Review of Palaeobotany and Palynology xxx (xxxx) xxx-xxx

Contents lists available at ScienceDirect

Review of Palaeobotany and Palynology

journal homepage: www.elsevier.com

Oceanic Island forests buried by Holocene (Meghalayan) explosive eruptions: Palaeobiodiversity in pre-anthropic volcanic charcoal from Faial Island (Azores, Portugal) and its palaeoecological implications

C.A. Góis-Marques [a, b, *], J. Rubiales [c], L. de Nascimento [d], M. Menezes de Sequeira [b, e], J.M. Fernández-Palacios [d], J. Madeira [a]

[a] Departamento de Geologia, Faculdade de Ciências da Universidade de Lisboa and Instituto Dom Luiz (IDL), Laboratório Associado, Universidade de Lisboa, Campo Grande, 1749-016 Lisboa, Portugal
[b] Madeira Botanical Group (GBM), Faculdade de Ciências da Vida, Universidade da Madeira, Campus da Penteada, 9000-390, Funchal, Portugal
[c] Unidad de Botánica, Departamento de Sistemas y Recursos Naturales, Escuela Técnica Superior de Ingeniería de Montes, Forestal y del Medio Natural, Universidad Politécnica de Madrid, Ciudad Universitaria, Madrid, Spain
[d] Island Ecology and Biogeography Group, Instituto Universitario de Enfermedades Tropicales y Salud Pública de Canarias (IUETSPC), Universidad de La Laguna (ULL), Avda. Astrofísico Francisco Sánchez s/n, La Laguna 38200, Canary Islands, Spain
[e] CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Pólo dos Açores, 9501-801 Ponta Delgada, Azores, Portugal

ARTICLE INFO

Article history:
Received 9 August 2019
Received in revised form 25 September 2019
Accepted 26 September 2019
Available online xxx

Keywords:
Macaronesia
Azores archipelago
Pyroclastic density current
Charcoalified wood
Mummified wood
Palaeovegetation

ABSTRACT

In Faial Island (Azores Archipelago, North Atlantic Ocean), charcoalified and mummified wood fossils have been reported within late Holocene (Meghalayan) pyroclastic deposits from the Caldeira Formation. Due to their recent age, a detailed study conveys a snapshot into Azorean palaeophytodiversity and palaeovegetation, ca. 7–5 centuries before the arrival of Portuguese settlers to the Azores Islands. Here we provide the first detailed anatomical and taxonomical study of these wood fossils. In total, 41 samples were collected from seven localities, mainly from a ~ 1200 yr BP ignimbrite. Field work revealed autochthonous and paraautochthonous assemblages, with tree trunks in upright position. The anatomical study of the fossil woods resulted in the identification of *Juniperus brevifolia*, *Laurus azorica*, *Myrsine retusa*, *Morella faya*, *Picconia azorica*, *Prunus lusitanica subsp. azorica,* and *Vaccinium cylindraceum*. Two fossil assemblages are comparable to the proposed potential natural vegetation (PNV) for the Azores. Surprisingly, *P. lusitanica* subsp. *azorica* was the second most abundant fossil wood suggesting that this tree was more abundant in a recent past in Faial Island and probably in the archipelago. This is corroborated by historical accounts, and its modern scarcity was certainly anthropically driven. Identifying Holocene plant macrofossils are essential to properly reconstruct oceanic islands terrestrial palaeoecosystems, especially where forests with high percentage of entomophilous taxa are underrepresented in palaeopalynological limnic record. Further work is necessary to reconstruct Faial Island and Azores archipelago palaeovegetation which is essential to provide an ecosystem base-line for restoration and management.

1. Introduction

The interaction between explosive or effusive volcanic events and vegetation may provide ideal taphonomical environments for plants to be buried and preserved as charcoals or mummifications (e.g. Fritz, 1986; Spicer, 1989; Hudspith et al., 2010; Scott, 2010; Mustoe, 2018). Rapid burial of trunks and stems by hot volcanic materials can promote their pyrolysis resulting in a total or partial charcoalification without combustion (e.g. Scott, 2010). The product obtained is charcoal, a fairly inert material relatively enriched in carbon (e.g. Scott and Jones, 1991a; Scott and Jones, 1991b; Bird, 2013). From a volcanological point of view, the degree of charcoalification and reflectance can provide insights on the palaeotemperature of the volcanic event that buried the wood (e.g. Scott and Jones, 1991b; Scott and Glasspool, 2005; Hudspith et al., 2010). Mummified wood, i.e. almost unaltered wood with preservation of the original matter (Mustoe, 2018), can be preserved within cold phreatomagmatic deposits (e.g. Góis-Marques et al., in press). Finally, charcoal and mummified wood found associated with volcanic deposits have been used worldwide to date late Quaternary volcanic eruptions (e.g. Bryson et al., 2006).

From a palaeobotanical perspective, fossil charcoal preserves anatomical characters that can allow the identification of genera or species (e.g. Leny and Casteel, 1975; Hudspith et al., 2010; Scott, 2010; Mustoe, 2018), being direct evidence of the terrestrial palaeobiodiversity and palaeoecology of a given territory at a specific point in time. In the Macaronesian archipelagos (Azores, Madeira, Canaries and Cabo Verde), charcoalified wood fossils have been primarily used for radiocarbon dating, being either found within limnic sedi-

---

* Corresponding author at: Departamento de Geologia, Faculdade de Ciências da Universidade de Lisboa and Instituto Dom Luiz (IDL), Laboratório Associado, Universidade de Lisboa, Campo Grande, 1749-016 Lisboa, Portugal.
Email address: c.goismarques@gmail.com (C.A. Góis-Marques)

https://doi.org/10.1016/j.revpalbo.2019.104116
0034-6667/

ments (e.g. Rull et al., 2017b; Castilla-Beltrán et al., 2019), within or below volcanic deposits (e.g. Madeira et al., 1995; Geldmacher et al., 2000; Carracedo et al., 2007), or to infer Holocene palaeofire regimes through microcharcoal concentration in limnic sedimentary cores (e.g. Connor et al., 2012; Nogué et al., 2013; de Nascimento et al., 2016). Taxonomical studies of charcoal fossils in Macaronesia are almost largely absent, despite their potential to inform past diversity and ecology. Recently, some studies illustrate anatomically preserved wood (e.g. Pensa et al., 2015), but without a taxonomic identification. In the Canaries, several wood fossils have been reported (Schmincke, 1967; Nogales and Schmincke, 1969; García-Talavera et al., 1995; Rubiales et al., 2013), but only a fossil charcoal was identified from the Miocene of Gran Canaria as *Pinus canariensis* Sweet ex Spreng., (Anderson et al., 2009). Anthracological studies from archaeological sites are known for Macaronesia (e.g. Machado Yanes et al., 1997; Machado Yanes, 2007; Huebert, 2015; Astudillo, 2018).

Since the 19th century, several naturalists and geologists (e.g. Webster, 1821; Mouzinho de Albuquerque and Menezes, 1826; Hartung, 1860; Fouqué, 1873), reported the presence of mummified and charcoalified tree trunks imbedded in tephra deposits for almost all islands of the Azores archipelago (Góis-Marques and Menezes de Sequeira, 2015; Góis-Marques et al., in press). Since then, and with the advent of ^{14}C radiocarbon dating, charcoal and wood fossils have been actively collected for dating volcanic events in the Azorean islands (e.g. Shotton et al., 1968; Madeira et al., 1995; Madeira et al., 1998; Pacheco, 2015; Conte et al., 2019). However, so far, a palaeobotanical study to these macrofossils was never accomplished.

The Azores Islands were settled by the Portuguese in the mid-15th century, and the earliest descriptions of the Azorean Islands (e.g. Fernandes, 1508; Frutuoso, 1590a; Frutuoso, 1590b; Frutuoso, 1590c) account for the presence of forests composed of laurels and conifers, including a probable arboreal extinct 'Malva'(Malvaceae?) in São Miguel (Frutuoso, 1590a; Dias, 2007). It is calculated that the clearance and exploration of Azorean forests for almost 600 years by Portuguese settlers left less than 5% of native forests (Triantis et al., 2010) although this value does not correspond to a pristine vegetation. So far, the efforts to define the natural vegetation of Azores Islands have been based on historical descriptions (e.g. Dias, 2007), study of the surviving native vegetation (e.g. Dias et al., 2005; Elias et al., 2016), and inferred from palaeopalynological analysis of lakes and peatlands (van Leeuwen et al., 2005; Connor et al., 2012; Rull et al., 2017a; Rull et al., 2017b). Plant macrofossils, such as charcoal, leaves impressions or adpressions which are buried within or below pyroclastic deposits, can provide important information on past diversity and ecology (e.g. Burnham and Spicer, 1986; Burnham, 1994). However, the study of Azorean plant macrofossils was seldom used in this discussion (Góis-Marques et al., in press; Góis-Marques et al., 2019a). Moreover, quaternary micro- and macrofossils of plants are abundant in the Azores and Macaronesia islands, and have already demonstrated the presence of extirpated or extinct taxa (e.g. de Nascimento et al., 2009; Góis-Marques et al., 2019b).

In Faial Island, plant fossils are known since the beginning of the 20th century (Góis-Marques et al., in press). Previous attempts to identify mummified and charcoalified fossil woods from the Azores and Faial were provided by Forjaz et al. (1970). However, no methodology or anatomical reasoning was given to support those identifications (Góis-Marques et al., in press). Charcoalified and mummified woods found in Faial Island have been used in radiocarbon dating (e.g. Madeira et al., 1995; Madeira, 1998; Pacheco, 2001; Pacheco, 2015), but their systematic and palaeoecological value have been overlooked until now. Recent field work in Faial Island provided promising materials, where exceptionally preserved fossil woods (either mummified or charcoalified specimens) were found throughout the Island (Góis-Marques et al., in press).

In this paper we provide the first anatomical and taxonomical study of wood fossils for the Azores archipelago from charcoal samples collected within the pyroclastic deposits of the Late Holocene (Meghalayan) Caldeira Formation in Faial Island. Moreover, palaeophytodiversity and palaeovegetation data are compared to the Azores Potential Natural Vegetation (PNV) (Elias et al., 2016), and analysed in the light of the actual plant diversity and historical data. Finally, we discuss the implications of the palaeobiodiversity found for the reconstruction of Faial and Azores palaeovegetation.

2. Geological setting

The Azores archipelago lies in the central North Atlantic Ocean at the triple junction between the North American, Eurasian and Nubian plates (Fig. 1A), and is interpreted as the result of this complex tectonic setting coupled with a hot spot (Gente et al., 2003). The archipelago is composed of nine islands (western group: Corvo and Flores; central group: Faial, Pico, S. Jorge and Graciosa; eastern group: S. Miguel, S. Maria islands and Formigas Islets; Fig. 1B). Faial Island is 21 km long and 14 km wide, with a surface area of 170 km^2 and reaching a maximum elevation of 1043 m above sea level (a.s.l.). According to Madeira (1998) the subaerial part of the island is composed of two central volcanoes and two fissural volcanic zones (Fig. 1C): the Ribeirinha shield volcano, mapped as Ribeirinha Volcanic Complex, is the oldest edifice and spans in age from 850 to 360 ka (Feraud et al., 1980; Hildenbrand et al., 2012); the Caldeira Volcano, a stratovolcano straddling the western flank of Ribeirinha volcano is divided into a lower unit, the Cedros Volcanic Complex (130–115 ka; Hildenbrand et al., 2012), representing a dominantly effusive basaltic phase, and an upper trachytic unit whose products are included in the Caldeira Formation (< 16 ka BP; Madeira et al., 1995; Pacheco, 2001). The fissural volcanic systems are represented by the Almoxarife Formation (< 46 ka; Hildenbrand et al., 2012) in the east and the Capelo Volcanic Complex (~ 8 ka, Di Chiara et al., 2014) in the west, with the latest documented eruption in 1957–1958 (Capelinhos eruption).

The Caldeira Formation (or the Upper Group of Cedros Volcanic Complex sensu Pacheco, 2001) has a geological record of 12 sub-plinian and phreatomagmatic trachyte eruptions younger than 16 ka BP (Madeira et al., 1995; Pacheco, 2001; Pacheco, 2015), whose deposits preserved leaf impressions/adpressions, charcoalified and mummified wood, and palaeosols (e.g. Madeira et al., 1995; Pacheco, 2001; Góis-Marques et al., in press).

One of the most expressive volcanic eruptions of the Caldeira Volcano was the sub-plinian C11 event (Pacheco, 2001; Pimentel et al., 2015), ^{14}C dated at ca. 1200 to 1000 yr BP (Madeira et al., 1995; Pacheco, 2015), that lead to the formation of a caldera in the summit of Faial Island (Fig. 1C). Pimentel et al. (2015) reconstructed the C11 event through a detailed stratigraphic study of the pyroclastic deposits, dividing it into three members, represented by distinct facies: (i) the Brejo Member corresponding to the initial phreatomagmatic phase, mainly composed of ash tuffs covering a palaeosol with associated fossiliferous layers (see Góis-Marques et al., in press); (ii) the Inverno Member representing the sub-Plinian phase, producing coarse pumice fall deposits; and (iii) the Cedros Member representing the final phase, with the collapsing of the sub-plinian eruptive column over the north and eastern sectors of the island, forming pyroclastic density currents (PDC) that engulfed Faial's palaeovegetation. The high temperature of the PDC and the consequent ignimbrite deposits, produced the pyrolysis of the buried vegetation, preserving them as charcoal (Góis-Marques et al., in press). Two other sites, sampled near the Caldeira rim (no 6 and 7 in Fig. 1C), are phreatomagmatic breccias from previous explosive eruptions, most probably from the C7 or C8 events (see Pacheco, 2001;

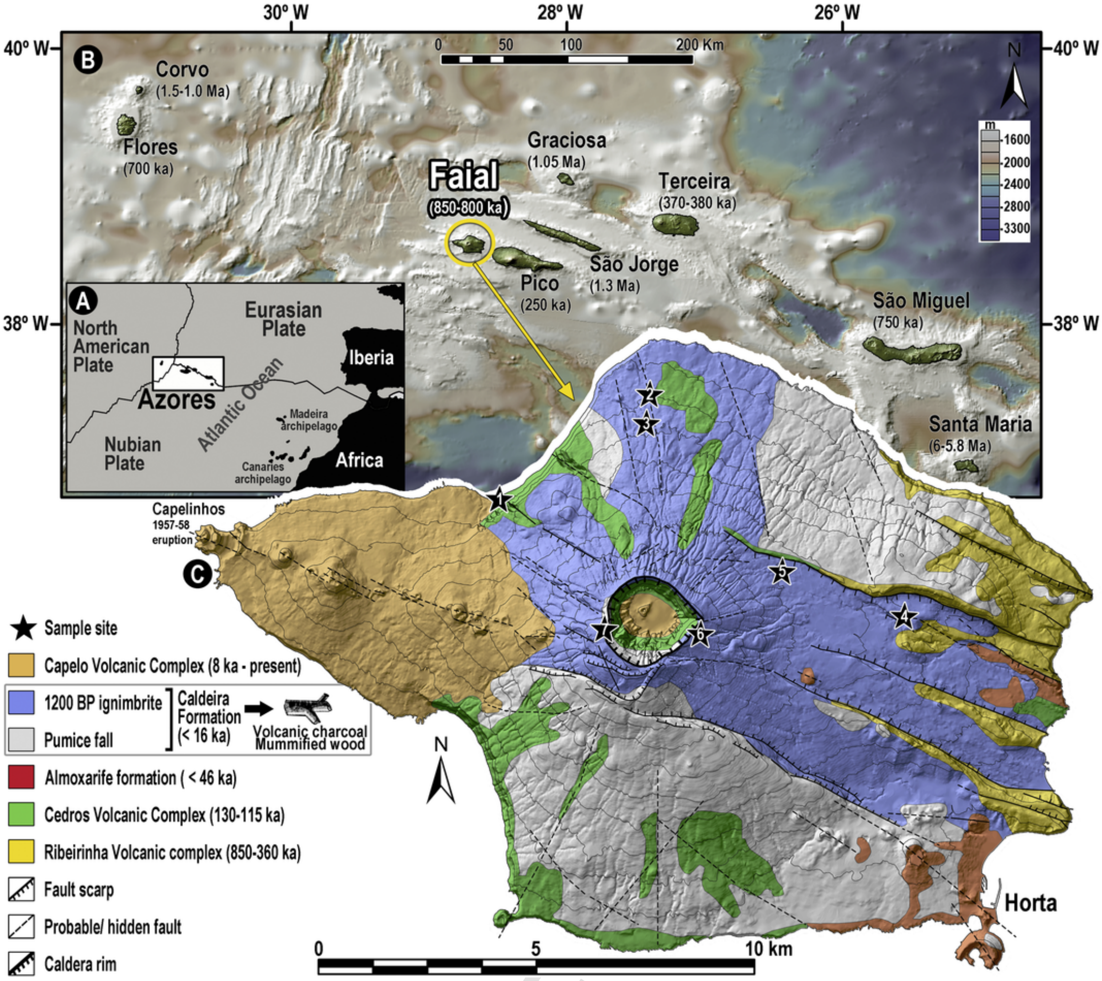

Fig. 1. Azores archipelago and Faial Island geological setting. **A**, Location and tectonic setting of Azores archipelago; **B**, Azores archipelago bathymetry (Digital elevation model generated in GeoMapapp (http://www.geomapapp.org/); Ryan et al., 2009), with the oldest known subaerial ages for each island; **C**, Simplified geological map of Faial Island, adapted from Madeira and Brum da Silveira (2003), showing the sites sampled (black stars): **1**. Fajã da Praia do Norte beach; **2** and **3**. South of Cascalho de Cima; **4**. Cancelas ash quarry; **5**. Cabouco Velho; **6** and **7**. West and East Caldera rim.

Pacheco, 2015), that contain mummified tree trunks (e.g. Madeira et al., 1995; Góis-Marques et al., in press).

3. The vegetation of Faial Island

The word 'Faial' is the Portuguese name for a forest dominated by *Morella faya* (Aiton) Wilbur, a botanical and vegetational toponomy that directly reflects the vegetation encountered by the 15th century Portuguese settlers in the island. The first written impression of Faial Island vegetation was given by Frutuoso (1590b), born in Ponta Delgada (São Miguel Island) ca. 1522, meaning that these are direct observations, by him or orally transmitted from the first settlers. He states that half of the island was covered by forests and describes the presence of endemic shrubs and trees still found today in the island (e.g. *Vaccinium cylindraceum* Sm. and *Laurus azorica* (Seub.) Franco).

The Azores archipelago, including Faial's vegetation has been described by several authors (Seubert and Hochstetter, 1843; Drouet, 1866; Trelease, 1897; Guppy, 1914; Tutin, 1953; Dansereau, 1970; Rivas-Martínez et al., 2001; Rivas-Martínez et al., 2002; Dias et al., 2005; Costa et al., 2012; Fernández-Prieto et al., 2012). Recently, Elias et al. (2016) published a potential natural vegetation model (PNV) where eight vegetation belts were proposed for the Azorean archipelago. For Faial Island, Elias et al. (2016) propose the occurrence of five attitudinal vegetation belts, from sea level to mountain top: **1**. *Erica-Morella* coastal woodlands (between 0 and 100 m a.s.l.), dominated by *Erica azorica* Hochst. and *M. faya*; **2**. *Picconia–Morella* low-land forest (between 100 and 300 m a.s.l) dominated by *Picconia azorica* (Tutin) Knobl. and *M. faya*.; **3**. *Laurus* submontane forest (between 300 and 600 m a.s.l.), dominated by *L. azorica*, with the co-occurrence of *P. azorica* and *M. faya* on the lower part and *Juniperus brevifolia* (Seub.) Antoine and *Ilex perado* Aiton subs*p. azorica* (Loes.) in the upper part; **4**. *Juniperus–Ilex* montane forest (between 600 and 900 m a.s.l.), dominated by *J. brevifolia* and *I. perado* subs*p. azorica*; **5**. *Calluna–Juniperus* altimontane scrubland, dominated by *Calluna vulgaris* (L.) Hull and *J. brevifolia* (above 900 m a.s.l.) on mountain ridges.

Currently, the landscape in Faial is dominated by pastures, exotic tree plantations (predominantly *Cryptomeria japonica* D. Don) and invasive species (e.g. *Pittosporum undulatum* Vent., *Hedychium gardnerianum* Sheppard ex Ker Gawl., *Hydrangea macrophylla* (Thunb.) Ser.) (e.g. Jardim et al., 2007). Faial's native vegetation is presently restricted to small patches on the East slope and inside the caldera, and coastal woodlands in the South coast of the island (Dias et al., 2007), within Faial Nature Park.

4. Materials and methods

Plant fossils were collected from different parts of Faial island (Góis-Marques et al., in press) in July of 2016. Previously known localities (e.g. Forjaz, 1960; Forjaz et al., 1970; Madeira et al., 1995; Madeira, 1998; Pimentel et al., 2015) were prospected for charcoalified or mummified wood. Additionally, new localities such as road cuts with visible charcoalified trunks were also sampled. Charcoalified wood was studied and identified under a reflected light microscope (LM) (see Leny and Casteel, 1975), and each sample studied in transverse surface (TS), radial longitudinal surface (RLS) and tangential longitudinal surface (TLS) sections. These were compared to the reference collection of Macaronesian woods at the 'Universidad Politécnica de Madrid' atlas and keys dealing with Macaronesian wood anatomy (e.g. Peraza and Lopez de Roma, 1967; Schweingruber et al., 2011; Ferreira et al., 2012; Schweingruber et al., 2013), online databases 'InsideWood' (Wheeler, 2011: http://insidewood.lib.ncsu.edu/search) and 'The Xylem Database' (Schweingruber and Landolt, 2010: https://www.wsl.ch/dendropro/xylemdb/). Furthermore, selected samples were split into TS, RLS and TLS, mounted on metal stubs, gold sputter coated (to prevent sample charging) and observed on a JEOL JSM-5200LV scanning electron microscope (SEM) at the Microscopy Facility of the Faculty of Sciences of the University of Lisbon (FCUL-MF). Wood anatomy descriptions and measurements follow the International Association of Wood Anatomists (IAWA) list of microscopic features for softwood (Baas et al., 2004) and hardwood (Wheeler et al., 1989). Systematic taxonomy follows Menezes de Sequeira et al. (2012). Charcoal samples are deposited in the palaeobotanical collection of Madeira University herbarium (UMad-P).

5. Results

5.1. Field sampling

Seven localities were sampled for fossil woods, ranging in elevation from 20 m to 977 m a.s.l. (Fig. 1C). In total, 41 samples were collected (Table 1), 38 charcoalified wood samples related mainly to the 1200 yr BP C11 ignimbrite deposit (Madeira et al., 1995; Pimentel et al., 2015) and three mummified wood samples from the caldera rim related to the Caldeira Formation (< 16 ka) phreatomagmatic deposits. As numbered in Fig. 1C: **1**. Fajã da Praia do Norte beach: located on the North coast of the island at an elevation of ~ 22 to 30 m a.s.l., a section of the sea cliff cut in the C11 Cedros Member ignimbrite (Fig. 2B) supplied charcoalified trunks (Fig. 2E). The occurrence of charcoal at that location was already mentioned by Forjaz et al. (1970); **2** and **3**. South of Cascalho de Cima: along road cuts, at elevations between 190 and 280 m a.s.l., the exposures of the C11 ignimbrite contain charcoalified trunks (Fig. 2F); **4**. Cancelas ash quarry: located in the northeast part of the island at 365 m a.s.l.; this abandoned quarry (Fig. 2A) exposes a palaeoforest buried by the C11 ignimbrite creating a fossil forest with charcoalified tree trunks (Fig. 2C–D, G), some still in upright position and preserving the bark; degassing pipes from pyrolysis of the wood are common (Fig. 2C); **5**. Cabouco Velho: located in the northeast part of the island at an elevation of 510 m a.s.l., this ignimbrite outcrop also supplied charcoal samples; localities 4 and 5 were some of the sites of sampling of charcoal for ^{14}C dating by Madeira et al. (1995) which yielded an average radiocarbon age of 1200 yr BP; **6** and **7**. West and East Caldeira rim: in these sites, close to the caldera rim, mummified coniferous wood, still preserving the aroma, were entombed by phreatomagmatic explosion breccias. The east site (Fig. 3C–E) outcrop, at an elevation of 897 m a.s.l., displays 4 breccias separated by paleosols or erosional unconformities; a wood sample from the palaeosol underlying the top breccia was radiocarbon dated at 1660 ± 45 yr BP (ICEN-994), while the west site (Fig. 3A–B) corresponds to a small stream valley, at an elevation of 977 m, that exposes a breccia covering a palaeosol rich in trunks, one of which was dated at 1820 ± 45 yr BP (ICEN-972) (see Madeira et al., 1995 for further details).

5.2. Systematic palaeobotany

The identification of anatomical features on charcoalified wood presents some challenges (Falcon-Lang et al., 2012) due to the homogenization of cell walls and the shrinking of cellular structures due to pyrolysis occurring at temperatures above 300–325 °C (Scott, 2010 and references therein). Anatomical characters, easily described in extant woods by differential wall staining or cell content (e.g. axial parenchyma), are not easily discerned or even possible to see in charcoals. Moreover, as pointed out by Falcon-Lang et al. (2012), the charcoalification process leads to opacity of cellular walls, preventing the observation of several anatomical characters. The descriptions presented here consider these limitations and are based on LM and SEM observations.

Division: **Spermatophyta** Willk., 1854
Class: **Pinopsida** Burnett, 1835
Order: **PINALES** Gorozh., 1904
Family: **CUPRESSACEAE** Gray, 1821
Genus: ***Juniperus*** L., 1753
Juniperus brevifolia (Seub.) Antoine, 1857
(TS: Figs. 4A–C; RLS: Figs. 4D–F; TLS: Figs. 4G–I)
Material: Fai-21; Fai-28U; Fai-02A; Fai-02B; Fai-11.

Description in IAWA code (Baas et al., 2004): 3, 40, 42, 44, 55, 58, 59, 80, 87, 93, 96, 98, 102, 107.

Description: *Growth rings:* softwood with distinct growth rings boundaries, abrupt transition between earlywood and latewood (Fig. 4A–B); *Tracheids*: pitting predominantly uniseriate (Fig. 4D, F), intercellular spaces present but rare, latewood tracheid with thin-walls, tracheid pits with torus extensions and notched borders (Fig. 4F); *Axial parenchyma*: indistinguishable and transverse end walls not observed; *Ray composition and size*: tracheids absent, ray parenchyma with smooth walls (Fig. 4E); rays uniseriate up to 4 cells (Fig. 4G–I), average ray height 63.8 μm (min = 26.98 μm; max = 101.36 μm); *Cross-field pitting*: usually 2, cupressoid.

Comparison and remarks: In the Azores, two native conifers are known, the endemic *J. brevifolia* and native *Taxus baccata* L. (Menezes de Sequeira et al., 2012). Wood anatomy of the studied charcoals are comparable to the Macaronesian *Juniperus* described by de Palacios et al. (2014). It differs from *T. baccata* due to the absence of helical thickenings in tracheid cells (e.g. Crivellaro and Schweingruber, 2013). According to de Palacios et al. (2014), tracheid pits with torus extensions and notches in the outer border, differentiate *J. brevifolia* from other Macaronesian *Juniperus* species. Under reflected LM and SEM these characters were difficult to observe. Moreover, the warty layer and the nodular transverse end walls of axial parenchyma cells were also not observed, most probably due to homogenization during pyrolysis of the cell walls (Fig. 3C). Although charcoalification prevents the identification of anatomical key characters, this fossil wood most probably belongs to *J. brevifolia*. As a note, this tree occurs in the Azores from 0 to 1500 m a.s.l. (Elias and Dias, 2014). This ecological amplitude led to the recognition of infraspecific taxa by Elias and Dias (2014). The identification of Azorean infraspecific taxa thorough wood anatomy seems improbable as the recognition of specific taxa is already challenging (de Palacios et al., 2014 and references therein).

Class: Magnoliopsida Brongn.,1843.
Order: LAURALES Berchtold and Presl, 1820.

Table 1
List of sampled specimens in Faial island presented in this study with respective information on location, age and identification.

Field number	Preservation	Collection	Locality	Coordinates (WGS84)	Altitude	error	Age (^{14}C)	Volcanostratigraphy	Identification	Plate
Fai-02A	Mummified	UMad-P	East rim of the caldera	38°34′54”N; 28° 42′05”W	897 m	10 m	1820 ± 45 yr BP	c7(?) or c8 (?)	cf. *Juniperus brevifolia* (Seub.) Antoine	—
Fai-02B	Mummified	UMad-P	East rim of the caldera	38°34′54”N; 28° 42′05”W	897 m	10 m	1820 ± 45 yr BP	c7(?) or c8 (?)	cf. *Juniperus brevifolia* (Seub.) Antoine	—
Fai-09	Mummified?	UMad-P	Fajã da Praia do Norte beach	38°36′35”N; 28°45′24”W	22 m	7 m	~ 1200 yr BP	c11	Not studied	—
Fai-10A	Charcoal	UMad-P	Fajã da Praia do Norte beach	38°36′36”N; 28°45′18”W	30 m	17 m	~ 1200 yr BP	c11	*Laurus azorica* (Seub.) Franco	—
Fai-10B	Charcoal	UMad-P	Fajã da Praia do Norte beach	38°36′36”N; 28°45′18”W	30 m	17 m	~ 1200 yr BP	c11	*Laurus azorica* (Seub.) Franco	—
Fai-10C	Charcoal	UMad-P	Fajã da Praia do Norte beach	38°36′36”N; 28°45′18”W	30 m	17 m	~ 1200 yr BP	c11	*Laurus azorica* (Seub.) Franco	—
Fai-10D	Charcoal	UMad-P	Fajã da Praia do Norte beach	38°36′36”N; 28°45′18”W	30 m	17 m	~ 1200 yr BP	c11	*Laurus azorica* (Seub.) Franco	—
Fai-11	Mummified	UMad-P	West rim of the caldera	38°35′06”N; 28°43′38” W	977 m	5 m	1660 ± 45 yr BP	c9	cf. *Juniperus brevifolia* (Seub.) Antoine	—
Fai-21	Charcoal	UMad-P	Cabouco Velho	38°35′47”N; 28°40′54”W	511 m	15 m	~ 1200 yr BP	c11	*Juniperus brevifolia* (Seub.) Antoine	—
Fai-28U	Charcoal	UMad-P	Cancelas ash quarry	38°35′12”N; 28°38′53”W	365 m	7 m	~ 1200 yr BP	c11	*Juniperus brevifolia* (Seub.) Antoine	Plate I
Fai-28A	Charcoal	UMad-P	Cancelas ash quarry	38°35′12”N; 28°38′53”W	365 m	7 m	~ 1200 yr BP	c11	*Laurus azorica* (Seub.) Franco	—
Fai-28C	Charcoal	UMad-P	Cancelas ash quarry	38°35′12”N; 28°38′53”W	365 m	7 m	~ 1200 yr BP	c11	*Laurus azorica* (Seub.) Franco	—
Fai-28D	Charcoal	UMad-P	Cancelas ash quarry	38°35′12”N; 28°38′53”W	365 m	7 m	~ 1200 yr BP	c11	*Laurus azorica* (Seub.) Franco	Plate II
Fai-28E	Charcoal	UMad-P	Cancelas ash quarry	38°35′12”N; 28°38′53”W	365 m	7 m	~ 1200 yr BP	c11	*Laurus azorica* (Seub.) Franco	—
Fai-28F	Charcoal	UMad-P	Cancelas ash quarry	38°35′12”N; 28°38′53”W	365 m	7 m	~ 1200 yr BP	c11	*Laurus azorica* (Seub.) Franco	—
Fai-28T	Charcoal	UMad-P	Cancelas ash quarry	38°35′12”N; 28°38′53”W	365 m	7 m	~ 1200 yr BP	c11	*Laurus azorica* (Seub.) Franco	—
Fai-28W	Charcoal	UMad-P	Cancelas ash quarry	38°35′12”N; 28°38′53”W	365 m	7 m	~ 1200 yr BP	c11	*Laurus azorica* (Seub.) Franco	—
Fai-28AA	Charcoal	UMad-P	Cancelas ash quarry	38°35′12”N; 28°38′53”W	365 m	7 m	~ 1200 yr BP	c11	*Laurus azorica* (Seub.) Franco	—
Fai-28M	Charcoal	UMad-P	Cancelas ash quarry	38°35′12”N; 28°38′53”W	365 m	7 m	~ 1200 yr BP	c11	*Morella faya* (Aiton) Wilbur	Plate III
Fai-28J	Charcoal	UMad-P	Cancelas ash quarry	38°35′12”N; 28°38′53”W	365 m	7 m	~ 1200 yr BP	c11	*Myrsine retusa* Aiton	Plate V
Fai-28B	Charcoal	UMad-P	Cancelas ash quarry	38°35′12”N; 28°38′53”W	365 m	7 m	~ 1200 yr BP	c11	*Picconia azorica* (Tutin) Knobl.	—
Fai-28H	Charcoal	UMad-P	Cancelas ash quarry	38°35′12”N; 28°38′53”W	365 m	7 m	~ 1200 yr BP	c11	*Picconia azorica* (Tutin) Knobl.	—
Fai-28I	Charcoal	UMad-P	Cancelas ash quarry	38°35′12”N; 28°38′53”W	365 m	7 m	~ 1200 yr BP	c11	*Picconia azorica* (Tutin) Knobl.	—
Fai-28K	Charcoal	UMad-P	Cancelas ash quarry	38°35′12”N; 28°38′53”W	365 m	7 m	~ 1200 yr BP	c11	*Picconia azorica* (Tutin) Knobl.	—
Fai-28L	Charcoal	UMad-P	Cancelas ash quarry	38°35′12”N; 28°38′53”W	365 m	7 m	~ 1200 yr BP	c11	*Picconia azorica* (Tutin) Knobl.	—
Fai-28R	Charcoal	UMad-P	Cancelas ash quarry	38°35′12”N; 28°38′53”W	365 m	7 m	~ 1200 yr BP	c11	*Picconia azorica* (Tutin) Knobl.	—
Fai-28S	Charcoal	UMad-P	Cancelas ash quarry	38°35′12”N; 28°38′53”W	365 m	7 m	~ 1200 yr BP	c11	*Picconia azorica* (Tutin) Knobl.	Plate VII
Fai-28G	Charcoal	UMad-P	Cancelas ash quarry	38°35′12”N; 28°38′53”W	365 m	7 m	~ 1200 yr BP	c11	*Prunus lusitanica L. Subsp. azorica* (Mouill.) Franco	Plate VI
Fai-28O	Charcoal	UMad-P	Cancelas ash quarry	38°35′12”N; 28°38′53”W	365 m	7 m	~ 1200 yr BP	c11	*Prunus lusitanica* L. subsp. *azorica* (Mouill.) Franco	—
Fai-28P	Charcoal	UMad-P	Cancelas ash quarry	38°35′12”N; 28°38′53”W	365 m	7 m	~ 1200 yr BP	c11	*Prunus lusitanica* L. subsp. *azorica* (Mouill.) Franco	—

Table 1 (*Continued*)

Field number	Preservation	Collection	Locality	Coordinates (WGS84)	Altitude	error	Age (^{14}C)	Volcanostratigraphy	Identification	Plate
Fai-28Q	Charcoal	UMad-P	Cancelas ash quarry	38°35′12”N; 28°38′53”W	365 m	7 m	~ 1200 yr BP	c11	*Prunus lusitanica* L. subsp. *azorica* (Mouill.) Franco	—
Fai-28V	Charcoal	UMad-P	Cancelas ash quarry	38°35′12”N; 28°38′53”W	365 m	7 m	~ 1200 yr BP	c11	*Prunus lusitanica* L. subsp. *azorica* (Mouill.) Franco	—
Fai-28X	Charcoal	UMad-P	Cancelas ash quarry	38°35′12”N; 28°38′53”W	365 m	7 m	~ 1200 yr BP	c11	*Prunus lusitanica* L. subsp. *azorica* (Mouill.) Franco	—
Fai-28Y	Charcoal	UMad-P	Cancelas ash quarry	38°35′12”N; 28°38′53”W	365 m	7 m	~ 1200 yr BP	c11	*Prunus lusitanica* L. subsp. *azorica* (Mouill.) Franco	—
Fai-28Z	Charcoal	UMad-P	Cancelas ash quarry	38°35′12”N; 28°38′53”W	365 m	7 m	~ 1200 yr BP	c11	*Prunus lusitanica* L. subsp. *azorica* (Mouill.) Franco	—
Fai-28N	Charcoal	UMad-P	Cancelas ash quarry	38°35′12”N; 28°38′53”W	365 m	7 m	~ 1200 yr BP	c11	*Vaccinium cylindraceum* Sm.	Plate IV
Fai-29A	Charcoal	UMad-P	South of Cascalho de Cima	38°37′57”N; 28°42′54”W	191 m	5 m	~ 1200 yr BP	c11	*Prunus lusitanica* L. *subsp. azorica* (Mouill.) Franco	—
Fai-29B	Charcoal	UMad-P	South of Cascalho de Cima	38°37′57”N; 28°42′54”W	191 m	5 m	~ 1200 yr BP	c11	*Prunus lusitanica* L. subsp. *azorica* (Mouill.) Franco	—
Fai-29C	Charcoal	UMad-P	South of Cascalho de Cima	38°37′57”N; 28°42′54”W	191 m	5 m	~ 1200 yr BP	c11	*Prunus lusitanica* L. subsp. *azorica* (Mouill.) Franco	—
Fai-30A	Charcoal	UMad-P	South of Cascalho de Cima	38°37′32”N; 28°42′49”W	280 m	27 m	~ 1200 yr BP	c11	*Laurus azorica* (Seub.) Franco	—
Fai-30B	Charcoal	UMad-P	South of Cascalho de Cima	38°37′32”N; 28°42′49”W	280 m	27 m	~ 1200 yr BP	c11	*Laurus azorica* (Seub.) Franco	Plate II

Family: LAURACEAE Juss., 1789.

Laurus azorica (Seub.) Franco, 1960

(TS: Figs. 5A–B; RLS: Figs. 5C–D; TLS: Figs. 5E–G)

Material: Fai-10A, Fai-10B, Fai-10C, Fai-10D, Fai-28A, Fai-28C, Fai-28D, Fai-28E, Fai-28F, Fai-28T, Fai-28W, Fai-28AA, Fai-30A, Fai-30B.

IAWA code (Wheeler et al., 1989): 1, 4, 9, 10, 13, 22, 25, 31, 41, 49, 53, 61, 65, 69, 98, 106, 112, 115.

Description: *Growth rings:* hardwood with distinct growth rings boundaries (Fig. 5A); *Vessels:* wood semi-ring-porous, vessel grouping solitary or 2–4 vessels, outline vessel round to angular (Fig. 5A–B), mean tangential diameter of vessel lumina between 50 and 100 µm ($\bar{X}$=100.5 µm; n=30), 40–100 vessels per mm^2 ($\bar{X}$=41.3 vessels per mm^2); vessel element length mean ≤ 350 µm ($\bar{X}$=234 µm; n=35); vessels with simple perforation plates (Fig. 5F–G), intervessel pits alternate and small (4–7 µm) (Fig. 5G); Vessel–ray pits rounded to irregular; *Fibers:* fibers simple and septate, ranging from thin (in early wood) to thick-walled in latewood (e.g. Fig. 5D, F); *Rays:* ray width 4 cells, height < 500 µm (Fig. 5C–D), rays parenchyma cells with small pits (Fig. 5E), procumbent with square marginal cells (Fig. 5H–I).

Comparison and remarks: the only known native Lauraceae in the Azores is the endemic *L. azorica* (Menezes de Sequeira et al., 2012), although other Macaronesian and European Lauraceae were introduced in several Azorean islands (e.g. *Ocotea foetens* (Aiton) Baill., *Laurus nobilis* L.; see Silva et al., 2005). Macaronesian Lauraceae wood anatomy is very similar (except for *Apollonias barbujana* (Cav.) Bornm.; see Loutfy, 2009). The studied samples are comparable to *L. azorica* wood anatomy (e.g. Peraza and Lopez de Roma, 1967; Loutfy, 2009; Schweingruber and Landolt, 2010; Schweingruber et al., 2011; Wheeler, 2011; Matos et al., 2019), particularly the vessel tangential lumina length and distribution and grouping, the mean vessel length, the presence of simple perforation plates, and septate fibers. In some specimens, latewood fiber walls are thick, without visible lumina or septa and totally vitrified (e.g. Fig. 5D). Loutfy (2009) states the presence of scalariform perforations in *L. azorica*, however we did not observe this character in our samples. The presence of extinct or extirpated Lauraceae in the Azores, although improbable, as the first historical descriptions only mention the presence of *L. azorica* (Frutuoso, 1590b; Frutuoso, 1590a; Frutuoso, 1590c), is not impossible. Leaf fossils presumably belonging to *Ocotea foetens* (Aiton) Baill. have been described for São Miguel (Diniz, 1962), although their taxonomical affinities still need to be revised (see Góis-Marques et al., in press). Today, *L. azorica* occurs in all Azorean islands (Silva et al., 2010), being an important tree in the extant Azorean natural forests (e.g. Jardim et al., 2007; Elias et al., 2016).

Order: MYRICALES Rich., 1835.

Family: MYRICACEAE Rich. ex Kunth, 1817.

Morella faya (Aiton) Wilbur, 1994.

(TS: Figs. 6A–C; TLS: Figs. 6D–H; RLS: Figs. 6I–K)

Material: Fai-28M.

IAWA code (Wheeler et al., 1989): 1, 5, 7, 10, 11, 12, 14, 15, 20, 21, 24, 25, 31, 41, 49, 53?, 57, 63, 65, 69, 97, 106, 112.

Wood description: *Growth rings:* hardwood with distinct growth rings boundaries (Fig. 6A); *Vessels:* wood diffuse-porous (Fig. 6A), radial pattern, with clusters common (Fig. 6A); outline angular (Fig. A–C), perforation plates simple and scalariform with ≤ 10 bars (Fig. 6B–C), intervessel pits scalariform and alternate (Fig. 6G–H), alternate pits minute to small; vessel–ray pits apparently simple and rounded; mean tangential diameter of vessel lumina between 50 and 100 µm ($\bar{X}$=57 µm; n=32), ranging from 38.08 to 70.72 µm, 40–100 vessels per square millimeter ($\bar{X}$=47 vessels/mm^2; n=141); vessel element up to 340 µm (maximum height measured); sclerotic tyloses present (Fig. 6A); *Fibers*: fibers pits common in both ra-

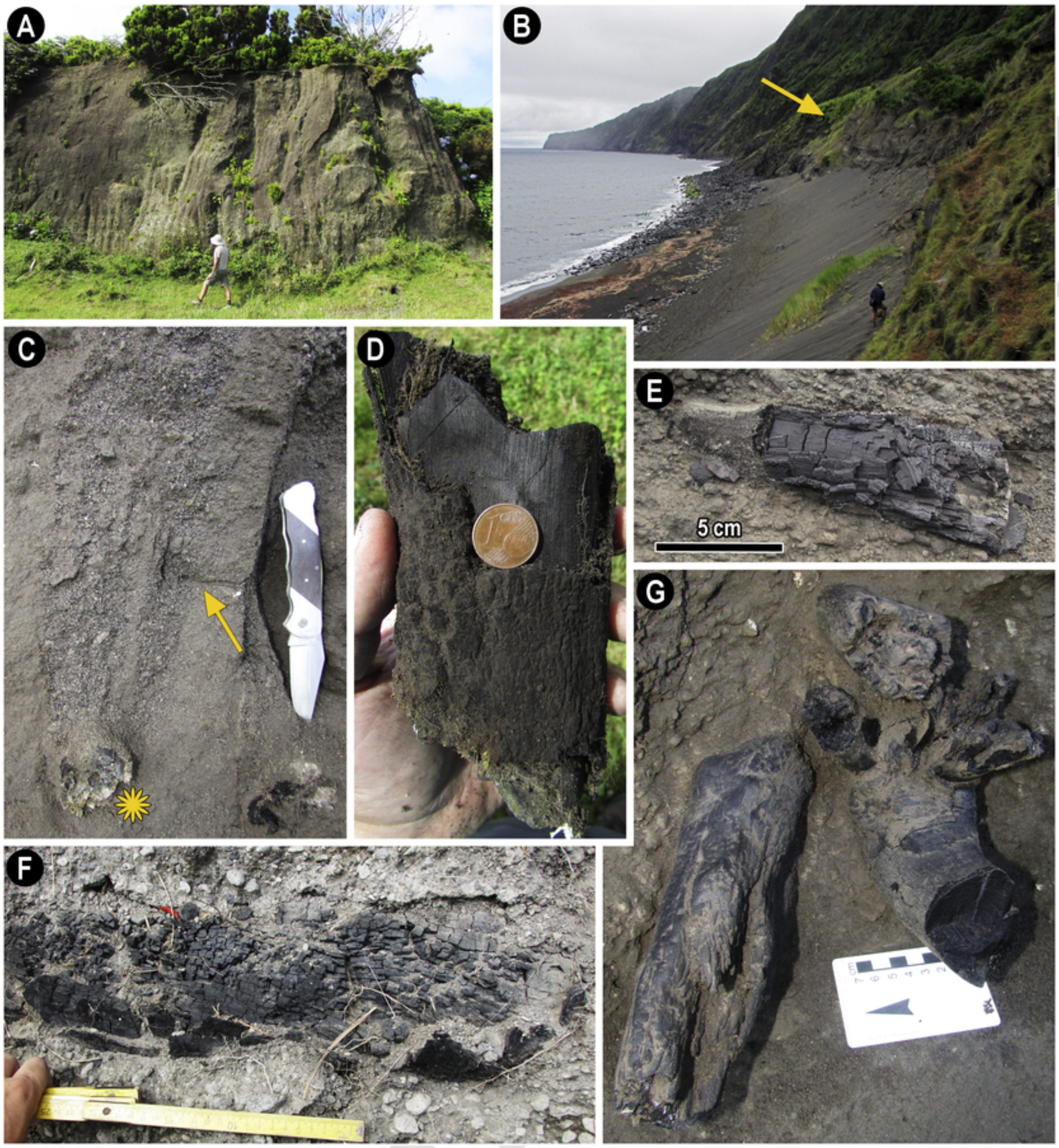

Fig. 2. Selected outcrops and associated charcoals from Faial Island. **A**, Cancelas ash quarry outcrop; **B**, Fajã da Praia do Norte beach outcrop; **C**, charcoal (star) from Cancelas ash quarry associated with degassing pipes (arrow; pocketknife ~ 20 cm); **D**, charcoal from Cancelas ash quarry showing the bark attached (coin diameter: 1,6 cm); **E**, charcoalified stem found in Fajã da Praia do Norte beach; **F**, Charcoalified trunk found in Cascalho de Cima locality; **G**, trunks from Cancelas ash quarry (scale bar in cm).

dial but rarer in tangential walls, septate, thin- to thick-walled (Fig. 6E); *Rays:* rays width 1–3 cells, heterocellular (Fig. 6D–E), height < 1 mm, ray cells pitted (Fig. 6B, F and J), body ray cells procumbent with 1–3 square marginal cells (Fig. 6I–J), perforated ray cells rare, presenting scalariform perforations (Fig. 6K); Rays per mm: 4–12/mm.

Comparison and remarks: The wood anatomy of *M. faya* was studied and illustrated by various authors (e.g. Carlquist, 2002; Schweingruber and Landolt, 2010; Schweingruber et al., 2011; Wheeler, 2011). Sample Fai-28M best fits within the wood anatomy of *M. faya,* especially to the presence of vessels with scalariform perforations with < 10 bars. Carlquist (2002) published a detailed study on Myricaceae wood anatomy. *Morella faya* is comparable to our sample, showing similar mean tangential diameter of vessel lumina (54 μm), comparable vessels per square millimeter, although lower (34 vessels/mm^2), number of bars on vessel perforations similar (9 bars), and similar ray anatomy and size. Growth rings boundaries are visible in our sample, but Carlquist (2002) did not observe them in *M. faya* from Hawaii. However, Schweingruber et al. (2011) and Pupo-Correia (2005) illustrate specimens from Madeira Island with clear growth rings. *M. faya* is present in all Azorean islands (Silva et al., 2010).

Order: ERICALES Bercht. & J. Presl Berchtold and Presl, 1820.

Family: ERICACEAE Juss., 1789.

Vaccinium cylindraceum Sm., 1819.

(TS: Figs. 7A–C; TLS: Figs. 7D–H; RLS: Figs. 7I–K)

Material: Fai-28N.

IAWA code (Wheeler et al., 1989): 1, 4, 6, 7, 11, 12, 14, 17, 20, 21, 26, 30, 36, 37, 40, 50, 53, 63, 65, 69, 98, 102, 103, 106, 107, 112.

Wood description: *Growth rings:* hardwood, distinct growth rings boundaries; *Vessels:* wood diffuse-porous (Fig. 7A–B), vessels in tangential, diagonal and radial pattern and clusters common (Fig. 7A); vessels outline angular (Fig. 7B), perforation plates scalariform with 20–40 bars (Fig. 7G–H, 7K), intervessel pits scalariform to opposite and small (7–10 μm) (Fig. 7G); vessel–ray pits with distinct borders similar to intervessel pits in size and shape throughout the ray cell (Fig. 7C); vessel elements with helical thickenings through the

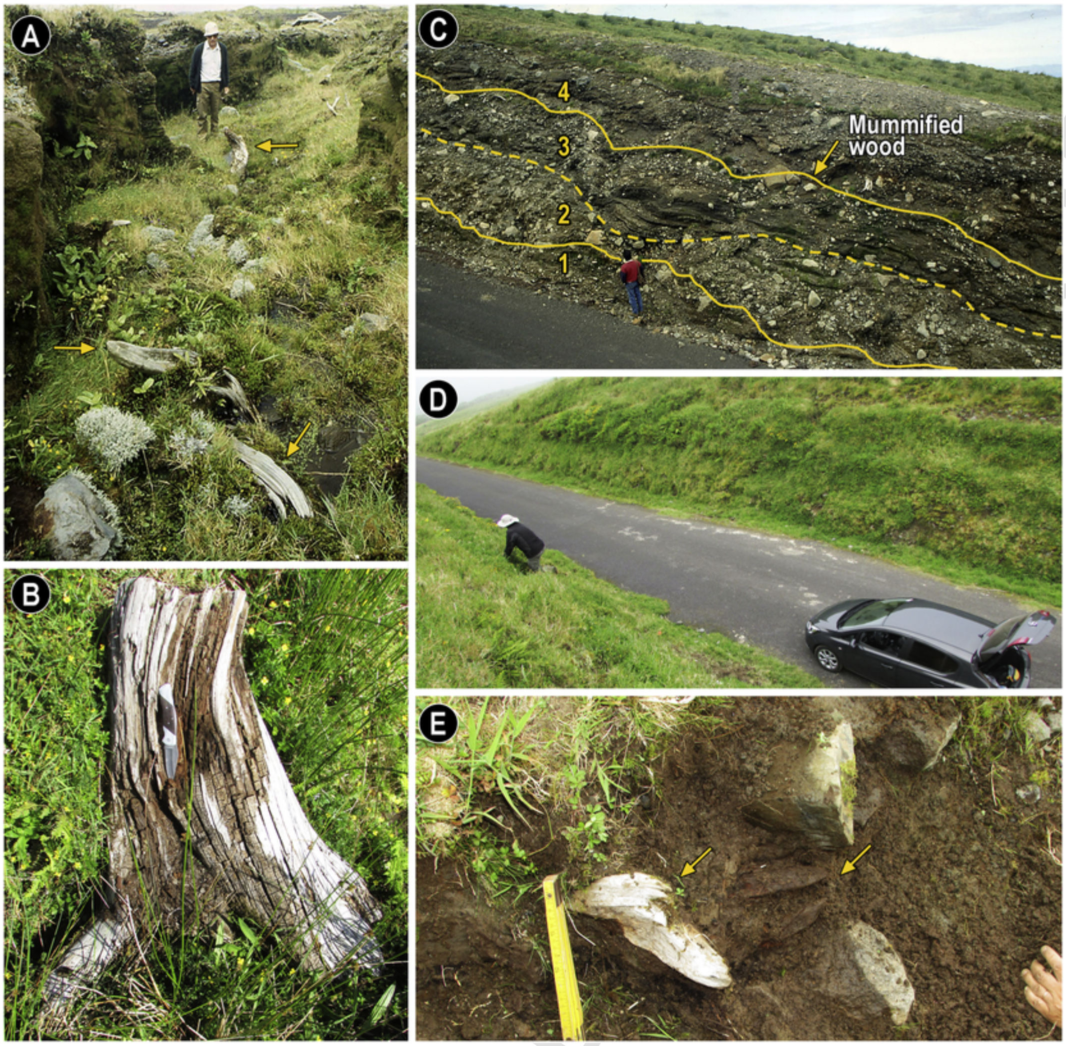

Fig. 3. Selected outcrops and associated mummified wood from Faial Island. **A**, Mummified woods cf. *Juniperus brevifolia* (arrows) found in the west part of Caldera rim, ca. early 1990 (Photo by José Madeira); **B**, same outcrop in 2016 still with mummified wood; **C**, phreatomagmatic deposits in the East part of the Caldera rim, with four phreatomagmatic breccias and associated mummified wood (photo by José Madeira ca. early 1990); **D**, same outcrop in 2016; **E**, example of mummified woods found below breccia no 4 dated at 1820 ± 45 yr BP.

body (Fig. 7E, G–H), mean tangential diameter of vessel lumina between ≤ 50 µm ($\bar{X}$ = 26.31 µm; n = 30), ranging from 18.36 to 38.42 µm, ≥ 100 vessels per square millimeter ($\bar{X}$ = 254 vessels/mm^2; n = 762); mean vessel element length ranging 350–800 µm ($\bar{X}$ = 573.7 µm; n = 11); *Fibers*: fibers pits common in both radial and tangential walls, septate, thin- to thick-walled; *Rays:* rays larger than 4–10 seriate, height > 1 mm although smaller rays occur (Fig. 7D, F); ray cells with perforated plates (Fig. 7F), body ray cells procumbent with one to 2–4 rows of upright marginal cells (Fig. 7I-K).

Comparison and remarks: Fai-28N is the single sample that presents vessels with > 20 scalariform perforations. Due to similar anatomical characters, vessel tangential lumina size and similar (although lower) vessels/mm^2, this specimen seems to correspond to *Vaccinium* L. The Azorean endemic *V. cylindraceum* still lacks a formal anatomical description. However, the sample studied best fits the Madeiran *V. padifolium* (=‘*V. maderense*’) in the “Xylem Data Base” (Schweingruber and Landolt, 2010). Phylogenetically, these species are sister taxa, clustering together within the *Vaccinium* Andean clade (see Kron et al., 2002), and most probably sharing identical wood anatomy. The vessels pattern in TS, lumina tangential vessel size and vessels/mm^2 approximate more to *V. padifolium*, vessels with helical thickenings through the body and simple pits through the ray cell walls. It differs in the number of bars in the scalariform perforation, having a higher number of bars (> 20) than proposed for *V. padifolium* ($\bar{X}$ = 3 bars, ranging from 1 to 6; Lens et al., 2004). However, *V. padifolium* illustrated by Schweingruber and Landolt (2010) shows scalariform perforation up to 15 bars (Lens et al., 2004), and similar to the ones found in Fai-28N. Another similar wood is *Ilex perado* Aiton subsp. *azorica* (Loes.) Tutin, although the tangential vessel length is higher (50–100 µm) and vessel/mm^2 is lower (40–100 vessel/mm^2) (Baas, 1973). Nowadays the endemic *V. cylindraceum* occurs in all Azorean islands including in Graciosa Island where it was introduced (Silva et al., 2010).

Order: PRIMULALES Lindl., 1833.
Family: MYRSINACEAE R. Br., 1810.
Myrsine retusa Aiton, 1789.
(TS: Figs. 8A–C; RLS: Figs. 8D–G; TLS: Figs. 8H–J)
Specimen: Fai-28J.

IAWA code (Wheeler et al., 1989): 2, 5, 7, 9, 12, 13, 20, 22, 24, 31, 40, 48, 62, 63, 65, 69, 98, 102, 105, 110, 114.

Wood description: *Growth rings*: hardwood with boundaries vague, presenting tangential and radial traumatic canal splits (

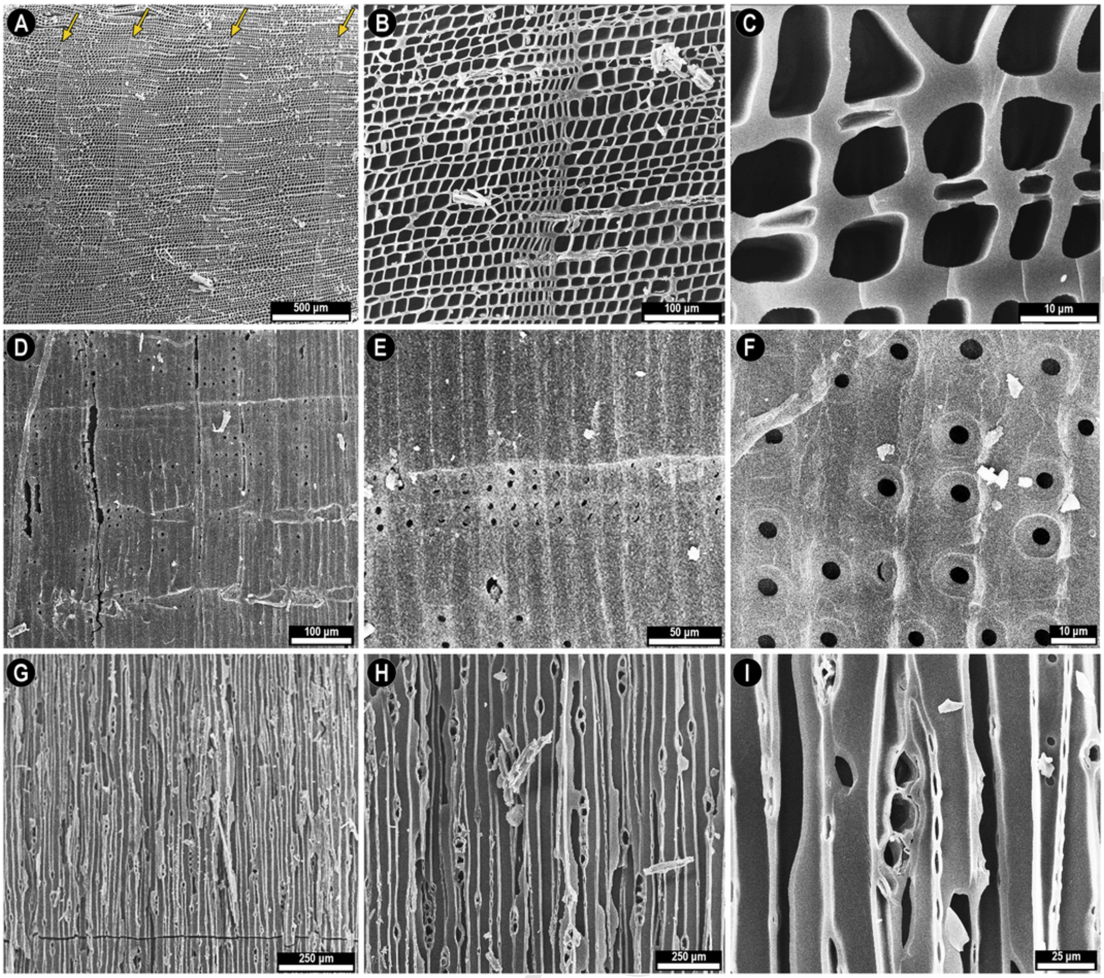

Fig. 4. *Juniperus brevifolia* (Seub.) Antoine anatomy (Fai-28U) SEM photographs in TS, TLS and RLS. **A**, General TS view showing the growth ring boundaries (arrows); **B**, TS, detail of early wood to late wood transition, **C**, TS, detail showing the homogenization of the cell walls caused by charcoalification above > 300 °C; **D**, RLS general view; **E**, RLS, cross-field pits apparently cupressoid, with two per crossfield, **F**, RLS, detail of tracheids showing uniseriate bordered pits **G**, general TLS view; **H**, TLS, showing uniseriate 1–4 ray vessels, **I**, TLS, detail showing a uniseriate 3 ray vessel.

Fig. 8A–B, D–E); *Vessels*: wood diffuse-porous, rarely mainly solitary or rarely in radial multiples of 2–4 (Fig. 8A–B), outline angular (Fig. 8C), perforation plates simple, intervessel pits minute (≤ 4 µm), scalariform or alternate (Fig. 8F), vessel-ray pits similar to intervessel pits in size and shape throughout the ray cell, mean tangential diameter of vessel lumina between ≤ 50 µm ($\bar{X}$ = 29.4 µm; n = 31); 20–40 vessels per square millimeter ($\bar{X}$=29.67 vessels/mm^2; n = 228); vessel element length not measured*; fibers*: fibers with distinctly bordered pits in both radial and tangential walls, septate, thin- to thick walled (Fig. 8F), fiber length not measured; *Rays*: 4–10 seriate (Fig. 8G), height > 1 mm (Fig. 8D–E) ray cells upright and square, sheath cells present (Fig. 8H–J), ≤ 4 rays/mm.

Comparison and remarks: the wood anatomy of this single specimen clearly fit *Myrsine* L., and most probably representing the endemic azorean *M. retusa* (Menezes de Sequeira et al., 2012). Detailed wood anatomy of *M. retusa* was never investigated, but close taxa were analyzed and illustrated in detail (e.g. Lens et al., 2005; Schweingruber et al., 2013; de Luna et al., 2018), and showing a comparable wood anatomy. Shared characteristics with *Myrsine* spp. wood are the presence of multiseriate ray cells and upright cells, vessels mostly solitary, angular (although de Luna et al., 2018, describes species ranging from circular to oval) and with a small tangential diameter (< 50 µm), vessels with alternate pits and simple perforations, fibers septate and with simple pits (e.g. Lens et al., 2005). Radial traumatic splits, viewed in TS and TLS (Fig. 8B, D) occur throughout the sample, most probably traumatic gas pipes formed by the instant and intense heat from the engulfing PDC. *Myrsine* wood shows characteristics similar to paedomorphic wood (e.g. Carlquist, 1962; Carlquist, 1974; Carlquist, 2001), which is closely associated with plants with insular woodiness (e.g. Carlquist, 1974; Dulin and Kirchoff, 2010). Remarkably, the sample Fai-28J resembles in TS and TLS the wood anatomy described for some lobelioid Hawaiian woody Campanulaceae (see Carlquist, 1969).

Order: ROSALES Bercht. & J.Presl Berchtold and Presl, 1820.

Family: ROSACEAE Juss. 1789.

Prunus lusitanica L. subsp. *azorica* (Mouill.) Franco.

(= *Prunus azorica* (Mouill.) Rivas Mart. & Lousã & Fern.Prieto & E.Días & J.C.Costa & C.Aguiar)

(TS: Figs. 9A–C; RLS: Figs. 9D–F; TLS: Figs. 9G–I)

Material: Fai-28G, Fai-28O, Fai-28P, Fai-28Q, Fai-28V, Fai-28X, Fai-28Y, Fai-28Z, Fai-29A, Fai-29B, Fai-29C.

IAWA code (Wheeler et al., 1989): 1, 4, 6, 7, 10, 11, 12, 13, 22, 24, 30, 36, 37, 40, 50, 52, 62, 66, 68, 98, 107, 115.

Wood description: *Growth rings:* hardwood, distinct growth rings boundaries (Fig. 9A–B); Vessels: semi-ring-porous, vessels in tangential, diagonal and radial pattern, vessels in multiples of 4 or

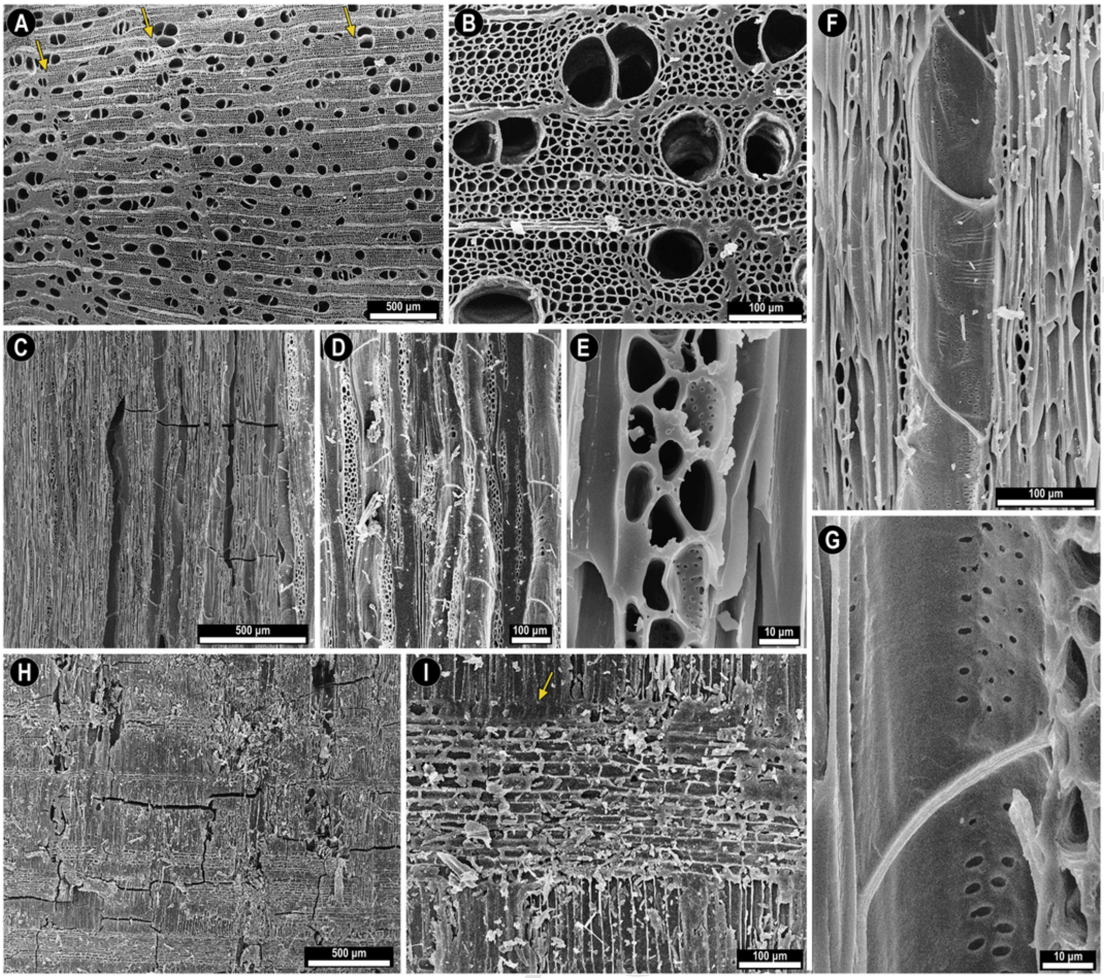

Fig. 5. *Laurus azorica* (Seub.) Franco (Fai-28D and Fai-30B) SEM photographs in TS, TLS and RLS. A, Fai-28D, general TS showing diffuse-porous and growth ring boundaries (arrows); B, Fai-28D, detail of TS depicting solitary or 2 vessels grouping; C, Fai-30B general view of TLS; D, Fai-28D, TLS section on latewood showing homogenized fibers; E, Fai-30B detail of the heterocellular ray cells; F, Fai-30B, detail in TLS of the vessels, showing simple perforation plates; G, Fai 28B, TLS, detail of the vessel alternate pitting; H, Fai-28D, RLS general view; I, Fai-28D, RLS, ray cells procumbent with square marginal cells (arrow).

in clusters, vessel outline oval to angular (Fig. 9A–C), perforation plates simple (Fig. 9G); intervessel pits alternate and minute (≤ 4 µm); Vessel–ray pits similar to intervessel pits in size and shape throughout the ray cell; helical thickenings throughout body of vessel element (Fig. 9E, F, H); mean tangential diameter of vessel lumina ≤ 50 µm ($\overline{X}$ = 47.4 µm; n = 30); ≥ 100 vessels per mm^2 ($\overline{X}$ = 147.8 vessels per mm^2); mean vessel element length (X = 288.9 µm; n = 20); *Fibers*: Fibers with distinctly bordered pits; nonseptate fibers present; fibers thin walled; *Rays:* rays uniseriate or 4–10 seriate, ray height of large rays < 1 mm (X = 689.3 µm; n = 13); rays per linear mm: 4.

Comparison and remarks: in Macaronesia two native *Prunus lusitanica* subspecies are known, *P. lusitanica* subsp. *hixa* (Willd.) Franco in Madeira and Canary Islands, and *P. lusitanica* subsp. *azorica* (Mouill.) Franco (Acebes Ginovés et al., 2010; Menezes de Sequeira et al., 2012). We compared our samples to the continental subsp. *P. lusitanica* subsp. *lusitanica* and to *P. lusitanica* subsp. *hixa* (Peraza and Lopez de Roma, 1967; Zhang, 1992; Schweingruber and Landolt, 2010; Wheeler, 2011). To date a detailed wood anatomy of the Azorean subspecies is lacking. Comparison of the fossil samples to extant woods of *P. lusitanica* shows a perfect match of wood anatomy. TS shows the same vessel size and organization; TLS vessels share identical helical thickenings and simple perforation plates and RLS and TLS shows the same ray characteristics with *P. lusitanica*. Today, *P. lusitanica* subsp. *azorica* is a very rare tree that occurs in Flores, Faial, Pico, S. Jorge, Terceira and S. Miguel (Silva et al., 2010).

Order: GENTIANALES Juss. ex Bercht. & J. Presl Berchtold and Presl, 1820.

Family: OLEACEAE Hoffmanns. & Link, 1809.

Picconia azorica (Tutin) Knobl., 1934.

(TS: Figs. 10A–C; RLS: Figs. 10D–F; TLS: Figs. 10G–I)

Specimens: Fai-28B, Fai-28H, Fai-28I, Fai-28L, Fai-28R, Fai-28S.

IAWA code (Wheeler et al., 1989): 1, 5, 8, 11, 12, 13, 22, 24, 30, 36, 37, 40, 66, 69, 97, 106, 165, 189.

Wood description: *Growth rings*: hardwood with distinct growth rings boundaries (Fig. 10A–B); *Vessels:* diffuse-porous, vessels displaying dendritic pattern and clustered (Fig. 10A–C); vessel outline rounded, less frequently angular (Fig. 10B–C), perforation plates simple, intervessel pits alternate and small (Fig. 10F, I), pits with membrane and torus cavity (Fig. 10I), helical thickenings throughout body of vessel element, mean tangential diameter of vessel lumina ≤ 50 µm ($\overline{X}$ = 48.03 µm; n = 31); *Ground tissue fibers*: Fibers thin to thick-walled and nonseptate; *Rays:* ray width 1–3 cells (Fig. 10D–E), and height up to 10 cells, with less than 1 mm ($\overline{X}$ = 168.6 µm; n = 30) (Fig. 10D, G–H), heterocellular and with intercellular spaces (

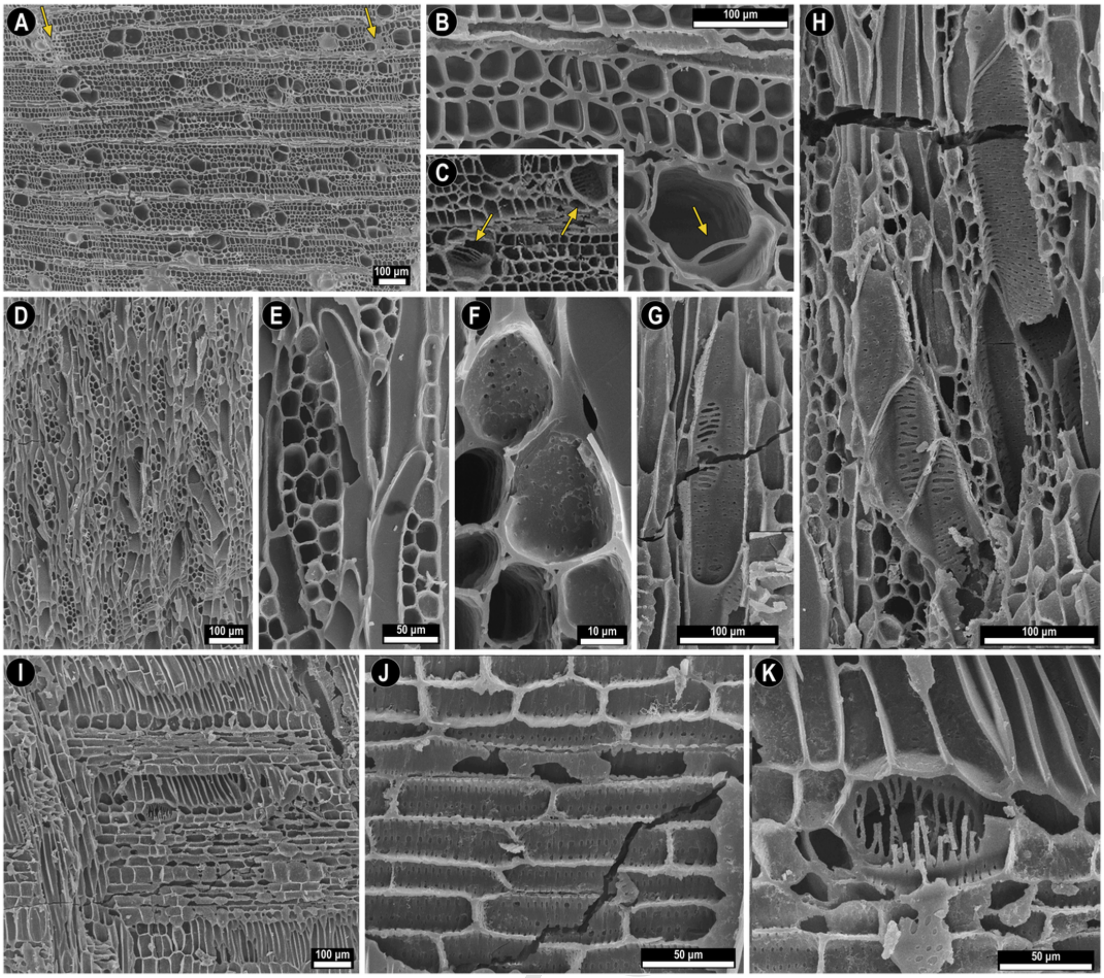

Fig. 6. *Morella faya* (Aiton) Wilbur SEM photographs in TS, TLS and RLS. **A**, General TS view showing the wood diffuse-porous and growth ring boundaries (arrows); **B**, detail of the TS showing a vessel with a broken scalariform perforation with one bar (arrow), fibers and ray cells; **C**, detail of Fig. A, where scalariform perforations are visible in the interior of vessels (arrows); D, general view of TLS; **E**, detail of the rays and fibers; **F**, detail of the heterocellular ray cells; **G–F**, intervessel pitting ranging from scalariform to alternate; **I**, general view of RLS; **J**, detail of the procumbent cells; **K**, detail of a perforated ray cells, with scalariform perforations.

Fig. 10E), body ray cells procumbent with one row of square marginal cells (Fig. 10G–H).

Comparison and remarks: Macaronesian native and endemic Oleaceae are represented by taxa included in the genera *Olea* L., *Jasminum* L., *Phillyrea* L., and *Picconia* DC. (Acebes Ginovés et al., 2010; Menezes de Sequeira et al., 2012), all sharing similar wood anatomy (e.g. Baas et al., 1988; Schweingruber et al., 2013). Among these genera, *Olea, Phillyrea* and *Picconia* are proposed to be part of an artificial group (Group V in Baas et al., 1988), based on similar wood anatomy. *Picconia* wood is differentiated from other Macaronesian Oleaceae by the occurrence of inter-vessel and inter-tracheary pits with tori (Dute et al., 2008; Ferreira et al., 2012), which also occur in the studied charcoal specimens (see Fig. 6F). The studied charcoal specimens have an identical wood anatomy to *Picconia*, especially in TS the vessels forming a dendritic pattern, and having a similar tangential diameter, and in TLS showing helical thickenings, associated with perforation plates, ray cells with less than 1 mm, and the inter-vessel and inter-tracheary pits with tori. In Macaronesia, two *Picconia* spp. are recognized, *P. azorica* in the Azores archipelago and *P. excelsa* in Madeira and Canaries archipelagos (Acebes Ginovés et al., 2010; Menezes de Sequeira et al., 2012). Ferreira et al. (2012), described in detail the wood anatomy of *P. azorica*, and comparing it to *P. excelsa,* and a separation between the two species based on wood anatomy is subtle, but due to the remarkable wood anatomy similarity, age and location these remains can be attributed to *P. azorica*. As a final note, although charcoalified, the trunks were the hardest of the charcoals to hand split into sections. This attests the hardness of *P. azorica* that was valued for construction and woodworking since the colonization of Macaronesian Portuguese archipelagos (Ferreira et al., 2012).

6. Discussion

6.1. Taphonomy and fossil-diagenesis

All specimens found within the 1200 yr BP ignimbrite were totally charcoalified (except Fai-09), implying that the PDC and the deposited ignimbrite remained at high temperatures (> 250 °C; Scott, 2010) for enough time to allow total pyrolysis of the buried trees. This is corroborated by degassing pipes coming from the buried trunks (Fig. 2C); this is in contrast to descriptions of historical explosive eruptions in North America, South America and in the British West Indies and their effects on vegetation (e.g. Spicer, 1989; Scott, 2010; Major et al., 2013). Second, several of the studied charcoalified trunks were found in the horizontal or sub-horizontal position (e.g. Fig. 2E, F), probably snapped and transported by the PDC. How-

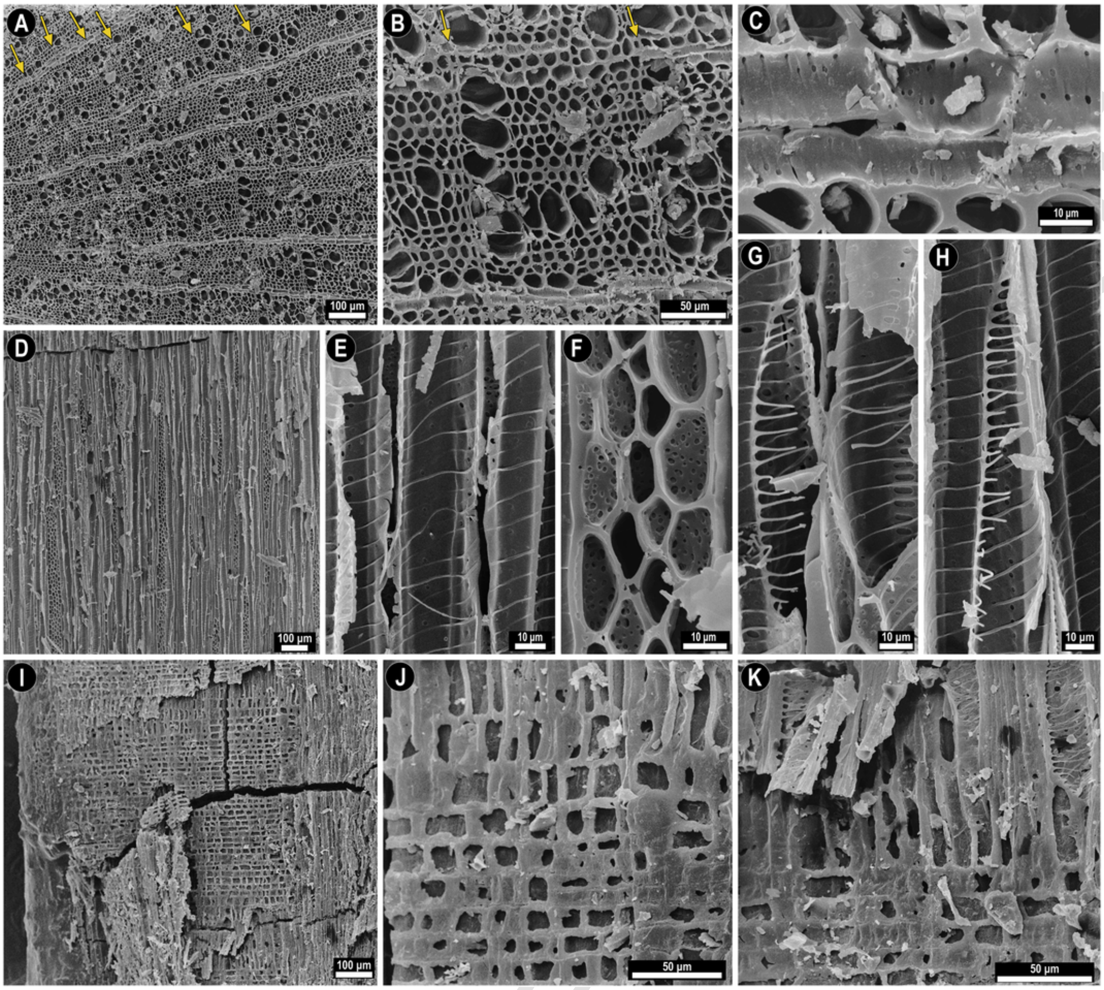

Fig. 7. *Vaccinium cylindraceum* Sm. (Fai-28N) SEM photographs in TS, TLS and RLS. **A**, TS general view showing vessels diffuse-porous and distinct growth rings (arrows); **B**, Detail of TS, with two growth rings (arrow) and vessels in tangential, diagonal and radial pattern; **C**, TS, detail of the simple pitted ray cells; **D**, TLS general view; **E**, TLS, vessels with helical thickenings, **F**, TLS of a ray with simple pits; **G** and **F**, vessels with scalariform perforation plates; **I**, RLS general view of ray cells; **J**, detail of procumbent and marginal upright ray cells; **K**, detail showing scalariform perforations associated with procumbent and marginal upright ray cells.

ever, some of the trees could have been thrown down by the PDC and buried without further transport (e.g. Scott, 2010). A minimal transport is supported by the presence of bark still attached to the charcoalified specimens (e.g. Fig. 2D). Reports on the effects of PDC (either cold or burning PDC) on trees is usually the bark strip on the vent-side, although this could be dependent on the taxon, PDC magnitude and temperature (see Major et al., 2013). Other charcoalified trunks entombed in the ignimbrite had no bark, most probably due to abrasion and destruction during transport. The total or partial lack of bark is also seen in the mummified wood (Fig. 1A, B and E) collected in the phreatomagmatic deposits, most probably stripped by similar processes. Moreover, in Cancelas quarry (site 4; Fig. 1C; 2A), charcoalified trunks were found in the upright position (see Pimentel et al., 2015, fig. 11a), with bark still attached around the stem (Fig. 2D). This reveals that tree trunks were buried and charred in situ by the burning ignimbrite, preserving a T^0 assemblage sensu DiMichele and Falcon-Lang (2011). T^0 assemblages associated with explosive volcanism reported in the literature are geologically much older and related to ash-fall deposits (e.g. Rößler et al., 2012; Wang et al., 2012). However, comparable situations are described associated with ignimbrites in historical PDC, were rotted boles are in situ after the passage of the PDC and subsequent burial (e.g. Fritz, 1986; Scott and Glasspool, 2005; Major et al., 2013). Third, information about the temperature of the PDC that charred the woods can be retrieved from SEM. All charcoals present homogenization of the cell walls. This indicates that the PDC and the ignimbrite were at temperatures > 235 °C (Scott, 2010). For Faial, the use of charcoal reflectance values and cell walls homogenization as a proxy to infer PDC and ignimbrites paleotemperatures, are inexistent. However, in São Miguel, charcoal recovered from ignimbrites gave reflectance values indicating temperatures up to 460 °C (Pensa et al., 2015). Finally, Faial charcoals showed an exceptional anatomical preservation under SEM (Figs. 4–9), as already previewed in LM (Góis-Marques et al., in press). The catastrophic event of a PDC allowed the rapid burial and charring of the wood, and simultaneously, prevented further decomposition and erosion, as charcoal is relatively inert (e.g. Scott and Jones, 1991b). Such an event allowed the preservation of the anatomy in exquisite detail allowing the study and identification of plant taxa.

6.2. Identifications and paleophytodiversity

Our identification approach was to compare the fossil woods with Azorean taxa and to the most similar Macaronesian or continental taxa. The Azores flora is composed of a reduced number of trees and shrubs when compared to other Macaronesian archipelagos, many being endemic (Menezes de Sequeira et al., 2012). However, it is im-

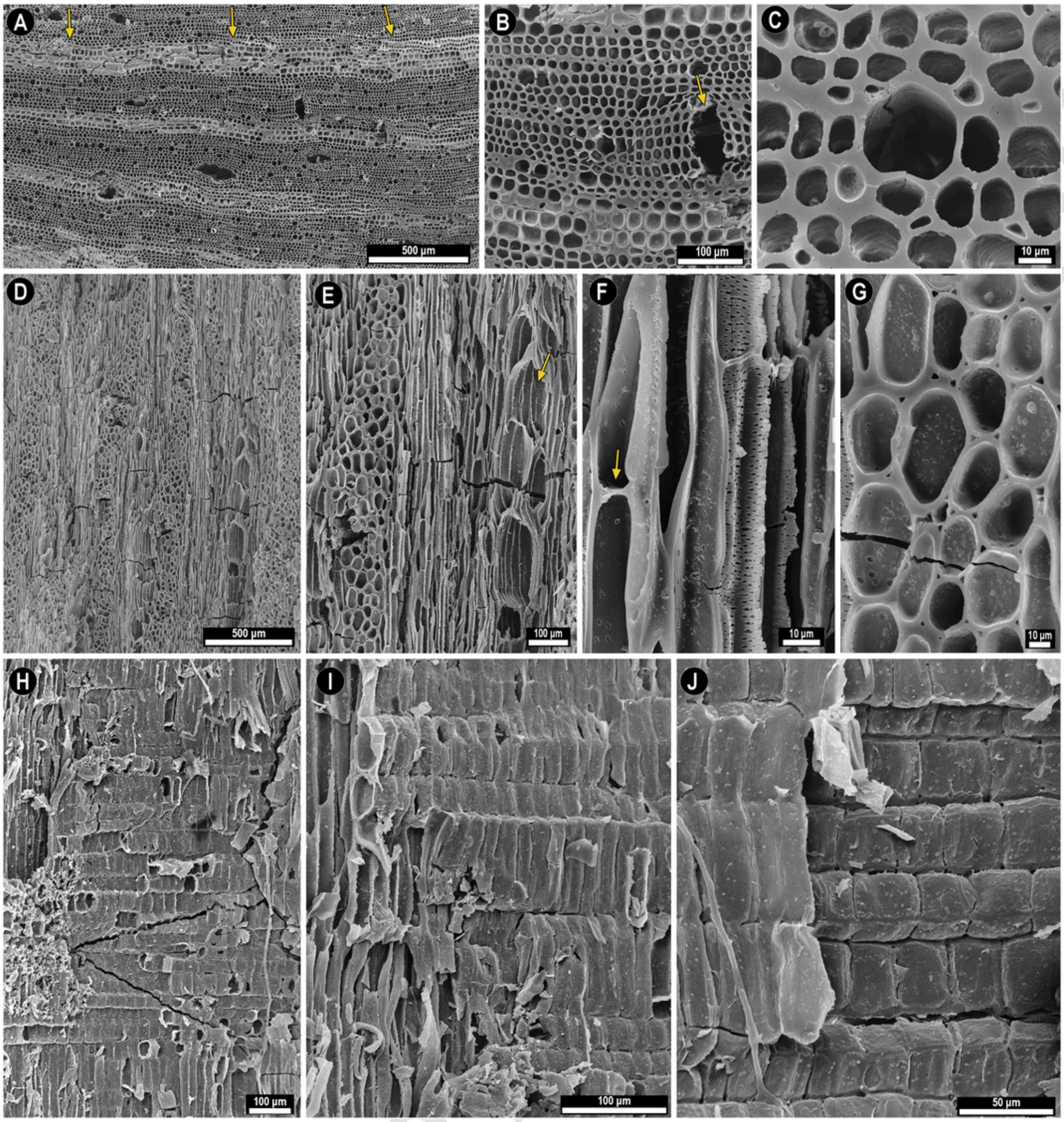

Fig. 8. *Myrsine retusa* Aiton (Fai-28 J) SEM photographs in TS, TLS and RLS. **A**, TS general view showing the large rays, small vessels and traumatic rips along the wood; **B**, TS detail, showing a tangential traumatic rip (arrow); **C**, TS detail showing a vessel (V) with angular outline and homogenized cell walls; **D**, general view of a TLS, showing the multiseriate rays > 1 mm; **E**, Detail of **D**, displaying large ray cells, contrasting with the small size of fibers and vessels and a traumatic rip (arrow); **F**, TLS detail of the fibers, with simple pits and septate (arrow), and vessels with scalariform or alternate pitting; **G**, TLS detail of a heterocellular ray, showing intercellular spaces and simple pitting; **H**, RLS general view of a ray; **I**, RLS, detail of the same ray showing upright and square cells; **J**, detail of upright (sheath cells) and square cells.

portant to emphasize that some of these taxa still lack a formal (or detailed) wood description (e.g. *M. retusa*, *V. cylindraceum, P. lusitanica* subsp. *azorica*). Endemicity is probably reflected into the wood anatomy, and fundamental knowledge of this is important to distinguish taxa in the fossil record.

Since the early 19th century, fossil woods, either charcoalified or mummified, are described in botanical and geological Azorean literature however the identifications are given without a scientific approach (Góis-Marques et al., in press and references therein). The collection of 41 specimens allowed identification of seven species based on wood anatomy (Table 1). All identified species correspond to endemic phanerophytes presently growing in Faial and other Azorean Islands (e.g. Silva et al., 2010; Menezes de Sequeira et al., 2012). Within Faial Island, it is the first time that *M. retusa*, *M. faya*, and *P. lusitanica* subsp. *azorica* have been recorded (Góis-Marques et al., in press). When compared with the Azorean macrofossil record (see Góis-Marques et al., in press), *P. lusitanica* subsp. *azorica* and *M. retusa* are new records. Moreover, pollen fossils from all taxa identified in this paper were also found in the Azorean limnic paleoecological record (see Connor et al., 2012).

Globally, the most abundant taxon was *Laurus azorica* (n = 14), followed by *Prunus lusitanica* subsp. *azorica* (n = 11), *Picconia azorica* (n = 7), *Juniperus brevifolia* (n = 5), while *Myrsine retusa*, *Vaccinium cylindraceum and Morella faya* account for the remaining (n = 3). The best exposed and sampled site was Cancelas quarry (Fig. 1C, site 4; n = 27 specimens), where the species *Laurus azorica* (n = 8), *Prunus lusitanica* subsp. *azorica* (n = 8) and *Picconia azorica* (n = 7), *Morella faya*, *Myrsine retusa*, *Vaccinium cylindraceum* and *Juniperus brevifolia* (n = 3) were recovered. In Cascalho de Cima sites (Fig. 1C, sites 2 and 3; n = 5), only *Prunus lusitanica* subsp. *azorica* (n = 3) and *Laurus azorica* (n = 2) were identified. Around the Caldera area and in Cabouco Velho (Fig. 1C, sites 6,7 and 5), *Junipe-*

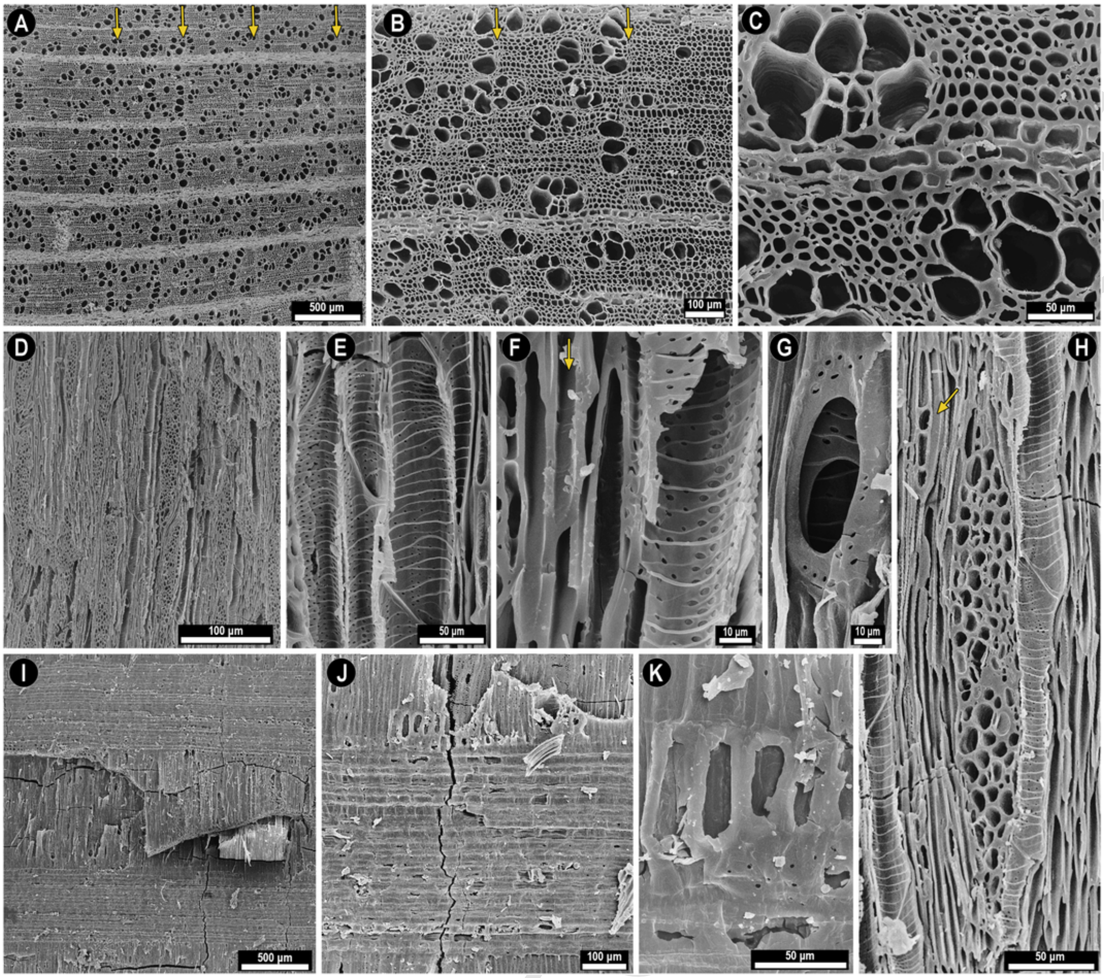

Fig. 9. *Prunus lusitanica* L. subsp. *azorica* (Mouill.) Franco (Fai-28G) SEM photographs in TS, TLS and RLS. **A**, TS general view with ring boundaries distinct (arrows); **B**, TS detail showing vessels in tangential, diagonal and radial pattern, and two ring boundaries (arrows); **C**, detail of B, showing the vessel clusters and the homogenization of the cell walls. **D**, TLS general view; **E**, detail of the vessels and the helical thickenings throughout the body of vessel element; **F**, intervessel pits alternate and minute and fibers septate and simple pits (arrow); **G**, RLS, vessel simple perforation plate; **H**, TLS detail of the uniseriate (arrow) and multiseriate rays; **I**, RLS general view; **J**, RLS showing procumbent and upright marginal cells; **K**, detail of the upright marginal cells.

rus brevifolia or cf. *Juniperus brevifolia* were the only species found (n = 4). In Fajã da Praia do Norte beach, only *L. azorica* was found (Fig. 1C, site 1; n = 4; one sample not studied).

6.3. Paleovegetation, PNV and current vegetation

The identified wood fossils suggests a fully forested island preceding the volcanic eruptions which eventually entombed them. Comparatively, today all sampled sites are highly anthropically modified landscapes, being transformed into pastures, *Cryptomeria japonica* plantations or areas invaded by several exotic plants (e.g. *Pittosporum undulatum*, *Hedychium gardnerianum*). Our data points to the presence of two main types of vegetation correlated with altitude, and comparable to the PNV proposed by Elias et al. (2016) (Fig. 11A). However, our results suggest some differences: In altitudes higher than 897 m a.s.l. only *J. brevifolia* or cf. *J. brevifolia* trunks were found (see Table 1). Although buried in slightly older deposits (1660 ± 45 yr BP 1820 ± 45 yr BP; see Madeira et al., 1995), these fossils attest the presence of a vegetation dominated by *J. brevifolia* in the higher reaches of Faial Island. The altitudinal occurrence of a juniper belt for the Azores islands have been discussed by several authors (Elias et al., 2016 and references therein). For Faial Island the presence of a *Juniperus–Ilex* montane forests associated with the Upper thermotemperate–Hyperhumid zone was proposed by Elias et al. (2016) (Fig. 11A). The second type of vegetation recognized is a laurel forest, found in Cancelas quarry (Fig. 1C, site 4; Fig. 11A–B), in Cascalho de Cima (Fig. 1C, site 2 and 3) and Fajã da Praia do Norte beach (Fig. 1C, site 1). For all these localities a *Laurus* submontane forest is modeled as the PNV (compare Fig. 1A–11A). In the Cancelas site, four main phanerophytes were identified from 27 specimens: *L. azorica*, *P. lusitanica* subsp. *azorica*, *P. azorica* and *M. faya* corresponding to an almost certain authocthonous fossil assemblage. In Cascalho de Cima *P. lusitanica* subsp. *azorica* and *L. azorica* were the only species identified, and in Fajã da Praia do Norte beach only *L. azorica* was found. Single specimens of *J. brevifolia*, *M. retusa* and *V. cylindraceum* were also found in Cancelas quarry, probably dragged by the PDC from an upper vegetation belt (i.e. *Juniperus–Ilex* montane forests; Fig. 11A–B), where these plants are common (Elias et al., 2016), corresponding to a allocthonous fossil assemblage. *Vaccinium cylindraceum* could also be associated with the shrub layer of the laurel forest. Our results agree with the *Laurus* submontane forest described in Elias et al. (2016) that occurs in Lower thermotemperate–Upper humid zones of Faial Island (Fig. 11A). However, extant Azorean forests, with dominance or co-domi-

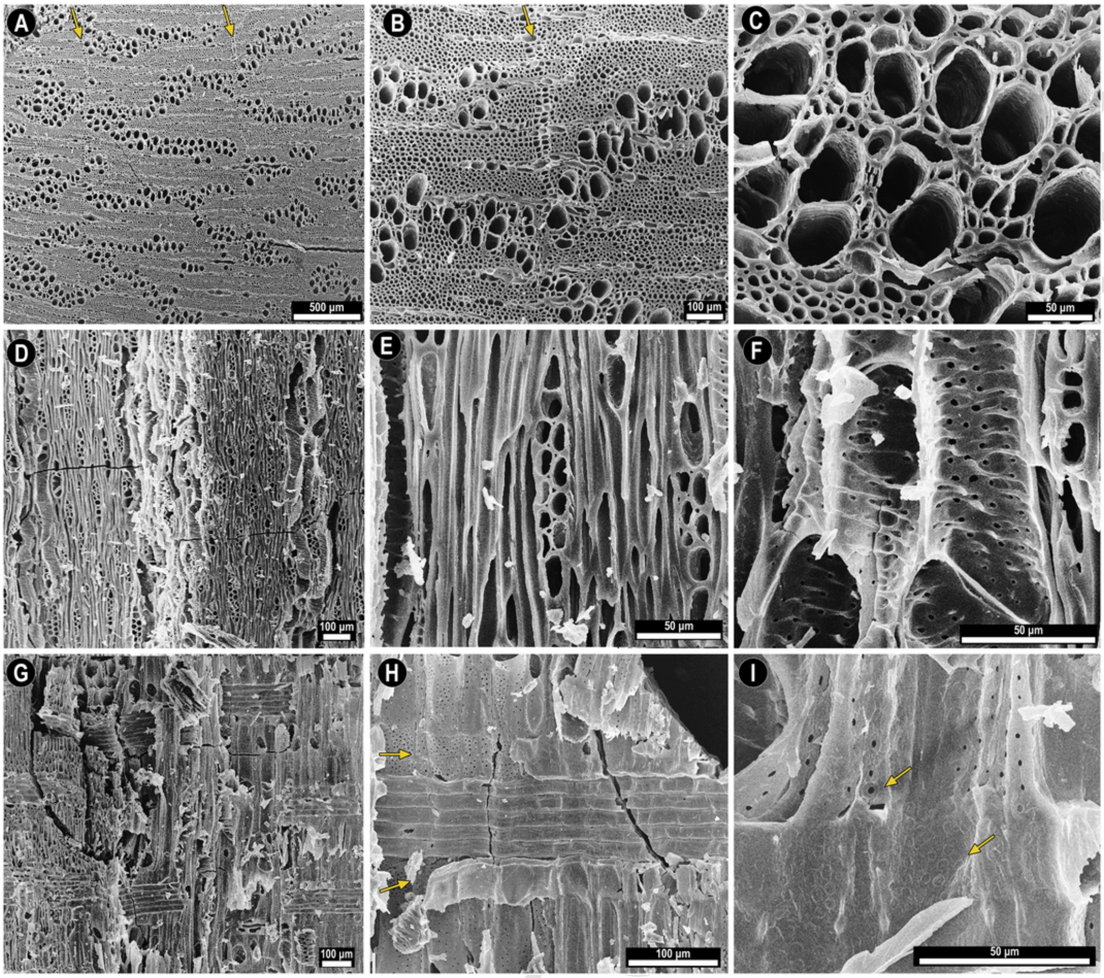

Fig. 10. *Picconia azorica* (Tutin) Knobl. (Fai-28S) SEM photographs in TS, TLS and RLS. **A**, TS general view showing vessels in dendritic pattern and ring boundaries distinct (arrows); **B**, TS detail of the ring (arrow) and the dendritic pattern; **C**, TS detail showing the vessel clusters and the homogenization of the cell walls; **D**, TLS general view; **E**, TLS detail of the rays and simple fibers; **F**, TLS detail of the vessels with helical thickenings and alternate small pits; **G**, RLS general view; **H**, RLS, detail of the ray procumbent and marginal cells (arrow); **I**, RLS, detail of the areolate pits (arrows).

nance of *P. lusitanica* subsp. *azorica,* are currently unknown. Vegetation descriptions of the Azores Islands (e.g. Dias et al., 2005; Elias et al., 2016) do not include *P. lusitanica* subsp. *azorica* as a dominant tree in the Azorean laurel forests. Only in one site in Terceira Island, *P. lusitanica* subsp. *azorica* (= *Prunus azorica* (hort. ex Mouill.) Rivas Mart., Lousã, Fern. Prieto, E. Dias, J.C. Costa & C. Aguiar) was identified as the dominant phanerophyte (see *Woodwardio radicantis–Prunetum azoricae*; Rivas-Martínez et al., 2001). Interestingly, the abundance of *Prunus* in our samples agrees with the Azorean historical accounts, where this tree is mentioned as abundant in all islands (Frutuoso, 1590a; Frutuoso, 1590b; Frutuoso, 1590c), and especially in São Miguel, furthermore Fernandes (1508), coeval with the Azores settlement, states the presence of large *L. azorica* but also the abundance of “Ginge” (the archaic Portuguese word for *Prunus lusitanica* subsp. *azorica*).

The value of the PNV concept has been debated in recent years, being criticized (e.g. Carrión and Fernández, 2009; Carrión, 2010; Chiarucci et al., 2010) and supported (e.g. Farris et al., 2010; Loidi et al., 2010; Somodi et al., 2012). Recently, Rull et al. (2017a), taking into account the contribution of Somodi et al. (2012), made a qualitative comparison of the pollen assemblages preserved in the Azorean paleoecological record (Connor et al., 2012; Rull et al., 2017a) to the proposed Azores PNV (Elias et al., 2016), verifying the similarity between both. Although our results are comparable to Azorean PNV, we found an unexpected abundance of *P. lusitanica* subsp. *azorica,* that differs from the *Prunus* abundance reported either in paleoecological pollen diagrams (Connor et al., 2012; Rull et al., 2017a), and from the modeled PNV (i.e. *Laurus* submontane forests). The near absence of this taxon in the paleopalynological record can be explained by the entomophilous pollination, contributing to a low representation in pollen fossil assemblages (de Nascimento et al., 2015 and references therein). This phenomenon is also observed with *L. azorica* pollen. Although *L. azorica* is one of the most abundant species found in our samples, *L. azorica* pollen is rarely preserved in the paleoecological record due to entomophily and thin pollen exine leading to fast degradation (de Nascimento et al., 2015 and references therein). This means that paleofloras dominated by entomophilous taxa, such as the Macaronesian laurel forests (Fernández-Palacios et al., 2019), will end up underrepresented in coeval palynological assemblages even if they are the most abundant and dominant species in a given territory, as already pointed out by Loidi et al. (2010), and empirically by actuopaleontological studies (de Nascimento et al., 2015). The absence of *P. lusitanica* subsp. *azorica* in the PNV models is due to this tree being a rare and endangered species (IUCN: Bilz, 2011). If this taxon is not observed or is underrepresented in neoecological surveys, it cannot be included in the modeled PNV.

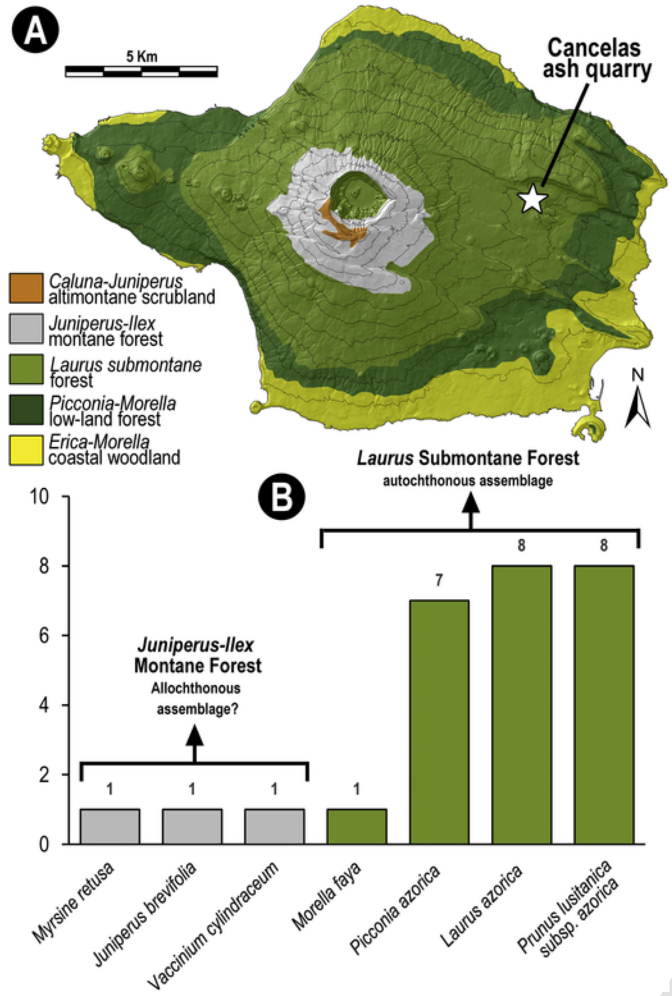

Fig. 11. The potential natural communities for Faial Island and the Cancelas ash quarry paleophytodiversity. **A**, Potential natural vegetation map for Faial Island based on Elias et al., 2016; **B**, paleophytodiversity and paleoecological interpretation of the Cancelas ash quarry charcoal assemblage.

The plant fossils preserved within deposit C11, which is between 1200 yr BP (Madeira et al., 1995) and 1000 yr BP (Pacheco, 2015), are important testimonies of an insular terrestrial paleoecosystem spatially preserved as a T^0 assemblage (see Góis-Marques et al., in press). Plant fossils found within the C11 deposits were part of a paleoforest growing 700–500 years before the Portuguese colonization of the Azores Islands. These fossils are the ideal ground proofs to test the Azorean PNV but also to reconstruct an ecological baseline (see Nogué et al., 2017), essential for a future floristic restoration and conservation of Faial Island. Moreover, this is probably applicable to other Azorean Islands, although further paleobotanical and palynological studies are needed (Góis-Marques et al., in press). Paleovegetation that is spatially preserved but time restricted (i.e. single volcanic event that led to the burial of insular forests), coupled with spatially restricted but with long-term information, such as the palynological record found in limnic sediments, are essential to the reconstruction of Azorean pre-anthropic vegetation.

6.4. Anthropic influence and extirpation?

Why did Azorean *Prunus* almost disappear, and other trees such as *L. azorica* did not? According to Frutuoso (1590a, 1590b, 1590c), *P. lusitanica* subsp. *azorica* was an abundant tree in all Azorean islands, growing together with other endemic and native trees. This situation is very similar to the one found in the charcoalified trees in Cancelas quarry. However, since the mid-15th century, the Azores natural landscapes were massively modified (Dias, 2007) by logging trees for fuel and construction, and opening the forests for agriculture and pastures (e.g. Dias, 2007). Habitat reduction is one of the main drivers of the reduction of this particular tree (Bilz, 2011). However, and as already pointed out by Frutuoso (1590a), *P. lusitanica* subsp. *azorica* is poisonous to cattle by ingestion. The symptoms and ecological clues of plant toxicity are described in detail: "…however, the foliage of 'ginja' [*P. lusitanica* subsp. *azorica*], on March onward, growing in highlands and darkening woodlands makes them (the cattle) to urinate blood." (Frutuoso, 1590a, pg. 212; translation by the authors). *Prunus* spp. are poisonous to ruminants (see Wagstaff, 2008 and references therein), due to the presence of cyanogenic glycosides. The active control of *P. lusitanica* subsp. *azorica* to avoid animal intoxication and death could most probably be a cause of its decline, along with the use of wood for fuel. The control of poisonous trees is not unknown in Portugal; for example, *Taxus baccata* L. was driven to an acute decline by shepherds (Draper and Marques, 2006) for this reason. Other hypotheses could be related to this tree being endozoochoric, having suffered from the negative effects of human colonization. The decline or even extinction of birds that acted as vectors cannot be ruled out, as the paleozoological fossil record has a record of extinct taxa (e.g. Rando et al., 2013; Alcover et al., 2015; Rando et al., 2017). The decline of *P. lusitanica* subsp. *azorica* was most probably a combination of causes, such as logging and habitat loss, associated with the loss of seed dispersers and an active population control, leading to the almost eradication of this tree.

Recently, Carine and Menezes de Sequeira (2019) proposed the existence of a Hookerian shortfall, an addition to several biological knowledge gaps that have been proposed (see Hortal et al., 2015 for further details). The Hookerian shortfall questions how human impact on pristine oceanic islands shaped the present diversity patterns observed today. The Faial Island fossil record points to a paleovegetation assemblage that differs from the observed and modeled (Elias et al., 2016) and that is more similar to the historical accounts (Fernandes, 1508; Frutuoso, 1590a; Frutuoso, 1590b; Frutuoso, 1590c). The study of Faial's medieval fossil forest will certainly contribute to fill the Azorean Hookerian shortfall.

7. Conclusions

Faial Island is a unique island within the Azores Archipelago to study pre-anthropic paleophytodiversity and paleovegetation, due to plant fossil preservation that resulted from Holocene recurrent explosive volcanism (especially the C11 event).

The detailed study of the wood anatomy of 41 samples allowed the identification of 7 phanerophytes, corresponding to extant taxa. The spatial distribution of the sites strongly suggests the presence of two vegetation belts. The identification of a forest preserved in situ, provides a unique view into a pristine Meghalayan vegetation within the Azores Islands. Unexpectedly, *Prunus lusitanica* subsp. *azorica* was the second most abundant fossil wood found, indicating that this tree was much more abundant in the recent past, as corroborated by historical accounts.

As a concluding remark, the recurrent explosive volcanism in Faial Island allowed the preservation of 'recent' macrofossils. These, in the context of a recently colonized but highly anthropically modified island, are the missing link to fully appreciate these paleoecosystems in a pristine state, and ideal to fill the knowledge gap of the Hookerian shortfall (Carine and Menezes de Sequeira, accepted). Further work is needed in Faial Island to have a full picture of the paleophytodiversity and paleovegetation buried by the C11 explosive volcanic activity.

Declaration of Competing Interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Uncited references

Brongniart, 1843
Brown, 1810
de Jussieu, 1789
Gorozhankin, 1904
Hoffmannsegg and Link, 1809–1820
Humboldt et al., 1817
Knoblauch, 1934
Lindley, 1833
Linnaeus, 1753
Smith, 1819
von Martius, 1835
Willkomm, 1854

Acknowledgements

We would like to thank Paloma de Palacios and Luis García (Universidad Politécnica de Madrid) to provide access to the Macaronesian wood reference collection; Adriano Pimentel (Azores University) to indicate some key localities in Faial Island; Artur Gil (Azores University) for helping with GIS data; Jorge Capelo (Instituto Nacional de Investigação Agrária e Veterinária) for fruitful discussion on Azores vegetation; Telmo Nunes (FCUL-MF) for SEM sample preparation and imaging; Ria Mitchell for the review that improved this manuscript. CAG-M would like to acknowledge financial support from ARDITI – Regional Agency for the Development of Research, Technology and Innovation, project M1420-09-5369-FSE-000001- PhD grant and JM to FCT-project UID/GEO/50019/2013 – Instituto Dom Luiz.

References

Acebes Ginovés, J.R., Catalina, L.A.M., Rodríguez Navarro, M.L., del Arco Aguilar, M., García Gallo, A., Pérez de Paz, P.L., Rodríguez Delgado, O., Martín Osorio, C.e., Wildpret de la Torre, W., 2010. Pteridophyta, Spermatophyta. In: Arechavaleta, M., Rodríguez, S., Zurita, N., García, A. (Eds.), Lista de especies silvestres de Canarias. Hongos, plantas y animales terrestres 2009, Gobierno de Canarias, Santa Cruz de Tenerife, España, pp. 119–172.

Aiton, W., 1789. Hortus Kewensis: A Catalogue of the Plants Cultivated in the Royal Botanic Garden at Kew, III, London.

Alcover, J.A., Pieper, H., Pereira, F., Rando, J.C., 2015. Five new extinct species of rails (Aves: Gruiformes: Rallidae) from the Macaronesian Islands (North Atlantic Ocean). Zootaxa 4057 (2), 151–190.

Anderson, C.L., Channing, A., Zamuner, A.B., 2009. Life, death and fossilization on Gran Canaria – implications for Macaronesian biogeography and molecular dating. J. Biogeogr. 36 (12), 2189–2201.

Antoine, F., 1857. Die Kupressineengattungen Arceuthos, Juniperus, und Sabina, 16, Wien.

Astudillo, F.J., 2018. Environmental and historical archaeology of the Galápagos islands: archaeobotany of Hacienda El Progreso, 1870–1920. Veg. Hist. Archaeobotany 27 (5), 737–751.

Baas, P., 1973. The wood anatomical range in Ilex (Aquifoliaceae) and its ecological and phylogenetic significance. Blumea 21 (2), 258–293.

Baas, P., Esser, P.M., van der Westen, M.E.T., Zandee, M., 1988. Wood anatomy of the Oleaceae. IAWA Bull. 9 (2), 103–182.

Baas, P., Blokhina, N., Fujii, T., Gasson, P., Grosser, D., Heinz, I., Ilic, J., Xiaomei, J., Miller, R., Newsom, L.A., Noshiro, S., Richter, H.G., Suzuki, M., Terrazas, T., Wheeler, E., Wiedenhoeft, A., 2004. IAWA list of microscopic features for softwood identification. IAWA J. 25 (1), 1–70.

Berchtold, B.V.v., Presl, J.S., 1820. O Prirozenosti Rostlin. Krala Wiljma Endersa, Prague, 322.

Bilz, M., 2011. *Prunus lusitanica* subsp. *azorica*. The IUCN Red list of Threatened Species 2011, e.T37577A10058878: Downloaded on .

Bird, M.I., 2013. Charcoal. In: Elias, S.A., Mock, C.J. (Eds.), Encyclopaedia of Quaternary Science. Elsevier Science, Amsterdam, The Netherlands, pp. 353–360.

Brongniart, A., 1843. Énumeration des genres de plantes cultivés au Muséum d'histoire naturelle de Paris. Fortin, Masson & Cie, Paris & Leipzig, 136.

Brown, R., 1810. Prodromus Florae Novae Hollandiae et Insulae Van-Diemen, Exhibens Characteres Plantarum. R. Taylor et socii, London, 590.

Bryson, R.U., Bryson, R.A., Ruter, A., 2006. A calibrated radiocarbon database of late Quaternary volcanic eruptions. eEarth Discuss 1, 123–134.

Burnett, G.T., 1835. Outlines of Botany, Including a General History of the Vegetable Kingdom in which Plants Are Arranged According to the System of Natural Affinities, 1. J. Churchill, London, 517.

Burnham, R.J., 1994. Plant deposition in modern volcanic environments. Earth Environ. Sci. Trans. R. Soc. Edin. 84 (3–4), 275–281.

Burnham, R.J., Spicer, R.A., 1986. Forest litter preserved by volcanic activity at El Chichon, Mexico; a potentially accurate record of the pre-eruption vegetation. PALAIOS 1 (2), 158.

Carine, M., Menezes de Sequeira, M., 2019. Sir Joseph Hooker on Insular Floras: human impact and the natural laboratory paradigm. Sci. Insularum.(submitted).

Carlquist, S., 1962. A theory of Paedomorphosis in dicotyledonous woods. Phytomorphology 12 (1), 30–45.

Carlquist, S., 1969. Wood Anatomy of Lobelioideae (Campanulaceae). Biotropica 1 (2), 47–72.

Carlquist, S., 1974. Island Biology. Columbia University Press, New York and London.

Carlquist, S., 2001. Comparative Wood Anatomy: Systematic, Ecological, and Evolutionary Aspects of Dicotyledon Wood. Springer-Verlag, Berlin, 448.

Carlquist, S., 2002. Wood and Bark anatomy of Myricaceae: relationships, generic definitions, and ecological interpretations. Aliso 21 (1), 7–29.

Carracedo, J.C., Badiola, E.R.g., Guillou, H., Paterne, M., Scaillet, S., Torrado, F.J.P.r., Paris, R., Fra-Paleo, U., Hansen, A., 2007. Eruptive and structural history of Teide Volcano and rift zones of Tenerife, Canary Islands. GSA Bull. 119 (9–10), 1027–1051.

Carrión, J.S., 2010. The concepts of potential natural vegetation (PNV) and other abstractions (trying to pick up fish with wet hands). J. Biogeogr. 37 (11), 2213–2215.

Carrión, J.S., Fernández, S., 2009. The survival of the 'natural potential vegetation' concept (or the power of tradition). J. Biogeogr. 36 (12), 2202–2203.

Castilla-Beltrán, A., de Nascimento, L., Fernández-Palacios, J.M., Fonville, T., Whittaker, R.J., Edwards, M., Nogué, S., 2019. Late Holocene Environmental Change and the Anthropization of the Highlands of Santo Antão Island. Cabo Verde, Palaeogeography, Palaeoclimatology, Palaeoecology.

Chiarucci, A., Araújo, M.B., Decocq, G., Beierkuhnlein, C., Fernández-Palacios, J.M., 2010. The concept of potential natural vegetation: an epitaph?. J. Veg. Sci. 21 (6), 1172–1178.

Connor, S.E., van Leeuwen, J.F.N., Rittenour, T.M., Knaap, W.O.v.d., Ammann, B., Björck, S., 2012. The ecological impact of oceanic island colonization – a palaeoecological perspective from the Azores. J. Biogeogr. 39 (6), 1007–1023.

Conte, E., Widom, E., Kuentz, D., França, Z., 2019. ^{14}C and U-series disequilibria age constraints from recent eruptions at Sete Cidades Volcano, Azores. J. Volcanol. Geotherm. Res

Costa, J.C., Neto, C., Aguiar, C., Capelo, J., Santo, M.D.E., Honrado, J., Pinto-Gomes, C., Monteiro-Henriques, T., Menezes de Sequeira, M., Lousa, M., 2012. Vascular plant communities in Portugal (Continental, the Azores and Madeira). Global Geobot. 2, 1–180.

Crivellaro, A., Schweingruber, F.H., 2013. Atlas of Wood, Bark and Pith Anatomy of Eastern Mediterranean Trees and Shrubs, with a Special Focus on Cyprus. Springer, Heidelberg.

Dansereau, P., 1970. Macaronesian studies IV. Natural ecosystems of the Azores. Rev. Can. Géogr. 24, 21–42.

de Jussieu, A.L., 1789. Genera plantarum secundum ordines naturales disposita, juxta methodum in horto Regio Parisiensi exaratum anno 1774. Herissant Typographum, Paris, 498.

de Luna, B.N., Freitas, M.d.F., Barros, C.F., 2018. Systematic and phylogenetic implications of the wood anatomy of six Neotropical genera of Primulaceae. Plant Syst. Evol. 304 (6), 775–791.

de Nascimento, L., Willis, K.J., Fernández-Palacios, J.M., Criado, C., Whittaker, R.J., 2009. The long-term ecology of the lost forests of La Laguna, Tenerife (Canary Islands). J. Biogeogr. 36 (3), 499–514.

de Nascimento, L., Nogué, S., Fernández-Lugo, S., Méndez, J., Otto, R., Whittaker, R.J., Willis, K.J., Fernández-Palacios, J.M., 2015. Modern pollen rain in Canary Island ecosystems and its implications for the interpretation of fossil records. Rev. Palaeobot. Palynol. 214, 27–39.

de Nascimento, L., Nogué, S., Criado, C., Ravazzi, C., Whittaker, R.J., Willis, K.J., Fernández-Palacios, J.M., 2016. Reconstructing Holocene vegetation on the island of Gran Canaria before and after human colonization. The Holocene 26 (1), 113–125.

de Palacios, P., Esteban, L.G., Fernández, F.G., García-Iruela, A., Conde, M., Román-Jordán, E., 2014. Comparative wood anatomy of Juniperus from Macaronesia. IAWA J. 35 (2), 186–198.

Di Chiara, A., Speranza, F., Porreca, M., Pimentel, A., D'Ajello Caracciolo, F., Pacheco, J., 2014. Constraining chronology and time-space evolution of Holocene volcanic activity on the Capelo Peninsula (Faial Island, Azores): the paleomagnetic contribution. Geol. Soc. Am. Bull. 126 (9–10), 1164–1180.

Dias, E., 2007. A Chegada dos portugueses às ilhas – o antes e o depois - Açores. In: Silva, J. (Ed.), Árvores e Florestas de Portugal: Açores e Madeira - A Floresta das Ilhas. 6. Público, Comunicação Social SA, Fundação Luso Americana para o Desenvolvimento e Liga para a Protecção da Natureza, pp. 137–164.

Dias, E., Mendes, C., Melo, C., Pereira, D., Elias, R., 2005. Azores Central Islands vegetation and flora field guide. Quercetea 7, 123–173.

Dias, E., Pereira, D., Medeiros, V., Mendes, J., Elias, R.B., 2007. V: Distribuição das principais manchas florestais: 1. Açores. In: Silva, S.J. (Ed.), Árvores e Florestas de Portugal: Açores e Madeira - A Floresta das Ilhas. 6. Público, Comunicação Social SA, Fundação Luso Americana para o Desenvolvimento e Liga para a Protecção da Natureza, pp. 299–322.

DiMichele, W.A., Falcon-Lang, H.J., 2011. Pennsylvanian 'fossil forests' in growth position (T^0 assemblages): origin, taphonomic bias and palaeoecological insights. J. Geol. Soc. 168 (2), 585–605.

Diniz, F., 1962. Vegetais dos tufos vulcânicos da ilha de São Miguel, Açores. In: Comunicações dos Serviços Geológicos de Portugal. Tomo XLVI pp. 317–329.

Draper, D., Marques, I., 2006. Taxus baccata en Portugal y sus perspectivas futuras frente al cambio global. In: Serra, L. (Ed.), El Tejo En El Mediterráneo Occidental: Jornadas Internacionales sobre el tejo y las tejeras en el Mediterráneo Occidental. Generalitat Valenciana, Valencia, pp. 171–176.

Drouet, H., 1866. Catalogue de la flore des iles Açores précédé de L'itinéraire d'un voyage dans cet archipel. J.-B. Bailliére & fils, Paris, 153.

Dulin, M.W., Kirchoff, B.K., 2010. Paedomorphosis, secondary woodiness, and insular woodiness in plants. Bot. Rev. 76 (4), 405–490.

Dute, R.R., Jansen, S., Holloway, C., Paris, K., 2008. Torus-bearing pit membranes in selected species of the Oleaceae. J. Alab. Acad. Sci. 79 (1), 12–22.

Elias, R.B., Dias, E., 2014. The recognition of infraspecific taxa in Juniperus brevifolia (Cupressaceae). Phytotaxa 188 (5), 241–250.

Elias, R.B., Gil, A., Silva, L., Fernández-Palacios, J.M., Azevedo, E.B., Reis, F., 2016. Natural zonal vegetation of the Azores Islands: characterization and potential distribution. Phytocoenologia 46 (2), 107–123.

Falcon-Lang, H.J., Wheeler, E., Baas, P., Herendeen, P.S., 2012. A diverse charcoalified assemblage of cretaceous (Santonian) angiosperm woods from Upatoi Creek, Georgia, USA. Part 1: wood types with scalariform perforation plates. Rev. Palaeobot. Palynol. 184, 49–73.

Farris, E., Filibeck, G., Marignani, M., Rosati, L., 2010. The power of potential natural vegetation (and of spatial-temporal scale): a response to Carrión & Fernández (2009). J. Biogeogr. 37 (11), 2211–2213.

Feraud, G., Kaneoka, I., Allègre, C.J., 1980. K/Ar ages and stress pattern in the Azores: geodynamic implications. Earth Planet. Sci. Lett. 46 (2), 275–286.

Fernandes, V., 1508. Das ilhas do Mar Oceano (Separata do "Manuscrito Valentim Fernandes-1508"). Acad. Hist. (1940) 7, 106–119.

Fernández-Palacios, J.M., Arévalo, J.R., Balguerías, E., Barone, R., Elias, R.B., de Nascimento, L., Delgado, J.D., Fernández Lugo, S., Méndez, J., Menezes de Sequeira, M., Naranjo, A., Otto, R., 2019. The Laurisilva: Canaries, Madeira and Azores. Macaronesia Editorial, Santa Cruz de Tenerife, 417.

Fernández-Prieto, J.A., Aguiar, C., Dias, E., 2012. Description of some new syntaxa from the Azores archipelago. Int. J. Geobot. Res. 2, 111–116.

Ferreira, R.C., Monaco, A.L., Picchio, R., Schirone, A., Vessella, F., Schirone, B., 2012. Wood anatomy and technological properties of an endangered species: Picconia azorica (Oleaceae). IAWA J. 33 (4), 375–390.

Forjaz, V.H., 1960. Notícia de alguns fósseis na ilha do Faial. Atlantida IV (1), 30–40.

Forjaz, V.H., Mojardino, J.L., Fernandes, N.S.M., 1970. Contribuição para o estudo das jazidas fossilíferas das ilhas do Faial, Pico, S. Jorge e Terceira (Açores). In: Comunicações dos Serviços Geologicos de Portugal. Tomo LIV pp. 27–37.

Fouqué, F., 1873. Voyages Géologiques aux Açores I. L' ile de Terceire. In: Revue des Deux Mondes, Cent Troisieme (Livraison du 1st Janvier). pp. 40–65.

Franco, J.A., 1960. Lauráceas Macaronésicas. Anais Inst. Super. Agron. 23, 89–104.

Fritz, W.J., 1986. Plant taphonomy in areas of explosive volcanism. In: Broadhead, T.W. (Ed.), Notes for a Short Course: Studies in Geology Organized by R.A. Gastaldo. 15. 15, University of Tennessee Department of Geological Sciences, pp. 1–9.

Frutuoso, G., 1590. Livro Quarto das Saudades da Terra, edition 1998, Instituto Cultural de Ponta Delgada, Ponta Delgada.

Frutuoso, G., 1590. Livro Sexto das Saudades da Terra, edition 1998, Instituto Cultural de Ponta Delgada, Ponta Delgada, 165.

Frutuoso, G., 1590. Livro Terceiro das Saudades da Terra, edition 1998, Instituto Cultural de Ponta Delgada, Ponta Delgada, 125.

García-Talavera, F., Sánchez-Pinto, L., Socorro, S., 1995. Vegetales fósiles en el complejo traquítico-sienítico de Gran Canaria. Rev. Acad. Canar. Cien. VII, 77–91.

Geldmacher, J., van den Bogaard, P., Hoernle, K., Schmincke, H.-U., 2000. The 40Ar/39Ar age dating of the Madeira Archipelago and hotspot track (eastern North Atlantic). Geochem. Geophys. Geosyst. 1 (2), 1–26.

Gente, P., Dyment, J., Maia, M., Goslin, J., 2003. Interaction between the Mid-Atlantic Ridge and the Azores hot spot during the last 85 Myr: emplacement and rifting of the hot spot-derived plateaus. Geochem. Geophys. Geosyst. 4 (10), 1–23.

Góis-Marques, C.A., Menezes de Sequeira, M., 2015. Darwin, Hooker and Arruda Furtado and the palaeobotany of Azores: rediscovering the first collections. Rev. Palaeobot. Palynol. 221, 47–51.

Góis-Marques, C.A., Elias, R.B., Steinbauer, M.J., de Nascimento, L., Fernández-Palacios, J.M., Menezes de Sequeira, M., Madeira, J., 2019. The loss of a unique palaeobotanical site in Terceira Island within the Azores UNESCO global geopark (Portugal). Geoheritagehttps://doi.org/10.1007/s12371-019-00401-1, (accepted).

Góis-Marques, C.A., Mitchell, R.L., de Nascimento, L., Fernández-Palacios, J.M., Madeira, J., Menezes de Sequeira, M., 2019. Eurya stigmosa (Theaceae), a new and extinct record for the Calabrian stage of Madeira Island (Portugal): ^{40}Ar/^{39}Ar dating, palaeoecological and oceanic island palaeobiogeographical implications. Quat. Sci. Rev. 206, 129–140.

Góis-Marques, C.A., de Nascimento, L., Menezes de Sequeira, M., Fernández-Palacios, J.M. and Madeira, J., in press. The Quaternary plant fossil record from the volcanic Azores Archipelago (Portugal, North Atlantic Ocean): a review. Hist. Biol.: 1–17.

Gorozhankin, I.N., 1904. Lektsii po morfologii i sistema-tike archegonialnykh rastenij. II Pteridophyta. I. Archispermae. A. I. Mamontov, Moscow.

Gray, S.F., 1821. A natural arrangement of British plants : according to their relations to each other as pointed out by Jussieu, De Candolle, Brown, &c. Vol 2, Baldwin, Cradock, and Joy, London, 757.

Guppy, H.B., 1914. Notes on the native plants of the azores as illustrated on the slopes of the mountain of Pico. Bull. Misc. Inform. (Royal Botanic Gardens, Kew) 1914 (9), 305–321.

Hartung, G., 1860. Die Azoren in iheer äusseren erscheinung und nach ihrer geognostischen natur. verlag von Wihelm Engelmann, Leipzig, 350.

Hildenbrand, A., Marques, F.O., Costa, A.C.G., Sibrant, A.L.R., Silva, P.F., Henry, B., Miranda, J.M., Madureira, P., 2012. Reconstructing the architectural evolution of volcanic islands from combined K/Ar, morphologic, tectonic, and magnetic data: the Faial Island example (Azores). J. Volcanol. Geotherm. Res. 241–242, 39–48.

Hoffmannsegg, J.C.v., Link, J.H.F., 1809–1820. Flore portugaise ou description de toutes les plantes qui croissent naturellement en Portugal avec figures coloriées, cinq planches de terminologie et une carte 1. Charles Fréderic Amelang, Berlin.

Hortal, J., Bello, F.d., Diniz-Filho, J.A.F., Lewinsohn, T.M., Lobo, J.M., Ladle, R.J., 2015. Seven shortfalls that beset large-scale knowledge of biodiversity. Annu. Rev. Ecol. Evol. Syst. 46 (1), 523–549.

Hudspith, V.A., Scott, A.C., Wilson, C.J.N., Collinson, M.E., 2010. Charring of woods by volcanic processes: an example from the Taupo ignimbrite, New Zealand. Palaeogeogr. Palaeoclimatol. Palaeoecol. 291 (1–2), 40–51.

Huebert, J.M., 2015. Anthropogenically driven decline and extinction of Sapotaceae on Nuku Hiva (Marquesas Islands, East Polynesia). The Holocene 25 (6), 1039–1046.

Humboldt, F.W.H.A.v., Bonpland, A.J.A., Kunth, K.S., 1817. Voyage de Humbolt et Bonpland. Sixième partie. Botanique. Nova Genera et Species Plantarum, 2. La Librairie Grecque-Latine-Allemande, Paris, 401.

Jardim, R., Menezes de Sequeira, M., Capelo, J., 2007. IV: Espécies florestais das ilhas: 2. Madeira. In: Silva, S.J. (Ed.), Árvores e Florestas de Portugal: Açores e Madeira - A Floresta das Ilhas. 6. Público, Comunicação Social SA, Fundação Luso Americana para o Desenvolvimento e Liga para a Protecção da Natureza, pp. 255–296.

Knoblauch, E.F., 1934. Oleaceae in Neue und seltene Arten II. Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem 11, 1078–1079.

Kron, K.A., Powell, E.A., Luteyn, J.L., 2002. Phylogenetic relationships within the blueberry tribe (Vaccinieae, Ericaceae) based on sequence data from MATK and nuclear ribosomal ITS regions, with comments on the placement of Satyria. Am. J. Bot. 89 (2), 327–336.

Lens, F., Kron, K.A., Luteyn, J.L., Smets, E., Jansen, S., 2004. Comparative wood anatomy of the Blueberry tribe (Vaccinieae, Ericaceae s.l.). Ann. Mo. Bot. Gard. 91 (4), 566–592.

Lens, F., Jansen, S., Caris, P., Serlet, L., Smets, E., 2005. Comparative wood anatomy of the Primuloid Clade (Ericales s.l). Syst. Bot. 30 (1), 163–183.

Leny, L., Casteel, R.W., 1975. Simplified procedure for examining charcoal specimens for identification. J. Archeol. Sci. 2 (153–159), .

Lindley, J., 1833. Nixus plantarum. Apud Ridgway et filios, Londini, 28.

Linnaeus, C., 1753. Species Plantarum, Exhibentes Plantas Rite Cognitas, Ad Genera Relatas, Cum Differentiis Specificis, Nominibus Trivialibus, Synonymis Selectis, Locis Natalibus, Secundum Systema Sexuale Digestas, 2. L. Salvius, Stockholm, 1200.

Loidi, J., del Arco, M., Pérez de Paz, P.L., Asensi, A., Díez Garretas, B., Costa, M., Díaz González, T., Fernández-González, F., Izco, J., Penas, , Rivas-Martínez, S., Sánchez-Mata, D., 2010. Understanding properly the `potential natural vegetation' concept. J. Biogeogr. 37 (11), 2209–2211.

Loutfy, M.H.A., 2009. Wood anatomy and its implications on the taxonomy of Apollonias Nees (Lauraceae). Feddes Repertor. 120 (1–2), 75–90.

Machado Yanes, M.d.C., 2007. Una visión de las Islas Afortunadas, a partir de los restos arqueológicos. Rev. Tabona 15, 71–90.

Machado Yanes, M.d.C., del Arco Aguilar, M.d.C., Vernet, J.-L., Ourcival, J.-M., 1997. Man and vegetation in northern Tenerife (Canary Islands, Spain), during the prehispanic period based on charcoal analyses. Veg. Hist. Archaeobotany 6 (3), 187–195.

Madeira, J., 1998. Estudos de Neotectónica nas ilhas do Faial, Pico e S. Jorge: uma contribuição para o conhecimento geodinâmico da junção tripla dos Açores. Universidade de Lisboa, 481.

Madeira, J., Brum da Silveira, A., 2003. Active tectonics and first paleoseismological results in Faial, Pico and S. Jorge islands (Azores, Portugal). Ann. Geophys. 46 (5), 733–771.

Madeira, J., Soares, Monge, Brum da Silveira, A., Serralheiro, A., 1995. Radiocarbon dating recent volcanic activity on Faial Island (Azores). Radiocarbon 37 (2), 139–147.

Madeira, J., Brum da Silveira, A., Serralheiro, A., Monge Soares, A., Rodrigues, C.F., 1998. Radiocarbon ages of recent volcanic events from the Island of S. Jorge (Azores). Comunic. IGM 84 (1), A189–A192.

Major, J.J., Pierson, T.C., Hoblitt, R.P., Moreno, H., 2013. Pyroclastic density currents associated with the 2008-2009 eruption of Chaitén Volcano (Chile): forest disturbances, deposits, and dynamics. Andean Geol. 40 (2), 324–358.

Matos, B., Borges Silva, L., Camarinho, R., Rodrigues, A.S., Rego, R., Câmara, M., Silva, L., 2019. Linking dendrometry and dendrochronology in the dominant Azorean tree Laurus azorica (Seub.) Franco. Forests 10 (7), 538.

Menezes de Sequeira, M., Espírito-Santo, D., Aguiar, C., Capelo, J., Honrado, J., 2012. Checklist da Flora de Portugal (Continental, Açores e Madeira). Associação Lusitana de Fitossociologia, Lisboa, 74.

Mouzinho de Albuquerque, L.d.S., Menezes, I.P.d.C., 1826. Observações sobre a ilha de São Miguel recolhidas pela commissão enviada à mesma ilha em Agosto de 1825. Impressão Régia, Lisboa, 43.

Mustoe, G.E., 2018. Non-mineralized fossil wood. Geosciences 8 (6), 223.

Nogales, J., Schmincke, H.U., 1969. El pino enterrado de la Cañada de Las Arenas. Cuader. Bot. Canar. 5, 23–25.

Nogué, S., de Nascimento, L., Fernández-Palacios, J.M., Whittaker, R.J., Willis, K.J., 2013. The ancient forests of La Gomera, Canary Islands, and their sensitivity to environmental change. J. Ecol. 101 (2), 368–377.

Nogué, S., Nascimento, L.d., Froyd, C.A., Wilmshurst, J.M., Boer, E.J.d., Coffey, E.E.D., Whittaker, R.J., Fernández-Palacios, J.M., Willis, K.J., 2017. Island biodiversity conservation needs palaeoecology. Nat. Ecol. Evol. 1, 0181 (1-9).

Pacheco, J., 2001. Processos associados ao desenvolvimento de erupções vulcânicas hidromagmáticas explosivas na ilha do Faial e sua interpretação numa perspectiva da avaliação do hazard e minimização do risco. Universidade dos Açores, 330.

Pacheco, J.M., 2015. ^{14}C ages of the last eruptive stage of Faial Island Caldeira volcano. Radiocarbon 57 (5), 1021–1027.

Pensa, A., Porreca, M., Corrado, S., Giordano, G., Cas, R., 2015. Calibrating the pTRM and charcoal reflectance (Ro%) methods to determine the emplacement temperature of ignimbrites: Fogo A sequence, São Miguel, Azores, Portugal, as a case study. Bull. Volcanol. 77 (18), 1–19.

Peraza, C., Lopez de Roma, A., 1967. Estudio de las principales maderas de Canarias. In: Ministério de Agricultura, Direccion General de Montes, Caza y Pesca Pluvial. Madrid, Instituto Florestal de Investigaciones Y Experiencias, p. 220.

Pimentel, A., Pacheco, J., Self, S., 2015. The ~ 1000-years BP explosive eruption of Caldeira Volcano (Faial, Azores): the first stage of incremental caldera formation. Bull. Volcanol. 77 (5), 1–26.

Pupo-Correia, A.M.C.d.N., 2005. Evolution of the Landscape of Madeira Island: Long-Term Vegetation Dynamics. Universidade da Madeira, 280.

Rando, J.C., Alcover, J.A., Olson, S.L., Pieper, H., 2013. A new species of extinct scops owl (Aves: Strigiformes: Strigidae: Otus) from São Miguel Island (Azores Archipelago, North Atlantic Ocean). Zootaxa 3647 (2), 15.

Rando, J.C., Pieper, H., Olson, S.L., Perreira, F., Alcover, J.A., 2017. A new extinct species of large bullfinch (Aves: Fringillidae: Pyrrhula) from Graciosa Island (Azores, North Atlantic Ocean). Zootaxa 4282 (3), 567–583.

Rivas-Martínez, S., Díaz, T.E., Fernández-González, F., Izco, J., Loidi, J., Lousã, M., Penas, A., 2001. Vascular plant communities of Spain and Portugal. Addenda to the syntaxonomical checklist of 2001. Part I Itenera. Geobotanica 15 (1), 1–432.

Rivas-Martínez, S., Díaz, T.E., Fernández-González, F., Izco, J., Loidi, J., Lousã, M., Penas, A., 2002. Vascular plant communities of Spain and Portugal. Addenda to the syntaxonomical checklist of 2001. Part II Itenera. Geobotanica 15 (2), 433–992.

Rößler, R., Zierold, T., Feng, Z., Kretzschmar, R., Merbitz, M., Annacker, V., Schneider, J.W., 2012. A snapshot of an early Permian ecosystem preserved by explosive volcanism: new results from the Chemnitz petrified forest, Germany. PALAIOS 27, 814–834.

Rubiales, J.M., Díez, A., Génova, M., Ballesteros, J., de Nascimento, L., Fernández-Palacios, J.M., 2013. Late Holocene Wood remains from Alluvial/ Colluvial Deposits in the Caldera de Taburiente National Park (La Palma, Canary Islands). In: Fernández-Palacios, J.M., et al. (Eds.), Climate change perspectives from the Atlantic: past, present and future. Servicio de Publicaciones Universidadd e La Laguna, La Laguna, pp. 233–247.

Rull, V., Connor, S., Elias, R., 2017. Potential natural vegetation and pre-anthropic pollen records on the Azores Islands in a Macaronesian context. J. Biogeogr. 44 (11), 2137–2440.

Rull, V., Lara, A., Rubio-Inglés, M.J., Giralt, S., Gonçalves, V., Raposeiro, P., Hernández, A., Sánchez-López, G., Vázquez-Loureiro, D., Bao, R., Masqué, P., Sáez, A., 2017. Vegetation and landscape dynamics under natural and anthropogenic forcing on the Azores Islands: a 700-year pollen record from the São Miguel Island. Quat. Sci. Rev. 159, 155–168.

Ryan, W.B.F., Carbotte, S.M., Coplan, J.O., O'Hara, S., Melkonian, A., Arko, R., Weissel, R.A., Ferrini, V., Goodwillie, A., Nitsche, F., Bonczkowski, J., Zemsky, R., 2009. Global multi-resolution topography synthesis. Geochemis. Geophys. Geosyst. 10 (3).

Schmincke, H.-U., 1967. Mid-Pliocene fossil wood from Gran Canaria. Preliminary note. Cuader. Bot. 2, 19–20.

Schweingruber, F., Landolt, W., 2010. The Xylem Database: A Web Product of the Swiss Federal Research Institute WSL.

Schweingruber, F.H., Börner, A., Schulze, E.-D., 2011. Atlas of Stem Anatomy in Herbs, Shrubs and Trees I. Springer-Verlag, Heidelberg, 495.

Schweingruber, F.H., Börner, A., Schulze, E.-D., 2013. Atlas of Stem Anatomy in Herbs, Shrubs and Trees II. Springer-Verlag, Heidelberg, 415.

Scott, A.C., 2010. Charcoal recognition, taphonomy and uses in palaeoenvironmental analysis. Palaeogeogr. Palaeoclimatol. Palaeoecol. 291 (1), 11–39.

Scott, A.C., Glasspool, I.J., 2005. Charcoal reflectance as a proxy for the emplacement temperature of pyroclastic flow deposits. Geology 33, 589–592.

Scott, A.C., Jones, T.P., 1991. Fossil charcoal: a plant-fossil record preserved by fire. Geol. Today 7 (6), 214–216.

Scott, A.C., Jones, T.P., 1991. Microscopical observations of recent and fossil charcoal. Microsc. Anal. 25, 13–15.

Seubert, M., Hochstetter, C., 1843. Uebersicht der Flora der azorischen Inseln. Archiv für Naturgeschichte 9 (1), 1–24.

Shotton, F.W., Blundell, D.J., Williams, R.E.G., 1968. Birmingham University radiocarbon dates II. Radiocarbon 10 (2), 200–206.

Silva, L., Pinto, N., Press, B., Rumsey, F., Carine, M., Henderson, S., Sjögren, E., 2005. Lista das plantas vasculares (Pteridophyta e Spermatophyta). In: Borges, P.A.V., et al. (Eds.), A list of the terrestrial fauna (Mollusca and Arthropoda) and flora (Bryophyta, Pteridophyta and Spermatophyta) from the Azores. Direcção Regional do Ambiente e Universidade dos Açores, Horta, Angra Do Heroísmo e Ponta Delgada, pp. 131–155.

Silva, L., Moura, M., Schaefer, H., Rumsey, F., Dias, E.F., 2010. Lista das Plantas Vasculares (Tracheobionta). In: Borges, P.A.V., Costa, A., Cunha, R., Gabriel, R., Gonçalves, V., Martins, A.F., Melo, I., Parente, M., Raposeiro, P., Rodrigues, P., Santos, R.S., Silva, L., Vieira, P., Vieira, V. (Eds.), A List of the Terrestrial and Marine Biota from the Azores. Cascais, Princípia, pp. 117–146.

Smith, J.E., 1819. Vaccinium. In: Rees, A. (Ed.), The Cyclopaedia; or, Universal Dictionary of Arts, Sciences and Literature. Longman, Hurst, Rees, Orme & Brown, London.

Somodi, I., Molnár, Z., Ewald, J., 2012. Towards a more transparent use of the potential natural vegetation concept – an answer to Chiarucci et al. J. Veg. Sci. 23 (3), 590–595.

Spicer, R.A., 1989. The formation and interpretation of plant fossil assemblages. In: Callow, J.A. (Ed.), Advances in Botanical Research. Vol. 16, Academic Press, pp. 95–191.

Trelease, W., 1897. Botanical Observations on the Azores. (Eighth Annual Report of The Missouri Botanical Garden).

Triantis, K.A., Borges, P.A.V., Ladle, R.J., Hortal, J., Cardoso, P., Gaspar, C., Dinis, F., Mendonça, E., Silveira, L.M.A., Gabriel, R., Melo, C., Santos, A.M.C., Amorim, I.R., Ribeiro, S.P., Serrano, A.R.M., Quartau, J.A., Whittaker, R.J., 2010. Extinction debt on oceanic islands. Ecography 33 (2), 285–294.

Tutin, T.G., 1953. The vegetation of the Azores. J. Ecol. 41 (1), 53–61.

van Leeuwen, J.F.N., Schäfer, H., Knaap, W.O.v.d., Tammy, M.R., Björck, S., Ammann, B., 2005. Native or introduced? Fossil pollen and spores may say. An example from the Azores Islands. In: Nentwig, W.e.a. (Ed.), Biological Invasions – from Ecology to Control. NEOBIOTA 6, pp. 27–34.

von Martius, C.F.P., 1835. Conspectus Regni Vegetabilis Secundum Characteres Morphologicos Praesertim Carpicos in Classes Ordines et Familias Digesti, Adjectis Exemplis Nominibusque Plantarum Usui Medico Technico et Oeconomico Inservientium. Joh. Leonard Schrag, Nürnberg, 72.

Wagstaff, D.J., 2008. International Poisonous Plants Checklist: An Evidence-Based Reference. CRC Press, Taylor & Francis Group, 443.

Wang, J., Pfefferkorn, H.W., Zhang, Y., Feng, Z., 2012. Permian vegetational Pompeii from Inner Mongolia and its implications for landscape paleoecology and paleobiogeography of Cathaysia. Proc. Natl. Acad. Sci. 201115076.

Webster, J.W., 1821. A Description of the Island of St. Michael, Comprising an Account of its Geological Structure. R. P. & C. Williams, Boston, 243.

Wheeler, E.A., 2011. InsideWood - a web resource for hardwood anatomy. IAWA J. 32 (2), 199–211.

Wheeler, E.A., Baas, P., Gasson, P.E., 1989. IAWA list of microscopic features for hardwood identification. IAWA J. 10 (3), 219–332.

Wilbur, R.L., 1994. The Myricaceae of the United States and Canada: genera, subgenera, and series. Sida 16 (1), 93–107.

Willkomm, M., 1854. Anleitung zum studium der Wissenschaftlichen Botanik, 2. Friedrich Fleischer, Leipzig, 530.

Zhang, S.-Y., 1992. Systematic wood anatomy of the Rosaceae. Blumea 37 (1), 81–158.