inference would be speculative. After these dates, the lowering of the lake levels was due to artificial draining and coincided with wetter climates, as documented in both the palaeoclimatic and instrumental records (Björck et al. 2006, Hernández et al., 2016). Correlations with the palaeoclimatic record of Lake Caveiro on Pico Island (Björck et al., 2006), in terms of the moisture balance, are difficult to establish at this stage, but the information is provided to facilitate eventual comparisons (Figure 6). Dating errors should also be taken into account, although they do not significantly affect comparisons. Further and more detailed paleoclimatic studies based on the same core analyzed here using independent proxies, notably biomarkers, is in progress (Rubio-Inglés, 2016).

Discussion and conclusions

Early settlement

The possibility of human settlement far before the official human occupation of the Azores deserves special attention. Pollen zone AZ1 (AD 1273±40 to 1358±40) has been interpreted in terms of limited human disturbance manifested as local forest burning, cereal cultivation and possibly animal husbandry within the caldera of Sete Cidades. There is no known historical documentation in support of this hypothesis, as the purported disturbance would have taken place by AD 1287±40, between 100 and 180 years before the official discovery of São Miguel Island (AD 1427) and between 120 and 200 years before the official settlement of the Archipelago (AD 1449). The date of the potential landscape disturbance is closer, but still ca. 50 years earlier, to the first maps representing São Miguel Island (AD 1339). An eventual artifact of the age-depth model is unlikely because the suggested disturbance event coincides with a radiocarbon date calibrated to AD 1291 (1266-1387) (Table 1). Downward pollen percolation through sediments and sample contamination can also be dismissed because other pollen types from introduced plants—notably *Pinus pinaster* and *Cryptomeria japonica*, whose abundance is significantly higher than that of cereals—do not show similar patterns. Therefore, it is suggested that the caldera of Sete Cidades was settled by humans by the end of the 13th century, almost immediately after the cessation of the latest known volcanic event. The extent of this settlement, both in space and time, cannot be inferred from the available information, but it suggests that São Miguel Island was already colonized about a century and a half before its official discovery. This situation is not unique in the Macaronesian archipelagos. For example, Rando et al. (2014), using radiocarbon dating of vertebrate bones, proposed that humans could have reached Madeira four centuries before its official colonization by Europeans. Similar "surprises" have been recorded in other oceanic islands abroad, for example, Easter Island (South Pacific), where recent palynological studies suggested human settlement more than a millennium before the more accepted dates (Cañellas-Boltà et al., 2013). It would be interesting to investigate whether this phenomenon is more general than usually thought.

Landscape dynamics

Comparison of vegetation changes, as deduced from the pollen and spores of terrestrial plants, with palaeoenvironmental trends inferred from sedimentology, aquatic plants and algae provide an initial comprehensive view of landscape development in the São Miguel Island. As a first appraisal, this view should be verified by further multiproxy studies that are already in progress. On the basis of the currently available evidence, the following insights may be advanced as working hypotheses. At the end of the MCA, the catchment was occupied by laurifolia forests dominated by native trees (*Juniperus brevifolia* and *Morella faya*). Lake Azul was shallower than at present (lowstand) and likely restricted to its present-day deeper part (NE) and its present basin was likely covered by forests. *Juniperus brevifolia*, a species that tolerates permanent inundation (Dias et al., 2005), could have been especially important in the wetlands around the lake, as indicated by the pollen peak at the base of the diagram (Figure 3). Laurifolia forests continued to be dominant at the beginning of the LIA, but *Morella faya* was the main tree due to a *Juniperus brevifolia* decline. Climates then became wetter, and lake levels started to steadily increase. The latest volcanic eruption (P17) was already completed when the first human settlers reached the caldera, where they began to perform cereal cultivation and animal husbandry. Settlements were small, and the effects on vegetation were local and limited, except in the case of *Juniperus brevifolia*, which virtually disappeared from the catchment by the end of the 14th century. The wood of this species, locally called "cedro do mato" (bush cedar), is highly valued and has been intensively used throughout history for a variety of purposes in the quotidian human life, whereas the wood of *Morella faya* is not of the same quality (Dias, 2007). In addition, as mentioned above, *Juniperus brevifolia* develops well in permanent aquatic habitats, where other forest species cannot survive. The combination of water availability and quality wood makes the present-day basin of Lake Azul the preferred site for initial human settlement. If this is true, the deeper parts of the basin should contain the corresponding evidence. It would be interesting to develop complementary palaeobotanical (seeds, phytoliths, starch) and biomarker (DNA, fecal lipids) studies to corroborate this possibility.

The first significant vegetation change recorded in Lake Azul occurred at the onset of the large-scale occupation of the island by the Portuguese (AD 1449), when a lake similar to the present Lake Azul occupied the basin. The native forests were removed by fire and were replaced by a mosaic vegetation of low forests/shrublands dominated by *Erica azorica* and *Myrsine africana*, as well as pastures. The climate and lake levels would have been oscillating during those times, but further studies are needed to define these trends more precisely. The main economic activity was forest (mainly *Erica*) exploitation until AD 1774, when cereal crops and pastures took the lead, coinciding with lake levels higher than today (highstand). The latest remarkable landscape transformation, i.e., the large-scale establishment of forests dominated by introduced trees (*Pinus pinaster*, *Cryptomeria japonica*), coincided with the end of the highstand phase, when lake levels began to decrease likely due to climatic forcing, at least until AD 1937, when the drainage tunnel contributed to lake lowering. A change in forest dominance from *Pinus pinaster* to *Cryptomeria japonica* occurred in the middle 20th century for official management reasons. The continued development of agricultural and animal husbandry activities significantly contributed to the eutrophication of Lake Azul, causing changes in the extent and composition of the littoral vegetation and the planktonic communities.

Comparison with other Azores records

The results of our study agree with the general conclusion of Connor et al. (2012) that human activities overcame natural factors, such as climatic change or volcanic events, as the drivers of vegetation change in the Azores. Overall, our pollen record is similar to those of Connor et al. (2012) in both taxonomic composition and ecological succession, with some differences likely due to local conditions and differences in elevation, as well as to the degree of anthropic disturbance. In this sense, São Miguel is one of the more modified islands of the archipelago, whereas Pico and Flores, the islands studied by Connor et al. (2012), are among the more pristine (Dias, 2007). In addition, our lake (Azul) is situated at 260 m elevation, whereas those of Connor et al. (2012) are at 530 m (Lake Rasa), 903 m (Lake Caveiro) and 873 m (Pico bog), which results in differences in terms of vegetation. A significant difference is that in all the Pico and Flores diagrams available, *Juniperus brevifolia* is dominant and did not disappear after human colonization as it did in our Azul record. This could be due to a combination of differential human impact and elevation because the species is currently restricted to a few protected locations on São Miguel, in contrast to to Pico, where it is a significant element of the mid- to high-elevation forests and shrublands (Dias et al., 2005). Another remarkable difference is the relatively high abundance of *Erica azorica* in our record compared to Pico and Flores, which may also be explained by differences in elevation and human practices across islands. Also noteworthy is the high abundance of *Cryptomeria japonica* and *Pinus pinaster* in our record during the last centuries and their scarcity in the pollen diagrams of Pico and Flores Islands. The grasses also show relevant disparities; they are relatively constant in Azul, whereas in Pico and Flores, they remain at lower levels until human colonization, when they experience a significant and relatively abrupt increase. Due to the poor taxonomic resolution of this pollen type, any explanation would be highly speculative; however, the development of extensive historically documented pastures could be involved. The similarity of the Poaceae and the *Plantago lanceolata* curves in the Rasa, Caveiro and Pico diagrams supports this statement.

A major difference between the São Miguel and the Pico/Flores records is the presence/absence of cultivated grasses or cereals. As discussed previously, the patterns of occurrence of *Secale cereale*, *Zea mays* and other cereals are essential to appraise the colonization history of São Miguel Island and the further development of cereal cultivation through history. In the Pico and Flores records, however, *Secale cereale*, *Zea mays* and other cereals appear in very low amounts only in the Rasa diagram after human settlement (Connor et al., 2012). Historical documents report that cereal cultivation was restricted to the lowlands for climatic reasons (Moreira, 1987). This fact, together with the lower anthropogenic incidence on Pico and Flores Islands, could explain the significant occurrence of all types of cereal pollen in the lowland Azul record of São Miguel, their poor representation in the mid-elevation Lake Rasa record (Flores) and their absence in the high-elevation Pico diagrams (Lake Caveiro and Pico bog). The cereal pollen records also have noticeable differences with regard to human settlement patterns. The pre-impact phase of Connor et al. (2012) extends to 400-500 cal BP, depending on the site, which coincides with our São Miguel record, where the large-scale colonization of the island started after AD 1420 (~530 cal BP). These figures agree with the official settlement dates documented in historical records. However, one of the more striking results of our analysis is the likely earlier human occupation of São Miguel, possibly some 100-180 years before the official dates, a fact that has not been recorded in the Pico and Flores diagrams. Again, local differences, notably the above-mentioned unsuitability of the mid-high elevation Pico and Flores coring sites to capture cereal cultivation, may explain this discrepancy. It is possible that early colonization events were restricted to the lowlands and/or that they were not widespread across the whole archipelago. In either case, the local nature of these initial settlements and their limited impact on general landscape features, as well as the paucity of palaeoecological studies available to date, make a sound assessment difficult. Our results suggest that the lowland lakes near the coast would be the most suitable sites to document potential early colonization events; hence, the palaeoecological study of such environments is encouraged.

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Table 1. AMS ^{14}C dates obtained for core AZ11_02 (Rubio-Inglés, 2016).

Depth (mm)	Lab. reference	Radiocarbon age	Calibrated age (2σ)	α13C (‰)	Material
55	Beta-326594	154.4 ± 0.4 pMC	1989–1991 AD	-32.7	Plant macrorest
460	Beta-316595	200 ± 30 BP	141-303 BP	-28.6	Plant macrorest
610	Beta-331408	410 ± 30 BP	330-519 BP	-25.8	Pollen concentrate
860	Beta-331410	690 ± 30 BP	563-684 BP	-25.3	Plant macrorest

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Figure captions

1. Location map. A) The Azores archipelago in the Macaronesian context. A – Azores Islands (Portugal), M – Madeira Islands (Portugal), C –Canary Islands (Spain), V – Cape Verde Islands. P – Portugal (highlighted in black), S - Spain. B) Topographic map of the island of São Miguel with its calderas and the lakes inside them (white areas). C) The caldera of Sete Cidades, showing the lakes inside (LA – Lake Azul, LV – Lake Verde, LS – Lake Santiago). The coring site is indicated by a white dot. SC – Village of Sete Cidades.

2. Bathymetry of Lake Azul in 0.5-m contour intervals showing the topographic features described in the text. The SW-NE cross-section is represented below. Sediments are represented in brown.

3. Percentage pollen diagram of core AZ11-02-01. Cereals are expressed in presence (yellow dots)/absence patterns. Elements below 0.5% of the total were represented as "others", which include *Prunus azorica*, *Quercus ilex* and *Tilia* (trees), *Daboecia azorica*, *Vaccinium cilindraceum* and *Viburnum treleasei* (shrubs) and Chenopodiaceae/Amaranthaceae, *Echium*, *Euphorbia*, Fabaceae, *Frangula azorica*, *Galium*, *Rubus* and *Sedum* (herbs). Elements outside the pollen sum are depicted at the right side, after the pollen summary column. Charcoal is expressed in concentration units (particles per gram of sediment). Solid lines indicate x10 exaggeration.

4. Microphotographs of keystone palynomorphs. A) Pollen of *Secale cereale* from a sample situated at 80 cm depth. B) Fragment of epidermis with stomata of *Laurus azorica* from a sample situated at 98 cm depth.

5. Percentage diagram showing the palynomorphs selected for lek-level reconstruction, together with the lithology and the pollen zones for comparison. Present-day values of *Myriophyllum alterniflorum* and *Botryococcus* spp. are indicated by vertical dashed lines. Green arrows – rising lake levels; brown arrow – dropping lake levels. OC – Official Colonization, ES – Early Settlement, DT – Drainage Tunnel.

6. Correlations between the Lake Azul record and other pertinent palaeoclimatic reconstructions. OC – Official Colonization, ES – Early Settlement, DT – Drainage Tunnel.

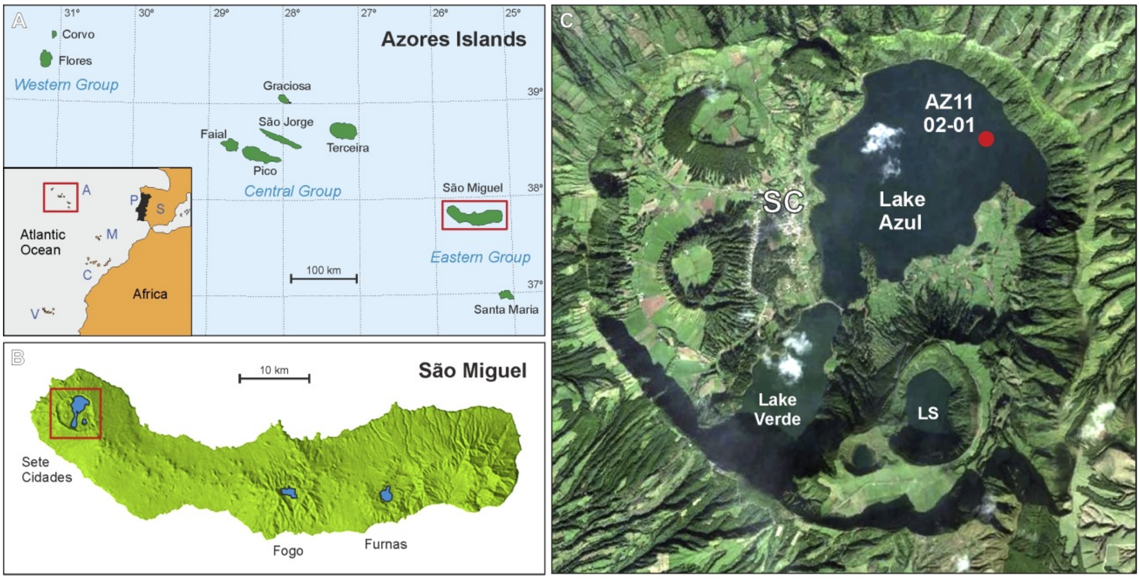

A
31°
30°
29°
28°
27°
26°
25°
Corvo
Flores
Western Group
Azores Islands
Graciosa
39°
São Jorge
Faial
Terceira
Pico
Central Group
São Miguel
38°
Eastern Group
100 km
37°
Santa Maria
Atlantic Ocean
Africa
B
10 km
São Miguel
Sete Cidades
Fogo
Furnas
C
AZ11 02-01
SC
Lake Azul
Lake Verde
LS

Figure 1

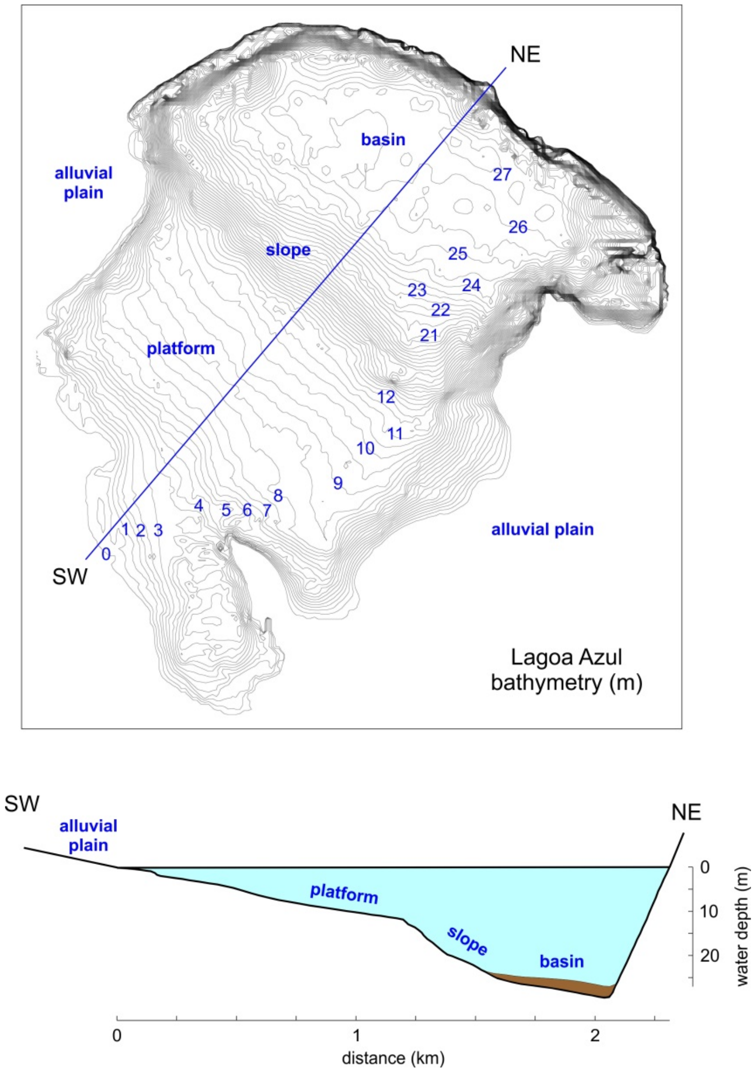
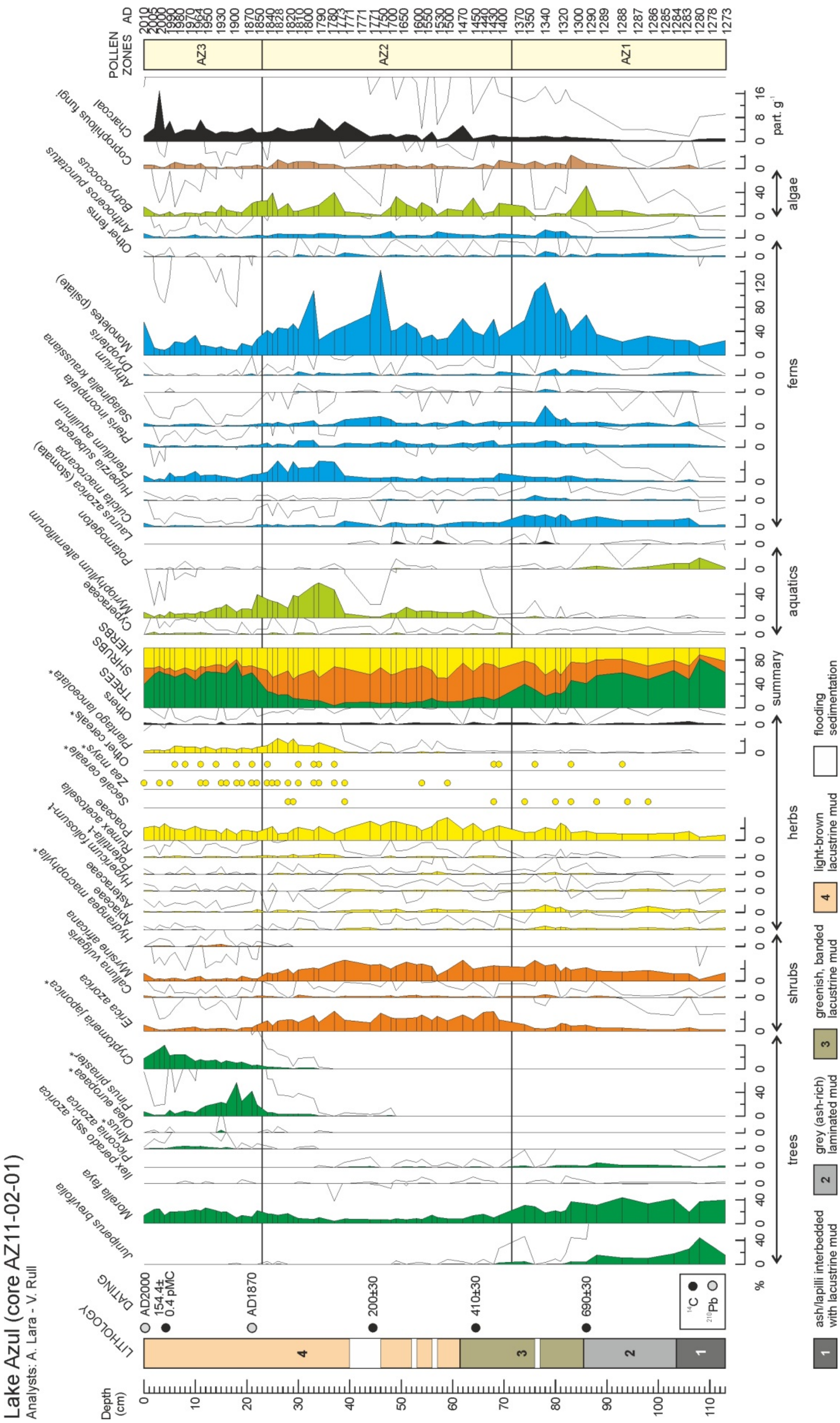

NE
basin
alluvial plain
slope
platform
27
26
25
24
23
22
21
12
11
10
9
8
4 5 6 7
1 2 3
0
SW
alluvial plain
Lagoa Azul bathymetry (m)
SW
alluvial plain
NE
platform
slope
basin
0
10
20
water depth (m)
0
1
2
distance (km)

Figure 2



Lake Azul (core AZ11-02-01)
Analysts: A. Lara - V. Rull
Depth (cm)
LITHOLOGY
DATING
AD2000
154.4± 0.4 pMC
AD1870
200±30
410±30
690±30
POLLEN ZONES
AZ3
AZ2
AZ1
trees
shrubs
herbs
summary
aquatics
ferns
algae
part. g-1
Juniperus brevifolia
Morella faya
Ilex perado ssp. azorica
Picconia azorica
Alnus*
Olea europaea*
Pinus pinaster*
Cryptomeria japonica*
Erica azorica
Calluna vulgaris
Myrsine africana
Hydrangea macrophylla*
Apiaceae
Asteraceae
Hypericum foliosum-t
Potentilla-t
Rumex acetosella
Poaceae
Secale cereale*
Zea mays*
Other cereals*
Plantago lanceolata*
Others
TREES
SHRUBS
HERBS
Cyperaceae
Myriophyllum alterniflorum
Potamogeton
Laurus azorica (stomata)
Culcita macrocarpa
Huperzia suberecta
Pteridium aquilinum
Pteris incompleta
Selaginella kraussiana
Athyrium
Dryopteris
Monoletes (psilate)
Other ferns
Anthoceros punctatus
Botryococcus
Coprophilous fungi
Charcoal
ash/lapilli interbedded with lacustrine mud
grey (ash-rich) laminated mud
greenish, banded lacustrine mud
light-brown lacustrine mud
flooding sedimentation

Figure 3

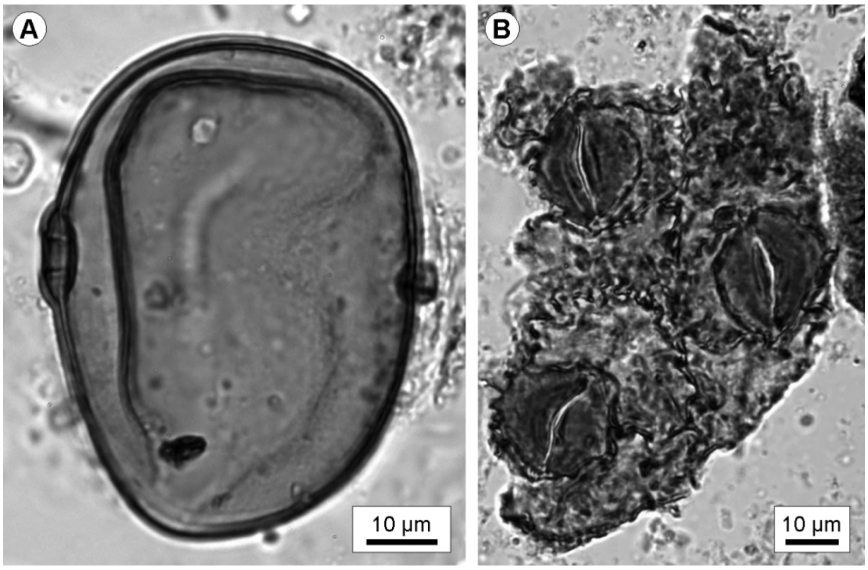
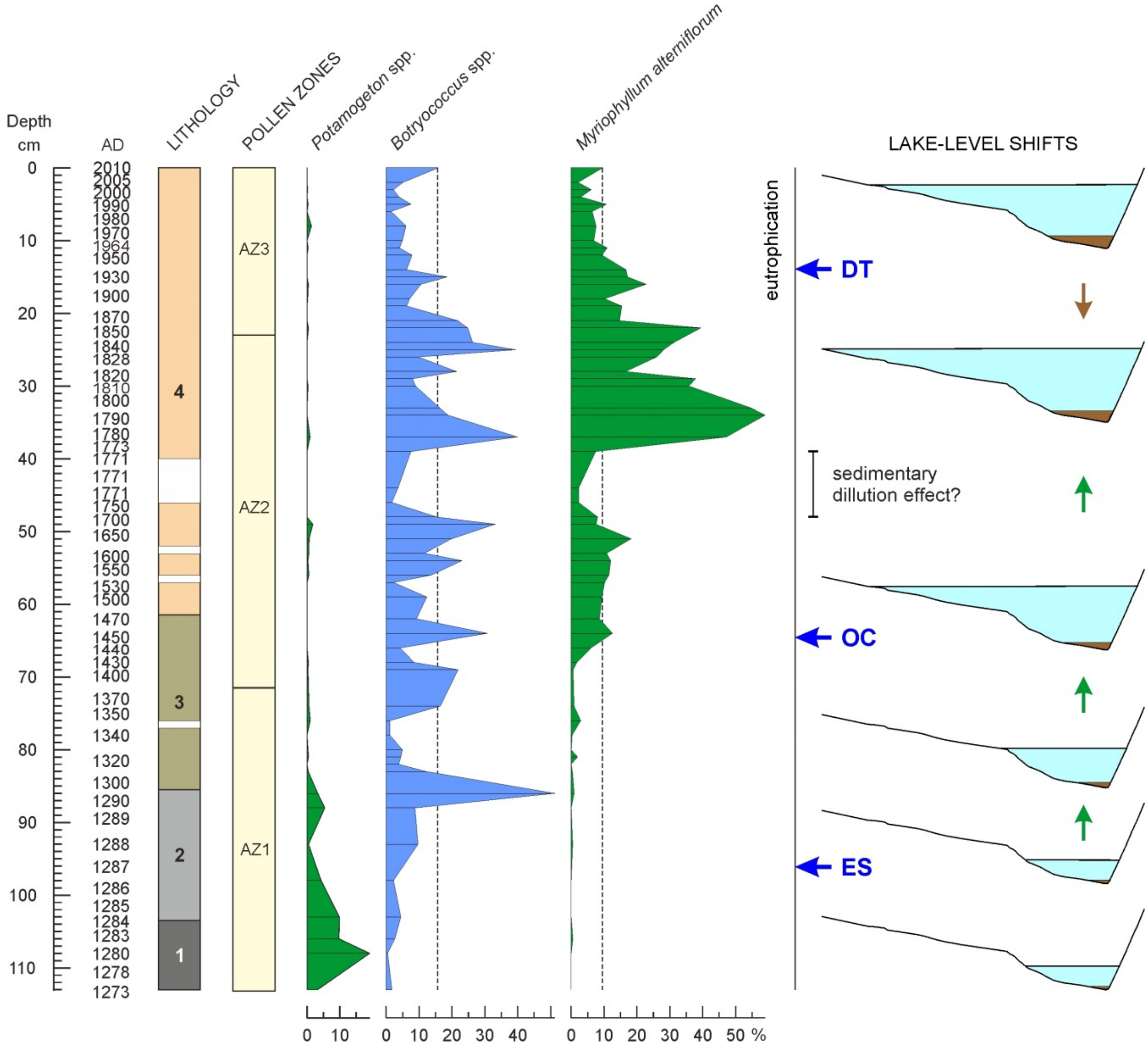


Figure 4



Depth
cm
AD
LITHOLOGY
POLLEN ZONES
Potamogeton spp.
Botryococcus spp.
Myriophyllum alterniflorum
LAKE-LEVEL SHIFTS
AZ3
AZ2
AZ1
4
3
2
1
eutrophication
DT
OC
ES
sedimentary
dillution effect?
0 10
0 10 20 30 40
0 10 20 30 40 50 %

Figure 5

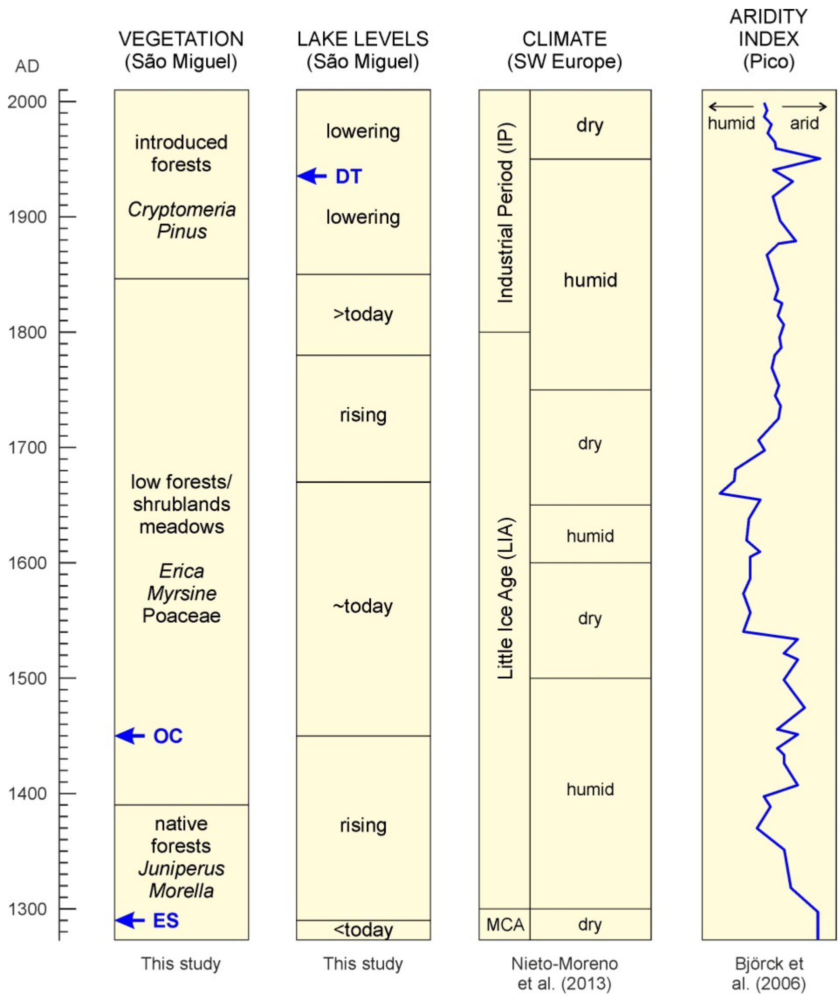

AD
VEGETATION (São Miguel)
LAKE LEVELS (São Miguel)
CLIMATE (SW Europe)
ARIDITY INDEX (Pico)
2000
1900
1800
1700
1600
1500
1400
1300
introduced forests
Cryptomeria
Pinus
low forests/ shrublands meadows
Erica
Myrsine
Poaceae
OC
native forests
Juniperus
Morella
ES
lowering
DT
lowering
>today
rising
~today
rising
<today
Industrial Period (IP)
Little Ice Age (LIA)
MCA
dry
humid
dry
humid
dry
humid
dry
humid
arid
This study
This study
Nieto-Moreno et al. (2013)
Björck et al. (2006)

Figure 6

Highlights

- The original Azorean laurisilvas were removed after the official human settlement (AD 1449)
- Current vegetation established after a second deforestation (AD 1774) and the introduction of exotic trees
- Modern landscapes are almost totally anthropogenic, climatic shifts have been less influential
- Lake levels increased until a maximum (AD 1778-1852) and then decreased to present-day values
- The island was likely colonized by humans a century and a half before the official settlement