SYNTHESIS

A reconstruction of Palaeo-Macaronesia, with particular reference to the long-term biogeography of the Atlantic island laurel forests

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Note: Within the text we have followed Rio *et al.*'s (1998) recommendation of incorporating the Gelasian Age (2.6–1.8 Ma) within the Pleistocene, thus yielding a Pliocene/Quaternary limit at 2.6 Ma.

ABSTRACT

Macaronesia is a biogeographical region comprising five Atlantic Oceanic archipelagos: the Azores, Madeira, Selvagen (Savage Islands), Canaries and Cape Verde. It has strong affinities with the Atlantic coast of the Iberian Peninsula and the north-western fringes of Africa. This paper re-evaluates the biogeographical history and relationships of Macaronesia in the light of geological evidence, which suggests that large and high islands may have been continuously available in the region for very much longer than is indicated by the maximum surface area of the oldest current island (27 Ma) – possibly for as long as 60 million years. We review this literature, attempting a sequential reconstruction of Palaeo-Macaronesia from 60 Ma to the present. We consider the implications of these geological dynamics for our understanding of the history of colonization of the present islands of Macaronesia. We also evaluate the role of these archipelagos as stepping stones and as both repositories of palaeo-endemic forms and crucibles of neo-endemic radiations of plant and animal groups. Our principal focus is on the laurel forest communities, long considered impoverished relicts of the Palaeo-tropical Tethyan flora. This account is therefore contextualized by reference to the long-term climatic and biogeographical history of Southern Europe and North Africa and by consideration of the implications of changes in land–sea configuration, climate and ocean circulation for Macaronesian biogeography. We go on to provide a synthesis of the more recent history of Macaronesian forests, which has involved a process of impoverishment of the native elements of the biota that has accelerated since human conquest of the islands. We comment briefly on these processes and on the contemporary status and varied conservation opportunities and threats facing these forests across the Macaronesian biogeographical region.

Keywords

Canarian volcanic province, geological history, historical biogeography, island biogeography, island ontogeny, laurisilva, Macaronesia, oceanic islands, palaeo-endemic, Tethyan biogeography.

INTRODUCTION

The name Macaronesia stems from the classical Greek words *makarios* (meaning happy) and *nessos* (meaning islands). Macaronesia is a biogeographical rather than a political entity, which is based on the existence of many shared elements in the floras and faunas of the constituent archipelagos. The origin of this name is attributed to the British botanist Philip Barker Webb, around AD 1835, although it seems that he intended the term to encompass only Madeira, the Selvagen archieplago (Savage Islands) and the Canaries, the nucleus of the region (Stearn, 1973). Engler (1879) may have been the first author to include the Azores in the Macaronesian region, and it was not until 1961 that Pierre Dansereau argued for the inclusion of the Cape Verde islands (Vanderpoorten *et al.*, 2007), so that today the Macaronesian region (or province) is widely
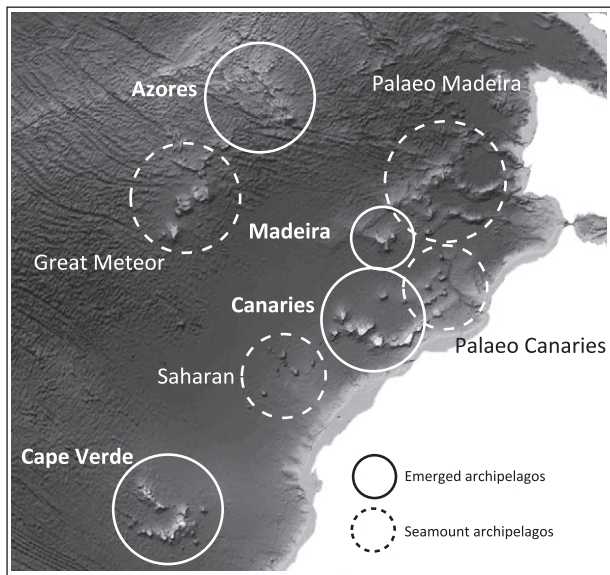
Figure 1 Empty ocean bathymetry showing the Northeast Atlantic Ocean region. Besides the actual emerged archipelagos forming the Macaronesia region (Azores, Madeira with Selvagens, Canaries and Cape Verde), other seamount archipelagos, such as Palaeo-Madeira and Palaeo-Canaries (between those island groups and the Iberian Peninsula), the Great Meteor archipelagos (south of the Azores) and the Saharan archipelago (south-west of the Canaries), are also shown. Source: Google Earth, modified.

considered to comprise these five volcanic archipelagos – the Azores, Madeira, Selvagen, Canaries and Cape Verde – located at distances varying from 96 to 1500 km off the Iberian Peninsula and North Africa (Fernández-Palacios & Dias, 2001; Fernández-Palacios, 2010) (Fig. 1). The region attains a maximum age of 27 Ma in its oldest current island, Selvagem Grande (Selvagen archipelago; Geldmacher et al., 2001).

Although the North Atlantic archipelagos of Macaronesia were the subject of study by some of the outstanding natural scientists of the 18th and 19th centuries, including German (von Humboldt, von Buch, Hartung, Bolle), French (Feulliee, Bory de Saint Vicent, Berthelott) and British (Webb, Hooker, Wollaston, Masson) scientists, attention within island science thereafter shifted elsewhere, mostly to the Pacific, and especially to Hawaii, the Galápagos and Wallacea. Within the last two decades, however, the development and application of new research techniques (e.g. multi-beam technologies to scrutinize the ocean floors, and phylogenetic and phylogeographic molecular analyses) have proved especially fruitful for Macaronesia, providing many new empirical and theoretical insights (reviewed in Juan et al., 2000; Whittaker & Fernández-Palacios, 2007).

The aim of the present paper is to provide an updated synthesis of recent geological, palaeoclimatological and biogeographical studies. Such a synthesis may encourage the development of new research projects in this exceptional biogeographical and evolutionary model system, which may illuminate as yet incompletely understood topics in island biology, such as the relative importance of vicariance versus dispersal in shaping insular biotas (Grehan, 2001; Heads, 2010; Renner, 2010; Renner et al., 2010); the role of islands as regions/refugia from which taxa might 'back-colonize' continents (Carine et al., 2004; Bellemain & Ricklefs, 2008); the prevalence of niche pre-emption as an evolutionary force within lineages (Silvertown et al., 2005); or the roles played by speciation, extinction and migration in shaping insular communities (Whittaker et al., 2008; Triantis et al., 2010), to mention but a few.

We begin with a section dedicated to the distinctive ontogeny of oceanic islands, exemplified by the Madeiran and Canarian islands. Following this, and based on the emerging picture of the North Atlantic abyssal bathymetry and chronology, we attempt to reconstruct the changing configuration of this island region over about the last 60 Myr. We go on to consider the regional and general biogeographical consequences of the existence of Palaeo-Macaronesia, in the light of the general progressive climate deterioration of the Neogene, focusing on the fate of the so-called Palaeotropical geoflora inhabiting the borders of the Tethys Sea. The Macaronesian laurel forests have long been viewed as a largely relictual element of this flora and to constitute a largely palaeo-endemic element, notwithstanding the existence of a number of spectacular recent radiations of plant taxa within Macaronesia (Whittaker & Fernández-Palacios, 2007). Given that they are an important and ancient element of the Macaronesian flora, we therefore provide both a short account of the origin and spread of the Lauraceae, and a summary of the changing status of the laurel forests in Macaronesia in response to environmental (especially climatic) change from the Miocene to the present day. A final section highlights the fate of the laurel forests following human colonization of the islands and the need for a research agenda that contributes to the long-term conservation of this relictual ecosystem.

PHASES IN THE ONTOGENY OF HOTSPOT ISLANDS

Remote volcanic islands behave, in the long term, rather like biological individuals. That is, they follow an ontogeny in which they are born, grow, and acquire their maximum area and elevational range, before erosion and subsidence reduce them once again to below sea level (e.g. Menard, 1986; Carracedo, 1999; Stuessy, 2007; Whittaker & Fernández-Palacios, 2007; Whittaker et al., 2008). This is particularly clearly shown in hotspot archipelagos such as Hawaii and the Canaries. Moreover, although not all Macaronesian archipelagos necessarily have origins and dynamics describable by a simple hotspot model, this generalized ontogeny has been followed repeatedly, to varying degrees, across the region. The process of island building can nonetheless be a prolonged one, and it can be complex. Thus, for example, Tenerife (Canary Islands) is generally considered to have emerged initially as two or possibly three separate islands, the oldest dating back to c. 11 Ma, and these proto-islands fused into the single

present-day island only within the last 3.5 Myr (Carracedo, 2006). One persuasive analysis suggests that the oldest section formed was the (Central) Miocene shield, with the Teno (late Miocene) and Anaga (Pliocene) massifs developing subsequently – Anaga for a long time as a separate island – but with the present surface of the central section of the island formed almost entirely from relatively recent (<3.5 Ma) post-erosive volcanism (Guillou *et al.*, 2004).

During their life span, volcanic oceanic islands are often subject to a series of catastrophic events through further volcanism, caldera collapse, mega-landslips, etc. In these aspects of their geological dynamics, they are thus clearly different from other (land bridge and microcontinental) island groups (Whittaker & Fernández-Palacios, 2007).

To simplify, we can distinguish six stages in a hotspot island's life cycle (Fernández-Palacios & Whittaker, 2010): stage A – birth and submarine construction; stage B – emergence and subaereal construction; stage C – erosion and dismantling dominant; stage D – reduction to a low-lying plain (or, in certain circumstances, to atoll form); stage E – terminal disappearance; and stage F – guyot (flat-summit seamount). We next exemplify the various stages, illustrating how they can coexist within a single archipelago, such as the Canaries or Madeira, where there is a sufficient span of island ages to allow the observation of the various island phases.

Figure 2 shows the evolution of the Madeiran and Canarian archipelagos through time. Stage A is represented by seamounts such as Las Hijas (Canaries), which have yet to emerge, and which are thought to be located at present over the archipelago's principal mantle plume. La Palma, El Hierro and Tenerife represent stage B, during which the islands are still being built, as testified by their recent volcanic activity. These islands achieve great heights, both above sea level (3000–4000 m) and especially when measured from the ocean floor, which in this part of the North Atlantic is located some 3 to 4 km beneath the sea level. These two first phases are not represented today in the Madeiran archipelago.

Stage C, the 'erosion and dismantling' phase, is represented by Madeira and in the Canaries by Gran Canaria and La Gomera, volcanic structures that had much greater elevations and areas in the past. In these two Canarian islands, destructive processes now dominate over constructive processes, with the exception of the north-eastern part of Gran Canaria, where volcanic activity (although not in the historical period) is still present (Carracedo, 2003). The most recent volcanic activity in La Gomera has been dated to 1.92 Ma (Paris *et al.*, 2005). It is in the early phase of erosion that islands achieve their maximal topographical complexity, and, despite losing the summit ecosystems owing to erosion, they nonetheless retain (or continue to generate) relatively high numbers of single-island endemics (Whittaker *et al.*, 2007, 2008).

Stage D, the 'basal plain', is well represented in Madeira by Porto Santo and Selvagem Grande (Selvagen archipelago) and in the Canaries by Mahan (the single volcanic edifice that includes both Lanzarote and Fuerteventura). Fuerteventura, today only 800 m high, is considered to have been 3300 m high in the past (Stillman, 1999). Nevertheless, Fuerteventura and especially Lanzarote have not become entirely dormant, and this volcanic activity has been important in continuing to rejuvenate the island(s). Despite having been much higher in the past, today only low-elevation habitats are present.

Stage E, 'terminal disappearance', is represented by Selvagem Pequena and Ilheu de Fora, islets within the Selvagen archipelago belonging politically to Madeira but built by the Canarian hotspot. They are fragmented structures, lower than 30 m, which suggests that they may soon disappear below sea level. Finally, stage F, the 'guyot' phase, is exemplified by several flat-topped seamounts, such as Seine, Coral Patch and Unicorn in the Madeiran volcanic province, and Amanay, Conception and Dacia in the Canarian province (Table 1).

THE RECONSTRUCTION OF PALAEO-MACARONESIA

Consistent with previous work on the Hawaiian system (e.g. Price & Clague, 2002) and the Galápagos (Hoernle *et al.*, 2002), there is now increasing evidence of a significant history of Macaronesian landmasses extending back in time
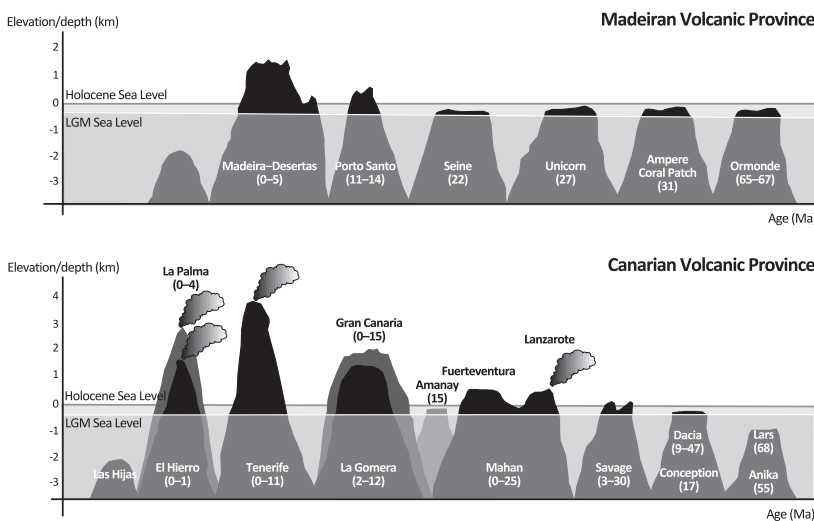
Figure 2 The Madeiran and Canarian volcanic provinces, with the various stages of the island cycle represented. The interval of volcanic activity is given in brackets. This is an original figure based on several sources discussed in the text.

Table 1 Seamounts of the Madeiran and Canarian volcanic provinces. Sources: Geldmacher *et al.* (2001, 2005); Acosta *et al.* (2005). Note that Mahan is the name for the former island represented today by the separate islands of Lanzarote and Fuerteventura, which were joined together as recently as the late Pleistocene. Ages are approximate and are shown here without error margins.

Name	Location	Isolation (km)	Age (Ma)	Minimal depth (m)
Madeiran province				
Ormonde	36°02′ N 11°09′ W	200 (Iberia)	65–67	<50
Gettysburg	36°31′ N 11°34′ W	240 (Iberia)	?	63
Ampere	35°00′ N 12°48′ W	404 (Iberia)	31	59
Coral Patch	34°56′ N 11°57′ W	300 (Iberia)	31	?
Unicorn	34°47′ N 14°35′ W	525 (Africa)	27	?
Seine	33°45′ N 14°45′ W	485 (Africa)	22	86
Canarian province				
Lars (Agadir Seamount)	32°50′ N 13°10′ W	345 (Africa)	68	900
Anika	31°34′ N 12°59′ W	285 (Africa)	55	?
Nico	30°50′ N 13°00′ W	260 (Africa)	?	?
Last Minute	30°10′ N 14°50′ W	340 (Africa)	?	?
Dacia	31°15′ N 13°45′ W	355 (Africa)	47	80
Conception	30°00′ N 12°50′ W	182 (Africa)	>17	120
Amanay	28°15′ N 14°45′ W	25 (from Mahan)	15	25

beyond the age of the oldest currently emergent islands, and probably providing a considerably longer continuous insular history of large islands than for either of these classic evolutionary systems (cf. Grehan, 2001; Neall & Trewick, 2008; Clague *et al.*, 2010). The improvements achieved in recent decades in our knowledge of oceanic bathymetry, mainly as a consequence of the use of new multi-beam technologies, have led to the discovery of several submarine chains and guyots located in the oceanic depths both among the archipelagos and between them and the European and African continents (Table 1).

Geldmacher *et al.* (2001, 2005) contend that the Macaronesian seamounts were created by the Palaeogene (64–25 Ma) activity of the same mantle-plume hotspots as much more recently (from the Miocene onwards) built the islands that form the current Madeiran and Canarian archipelagos (Fig. 3). The Selvagen Islands and neighbouring large seamounts, located north and north-east of the Canary Islands on the same bathymetric high, have similar geochemical (major and trace element and Sr–Nd–Pb–Hf isotopic) compositions to the Canary Island magmatic rocks, but different compositions from the Madeiran rocks to the north. Therefore, the two archipelagos are related to different mantle-plume hotspots (Hoernle & Carracedo, 2009).

Furthermore, two more submerged archipelagos, owing their origins to other hotspots, have been discovered in the Macaronesian region. These are: first, the Saharan archipelago, a group of 4 to 5 seamounts located some 300 km south of the Canarian island of El Hierro (Patriat & Labails, 2006); and second, the Great Meteor seamount, covering an area of 1200 km^2, rising from the ocean floor at −4800 m, peaking just 270 m below the present sea level, and located on the African plate approximately 800 km south of the Azorean island of Santa María and 1600 km off the African mainland (Bartsch, 2008) (Fig. 1).

As described elsewhere for other oceanic islands, once the volcanic activity has finally ceased, these former islands (guyots today) are progressively depleted by destructive processes such as mass-wasting and marine erosion until they are reduced to their present sub-surface form (Smoot, 1995). Many such islands, especially in the Central Pacific, also experience very significant subsidence owing to their mass as they move away from the magma source; for example, estimates for some Hawaiian islands suggest subsidence by as much as 1000 m (e.g. Price & Clague, 2002). Indeed, if the same degree of sea-floor subsidence affecting Hawaii had affected the Canaries, the archipelago today would be composed of just three emergent islands: the central part of Tenerife, La Palma and El Hierro (Carracedo *et al.*, 2002; Carracedo, 2006). However, such a large degree of subsidence does not appear to have occurred in this sector of the Atlantic floor (Carracedo *et al.*, 1998; Meco *et al.*, 2005) owing to its proximity to a passive continental margin and to the antiquity and rigidity of the oceanic crust on which the Canaries rest, allowing several seamounts to maintain a summit within 120–150 m of the present sea level. These shallowly submerged seamounts would have been emergent during the extreme glacial sea-level minima, forming an array of stepping stones distributed between the present-day islands and the Iberian Peninsula and North Africa (Kämmer, 1982; García-Talavera, 1999) (Fig. 4g). We thus need to take into account in our biogeographical reconstructions the existence of former islands, and the emergence of at least some of these 'lost' islands as Pleistocene stepping stones. These former and intermittently re-emergent islands, which we may designate as constituting the Palaeo-Macaronesian region, have probably played a major role in the shaping of contemporary Macaronesian biotas and communities (cf. Carine *et al.*, 2004).

In addition to the largely flat-topped seamounts, recent discoveries include volcanic structures with peak-form
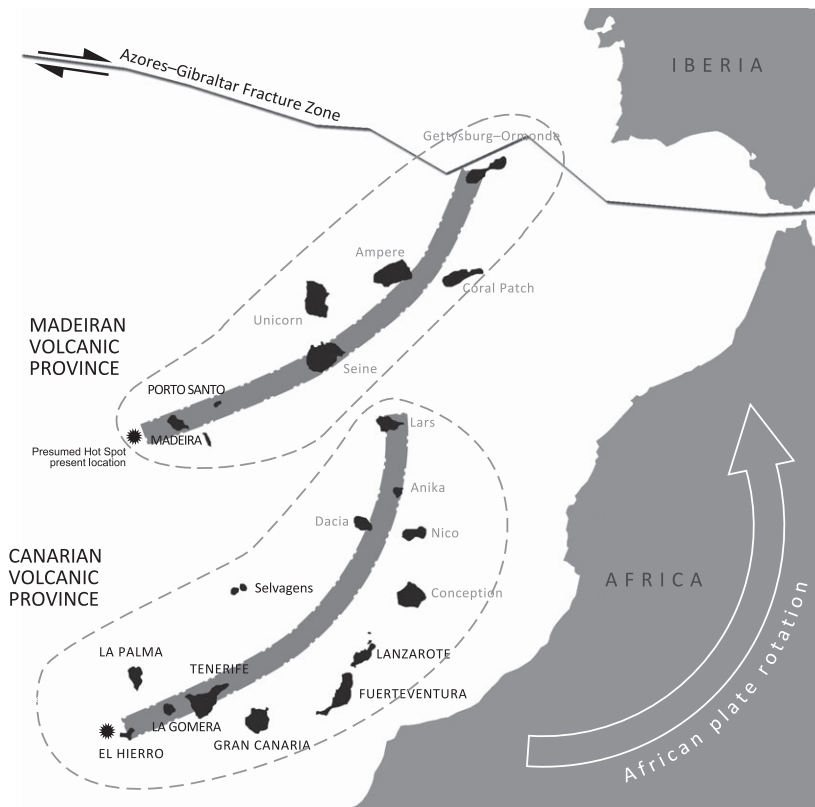
Figure 3 Map showing the Madeiran and Canarian volcanic provinces (denoted by dashed lines), including islands and associated seamounts in the Northeast Atlantic Ocean. Thick lines within each province mark the centres of possible hotspot tracks. Based on Geldmacher *et al.* (2005), slightly modified.

summits – apparently much younger and not-yet-emerged islands. For example, in the abyssal plain south-west of El Hierro there are peaks rising some 1500 m above the general level of the ocean floor. Although they remain 2500 m below the ocean surface, these seamounts, the most notable of which is named 'Las Hijas' (Rihm *et al.*, 1998), represent volcanic structures that may emerge in the future to add new islands to the archipelago, providing that the volcanic activity that created them continues for several million years.

Although involving a significant degree of uncertainty, the geological dating and morphological analysis of the older seamounts of Palaeo-Macaronesia can potentially enable the reconstruction of their sequence of emergence and submergence and thus of their past availability as targets for colonization by propagules of species within past mainland source-pool communities. Moreover, available plate tectonic scenarios (Smith *et al.*, 1994; Scotese, 2004) suggest that when these seamounts were still islands, they were located much closer to the Iberian Peninsula. They would also have been affected by the east-to-west warm circum-equatorial marine current that flowed through the Tethys Sea. In comparison with the present-day configuration of Macaronesia, these circumstances suggest an enhanced ease of colonization of these former islands from Iberia and North Africa.

The oldest of these seamounts, Ormonde in the Madeiran volcanic province and Lars (also known as the Agadir Seamount) in the Canarian volcanic province, date back to 60 Ma (Geldmacher *et al.*, 2001, 2005), that is, to the start of the Tertiary, when the Tethys Sea was still open. Thus,

Palaeo-Macaronesia is twice or three times as old as hitherto generally recognized by biogeographers (Fernández-Palacios & Dias, 2001). Furthermore, as light can penetrate down to the depths reached by many of the seamount summits (*c.* 120 m or less), photosynthetic benthic communities can be found around them, with the summits acting as submarine islands, separated from similar summits by dark abyssal plains 3–4 km deep. Many of these summit-illuminated seamounts have been found to support regional endemic, or even exclusively endemic, invertebrate species, thus contributing directly to contemporary Macaronesian biodiversity (Beck *et al.*, 2002). In addition, the role of these seamounts as stepping stones has very recently been suggested to explain the haplotype differences found among populations of endemic Macaronesian gastropods (van den Broeck *et al.*, 2008).

In Fig. 4(a)–(h), we attempt a speculative reconstruction of the developmental history of the Macaronesian region for the last 60 Myr as a means of initiating further exploration of the significance of this deep history of events for contemporary biogeographical and evolutionary patterns and processes. We have attempted this reconstruction based on: (1) the geological ages of the basal shields of both submerged and emergent islands (Geldmacher *et al.*, 2001, 2005); (2) the present minimum depth of the seamounts (various sources); (3) the general lack of evidence of crustal subsidence in this area of the Atlantic Ocean (Carracedo *et al.*, 1998; Meco *et al.*, 2005); and finally (4) the known pattern of eustatic variation in sea level during the Cenozoic (Miller *et al.*,
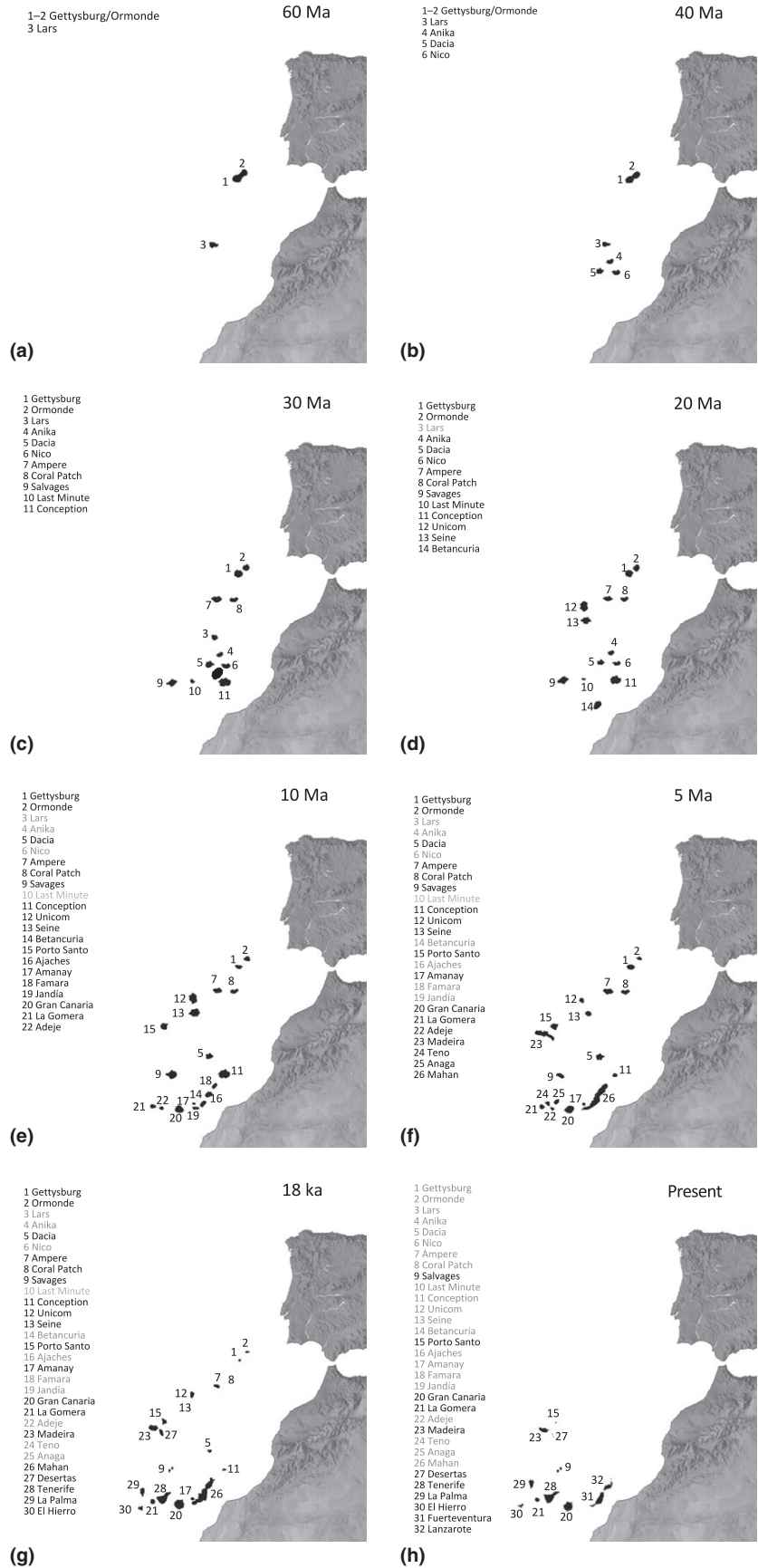
Figure 4 Hypothetical reconstruction of Palaeo-Macaronesia, compiled from various publications cited herein, and drawn alongside the contemporary continental coastline, although the position and form of the continents have varied substantially over this time period: (a) 60 Ma, (b) 40 Ma, (c) 30 Ma, (d) 20 Ma, (e) 10 Ma, (f) 5 Ma, (g) 18 ka and (h) present. Sources: all original except (g), redrawn from García-Talavera (1999). Note that the seamount and island stages depict the present positions of the palaeo-islands and not their 'relative' time progression (e.g. the Gettysburg/Ormonde island/seamount is shown in the same position at 60 Ma as at present, whereas this island was located approximately at the current location of El Hierro around 60 Ma). Names of the emerged islands at the designated date are given in bold.

2005). For ease of visualization, we make the further simplifying (and somewhat unrealistic) assumption of accepting Iberia and North Africa as occupying their current geographical positions.

In addition to the changes caused by the mountain-building and erosional processes forming and destroying volcanic oceanic islands, the emergence of the higher of the seamounts (those within 120 m of current sea level) during the eustatic sea-level minima of the glacial periods will have repeatedly transfigured the map of Macaronesia. Sea-level minima would have corresponded to significant increases in the number of islands, and in the area and elevation of extant islands, while simultaneously diminishing between-island and mainland–island distances. For instance, the Canaries have repeatedly doubled and halved their emerged area (García-Talavera, 1999), shortening the minimum distance between the archipelago and the African mainland from 96 to just 60 km (Fig. 4g). Hence, the emerged seamounts will have acted as stepping stones, facilitating the movement of species populations from the European or African mainland to Macaronesia and occasionally in the opposite direction (e.g. Carine *et al.*, 2004). They will also have facilitated exchanges among the Macaronesia archipelagos, for instance from Madeira or the Canaries to the Azores, via the Josephine or Great Meteor archipelagos, or from the Canaries to the Cape Verde Islands, via the Saharan archipelago (cf. Carine, 2005; van den Broeck *et al.*, 2008).

THE NEOGENE CLIMATIC DETERIORATION AND ITS EFFECTS ON THE IBERIAN AND NORTH AFRICAN PALAEOTROPICAL GEOFLORA

Note: In discussing fossil and microfossil literature below we have sometimes given specific names without qualification, even though in the original sources the determination to species level is not always given with certainty.

The Palaeogene Period (64–25 Ma) was characterized in Southern Europe and North Africa by the influence of the warm east-to-west circum-equatorial global marine current, which connected the Indian and the Atlantic oceans through the Tethys Sea. This influence ensured the prevalence of high temperatures and monsoon summer rains, yielding a wet-tropical climate in the region (Uriarte, 2003). At this time, Southern Europe took the form of a set of large islands, dotted in the Tethys Sea, rather than the continent we recognize today. The world-wide absence of ice caps during the mild climate of the Palaeogene corresponded to high sea levels and the existence of epicontinental seaways. For instance, the Turgai (or West Siberian) Seaway connected the Tethys and Paratethys seas with the Arctic Ocean, while in the North American region the Inter-American seaway connected the Gulf of Mexico with the Arctic Ocean (Uriarte, 2003). The existence of these seaways was only one aspect of the radically different land–sea configuration of this period compared with the present day. The availability of intercontinental land bridges, such as the North Atlantic land bridge, which connected West Europe with Atlantic North America

via Scotland–Greenland (Iceland did not form until about 16–13 Ma; Foulger, 2006), or the Bering land bridge, which connected East Asia with Pacific North America, via the Chukotka Peninsula and Alaska, accounts for the existence of floral relationships that otherwise appear bizarre. For instance, Europe was floristically closer to eastern North America than to West Asia, with the Palaeogene floras of the two former regions sharing the *Normapolles* pollen type, whereas East Asia was floristically closer to western North America than to Europe, with East Asia and western North America sharing the *Aquilapollenites* pollen type (Barrón & Peyrot, 2006).

In the Palaearctic region, the land at both margins of the Tethys Sea was populated from the Late Cretaceous to the Late Miocene by the so-called Palaeotropical geoflora (Mai, 1989, 1991), a flora comprising a mixture of conifers (e.g. *Tetraclinis*), palms (*Phoenix, Chamaerops, Sabal*, etc.), trees of lauroid-shape leaves [*Laurophyllum, Daphnogene, Cinnamomum, Litsea, Neolitsea, Laurus, Ocotea, Persea* (all Lauraceae), *Quercus, Castanopsis* (Fagaceae), or *Visnea* (Theaceae)] and ferns (*Culcita, Woodwardia, Dryopteris, Osmunda, Trichomanes, Davallia, Diplazium, Hymenophyllum*) (Barrón & Peyrot, 2006) (Table 2).

From the Eocene onwards, but especially after the end of the Oligocene, several complex global-scale tectonic events created the context for a progressive climatic deterioration, culminating with the Pleistocene glaciations, which had a heavy impact on the Holarctic tropical-like flora (Mai, 1989, 1991).

Within Europe, the Iberian Peninsula was the last refugium of the Palaeotropical geoflora, which persisted there, although impoverished, until the late Pliocene (i.e. the Piacenzian, 3.5–2.6 Ma), having been extinguished from the rest of the continent as a result of the climatic deterioration. The most recent Iberian fossil remains of several Lauraceae genera (*Apollonias, Cinnamomum, Daphnogene, Lindera, Ocotea, Persea* and *Sassafras*) date to this period (Postigo Mijarra *et al.*, 2009).

Hence, today, the major refugia of the Palaeotropical flora in the Holarctic are predominantly found outside Europe. They include localities in Southeast Asia, Korea/Japan, the Anatolian Peninsula, California and a strip in eastern North America located between the Atlantic coast and the Appalachian chain (Mai, 1989, 1991; Milne, 2006), together with the Macaronesian archipelagos.

The responses of the tropical flora to the climatic deterioration may be divided into six forms (Table 3). First, species may have responded adaptively to the Mediterranean-type climate, that is, to a regime of wet, cool-to-cold winters and dry, warm-to-hot summers, which implies the need to withstand two distinct stresses in a single annual cycle: summer drought and winter cold. We may speculate that species such as *Arbutus unedo, Rhamnus alaternus, Viburnum rigidum* and *Phillyrea angustifolia*, which remain members of the Mediterranean-type forests, may have undergone this form of adaptive response.

Table 2 Examples of laurel forest tree fossils found in the Western European area.

Locality	Age (Ma)	Genera	Reference
Gelinden, Belgium	Palaeocene (65–56)	Lauraceae (*Persea*, *Laurus*), Fagaceae (*Quercus*, *Castanopsis*), Theaceae (*Visnea*), Arecaceae (*Phoenix*, *Chamaerops*, *Sabal*)	de Saporta, 1881
Cervera, Catalonia, Spain	Lower Oligocene (35–29)	17 species of Lauraceae (*Lindera*)	Sanz de Siria, 1985, 1992
Izarra, Basque Country, Spain	Lower Miocene (23–11)	Lauraceae (*Daphnogene*, *Laurophyllum*), *Myrica*, *Juglans*, *Quercus*, *Byttneriophyllum*	Barrón, 1999
Moruelos, Aragón, Spain	Lower Miocene (23–11)	*Laurophyllum*, *Daphnogene*, *Neolitsea*	Barrón & Diéguez, 2001
Cerdaña, Catalonia, Spain	Upper Miocene (11–5)	*Persea princeps*, *Daphnogene*, *Laurophyllum*, *Ocotea*, Myrsinaceae, *Quercus drimeja*, *Quercus mediterranea*	Barrón, 1996
Central Massive, France	Pliocene (5–2.6)	*Ocotea*, *Laurus*, *Apollonias*, *Glyptostrobus*, *Liriodendron*,	de Saporta & Marion, 1876
Lower Catalonia, Spain	Pliocene (5–2.6)	*Laurus*, *Persea*, *Cinnamomum*, *Lindera*, lauroid-leaved *Quercus*	Almera, 1894; Sanz de Siria, 1987

Table 3 Responses of the Iberian (Tethyan) palaeoflora to the climatic deterioration marking the end of the Tertiary period. Source: Benito Garzón & Sainz de Ollero (2002).

Responses	Examples
Apparent or inferred adaptation to the Mediterranean climate	*Arbutus unedo*, *Rhamnus alaternus*, *Viburnum rigidum*, *Phillyrea angustifolia*
Survival in Iberian and Macaronesian refugia	*Laurus*, *Prunus lusitanica*, *Culcita macrocarpa*, *Davallia canariensis*, *Diplazium caudatum*, *Dryopteris guanchica*, *Woodwardia radicans*
Extinction in Iberia and survival in Macaronesia (Macaronesian palaeoendemics)	*Persea*, *Ocotea*, *Apollonias*, *Visnea*, Myrsinaceae
Extinction in Iberia and survival in other Asiatic and American Tertiary refugia	*Magnolia*, *Cinnamomum*, *Liquidambar*, *Liriodendron*
Extinction in Macaronesia and survival in other continental (Europe, Africa) refugia	*Tetraclinis articulata*, *Ulmus minor*
Global extinction	*Daphnogene*, *Laurophyllum*, laurophyll *Quercus*

Second, other species may have shown limited adaptive responses but persisted as relicts in particular Iberian refugia characterized by a high mean annual precipitation (Cádiz Mountains, Central chain, Galicia, Cantabrian coastal chain), or in particular river basins (e.g. Tagus), where the tropical moisture is to some degree substituted by water flowing from mountain headwaters. Some tree species such as *Laurus*, *Prunus lusitanica*, *Tetraclinis articulata*, shrubs such as *Rhododendron ponticum*, and especially ferns such as *Culcita macrocarpa*, *Davallia canariensis*, *Diplazium caudatum*, *Dryopteris guanchica*, *Hymenophyllum tunbrigense*, *Trichomanes speciosum* and *Woodwardia radicans* are found in such locations (Blanco *et al.*, 1998). Many of these species also

inhabit the Macaronesian archipelagos, where the impact of the regional climate deterioration has been buffered, both by the oceanic influence and by the ease of elevational migration, thus giving rise to small but continuously available refugia. In the case of *Laurus*, perhaps the best representative of this Palaeotropical geoflora, an ability to withstand a degree of aridity (Rodríguez-Sánchez & Arroyo, 2008) has allowed this genus to maintain a fairly broad distribution within the Mediterranean Basin, with the existence of several populations ranging from the Pontic Mountains in Anatolia to Macaronesia, including some Moroccan refugia (Rodríguez-Sánchez *et al.*, 2009).

Third, another group of species survived on Macaronesian islands but became extinct in Iberia. Among them we can include tree species in genera such as *Apollonias*, *Clethra*, *Ocotea*, *Persea*, *Picconia*, *Pleiomeris* and *Visnea*, all of which are Macaronesian palaeoendemics in the sense that they have undergone only limited evolutionary change or radiation on the Macaronesian islands, remaining close to their ancestral form. Some of these taxa are also endemic at the generic level: *Pleiomeris*, *Picconia*, *Visnea* and (possibly) *Apollonias*.

Fourth, other taxa failed to survive in Iberia and may never have managed to colonize Macaronesian islands because of limited over-water dispersal ability, but have persisted in other Tertiary refugia, such as within the North American Appalachian chain (*Carya*, *Magnolia*) or in parts of Southeast Asia (*Cinnamomum*, *Juglans*, *Zelkova*). Some taxa have persisted in both of these areas, for example *Liquidambar* and *Liriodendron*, thus providing striking examples of disjunct distributions (Axelrod, 1975).

Fifth, there are some taxa still extant in continental refugia that have been discovered as fossils or microfossils in Macaronesia (*Carpinus*, *Tetraclinis articulata*, *Ulmus minor*) (Heer, 1855; Andersson *et al.*, 2009; de Nascimento *et al.*, 2009).

Finally, some taxa became globally extinct; examples include *Daphnogene*, *Laurophyllum* and lauroid-leaved species of *Quercus*.

BIOGEOGRAPHICAL CONSEQUENCES OF THE EXISTENCE OF PALAEO-MACARONESIA SINCE 60 MA

Macaronesia has long been regarded as a floristic crossroads (e.g. Hooker, 1866; Engler, 1879). In it, (1) a group of very old (i.e. palaeoendemic) Tethyan tropical ferns and trees of 'continental' origin have been able to survive the generally dramatic climate deterioration of the Pliocene–Pleistocene (Rodríguez-Sánchez & Arroyo, 2008; Rodríguez-Sánchez *et al.*, 2009); these coexist with (2) a group of younger [although still Tertiary (Vargas, 2007; Kim *et al.*, 2008)] species that have diversified *in situ* (i.e. they are neoendemics) from comparatively few (mainly African and Mediterranean) colonization events (Bramwell, 1976, 1985; Kim *et al.*, 2008); and also alongside (3) many native non-endemic species shared with North Africa and the Mediterranean (Médail & Quézel, 1999).

Despite constituting only an impoverished version of the original Tethyan Tertiary laurel forest (Hooker, 1866; Sunding, 1979), the Macaronesian laurel forest is still rich in palaeoendemics, including about 40 Madeiran/Canarian species (Bramwell, 1976, 1985; Sunding, 1979; Höllermann, 1981). These comprise both geographic palaeoendemics (species or genera still extant in other parts of the world but lost from the Mediterranean, as, for instance, is the case for *Persea*, *Ocotea* and *Clethra*) and taxonomic palaeoendemics (species or genera isolated within their clades as a result of past continental extinction, such as *Apollonias*, *Picconia*, *Pleiomeris* or *Visnea*) (Cronk, 1992; Vargas, 2007). This relictual laurel forest was later enriched with more recent floristic elements, such as the Afro-Arabian heather *Erica arborea*, which was already present in Madeira by *c.* 2 Ma (Heer, 1855) and which appears to have colonized Macaronesia from the nearby continents at least twice (Désamoré *et al.*, 2010).

Recent phylogeographic analyses of both Macaronesian cryptogams (Vanderpoorten *et al.*, 2007; Aigoin *et al.*, 2009) and spermatophytes (Vargas, 2007) support earlier work in highlighting that the Macaronesian flora consists of a mixture of palaeoendemics and neoendemics. Such studies have also clearly demonstrated the role of Macaronesia in providing Pleistocene refugia for species that were later able to re-colonize Iberia or North Africa, as has been inferred for the moss *Radula linderbergiana* (Laenen *et al.*, 2010) and for members of the spermatophyte genera *Aeonium*, *Sonchus* and *Convolvulus*, among others (Caujapé-Castells, in press).

While the island ages of several contemporary Macaronesian islands overlap by several million years with the long period of dominance of the Palaeotropical flora in the source region, Palaeo-Macaronesia provided opportunities for the colonization of high islands (of varied major habitat types) perhaps stretching unbroken as far back as the start of the Tertiary (*c.* 65 Ma) and over distances of less than 200 km from both the Iberian Peninsula and North Africa. Over this time, both source floras and the availability of dispersal vectors may have changed dramatically.

Acknowledgement of the antiquity of Palaeo-Macaronesia makes it easier to account for the presence of relictual and in some cases palaeo-endemic floral elements in the laurel forests of contemporary Macaronesia. That the Macaronesian laurel forests are impoverished versions of the Tethyan floras can be accounted for by the limited area of the islands, by climatic or habitat requirements not being met, and also by the limited ocean-crossing dispersal abilities of species specialized to dispersal by terrestrial vertebrates or by birds that lack the ability to cross significant stretches of water.

We may further speculate that the progressive climatic deterioration experienced in the Tethyan region was less pronounced on the islands, mainly owing to the buffering effect of the Atlantic Ocean and the latitudinal span provided amongst the islands. The range in elevation within higher islands also allowed for vertical migration of the laurel forest elements in response to fluctuations in climate.

Examination of the known geological ages of the basal shields forming the Palaeo-Macaronesian archipelagos (Geldmacher *et al.*, 2001, 2005) indicates that several islands, representing different stages of island ontogeny, almost certainly existed simultaneously. The older islands were located closer to the Iberian Peninsula, while the new ones were being formed by the hotspot activity some hundreds of kilometres to the south-west, owing to the slight counter-clockwise rotation of the African Plate (Geldmacher *et al.*, 2001, 2005). These new islands were located further away from Iberia, but also downstream from the circum-tropical global marine current and the trade winds. Thus, the Palaeotropical flora might have colonized the younger and contemporary islands from two distinct routes, either directly from the continent, or, as evidenced in molecular phylogenies for many extant island lineages, much more probably in stepping-stone fashion from the older islands of Palaeo-Macaronesia.

The colonization process of the more recent islands was probably characterized by a progressive impoverishment in the Palaeotropical ecosystem assemblage, as some species present on the old islands simply failed to reach the new ones. Nevertheless, some species that might have evolved *in situ* to yield Palaeo-Macaronesian neoendemic species on the old islands might not have vanished with the submerging islands, but instead have survived on different islands after successful 'progression rule' intra-archipelago (or inter-archipelago) dispersal events (Wagner & Funk, 1995; Juan *et al.*, 2000; Whittaker & Fernández-Palacios, 2007).

In addition to its significance for Macaronesian biogeography, recognition of the availability of emerged islands in the East Atlantic Ocean, close to Europe and Africa, since *c.* 60–65 Ma has broader global biogeographical implications. For instance, these islands may have contributed to trans-Holarctic dispersal after the closure of the North Atlantic land bridge (Scotland–Greenland) – an event associated with the deterioration of the climate *c.* 40 Ma (Mai, 1989, 1991; Milne & Abbott, 2002; Milne, 2006). Although the Bering land bridge connecting East Asia with western North America remained

open until *c.* 5 Ma (Milne, 2006), its climate was latterly too cold for the exchange of Palaeotropical floral elements to occur.

Interestingly, Daniel Axelrod, in his seminal paper about the Madrean (palaeovegetation of the Sierra Madre chains in Mexico) and Tethyan flora relationships (Axelrod, 1975), discusses the possibility of a late Holarctic connection via the Atlantic islands, within the framework of a significantly narrower Atlantic Ocean. Although the Azores archipelago (identified by Axelrod as a candidate locality) is rather younger than required, with Santa Maria, its oldest island, being only 8 Myr old (França *et al.*, 2005), the submerged archipelago of Great Meteor, located 800 km south of the Azores, and for which ages of 16 Ma have been given (Weigel & Grevemeyer, 1999), might have aided in this trans-Atlantic long-distance dispersal. It could have acted as a stepping stone between the American mainland and the Old World mainland, or even between the American mainland and other, more easterly archipelagos (Palaeo-Madeira and Palaeo-Canaries). The importance of such long-distance dispersal events in shaping the biotas of entire archipelagos and continents is today widely recognized by many (e.g. Winkworth *et al.*, 2002; Särkinen *et al.*, 2007) but not all biogeographers, some of whom regard long-distance dispersal as a generally unsupported inference (e.g. Nelson & Ladiges, 2001; Heads, 2005, 2009). However, it seems to us that the vicariance–dispersalism controversy becomes more easily resolvable if it is accepted that islands have always been built and destroyed throughout the history of the great oceans, thus extending the time-scale over which such migrations have been possible, and allowing for the operation of 'stepping-stone' dispersal via now vanished islands and terrains (Morley, 2003; Carpenter *et al.*, 2010; Heads, 2010; Renner, 2010). For example, very recently Wen & Ickert-Bond (2009) highlighted a role for trans-Atlantic long-distance dispersal, together with the North Atlantic migration route, in the origin of the Madrean–Tethyan disjunctions. Here, the role of Palaeo-Macaronesia could have been especially relevant during the time interval between the definitive closure of the North Atlantic land bridge (*c.* 40 Ma) and the appearance of the oldest extant Macaronesian islands (Salvagem Grande and Fuerteventura, 30–20 Ma).

We may speculate that some Palaeotropical species that underwent extinction in the Iberian mainland before the start of the Miocene, *c.* 25 Ma, might also have colonized Palaeo-Macaronesian islands at some point before the oldest present-day islands emerged. For instance, Aigoin *et al.* (2009) report that the moss *Brachythecium percurrens*, endemic to Madeira, diverged from the most recent common ancestor within its family (Helicodontioideae) *c.* 40 Ma, significantly earlier than the appearance of the oldest extant Macaronesian island (Salvagem Grande, 27 Ma), which is perhaps most parsimoniously explained by a dispersal event to Palaeo-Macaronesia from the Tethys Sea margins, followed by subsequent stepping-stone dispersal through the current seamount chain until Madeira (just 5 Myr old) was reached. These islands, having mild maritime climates, might even have acted as Palaeogene

refugia for Iberian and North African taxa during periods of unfavourable climate in the continental areas.

Phylogenetic studies in Hawaii and elsewhere indicate that it is possible for neo-endemic archipelagic species to be older (as distinct lineages) than the islands on which they occur today (Wagner & Funk, 1995; Whittaker & Fernández-Palacios, 2007; Renner *et al.*, 2010; and references therein). Moreover, phylogenetic data for many island archipelago radiations frequently conform to a progression rule: a predominant pattern of colonization of younger islands from older ones, followed by further *in situ* divergence and diversification (Wagner & Funk, 1995; Whittaker & Fernández-Palacios, 2007). We regard it as probable that such processes have operated within Palaeo-Macaronesia and between these now vanished islands of present-day Macaronesia, significantly increasing the time that has been available for divergence between Macaronesian lineages and mainland source pools. This argues against relying too readily or simplistically on maximum island ages of existing islands in calibrating molecular clocks (for further discussion of related molecular dating issues see, for example, Grehan, 2001; Pulquério & Nichols, 2007; Andersson *et al.*, 2009; Heads, 2010; Inoue *et al.*, 2010).

THE LAUREL FOREST AND MACARONESIA: BIOGEOGRAPHICAL PATTERNS AND HYPOTHESES

The Lauraceae form a large family of woody plants (with the exception of the herbaceous parasite *Cassytha*), comprising about 50 genera and 2500–3500 species (Rohwer, 1993) distributed throughout tropical and subtropical latitudes, mainly in America, Madagascar and Australasia. According to the fossil evidence, Lauraceae appeared in the mid-Cretaceous, with basal lineages established in either Laurasian or Gondwanan late Cretaceous terrain (Chanderbali *et al.*, 2001). There are three main tribes (Laurae, Perseae and Cryptocaryae) within the family, with the first two seeming to form a single clade embracing the largest part of the family. Fossils of this clade, to which all five extant Macaronesian species (*Laurus novocanariensis, L. azorica, Ocotea foetens, Persea indica* and *Apollonias barbujana*) and the single Mediterranean extant species (*Laurus nobilis*) belong, appeared in Laurasia only in the Eocene, having possibly migrated from North Africa through a narrowing Tethys Sea rich in islands (Chanderbali *et al.*, 2001).

Today, the Lauraceae show a complex distribution pattern around the world, with a strong American and/or Asian presence but few African elements, pointing to an expansion from Laurasia followed by a subsequent divergence in tropical America. Phylogenetic analyses of the family (Rohwer, 2000; Chanderbali *et al.*, 2001) show the existence of two main clades respectively related to the Northern Hemisphere (Laurasian) and to the Southern Hemisphere (Gondwanan), with the *Ocotea* clade being simultaneously present within both palaeo-realms. Although the arrival and subsequent diversification of *Ocotea* in the Neotropics, where it is richer in species, has been postulated as the result of continental range expansions via

North America or Africa, phylogenetic results support a much later timing for this disjunction, clearly after the break-up of West Gondwana, thus supporting the role of (either trans-Atlantic or trans-Pacific) long-distance dispersal (Rohwer, 2000).

The ability of Lauraceae trees to achieve long-distance dispersal has been supported through several independent lines of evidence. On the one hand, the existence of various Lauraceae species on islands that have never been connected to the mainland, such as Macaronesia, with several of them very distant from the mainland, such as Flores (Azores) 1865 km off Iberia and 1930 km off Newfoundland, testify in this direction. On the other hand, recent phylogenetic analyses have highlighted the close similarity exhibited by Macaronesian and Moroccan populations of *Laurus azorica* (*L. novocanariensis*) and Iberian populations of *Laurus nobilis*, which are actually more closely related to Macaronesian populations of *L. novocanariensis* or *L. azorica* than to Italian, Greek and Turkish populations of the same species (Arroyo-García *et al.*, 2001; Rodríguez-Sánchez *et al.*, 2009). According to these studies, the data point to a recent and rapid expansion of *Laurus* from Iberia to Macaronesia, but a dispersal in the opposite direction cannot be ruled out, especially given that *Laurus* was already present in Madeira at least 2 Ma (Heer, 1855) and that there is evidence for a number of back-colonizations of Macaronesian taxa to Iberia (e.g. Carine *et al.*, 2004; Caujapé-Castells, in press; Laenen *et al.*, 2010). Noting that genetic diversity of Macaronesian *Laurus* is greater than that of Iberian populations, Rodríguez-Sánchez *et al.* (2009) argue that the Macaronesian *Laurus* have probably been isolated for a lengthy period of time (consistent with the age of fossils according to Heer, 1855). Moreover, the same authors report that Madeiran, Canarian and Moroccan haplotypes are basal to Azorean and Iberian populations, suggesting that the latter could be derived from the former. These observations are consistent with the notion that the Macaronesian region has acted as an important refugium for Tertiary Iberian plants.

Consistent with the above arguments but in an entirely separate geographical context, Carpenter *et al.* (2010) have reported the occurrence of Lauraceae macrofossils in samples taken from the submerged summit of a Palaeocene volcanic palaeo-island, located close to the Ninetyeast Ridge in the Indian Ocean (which probably originated in the former activity of the Kerguelen hotspot). For these authors this constitutes clear support for the role of small oceanic islands in long-distance island-hopping dispersal events that may explain the biotic interchanges between Australia and Africa, largely after the break-up of eastern Gondwana (and see Renner, 2010).

Given the geological and geomorphological dynamics of the islands and the predominance of igneous rock types, the fossil evidence of plant species from sedimentary deposits is comparatively scarce. However, Andersson *et al.* (2009) argue that the burial of vegetation and soils in volcanic eruptions has been a repeated pattern of events and thus that further exploration of palaeofloras may well prove fruitful. The most important site analysed to date is still the classic Pliocene–Pleistocene deposit of São Jorge in Madeira, discovered by Heer (1855), and later dated by Charles Lyell (1864) as probably belonging to the late Pliocene, which means within today's lower Pleistocene limits (Rio *et al.*, 1998). Although his taxonomic determinations proved controversial (Bunbury, 1859), according to Heer several laurel forest species were present in the São Jorge material, many of them still extant in Macaronesia, including ferns (*Osmunda regalis*, *Trichomanes speciosum*, *Asplenium marinum*, *Woodwardia radicans*, *Davallia canariensis*, *Pteridium aquilinum*) and shrubs or trees (*Myrica faya*, *Laurus azorica*, *Rosa canina*, *Myrtus communis*, *Clethra arborea*, *Erica arborea*, *Vaccinium padifolium* and *Frangula azorica*). Of these taxa, *Frangula azorica* is today extinct in Madeira but the species remains extant in the Azores. A second group of tree species that have been lost from Madeira includes *Ilex hartungi*, *Ulmus minor*, *Corylus australis* and *Pistacia phaecum*. Interestingly, the genus *Pistacia*, although no longer native in Madeira, is an important component of the Mediterranean-like thermophilous woodlands in the Canaries, where two different species (*Pistacia atlantica* and *Pistacia lentiscus*) that participate in such forests in Southern Europe and North Africa coexist. These Madeiran records provided an early indication of the antiquity of elements of the Mediterranean forest within Macaronesia, although, as argued herein, their colonization is actually likely to have been very much earlier and well in advance of the onset of the Pleistocene glacials.

Andersson *et al.* (2009) have recently published data from a late Miocene–Pliocene sedimentary deposit from the summit region of Gran Canaria, dated to *c.* 4 Ma. Among many laurophyll species, some yet to be determined, they found *Arbutus canariensis* and, surprisingly, also the conifer *Tetraclinis articulata*, a species abundant in North Africa but restricted today in Europe to an area near Cartagena (Iberian Peninsula) and Malta, where it is the national tree. It was not previously considered a Macaronesian island native. Its presence has also been confirmed in the lower Miocene subtropical flora of Izarra, Spain (Barrón, 2003). Interestingly, the genus *Arbutus* (represented in the Canarian laurel forest by the endemic *Arbutus canariensis*, a sister species to the widely Mediterranean-distributed *Arbutus unedo*) is considered by Benito Garzón & Sainz de Ollero (2002) to be an example of a member of the European Palaeotropical flora that has adapted to the Mediterranean climate (Table 4). *Arbutus* is one of the very few Canarian laurel forest tree genera (together with *Viburnum* and *Pleiomeris*) not present (at least today) in Madeira.

Another recent study, based on pollen analysis from Tenerife, has revealed that two tree taxa (*Carpinus* possibly *betulus* and *Quercus* sp. or spp.), not previously considered native to Macaronesia, once grew in the area around La Laguna (de Nascimento *et al.*, 2009). These pollen types, which were abundant in the record before the arrival of the first settlers on Tenerife (*c.* 2500 BP), had disappeared by around the time of

Table 4 Palaeogeological and palaeoclimate events in the Canaries and possible biogeographical consequences. The most significant geological events during the Cenozoic and their influence on world climate and biogeography are included.

Chronology	Evidence	Authors	Biogeographical consequence
60–25 Ma (Palaeogene)	Emergence (and consequent submergence) of islands of Palaeo-Macaronesia	Geldmacher *et al.* (2001, 2005)	Existence of islands in the Atlantic prone to be colonized from Europe and North Africa
55–45 Ma (Eocene)	Tibet Plateau uplift, owing to the collision of India and Eurasia	Barrón & Peyrot (2006)	Closure of the exit way of Siberian cold and dry air masses to South Asia. The European laurel forest began to be displaced
45–29 Ma (Eocene–Oligocene)	Opening of the Drake Strait separating South America from Antarctica	Barrón & Peyrot (2006)	Antarctica became isolated and began its deep freeze. Sea level diminished and epicontinental seas (i.e. Inter-American and Turgai) disappeared
19–12 Ma (Miocene)	Collision of the Turkish and Arabian plates → Tethys Sea–Indian Ocean definitive separation	Barrón & Peyrot (2006)	End of the circum-equatorial warm sea current, which subsequently had to round Africa → Central European climate deterioration. The Mediterranean became definitively an interior sea, closed to the east, although still open to the Atlantic
25–5 Ma (Miocene)	Emergence of the oldest extant Canaries: Fuerteventura (21 Ma), Ajaches (15), Gran Canaria (15), Famara (10), La Gomera (12), Adeje (11.5), Teno (8) and Anaga (6); and of Amanay (15 Ma), which is now reduced to a seamount	Various sources	First palaeoclimate records. Information about Canarian Palaeogene climate can also be inferred from a knowledge of European and North African climate
25–5 Ma (Miocene)	Guinean coastal fauna → tropical climate with isothermic coastal waters throughout the year	Meco *et al.* (2003)	Absence of today's cold marine Canarian current
25–5 Ma (Miocene)	Fuerteventura's elevation reached 3300 m in the Miocene, before being subject to dominant erosional processes, including mega-landslides	Stillman (1999); Acosta *et al.* (2005)	The older islands were much higher and larger than today, and included habitats that they have since lost
c. 9–4 Ma (end of Miocene–middle Pliocene)	The presence of several shallow marine water genera (*Rothpletzia*, *Strombus*, *Nerita*, *Ancilla*, *Saccostrea* and *Siderastraea*) implies the existence of a tropical climate (similar to today's Guinea Gulf and Caribbean Sea climates): this is very warm and without seasonality but includes frequent large hurricanes	Meco *et al.* (2005)	The Mediterranean climate (cool, humid winters and warm, dry summers) was not yet present in the Canaries so there would have been little drought stress to threaten the laurel forest
6–5 Ma (Latest Miocene–Pliocene)	Gibraltar Strait reiterative closure	Barrón & Peyrot (2006)	Aridification of Europe and N Africa. Mediterranean Sea desiccation and salinization. Desertization cycles in the Saharan region
c. 3.5 Ma	Emergence of La Palma	Carracedo *et al.* (2001)	Island colonization and species exchange follows

Table 4 Continued

Chronology	Evidence	Authors	Biogeographical consequence
3–2 Ma (Pliocene–Pleistocene transition)	The warm tropical climate shifts gradually to a general arid climate interrupted by several (about 10) strong and irregular rainy periods (each one lasting millennia), culminating in the onset of the Pleistocene glacial.	Meco *et al.* (2006)	
3.2–2.6 Ma (Late Pliocene)	Cool Canarian current (re-?)appears inducing continental aridity → start of the glacial–interglacial sequence that has continued through the Quaternary. The Canarian current is associated with a trade winds impulse	Meco *et al.* (2003); Rognon & Coudé-Gaussen (1996)	Formation of thick, extensive calcretes (*caliche*) in sites all over the Canaries. The thickest crust is the earliest, created after the very humid Miocene and Pliocene. The littoral origin of the carbonates forming these crusts proves that the sand deposition enables the formation of calcretes, which need sufficient warmth (evaporation) to be produced. Usually calcretes are formed over the surface of sand dunes in an arid, warmer period occurring after a pluvial. The present interglacial has not yet formed its calcrete layer
3.2–2.6 Ma (Late Pliocene)	First *Antophora* (a type of bee) nests known (Gran Canaria) formed in a general arid climate with humid episodes (palaeosols)	Meco *et al.* (2006)	First evidence of climate change (tropical → Mediterranean) in the Canaries, very probably triggered by the onset of the Canarian marine current, and this by the onset of the glaciations
3.2–2.6 Ma (Late Pliocene)	Final closure of the Panama Isthmus	Barrón & Peyrot (2006)	Glaciation cycles; onset of the Mediterranean climate. Ice formation in the Arctic region and in the Antarctica Peninsula
2.6–0 Ma (Quaternary)	Fossiliferous palaeosols (with *Antophora* nests) → humid episodes (with vegetation) intercalated with calcrete deposits + heavy aeolian deposition and dunes formation → arid episodes	Meco *et al.* (2003)	
2.6–0 Ma (Quaternary)	The southward shift of the Azores High, owing to the glacial ice sheets, provoked the influence of the Westerlies at the Canarian latitude	Rognon & Coudé-Gaussen (1996)	Displacement of the trade winds 5–8° southwards (to Cape Verde) during glaciations
2.6–0 Ma (Quaternary)	West-to-east wind deposition of sand with shore origin during sea-level minima associated with glacial episodes	Rognon & Coudé-Gaussen (1996)	
c. 1.1 Ma	Emergence of El Hierro	Guillou *et al.* (1996)	Most recent case of colonization of a new island from older islands nearby, altering patterns of habitat availability and of endemism

Table 4 Continued

Chronology	Evidence	Authors	Biogeographical consequence
125 ka (Last interglacial, Eemian)	Tropical climate in the Canaries, with seawater temperature >23 °C for at least 6 months (as in Cape Verde currently)	Meco *et al.* (2003)	Senegalese marine fauna with *Siderastraea* corals in eastern and central Canaries
125 ka (Last interglacial, Eemian)	Fuerteventura coastline 5 m above the present sea level	Meco *et al.* (2006)	Slightly smaller, lower and more isolated Canary islands than today
125 ka (Last interglacial, Eemian)	The Senegalese gastropod fauna characterized the Canarian coasts, lasting until 83 ka in Gran Canaria	Meco *et al.* (2006)	Canarian sea temperature in the Eemian interglacial was as high as it is today in the Guinea Gulf
50–30 ka	Emergence of the islets north of Lanzarote	de la Nuez *et al.* (1997)	
50–5 ka	Multiple (up to 8) Aeolian/palaeosol deposits accumulated during arid phases in Fuerteventura and Lanzarote with a recurrence period of 5–7 ka, which stopped when conditions produced higher effective environmental moisture and soil formation	Ortiz *et al.* (2006)	Related to African palaeo-monsoon activity, which caused the predominance of trade winds during humid phases and of Saharan winds during arid episodes
18 ka (Last Glacial Maximum)	Predominance of Westerlies during the LGM	Rognon & Coudé-Gaussen (1996)	Possibility of back-colonization from Macaronesia to N Africa enhanced
14–13 ka	Climate became wetter; El Golfo landslide on El Hierro, displacing one-third of the land area into the sea	Rognon *et al.* (1989); Canals *et al.* (2000)	Dunes stabilized by vegetation in the eastern Canaries. On El Hierro, loss of area alters habitat availability
8 ka (Early Holocene)	Important humid period	Meco *et al.* (2006)	
5.5 ka (Middle Holocene)	Achievement of the present sea level on the African coast	Meco *et al.* (2003)	Present island area, elevation and isolation existing since 5.5 ka

the Castilian conquest (AD 1496), thus providing examples of human-induced extinction in the pre-historic period.

A BRIEF HISTORY OF THE COMPOSITION AND DISTRIBUTION OF THE MACARONESIAN NEOGENE LAUREL FOREST

Table 4 provides a synthesis of the most important geological and climatic events known to have occurred in the Canaries from the Miocene onwards. From the start of the Miocene (and probably much earlier) until the onset of the latest Pliocene glaciations and hence of the Mediterranean climate (*c.* 3.2 Ma) (Suc, 1984), shallow Canarian waters were characterized by the establishment of the so-called Guinean coastal fauna (*Siderastraea, Saccostrea, Rothpletzia, Strombus, Nerita, Ancilla*). As the name suggests, this fauna is distributed today in the Guinean Gulf, but it is also recorded as fossil fauna from several Canarian beaches. These assemblages indicate the existence of a tropical climate (including hurricanes) and of isothermic coastal waters throughout the year. These conditions were incompatible with the existence of the Canarian marine current (Meco *et al.*, 2005), which appeared or became functional only after the closure of the Panama Isthmus, which occurred *c.* 2.5 Ma.

The earliest evidence of a climatic deterioration in the Canaries linked to the onset of the glaciations is dated to around 4–3 Ma (Meco *et al.*, 2006). Prior to this, the warmer and wetter Miocene climate would have allowed a far greater extent of the laurel forest, in terms both of slopes (windward and leeward) on which it occurred and of elevational range. Nevertheless, the discovery of very ancient pine fossils (*c.* 13 Ma) in Gran Canaria (García-Talavera *et al.*, 1995) suggests the existence of a pine forest at high elevations, as remains the case today. The formation of the thermophilous woodlands should be a much more recent process, related to the arrival of plant species well adapted to withstand Mediterranean climates, namely ones characterized by winter cold and summer drought (Blondel & Aronson, 1999). The existence of several native non-endemic tree species (*Juniperus turbinata, Pistacia atlantica, Pistacia lentiscus, Phillyrea angustifolia*) argues for a recent arrival of these elements (Fernández-Palacios *et al.*, 2008).

During the Late Pliocene (*c.* 3 Ma), the warm tropical climate of the Mediterranean region gradually shifted to a generally arid climate interrupted by strong and irregular wetter periods (each one lasting millennia) that culminated in the onset of the Pleistocene glaciations. This change in regime was connected with the closure of the Panama Straits, the operation of the trade winds system and the (re-?)appearance of the cool Canarian marine current inducing continental aridity (Meco *et al.*, 2006). All over the Canaries this event is well recorded owing to the extensive formation of reiterative, thick, calcretes (*caliche*) in deposits of littoral origin. The thickest crust is the

oldest, created after the very humid Miocene and Pliocene. Usually calcretes are formed over the surface of sand dunes in an arid, warmer period occurring after a pluvial one (Meco *et al.*, 2006): their formation is thus indicative of environments in which sand deposition has occurred in combination with conditions of high evaporative demand.

Canarian deposits of late Pliocene age (3–2.9 Ma) record the shift from an essentially tropical to a Mediterranean-type climate. These deposits include fossiliferous palaeosols that are very rich in *Antophora* bee nests [or perhaps in ootheca (parcels of eggs) of *Dociostaurus* crickets (Acrididae)]. These features indicate the existence of humid episodes (with vegetation) intercalated with calcrete deposits and heavy aeolian deposition and dune formation, indicative of aridity (Meco *et al.*, 2006).

Furthermore, during the Pleistocene glacials, the southward shift of the Azores High was accompanied by the displacement of the trade winds 5°–8° southwards (to Cape Verde) and thus the enhanced influence of the Westerlies in the Canarian latitudes (Rognon & Coudé-Gaussen, 1996; Uriarte, 2003). This can be inferred from the west-to-east deposition of wind-blown sand of littoral origin during sea-level minima associated with the glacials. These recurrent episodes of the Westerlies have doubtless played a major role in enhancing opportunities for back-colonization from Macaronesia to North Africa, resulting in several examples of African endemics of earlier Canarian origin (e.g. in the genera *Aeonium*, *Convolvulus* and *Sonchus*) (Carine *et al.*, 2004; Caujapé-Castells, in press).

Carine's colonization-window hypothesis (Carine, 2005) envisages the opportunities for the establishment of new colonizers varying over time owing to the changing availability of the relatively uncontested space within the Macaronesian islands, as islands form or suffer extinction events. This idea may be extended to include the notion of dispersal windows, that is, periods such as the onset of the Westerlies, when dispersal opportunities to particular island groups may be significantly enhanced, resulting in pulses of arrivals rather than a steady rate over time (Caujapé-Castells, in press).

During the last (Eemian) interglacial (125 ka), the sea temperature was as high as that today in the Cape Verde Islands, with at least 6 months of the year >23 °C. This is demonstrated by fossils of the so-called Senegalese marine fauna (including *Siderastraea* corals) in the eastern and central Canaries. This fauna characterized the coasts of Gran Canaria until around 83 ka (Meco *et al.*, 2006). During the Eemian Interglacial, the coastline of Fuerteventura was about 5 m above the present sea level, thus indicating that the emergent Canary islands would have been very slightly lower, smaller and more isolated than they are today (neglecting changes resulting from the subsequent growth/erosional loss of land, for example the El Golfo landslide on the island of El Hierro).

The Pliocene and Pleistocene climatic deterioration, although much milder than in the continents, was also experienced in the Canaries, possibly impoverishing the laurel forests in species and restricting their distribution to the zone

Table 5 Potential (i.e. pre-human colonization) and present distribution of the Macaronesian laurel forest. Modified from Fernández-Palacios (2009).

Island	Potential area (thousands of ha)	Present area (thousands of ha)	Potential %
Gran Canaria	20	0.2	1
Tenerife	40	4	10
La Palma	20	6	30
La Gomera	9	4.6	52
El Hierro	6	2.5	42
Total Canaries	105	19	18
Madeira	60	15	25
Azores	200	6	3
Total Macaronesia	365	40	12.5

directly influenced by the cloud banks of the trade-wind inversion layer in the mid-elevations of the windward slopes of the high islands, where there is sufficient summer moisture. Geomorphological evidence suggests that the laurel forest has occupied approximately its present elevational extent at least since the last Pleistocene glaciation. While at lower elevations heavy debris movements took place during the late Pleistocene, in the present laurel forest belt mainly fine materials were transported, and humus horizons were formed within the interval 40 to 11 ka (Rohdenburg & Bork, 1979). This restriction of the laurel forest to the cloud belt has extended the area available to other forest formations in the Canaries: the pine forest above and the thermophilous woodlands below the laurel forest zone (but see de Nascimento *et al.*, 2009).

Immediately before the arrival of the first humans on the Canaries – berbers, who reached the islands at some point within the first millennium BC (del Arco *et al.*, 1997; Rando *et al.*, 1999) – the laurel forest was present in the high central and western islands and very probably in the summit regions of the eastern ones, as some small remnants of this vegetation type persist there today (Santos-Guerra, 1990). Whereas in the Canaries this laurel forest was restricted in distribution to the most favourable zones (windward mid-elevations), in Madeira the laurel forest was much more widely distributed (as is the case today), although here too it was probably absent from the coastal lowlands and summit, and was perhaps only minimally represented in the highest elevations of Porto Santo and The Desertas.

By contrast, in the Azores, immediately before the arrival of the first European settlers in AD 1432, the laurel forests occupied the islands from the coast to the summit, with the exception of the highest slopes of the Pico peak (2350 m), which are too cold for this formation. It has been estimated that immediately prior to human colonization, the laurel forest may have occupied about 200,000 ha in the Azores, 105,000 ha in the Canaries and some 60,000 ha in Madeira, yielding a total aera of 365,000 ha for the whole of Macaronesia (Fernández-Palacios, 2009). Today, only 40,000 ha remain (mainly in Madeira and La Gomera), about 12.5% of the potential area (Table 5).

THE MACARONESIAN LAUREL FOREST TODAY: DISTRIBUTION, SPECIES COMPOSITION AND HUMAN IMPACT

After the arrival of the first settlers in Macaronesia (during the first millennium BC for the Canaries, AD 1420–1430 for the Azores and Madeira, and 1456 for Cape Verde), the laurel forests were affected in varying ways. In the Canaries, these impacts were associated with the use of fire and opening of forests for grazing, whereas in the Azores and Madeira the forests were cleared for agriculture and cattle. There is no evidence that the laurel forest survived in Cape Verde into the present climatic period, so its absence cannot be attributed to human intervention. Nevertheless, we cannot rule out that in earlier periods the laurel forest may have been present there (Brochmann *et al.*, 1997).

In the Canaries, the use of fire by the Guanche people, together with the introduction of goats, sheep, pigs and rodents, had a heavy impact on the vegetation, even extinguishing some forest types (de Nascimento *et al.*, 2009). Later, the arrival of the Castilians (15th century), and the introduction of an agricultural development model, culminated in the disappearance of the majority of the laurel forest, especially in areas easily exploited for agriculture (Parsons, 1981). The laurel forests were almost completely eliminated from Gran Canaria, and were reduced to a fraction on the other islands, with the exception of La Gomera, on which a substantial area (now Garajonay National Park) remains forested.

In the Azores, the initial intensive conversion to agricultural and grazing land, coupled with the later development of timber (*Cryptomeria japonica*) production, the pillars of the economy, almost destroyed the laurel forest of the archipelago, which is now only represented in small, fragmented patches on the summits of São Miguel, Terceira, Pico and Flores. Fortunately, in Madeira the impact of colonization was not great enough to destroy the laurel forest, and several good stands of mature laurel forest have persisted in ravines and on cliffs. Hence, Madeira and La Gomera (Canaries) now provide the best remaining examples of the Atlantic laurel forest (Sziemer, 2000).

The laurel forest structure we know today is characterized by a canopy of variable height (10–40 m), dominated by up to 10 palaeoendemic tree species and by an understorey with seedlings, suckers and ferns (Santos-Guerra, 1990; Fernández-Palacios & Arévalo, 1998; Fernández-Palacios *et al.*, 2004a). Seedlings and suckers form banks around the parent trees. There are very few herb species growing inside this forest, and they are usually restricted to the light gaps where the canopy has been recently opened. Several fern genera (*Culcita*, *Davallia*, *Diplazium*, *Hymenophyllum*, *Lastrea*, *Osmunda*, *Stegnogramma*, *Trichomanes* and *Woodwardia*) that were part of the Palaeotropical flora are shared with the so-called Iberian refugia (the Cádiz Mountains, Algarve, Galicia, Cantabrian coast), constituting the strongest contemporary link between Palaeo-Iberian and Macaronesian laurel forests, although, in the latter, ferns are only present where the moisture availability is high enough.

CONCLUSIONS AND PROSPECTS

We would like to finish this paper with a brief comment on some important issues regarding the conservation of the Macaronesian laurel forests. On the one hand, despite its current regrettable conservation status, the spontaneous regeneration of laurel forest can today be observed in many places, mainly as a result of the shift in the economic development model, both in Madeira and the Canaries, from agriculture to mass tourism, but also because of the active protection policies developed by governments (Fernández-Palacios *et al.*, 2004b). Unfortunately, this is not the case within Gran Canaria (where the remnant laurel forest fragments were too small to enable spontaneous regeneration), or in the Azores, where the economy still relies on (exotic) timber production and the dairy industry (for implications, see Triantis *et al.*, 2010). Nevertheless, the best remaining formations of the Macaronesian laurel forest, as well as many of the places where it is recovering reasonably well, are protected.

On the other hand, as we have highlighted, our knowledge of the historical distribution ranges, of species compositional shifts throughout the Tertiary and Quaternary, and of the ecological–evolutionary dynamics of these forests is far from complete. Of particular importance is further research to delineate the extent of the human impact on Macaronesian forests, linked first to the aboriginal colonizers and second to the more recent Europeans conquerors, and to provide a baseline for designing realistic objectives for restoration and management efforts, including, for instance, the resolution of questions such as which species have been extirpated or extinguished, whether there are important functional types missing, and what were the insular and elevational distributions of the pre-human forest formations (see, for example, de Nascimento *et al.*, 2009; Triantis *et al.*, 2010). We anticipate that an increase in the knowledge and analyses of new fossil sites in Macaronesia will result in additions to the list of species lost from Macaronesia owing to climate change, loss of habitat, natural disasters, human impacts, or a combination of these factors.

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BIOSKETCH

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