BIOLOGICAL REVIEWS
Cambridge Philosophical Society
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Biol. Rev. (2024), **99**, pp. 2060–2081.
doi: 10.1111/brv.13112

In defence of the entity of Macaronesia as a biogeographical region

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ABSTRACT

Since its coinage *ca.* 1850 AD by Philip Barker Webb, the biogeographical region of Macaronesia, consisting of the North Atlantic volcanic archipelagos of the Azores, Madeira with the tiny Selvagens, the Canaries and Cabo Verde, and for some authors different continental coastal strips, has been under dispute. Herein, after a brief introduction on the terminology and purpose of regionalism, we recover the origins of the Macaronesia name, concept and geographical adscription, as well as its biogeographical implications and how different authors have positioned themselves, using distinct terrestrial or marine floristic and/or faunistic taxa distributions and relationships for accepting or rejecting the existence of this

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Biological Reviews **99** (2024) 2060–2081 © 2024 The Author(s). *Biological Reviews* published by John Wiley & Sons Ltd on behalf of Cambridge Philosophical Society.
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biogeographical region. Four main issues related to Macaronesia are thoroughly discussed: (*i*) its independence from the Mediterranean phytogeographical region; (*ii*) discrepancies according to different taxa analysed; (*iii*) its geographical limits and the role of the continental enclave(s), and, (*iv*) the validity of the phytogeographical region level. We conclude that Macaronesia has its own identity and a sound phytogeographical foundation, and that this is mainly based on three different floristic components that are shared by the Macaronesian core (Madeira and the Canaries) and the outermost archipelagos (Azores and Cabo Verde). These floristic components are: (*i*) the Palaeotropical-Tethyan Geoflora, formerly much more widely distributed in Europe and North Africa and currently restricted to the three northern archipelagos (the Azores, Madeira and the Canaries); (*ii*) the African Rand Flora, still extant in the coastal margins of Africa and Arabia, and present in the southern archipelagos (Madeira, the Canaries and Cabo Verde), and (*iii*) the Macaronesian neoendemic floristic component, represented in all the archipelagos, a result of allopatric diversification promoted by isolation of Mediterranean ancestors that manage to colonize Central Macaronesia and, from there, the outer archipelagos. Finally, a differentiating floristic component recently colonized the different archipelagos from the nearest continental coast, providing them with different biogeographic flavours.

Key words: Azores, biogeographical regionalization, Cabo Verde, Canaries, floristic relationships, island biogeography, island endemism, Macaronesia, Madeira, phytogeography.

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I. INTRODUCTION

The term *Makaron nesoi* stems from the ancient Greek words *μακάρων* [*makárōn*] (the blessed) and *νῆσοι* [*nêsoi*] (the islands), and thus means Fortunate Islands or Islands of the Blessed. It was used for the first time *ca.* 700 BCE by the Greek poet Hesiod [750–680 BCE] in his didactic poem *Εργα καὶ 'Ημέραι* [*Erga kai Hēmerai*] (*Works and Days*) in reference to the insular paradise where the heroes of Greek mythology went after their death. The Latinized term for Macaronesia, *Fortunatae Insulae*, appeared for the first time in 188 BCE, when the Latin comediographer Titus Maccius Plautus [255–185 BCE], used it in his work *Trinummus* (Three coins) (Martínez de Lagos & Quintero, 2006).

Beyond its ancient mythological origin, the term Macaronesia is frequently used in biogeography. In this context, it refers to a set of volcanic archipelagos located in the northeastern Atlantic Ocean off southwest Europe and northwestern Africa, which share a certain affinity in their biota. Macaronesia includes, in decreasing order of latitude, the archipelagos of the Azores, Madeira and Selvagens (all autonomous regions of Portugal), Canaries (an autonomous region of Spain) and Cabo Verde (a country) (Fig. 1). They encompass 40 islands larger than 1 km^2 and 420 small islands and islets of less than 100 ha (F. Médail, R. Vasconcelos, M. Nogales, A.D. Abreu, Y. Acosta, C. Damery, C. Grouard & J.M. Fernández-Palacios, in preparation). These archipelagos comprise a land area of *ca.* 14,600 km^2 and around 18,000 native terrestrial species of which *ca.* 6400 are endemic to this insular region [Florencio *et al.* (2021) and references therein].

Although Macaronesia has contributed numerous insights to the development of the natural and environmental sciences of islands (Florencio *et al.*, 2021), its validity as a biogeographical unit is still widely discussed (Lobin, 1982; Lüpnitz, 1995*a*; Fernández-Palacios & Dias, 2001; Vanderpoorten, Rumsey & Carine, 2007; Freitas *et al.*, 2019; Capelo, 2020). Clarification is needed on the following points: (*i*) does Macaronesia have enough biological identity to be considered a biogeographical unit, independent from the Mediterranean region? (*ii*) If so, is it merely a phytogeographical unit (as originally coined), or could the regionalization be extended to the terrestrial fauna and/or to the marine realm? (*iii*) Where are its geographical limits? (*iv*) At what level might Macaronesia qualify within a hierarchical regionalization scheme? The aim of this review is to address these questions.

II. ON THE TERMINOLOGY AND PURPOSE OF REGIONALISM

Before commencing our assessment of Macaronesia as a biogeographical unit, it is important to establish what we mean

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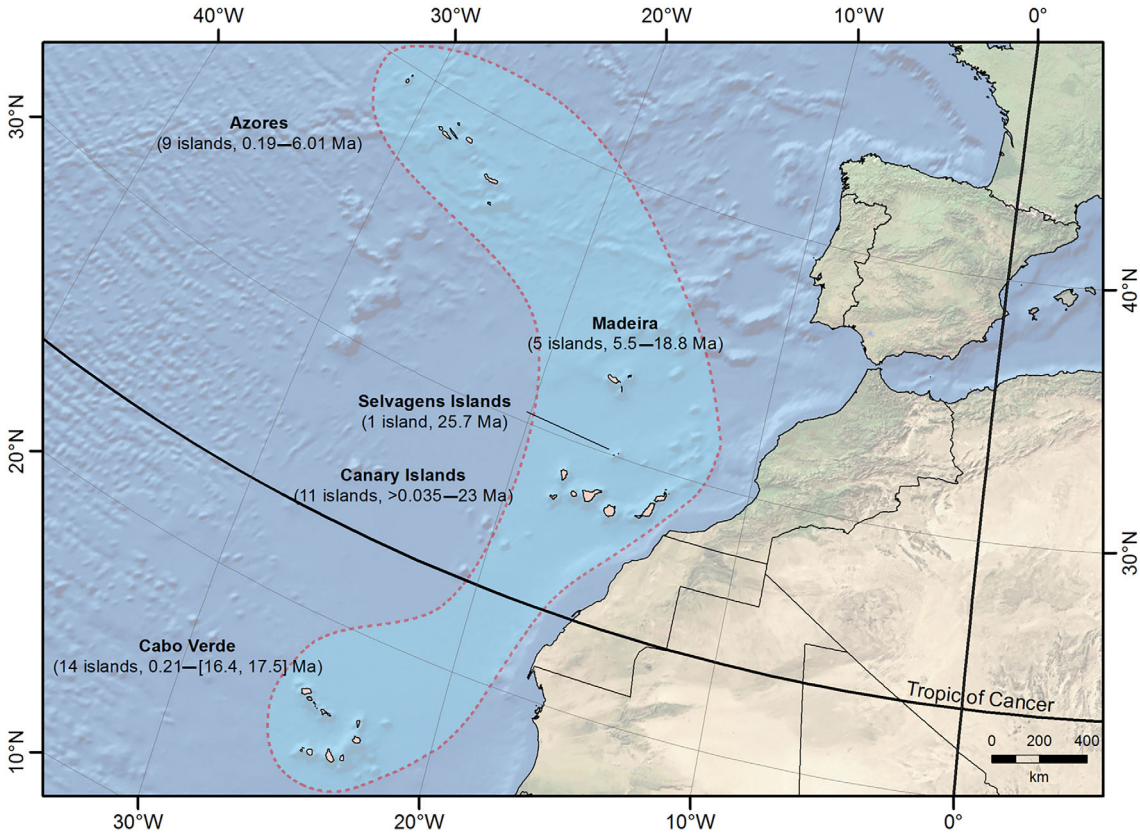

Fig. 1. Map of Macaronesia. Ma, million years ago. Source: extracted with kind permission from Florencio *et al.* (2021). https://doi.org/10.3389/fevo.2021.718169.

by biogeographical regionalization. According to Nelson (1978), an essay by Augustin-Pyramus de Candolle (1820) provided a decisive early contribution. In it, de Candolle wrote "From all of these facts, one may deduce that there are *botanical regions*; and by this term I denote whatever areas that, with the exception of introduced species, have a certain number of plants that to them are peculiar, and that can be called truly *aboriginal*" (translation in Nelson, 1978, p. 283). That is, for de Candolle, regions were essentially areas of plant endemism. Based on the limited data available to him, de Candolle listed 20 botanical regions, one of which was the Canaries, although he also noted that "each island that is isolated enough from a continent to have its own flora, is, in effect, another botanical region" (Nelson, 1978, p. 283).

When the first global zoogeographical regionalization scheme was proposed nearly 40 years later by Sclater (1858), it was based on data for birds and comprised six regions. This scheme was adopted and refined soon after by Wallace (1894), who wrote of zoogeographical regions as "…those primary divisions of the Earth's surface of approximately continental extent, which are characterised by distinct assemblages of animal types." (Wallace, 1894, p. 613). Expanding on this, Wallace argued that within a regionalization scheme, areas delimited should "…possess great individuality; whether exhibited by the *possession* of numerous peculiar species, genera, or families, or by the entire *absence* of genera or families which are abundant and widespread in some of the adjacent regions." (Wallace, 1894, p. 613).

Since then, biogeographers have continued to generate and discuss new regionalization schemes, varying in properties such as: (*i*) their global *versus* regional extent; (*ii*) the taxa or taxon used; (*iii*) whether based on data mostly considered at family, genus or species level; (*iv*) the geographical entities used (grid cells or "natural" geographical units of irregular shape and size); (*v*) the algorithm(s) used for classification; (*vi*) the number of units and levels of the hierarchy; and (*vii*) the terminology for each level (e.g. kingdoms/realms, regions, provinces).

The result is that we now have a plethora of regionalization schemes for the terrestrial world, as well as a smaller number for the marine realm (Briggs & Bowen, 2012; Costello *et al.*, 2017). However, modern global terrestrial biogeographical regionalization schemes, whether for plant or animal taxa, typically identify between six and eleven top-level "realms", within which groups of smaller islands such as those of Macaronesia fail to register as distinctive enough to qualify as a top-level realm (Nelson, 1978; Cox, 2001; Kreft & Jetz, 2010; Holt *et al.*, 2013; Rueda, Rodríguez & Hawkins, 2013; Whittaker *et al.*, 2013). In assessing whether Macaronesia holds merit as a biogeographical unit, we can therefore set aside the notion that it could be considered a realm. Hence, the question is one of whether

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it qualifies as a secondary- or tertiary-level group wherein (*i*) the internally shared floristic components among the archipelagos are sufficient and (*ii*) the relative distinctiveness of their biota from mainland source pools is strong enough to justify the claim that these archipelagos constitute a meaningful entity. For instance, one definition (Rivas-Martínez, 1987, p. 13) of a biogeographical [actually phytogeographical] region is: "an extended territory possessing a singular flora with endemic species, genera or families". It is well established that regionalizations based on data for one major taxonomic group can differ from those based on other groups, especially, if comparing phytogeographical and zoogeographical regionalizations. For instance, South Africa's Cape Province has been considered by many authors to constitute a top-level floristic "kingdom" (Capensis), independent of the Palaeotropical (or Ethiopian) kingdom (Takhtajan, 1986), but no one considers it as a top-level faunistic division.

Over time, the basis for biogeographical regionalization schemes has improved as our knowledge of species distributions has expanded and as numerical methods have been developed for more objective decision making on where to draw the boundaries between groups. These developments have included algorithms that capture the phylogenetic relatedness of shared and unique elements of the biotas (e.g. Holt *et al.*, 2013). Recent studies include phylogenetic information in quantitative biogeographical regionalization (Daru, Karunarathne & Schliep, 2020; Carta, Peruzzi & Ramírez-Barahona, 2022; Liu *et al.*, 2023) based on species distribution data and phylogenetic trees/phylogenetic similarity indices (phylogenetic beta diversity). Herein, however, we make reference to phylogenetic information (shared clades between archipelagos) in reevaluating the concept of Macaronesia, but applying a qualitative approach. This is because, unfortunately, complete phylogenetic trees and species distribution data for all archipelagos and the adjacent continental regions are not yet available at fine spatial resolution.

III. ORIGINS OF THE TERM MACARONESIA WITHIN PIONEERING PHYTOGEOGRAPHICAL STUDIES

The British historian William Stearn [1911–2001] attributed the coining of the Macaronesian phytogeographical concept to the British botanist, geologist and philanthropist Philip Barker Webb [1793–1854] (Fig. 2) around 1850, 4 years before his death (Stearn, 1973). Webb was a polyglot, who would have been familiar with the classic texts, Greek mythology and the history of the *Fortunatae Insulae*.

Actually, some years earlier, in 1832, the French sailor, explorer and botanist Jules Dumont D'Urville [1790–1842] had coined the terms Micronesia, Melanesia and Polynesia, each embracing specific island regions within the Pacific Ocean. This pioneering biogeographical subdivision of insular regions undoubtedly inspired Webb. Dumont D'Urville and Webb met in Paris in 1833, introduced by their mutual colleague, Sabin Berthelot (see below), and they became "enduring friends" (Duyker, 2014, p. 310).

Fig. 2. Portrait of the botanist and philanthropist Philip Barker Webb. Unknown author. Source: https://commons.wikimedia.org/wiki/File:Philip_Barker_Webb_1793-1854.jpg.

In an attempt to scrutinize exactly when and in which text the phytogeographical use of the term Macaronesia first appeared, we studied classic 19th century texts dealing with the Atlantic islands and their biota. The idea that these archipelagos shared some biotic affinities was already present in the works of the German geographer Alexander von Humboldt [1769–1859] and the German geologist Leopold von Buch [1774–1853]. Both visited the Canaries, but they never used the word "Macaronesia" when writing about these islands (von Humboldt & Bonpland, 1816; von Buch, 1825). The term Macaronesia is also absent from the *magnus opus* of Philip Barker Webb and the French naturalist and ethnologist Sabin Berthelot [1794–1880] *Histoire naturelle des Îles Canaries*, published between 1836 and 1850 (Webb & Berthelot, 1836–1850), where the authors had myriad opportunities for using it (Fernández-Palacios & Otto, 2020). Nevertheless, in 1840, Sabin Berthelot had indicated in the introduction to his *Étude de géographie botanique des îles Canaries* that the Canarian archipelago deserved the title of botanical region ("*l'archipel des Canaries mérite bien le titre de Région botanique*") (Berthelot, 1840, p. 4). This followed the

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first proposal by the Swiss botanist Augustin-Pyramus de Candolle [1778–1841] in his *Essai élémentaire de géographie botanique* to consider the Canaries as one of 20 botanical regions that he defined worldwide (de Candolle, 1820), although as noted above this was an incomplete list.

Recently, Mesquita, Menezes de Sequeira & Castel-Branco (2021) drew attention to the arrival of Richard Thomas Lowe [1802–1874] in Madeira in 1826, noting that his 1827 "Letter as Travelling Bachelor" justified his interest and that of other naturalists in the territories which are now known as Macaronesia by quoting a passage from von Humboldt (1814, p. 273) that read: "Though I flatter myself with having thrown some light on objects, which have been so often discussed by other travellers, I think nevertheless, that the natural history of this archipelago [Canaries] still offers a vast field to inquiry. … Let us hope, that some among them [naturalists on scientific expeditions], influenced by a love of science, and capable of pursuing a plan of several years, will devote themselves to the examination of the archipelagos of the Azores, Madeira, the Canaries, Cape Verde Islands, and the north-west coast of Africa". Lowe subsequently became an important figure in documenting the floristic relationships within Macaronesia, both by establishing contacts with other naturalists interested in these archipelagos and by visiting the Canaries (1857–1862), Cabo Verde (1864–1866) and Morocco (1859–1861) himself (see Mesquita *et al.*, 2023 for further details).

Based on our bibliographical review, the first published use of Macaronesia appeared in the work *Niger Flora or An Enumeration of the Plants of Western Tropical Africa*, edited in 1849 by William Jackson Hooker [1785–1865; father of Joseph Dalton Hooker]. This work contains a chapter entitled *Spicilegia Gorgonea* [*Spicilegia* meaning a compilation of unpublished notes, and *Gorgonium* being the classic word designating the Cabo Verde archipelago] dedicated to the flora of Cabo Verde, authored by Webb (1849), where he attributes to himself the coining of the term (p. 100): "The region to which the genus *Sinapidendron* belongs *we* (our emphasis) have elsewhere called Macaronesian. The two *Sinapidendrons* of the Cape de Verd islands differ from the Madeira and Canarian species….". In this quotation, there are two points that deserve comment. First we note that Webb had apparently coined the term in an earlier text, either authored by himself (perhaps using a majestic or a modesty plural), or with the collaboration of (an)other colleague(s), unfortunately not cited. Second, it is possible that Webb's conception of Macaronesia included only the archipelagos explicitly cited, that is Madeira, the Canaries and Cabo Verde, but not the Azores, where the genus *Sinapidendron* (Brassicaceae) is not present (Fernández-Palacios & Otto, 2020). [Note: of the three *Sinapidendron* species, two are endemic to Cabo Verde: first published in P. B. Webb (1849, p. 100), *Sinapidendron vogelii* Webb (syn. *Diplotaxis vogelii*) and *Sinapidendron gracile* Webb (syn. *Diplotaxis gracilis*); and one is endemic to the Canary Islands: first published in Christ (1888, p. 89), *Sinapidendron bourgeaui* Webb ex Christ (syn. *Brassica bourgeaui*). Presently the genus *Sinapidendron* is accepted as endemic to Madeira only.]

Intriguingly, within a separate chapter of the same volume, entitled *Notes on Madeira plants*, written by W.J. Hooker and J.D. Hooker (Hooker & Hooker, 1849), the term was again used (p. 75) and attributed to Webb: "The Canaries and Madeira, from their central position and various other causes, are the centre of this Botanical region, called by Mr. Webb the 'Macaronesian,' and exhibit more peculiarity than the Cape de Verds, (as far as they are at present known), or the Azores." It is interesting that these authors used the word *centre*, implying that the original formulation of Macaronesia by Webb may indeed have included the Azores besides Cabo Verde.

After the first mention of Macaronesia in *Spicilegia Gorgonea*, the term seems to disappear until being resurrected more than two decades later, in 1872, by the German geobotanist August Grisebach [1814–1879] in his book *Die Vegetation der Erde nach ihrer klimatischen Anordnung*. Grisebach (1872) used the term in the chapter dedicated to the oceanic islands, specifying that it was coined by Webb. Some years later, J.D. Hooker [1817-1911] again used the term in an 1878 book co-authored with the Irish botanist John Ball [1818–1889] entitled *Journal of a Tour in Marocco and the Great Atlas*, in an appendix written by him with the title: *On the Canarian Flora as compared with the Maroccan* (original spelling retained) (Hooker & Ball, 1878). Interestingly, Hooker vindicated the inclusion of the Canaries, Azores, Madeira (with Selvagens) and Cabo Verde islands within the region, while commenting in a footnote that the term was coined by Webb for referring exclusively to the Canarian flora (which is not true, at least of the 1849 text).

In 1879, the first reference to "Makaronesia" by the German plant botanist and phytogeographer, Adolf Engler [1844–1930], appears in his work *Versuch einer Entwicklungsgeschichte der extratropischen Florengebiete der Nördlichen Hemisphäre*. Here, he contends that Webb meant exclusively the Canaries (which seems to be wrong), and further suggests that Macaronesia should encompass the archipelagos of the Azores, Madeira and the Canaries, but not Cabo Verde (Engler, 1879). Later (Engler, 1914), he used the term including the four archipelagos, except in his 1910 book (Engler, 1910), where the Azores was excluded simply because it cannot be ascribed to Africa, which was the focus of the book.

The first appearance in the Spanish literature corresponds to a publication in 1880 by the military doctor and botanist Ramón Masferrer [1850–1884]. Masferrer lived for some years in Tenerife, where he studied the Canarian flora and vegetation. In 1880, he presented a query in the yearly session of the Spanish Society of Natural History about Webb's concept of Macaronesia, which Masferrer restricted to the Azores, Madeira and the Canaries. That same year, he used the term Macaronesia with this meaning in his work "*Recuerdos botánicos de Tenerife, o sea, datos para el estudio de la flora canaria*" (Masferrer, 1880–1882), and 2 years later, in "*Los laureles de las Islas Canarias*" (Masferrer, 1882), where again he attributed it to Webb. It can be concluded that, although the biogeographical meaning of the term is unanimously attributed to Philip Barker Webb, who certainly used it in 1849, there

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are still reasonable doubts about the archipelagos that were considered to be involved and the text where it appeared for the first time (Fernández-Palacios & Otto, 2020).

IV. ABOUT THE INDEPENDENCE OF THE MACARONESIAN PHYTOGEOGRAPHICAL REGION FROM THE MEDITERRANEAN

Several authors have debated whether Macaronesia holds sufficient distinctiveness to be considered an independent phytogeographical region. Those rejecting the validity of Macaronesia as an independent region include Meusel (1962, 1965), Lobin (1982), Beyhl *et al.* (1990), Lüpnitz (1995*a*), Rivas-Martínez (2009), and Rivas-Martínez *et al.* (2014, 2017), among others.

In the middle of the last century, Meusel (1962, 1965) was one of the first authors to question the validity of Macaronesia as an independent region, and suggested its fusion with the Mediterranean region, due to the strong links between their floras. He considered the Macaronesian woody flora to be a relictual by-product of millions of years of species sampling from the continent, producing a derived Mediterranean herbaceous flora, well adapted to the thermic and hydric stress of the Mediterranean climate. Some decades later, Lobin (1982) discarded the use of Macaronesia for phytogeographical purposes as anything other than a convenient geographical grouping. He considered the three northernmost archipelagos as a part of the Mediterranean region in the Holarctic Kingdom [i.e. realm], with (*i*) the Azores as a province of the Submediterranean subregion, and (*ii*) the Canaries, Madeira and the African enclave as a subregion on its own. The Cabo Verde islands he included as a province of the West Saharo-Sindian region of the Palaeotropic Kingdom.

Beyhl *et al.* (1990), when analysing the biogeographical location of Cabo Verde, concluded that both Macaronesian and Saharo-Sindian floristic components coexist there. The former prevails in the mountains of the highest islands, to which they would have retreated in response to the aridity linked to the end of the African Humid Period during the mid-Holocene (Berke *et al.*, 2012). According to Beyhl *et al.* (1990) such an event would have facilitated the arrival of the Saharo-Sindian flora that occupied the coasts of the highest islands and the whole area of the lower ones. Later, Beyhl, Mies & Ohm (1995) considered the laurel forest and the coastal succulent scrub as the floristic components connecting Macaronesia. However, they discard this biogeographical denomination for the four archipelagos on the grounds that these floristic components have different origins. Lüpnitz (1995*a*) went further, splitting the Macaronesian core: he ascribed the Azores to the Atlantic region and Madeira to the Mediterranean region (both within the Holarctic Kingdom), whereas the Canaries and Cabo Verde were joined together in the Saharan-Sindian region of the Palaeotropical Kingdom.

Although Rivas-Martínez (1987) initially supported the Macaronesian region, he later considered that Cabo Verde was only marginal to the grouping. Thus, in his synthesis of Macaronesia (Rivas-Martínez, 2009), he biogeographically dismantled Macaronesia, assigning the Canaries and Madeira to a subregion of the Mediterranean region, and placing the Azores in the Eurosiberian region of the same kingdom (Holarctic) and Cabo Verde in the Sahelian-Sudanian region of the Palaeotropic (also called Ethiopic) Kingdom. A distinctive feature of Rivas-Martínez's (2009) analysis is that he included macroecological criteria alongside the analysis of the chorological arrangement of shared taxa. Namely, he considered (macro-)bioclimatic variables and the distribution of major vegetation types, involving Temperate, Mediterranean and Tropical macrobioclimates. His underlying reasoning was that macrobioclimate is, for the most part, what defines the Earth's biomes, in correspondence with their distinctive vegetation responses. Vegetation at the biome level is strongly particular whether in physiognomy, characteristic taxa, trait syndromes and/or phylogeography (Mucina, 2019; Loidi, Navarro-Sánchez & Vynokurov, 2022). Under Rivas-Martínez's (2009) reasoning, the differences at the biome level found among archipelagos did not provide biogeographical support to the putative Macaronesian region, which should consequently be split among the corresponding continental regions. Accordingly, as the Azores share a temperate macrobioclimate with European continental territories, they should be assigned to the Eurosiberian region. Likewise, he argued that Madeira and the Canaries are predominantly Mediterranean both in macrobioclimate and floristic affinities; and Cabo Verde has a Tropical macrobioclimate and was therefore included in the Palaeotropic Kingdom.

Nevertheless, other plant biogeographers, such as Engler (1879, 1910, 1914), Dansereau (1961), Sunding (1973), Takhtajan (1986), Bolòs (1996) or Santos-Guerra (1977, 1999) defended the existence of significant floristic relationships and commonalities among the different archipelagos as vindicating the Macaronesian phytogeographical region *per se*. In particular, Engler (1879, 1910) was the first phytogeographer to emphasize the two differential characteristics of the Macaronesian archipelagos, as constituting: (*i*) a speciation centre of an ancient Mediterranean flora, and (*ii*) a refugium for relict Tethyan–Tertiary European flora.

Sunding (1973) also argued that while the inclusion of Cabo Verde in Macaronesia would incorporate several tropical species otherwise absent from the rest of the region, the clear connections of the Cabo Verde endemic flora with the other archipelagos supports such a decision. In a later work he retreated from this position, splitting Cabo Verde as a different subregion from the rest of Macaronesia (Sunding, 1979). In his comprehensive classification of floristic regions of the World, Takhtajan (1986) recognized a formal floristic entity defined as the Macaronesian region, including four provinces corresponding to each of the four main archipelagos. Takhtajan (1986) recognized the Mediterranean affinities of the Macaronesian archipelagos, placing Macaronesia within the Tethyan (Ancient Mediterranean) Subkingdom

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of the Holarctic Kingdom [contrasting with e.g. Cox (2001), who assigned Macaronesia to his African Kingdom]. Bolòs (1996) supported the independence of Macaronesia from the Mediterranean region based on a floristic analysis of both regions, which reveals the importance of the endemic floristic component in Macaronesia, but without commenting on the relationships of the extreme archipelagos to the rest of Macaronesia.

Santos-Guerra (1999) considered that the truly Macaronesian floristic component of the Cabo Verde flora, while clearly present in high-elevation areas of the highest islands, was very likely degraded in their lower parts and in the lowest islands. Thus, human impact most likely erased the Macaronesian affinity of Cabo Verde (see also Carine & Menezes de Sequeira, 2020). However, Duarte & Moreira (2002) assert that no historical documents or old plant collections suggest the presence of species in Cabo Verde that may have disappeared completely due to human activities. Morover, recent palaeoecological studies (Castilla Beltrán *et al.*, 2019, 2020, 2021*a*, 2023) show changes in vegetation after human arrival to these islands, but no sign of species disappearance.

In attempting to reconcile these disparate views, we suggest that it is critical to determine the methodological approach to regionalization that is required for the purpose in hand. In particular, should the approach adopted account for other criteria beyond traditional geographical, geological and, most relevantly, those based on the flora and vegetation types as analysed by current chorology and synchorology (i.e. chorology of vegetation types) (Capelo, 2020)? On the one hand, if comparison of the flora, vegetation and biomes is paramount, fragmentation models (such as that of Rivas-Martínez, 2009) are likely to prevail. On the other hand, if the analytical emphasis is on the sharing of infrageneric taxa, or clades, allowing documentation of shared lineages, despite distinct species being recognized in each archipelago (our approach), then a stronger argument can be constructed for Macaronesia as an entity. Examples of such shared taxa are *Erica* sect. *Chlorocodon* or *Euphorbia* sect. *Aphyllis* subsect. *Macaronesicae*. As in many classificatory exercises, the crux is then to establish if the internal similarities among archipelagos are unequivocally greater than the similarities to relatable continental regions.

A relevant perspective is introduced by the consideration of evolutionary criteria for interpreting the makeup of vegetation linking phytogeography to the assembly of plant communities after dispersal and diversification in the islands (e.g. Webb, 2000). Despite exhibiting great taxonomical affinities, many ecologically key species diverge by geographic speciation, that is inter-island dispersal followed by geographical isolation (Sunding, 1979; Kim *et al.*, 2008). Subsequently, plant communities in distinct archipelagos assemble through environmental filtering of these species in analogous environments. We should presuppose that, for the most part, niches among allopatric species (vicariant species sharing a common ancestor) were preserved. As a result, the communities of distinct archipelagos, although composed of distinct taxa, came to be strikingly similar physiognomically and phylogenetically. Although dispersal among islands should not be overlooked, geographic speciation should have been important in providing a local species pool for the community assemblage. Moreover, such plant communities are accounted for specifically by both syntaxonomy (classification of vegetation types) and biogeography.

An attempt to express an evolutionary perspective on island vegetation classification was that of Capelo (2020), where a method that accounted for phylogenetic similarity among species co-occurring in plots (*relevés*) was proposed. The resulting model yielded classes of woody vegetation spanning several archipelagos, named "coenoclasses" (*sensu* Deil, 1989), which are characterized by clades of allopatric species. Relevant results are that a single laurel forest coenoclass for the Azores–Madeira–Canaries group and a *Euphorbia–Echium* succulent scrub coenoclass spanning Madeira–Canaries–Cabo Verde appear. The coenoclasses are shared in a polythetic pattern and, although no coenoclass is present in the Azores and Cabo Verde, their vegetation still seems to express the palaeoclimatic and palaeobiogeographical unity of the three archipelagos involved in each vegetation unit. In short, if we consider infrageneric taxa or clades, and the vegetation units characterized by them, Macaronesia emerges again as a coherent plant geographical and evolutionary region.

V. ABOUT THE BIOGEOGRAPHICAL DISCREPANCIES ACCORDING TO DIFFERENT BIOTIC ASPECTS

According to Lobin (1982), the first approach towards considering Macaronesia as a floristic province (albeit without the label Macaronesia) was the work of Joaquim Frederik Schouw (1822), where the Azores, Madeira (albeit tentatively), Canaries and the mainland African Macaronesian enclave were together designated as the Province Sempervivorum within the Mediterranean Region (Lobin, 1982). For Schouw [1789–1852], this province was characterized by the genera *Aeonium* (Crassulaceae), the woody succulent *Euphorbia* (Euphorbiaceae) and *Kleinia* (Asteraceae).

In general, for geobotanists there is a consensus for the validity of a Macaronesian core or "central Macaronesia", constituted by Madeira, Selvagens and Canaries (Rivas-Martínez, 2009; del Arco & Rodríguez-Delgado, 2018). Although the geographically more extreme archipelagos (the Azores and Cabo Verde) share some characteristics with the Macaronesian core, the affinity between the two archipelagos is almost non-existent. Specifically, the Azores has Atlantic and Eurosiberian affinities, whereas Cabo Verde shows Sahelian and Tropical African affinities (see Section IV). The Azores also lack the xerophilous vegetation belts, which are common in the Canaries and Cabo Verde. The Azores are distinctive also in possessing montane rain forests, dominated by *Juniperus brevifolia* and *Ilex azorica*, which are unique to the Azores.

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However, laurel forests present clear affinities between the Azores, Madeira and Canaries, in spite of differences in the number of Lauraceae species on each archipelago (Mesquita *et al.*, 2007; Del Arco *et al.*, 2010; Elias *et al.*, 2016; Fernández-Palacios *et al.*, 2017).

With respect to the cryptogamic flora (restricted here to bryophytes, ferns and allies), Vanderpoorten *et al.* (2007) concluded that, based on floristic analyses, Cabo Verde belongs within the Tropical African cluster and is clearly detached from the rest of the Macaronesian archipelagos. The three northern archipelagos maintain their cohesion for liverworts and ferns, but not for mosses. This study showed that mosses group the Azores and Madeira, and include the Canaries in the North African cluster (Vanderpoorten *et al.*, 2007).

In his seminal vertebrate regionalization scheme, Alfred Russel Wallace placed all Macaronesian islands into the Palaearctic (Wallace, 1880), but since then treatments have varied. One of the first Macaronesian zoogeographers, Thomas Vernon Wollaston [1822–1878], explored the Madeiran and Canarian beetle fauna, and concluded that they form a solid zoogeographical unit (Wollaston, 1865), to which he incorporated Cabo Verde two years later (Wollaston, 1867) after realizing the close similarity of the beetle fauna in the three archipelagos. Nevertheless, more than a century later, in his monograph about the Canarian Carabidae beetles, Machado (1992) concluded that, although a Macaronesian humid component (related to the laurel forest) and a Macaronesian dry component (related to the *Euphorbia* shrubland) could be detected across the Atlantic archipelagos, the concept of a Macaronesian biogeographical region for carabids had no sense beyond its strict geographical value, and that Macaronesia should be split into Palaearctic (Azores, Madeira and Canaries) and Ethiopic/Palaeotropical (Cabo Verde) components, essentially extending into the ocean the sub-division of Africa through the Saharan region shown in many zoogeographical regionalization schemes based on vertebrate taxa (e.g. Holt *et al.*, 2013; Rueda *et al.*, 2013). The same conclusion was reached by Wunderlich (1991) when analysing the spider fauna of the Macaronesian islands. He asserted that the arachnids of Cabo Verde have a significant Ethiopian component, which contrasted with the clear Mediterranean and Palaearctic affinity of the spiders native to the rest of the archipelagos. Finally, for Pedro Oromí (personal communication) Cabo Verde only shares with the rest of the Macaronesian archipelagos some insects associated with coastal halophytic habitats, so that we cannot discount that they are also present on African coasts. Conversely, the Azorean connection with Madeira and the Canaries is closer, but largely due to their belonging to the Western Palearctic rather than to strict Macaronesian affinities, which are limited to few clades (e.g. *Calathus*, *Laparocerus*, *Tarphius*, etc.).

Before concluding about terrestrial zoogeography, we have to note that concerning native vertebrates, and leaving aside seabirds, bats (usually not used in biogeographical analyses due to their vagility) and amphibia (absent from Macaronesia), the relations are limited to some reptile (Mateo *et al.*, 2022) and bird (García-del-Rey, 2011) genera. The only archipelago that is known to have possessed native terrestrial mammals prior to human contact is the Canaries, which featured one extant (*Crocidura canariensis*) and three extinct (*Canariomys bravoi*, *C. tamarani* and *Malpaisomys insularis*) species (Rando *et al.*, 2011). Native reptiles are lacking from the Azores, but on the other archipelagos, several lineages have radiated (Canarian *Gallotia* lizards and *Chalcides* skinks, Caboverdean *Chioninia* skinks and *Hemidactylus* geckos), without colonizing other archipelagos. Nevertheless, some interesting Macaronesian connections linking the Selvagens with Madeira and the Canaries, and this last group with Cabo Verde, do exist. The native Selvagens lizard *Teira dugesii* is shared with Madeira whereas its native gecko, *Tarentola boettgeri*, is shared with the Canaries, both being Macaronesian endemics. Furthermore, in the Canaries *Tarentola* is a polyphyletic genus, as there are two additional lineages besides the one shared with the Selvagens. One of them, represented by *T. delalandii*–*T. gomerensis*, is ancestor to the 13 endemic Caboverdian *Tarentola* geckos, which derived from a single colonization event around 6 million years ago (Ma) (Mateo *et al.*, 2022). Finally, the relationships between the giant extinct Canarian tortoises (*Centrochelys burchardi* and *C. vulcanica*) and the Caboverdean *C. atlantica*, are uncertain. Unlike the other extinct reptiles mentioned, the Canarian and Caboverdean tortoises became extinct long before human colonization.

Few landbirds show clear cross-Macaronesian affinities, and none involving Cabo Verde. Among those that are shared between archipelagos, the Canarian bird, *Serinus canaria*, was at one point shared by the Canaries and Madeira, from which it later (*ca.* 0.32 Ma) colonized the Azores. Nevertheless, there is still high uncertainty about the colonization routes (Dietzen *et al.*, 2006; Illera, 2024). Another well-known example is the Berthelot pipit, *Anthus berthelotii*, shared by the three central Macaronesia archipelagos, which colonized first the Canaries, from which it later jumped to Madeira and the Selvagens (Illera, Emerson & Richardson, 2007; Martin *et al.*, 2023). A different colonization route was followed by the common chaffinch *Fringilla coelebs*, which first colonized the Azores <1 Ma, from Iberia, from where it colonized Madeira and then the Canaries, forming an allopatric superspecies (Marshall & Baker, 1999; Recuerda *et al.*, 2021). Finally, *Columba bollii* and *C. trocaz*, respectively the laurel forest pigeons of the Canaries and Madeira, are sister taxa, but colonization pathways are not yet clear: mainland to Canaries and later to Madeira, the other way round, or two independent colonizations (Dourado *et al.*, 2014; Valente *et al.*, 2017).

Other landbird taxa present in Macaronesia (*Regulus regulus*, *Sylvia atricapilla*, *Erithacus* spp.) have independently colonized the different archipelagos from the mainland, thus demonstrating a strong source-region effect rather than indicating inter-archipelago exchange as per the meta-archipelago concept (Whittaker *et al.*, 2018). Finally, consideration of other shared extant (*Motacilla cinerea*, *Turdus merula*) or extinct (*Chloris*, *Coturnix*, *Rallus*) taxa are still awaiting in-depth phylogenetic studies (J.C. Illera, personal communication).

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In any case, these between-archipelago affinities involve a very tiny fraction of the Macaronesian native vertebrates, so that it seems evident that the Macaronesian region does not hold in terms of terrestrial zoogeography.

Concerning the marine biota, Spalding *et al.* (2007) reviewed the Earth's marine ecoregions considering simultaneously the flora and fauna littoral biota (up to 200 m depth). Based on these analyses they split Macaronesia into (*i*) the Azores, Madeira and Canaries, all placed in an ecoregion included in the Lusitanian province of the Temperate North Atlantic realm and (*ii*) Cabo Verde, which is placed into an ecoregion of the West Africa Transition Province within the Tropical Atlantic realm. Recently, a marine biogeographical synthesis (Costello *et al.*, 2017), based on the analysis of the distribution areas of 65,000 marine animal and plant species, again split Macaronesia including the Azores and Madeira in their offshore and NW Atlantic realm, whereas the Canaries and Cabo Verde were included in their offshore South Atlantic realm.

Finally, Freitas *et al.* (2019) carried out a local study with better data resolution using different benthic animal and algal taxa. They suggested that there exists a Macaronesian core formed by Madeira, Selvagens and Canaries (which they called "Webbnesia" in deference to P.B. Webb), and they split off both Cabo Verde (due to its very high endemicity, a signal of the persistent isolation of its marine biota) and the Azores.

VI. ABOUT THE MACARONESIAN LIMITS (CONTINENTAL ENCLAVES)

The question of the geographical boundaries of Macaronesia is not just a matter of whether all of the archipelagos belong within it, but also of whether or not to recognize so-called Macaronesian continental enclaves. Two have been posited in the past. The first is the south-west Iberian coast (Serra da Arrábida and Ponta de Sagres) (Pinto da Silva & Teles, 1981). The second is an area of the Northwestern African coast extending between southern Morocco and northern Mauritania and, depending on the authors, from Cape Guir to Tarfaya (Peltier, 1973), from Agadir to Nouadhibou (Sunding, 1979), from Cape Guir to Cabo Blanco (Santos Guerra, 1999), or from Essaouira to Dakhla (Wildpret & Martín Osorio, 2006). Beyhl *et al.* (1995) concluded that, as the continental enclave is actually larger than the sum of the archipelagic areas, it should have its own entity and, thus, not be subordinated to the Macaronesian archipelagos. The idea behind the existence of the enclave is that the flora of these parts of Western Europe and North Africa have more affinities to the Macaronesian archipelagos than to the other mainland taxa outside the enclave. According to Evers (1964), this pattern is so clear for the fauna that he postulated the existence of former land bridge connections of the eastern Canaries to the African mainland, something that we now know never happened (Carracedo & Troll, 2016).

But this is tricky. If we compare entire native floras of enclaves, mainland and archipelagos, not focusing only on some particular shrub or tree species, and consider that the floras of NW Africa show a considerable proportion of annual species, many of them shared with the Mediterranean and Saharan region, and that Macaronesia has relatively few native annuals, whose native status is uncertain, this postulated affinity is not so clear. Indeed, Takhtajan (1986) recognized the South Morrocan province as one of the nine provinces he identified in the Mediterranean region, whereas for the Macaronesian region each archipelago (with the logical exception of the Selvagens) was recognized as an independent province. Actually, a precise phytogeographical comparison between southwestern Morocco (the "Argan area" western part of the Anti-Atlas mountains) and the neighbouring Canaries carried out by Médail & Quézel (1999) suggests that, in spite of some similarities regarding climate and flora (i.e. presence of succulent species and endemics shared by the two areas) in the lower zones, the Moroccan enclave belongs to the Mediterranean sub-region.

VII. ABOUT THE VALIDITY OF THE PHYTOGEOGRAPHICAL REGION LEVEL

The arguments of authors questioning the validity of Macaronesia as a phytogeographical entity (see Section IV) rest mainly, if not exclusively, in the biogeographical affinities deriving from the latitudinal location of the archipelagos, and thus, conditioned by current climates and bioclimates affecting them. Their isolation and oceanic character notwithstanding, this procedure obviously emphasizes the affinities of the archipelagos to the continental coastal fringes located at the same latitude. Yet, biogeography, as the science studying the geography of life, that is the geographical distribution of biodiversity and its causes, stems from two pillars: Historical and Ecological Biogeography (Nelson, 1978). Ecological Biogeography is centred in understanding the current causes of species distributions (e.g. the ecological requirements of the species, the species relationships or the community assemblages). By contrast, Historical Biogeography pays attention to past events, such as continental drift, island ontogeny, volcanic activity, Pleistocene glaciations, megalandslides, etc., which underlie processes such as dispersal, vicariance, extirpations, extinctions, etc. These processes shape current species distributions, for instance, explaining why a species is absent from a location where its environmental requirements could be met or where it was present in the past. Analyses that fail to consider simultaneously both pillars will be skewed, or at least limited in scope, from the very beginning. The Macaronesian region has comprised islands continuously over many tens of millions of years, and it cannot be neglected that its origin as a biogeographical region holds a signal of evolutionary and biogeographical dynamics extending through the Neogene, a period where not only was the climate of this part of the Earth very different from the

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present, but over which the relative connectivity of the region to potential source areas has changed greatly (Fernández-Palacios *et al.*, 2011).

Although the presently emerged islands are not very old, with the oldest being Selvagem Grande (*ca.* 26 Ma) (Geldmacher *et al.*, 2001; Mata *et al.*, 2013), and Fuerteventura (*ca.* 24 Ma) (Hoernle & Carracedo, 2009), Macaronesia has existed since the onset of the Paleogene (64 Ma) and presumably, for much longer, as the currently drowned archipelagos of Great Meteor (30–50 Ma) and Saharan seamounts (140 Ma), support these estimations. Regardless of their time of emergence, these archipelagos were from their very beginning gathering the more dispersive fraction of the continental floras, more probably from Africa and Europe than from North and South America. Furthermore, these colonizing species were assembled in unique combinations of terrestrial communities, which would produce endemic species given sufficient time in isolation and an absence of gene flow with the ancestral populations. Within the timespan of the currently oldest islands, it is very likely that Macaronesia has sampled preferentially from the closest mainland in Africa and Europe the three main floristic components that generate its present identity: (*i*) the Palaeotropical-Tethyan Geoflora; (*ii*) the African Rand flora; and (*iii*) the Mediterranean ancestors that, arriving to the islands over different timeframes and after persistent isolation, have diversified to produce the outstanding Macaronesian Neoendemic flora (Humphries, 1979; Gomes *et al.*, 1995; Carine *et al.*, 2010; Price *et al.*, 2018) (Fig. 3). These three floristic components constitute the essence of the Macaronesia phytogeographical region. In sum, the archipelagos support around 900 palaeo- and neoendemic vascular plant species (J.P. Price, J. Caujapé-Castells, C. García-Verdugo, R. Otto, M. Romeiras, M. Menezes de Sequeira & J.M. Fernández-Palacios, in preparation) and 46 endemic genera (25 endemic to the Canaries, five to Madeira, one to the Azores, one to Cabo Verde, and 14 others shared by more than one archipelago; del Arco & Rodríguez-Delgado, 2018) (Table 1). Furthermore, despite the absence of any plant species endemic to all the archipelagos, they do all share two lineages, namely the *Aeonium* alliance and *Tolpis* (see Table 4). At least 24 further lineages are shared among at least two archipelagos (Tables 2–4).

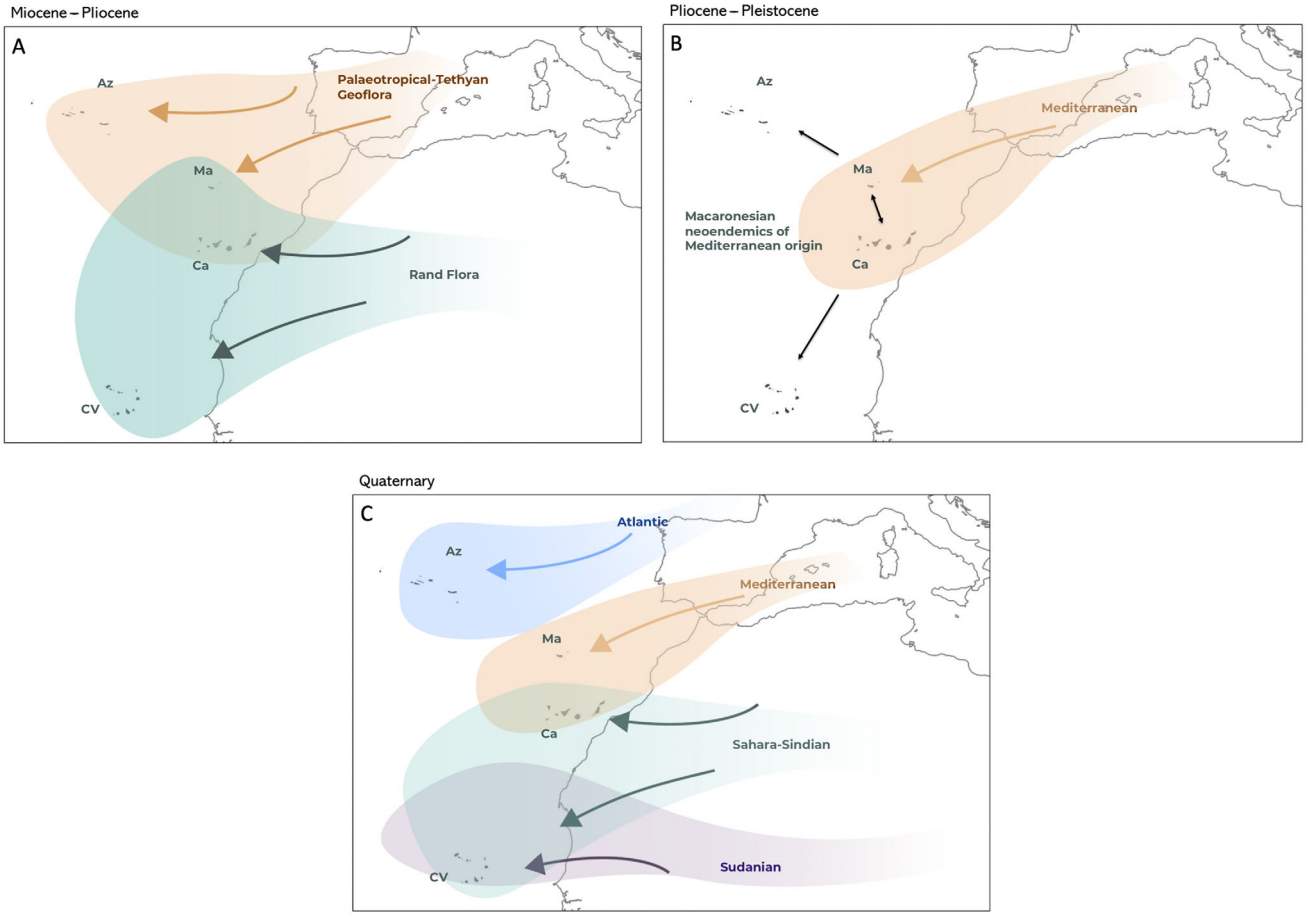

Fig. 3. Gradual incorporation of different continental floristic elements that have shaped the identity of Macaronesia. (A) The Palaeotropical-Tethyan Geoflora and the African Rand Flora in the Miocene–Pliocene. (B) The Macaronesian neoendemics of Mediterranean origin in the Pliocene–Pleistocene. (C) The Atlantic, the Mediterranean, the Saharo-Sindian and the Sudanian floristic elements in the Quaternary. Az, Azores; Ca, Canary Islands; CV, Cabo Verde; Ma, Madeira.

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Table 1. The distribution of the 46 Macaronesian endemic vascular plant genera (slightly modified from del Arco & Rodríguez-Delgado, 2018).

Genus	Azores	Madeira	Selvagens	Canaries	Cabo Verde
Aichryson	X	X		X	
Allagopappus				X	
Argyranthemum		X	X	X	
Atalanthus				X	
Azorina	X				
Babcockia				X	
Bencomia				X	
Bethencourtia				X	
Bystropogon				X	
Ceballosia				X	
Cedronella		X		X	
Chamaemeles		X			
Chrysoprenanthes				X	
Dicheranthus				X	
Dendriopoterium				X	
Gesnouinia				X	
Gonospermum				X	
Heberdenia		X		X	
Isoplexis		X		X	
Ixanthus				X	
Kunkeliella				X	
Lactucosonchus				X	
Marcetella		X		X	
Melanoselinum		X			
Monizia		X			
Monanthes			X	X	
Musschia		X			
Navaea				X	
Neochamaelea				X	
Normania		X		X	
Parolinia				X	
Pericallis	X	X		X	
Phyllis		X		X	
Picconia	X	X		X	
Pleiomeris				X	
Rutheopsis				X	
Schizogyne			X	X	
Semele		X		X	
Sinapidendron		X			
Spartocytisus				X	
Sventenia				X	
Tinguarra				X	
Todaroa				X	
Tornabenea					X
Vieraea				X	
Visnea		X		X	

Such data clearly support the identification of Macaronesia as a phytogeographical region.

During the Paleogene and Neogene, the most dispersive plant elements of the Tethyan Palaeotropical Geoflora (the forests occupying then Central and Southern Europe), colonized – very likely *via* endozoochory (Vargas, 2007) – the Macaronesian islands, resulting in an impoverished version of the original tropical forest that we call the Macaronesian laurisilva or laurel forest (Table 2) (Santos Guerra, 1990; Fernández-Palacios *et al.*, 2017). This forest, while persisting in the three northern Macaronesian archipelagos (the Azores, Madeira and the Canaries), completely vanished from the mainland due to the Pleistocene glaciations and constitutes a solid biogeographical link among these three archipelagos. Due to the climate refuge created by the trade winds (the "sea of clouds"), this very particular vegetation type has been able to withstand the summer aridity of the Mediterranean climate prevalent in the current interglacial in Madeira and the Canaries, with the laurel forest distribution on these archipelagos restricted to the

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Table 2. Palaeotropical-Tethyan Geoflora (laurisilva) lineages shared by the Azores with Madeira and/or the Canaries (Santos-Guerra, 1990; Fernández-Palacios *et al.*, 2017).

Lineage	Azores	Madeira	Canaries
Erica	*azorica*	*platycodon* ssp. *maderincola*	*platycodon* ssp. *platycodon*
Euphorbia	*stygiana/santamariae*	*mellifera*	*mellifera*
Frangula	*azorica*	*azorica* (extinct)	
Ilex	*perado ssp. azorica*	*perado* ssp. *perado*	*perado* ssp. *platyphylla/perado* ssp. *lopezlilloi*
Laurus	*azorica*	*novocanariensis*	*novocanariensis*
Morella	*faya*	*faya*	*faya*
Picconia	*azorica*	*excelsa*	*excelsa*
Prunus	*azorica*	*lusitanica* ssp. *hixa*	*lusitanica* ssp. *hixa*
Taxus	*baccata*	*baccata*	
Viburnum	*treleasei*		*rigidum*

elevational distribution of the sea of clouds, that is the windward slopes of the high islands, between 500 and 1500 m elevation (Fernández-Palacios *et al.*, 2017).

The canopy of this forest is formed by 20–30 tree species within genera belonging to tropical families (Clethraceae, Lauraceae, Myrsinaceae, Pentaphylacaceae, Pittosporaceae, etc.). Although some of these lineages are exclusive to one archipelago (such as *Clethra* and *Pittosporum* to Madeira or *Arbutus* and *Pleiomeris* to the Canaries), many are shared by Madeira and the Canaries (*Apollonias*, *Heberdenia*, *Ilex canariensis*, *Ocotea*, *Persea*, *Visnea*) or by the three archipelagos [*Ilex perado*, *Laurus*, *Morella* (Fig. 4B), *Picconia* (Fig. 4A), *Prunus*] (Table 2). These species are known as palaeoendemic trees because of their much wider past distribution, as shown by many fossils of the same or very similar species found in areas that were the margins of the Tethys Sea during the Palaeogene and Neogene (Bramwell, 1976; Sunding, 1979; but see Kondraskov *et al.*, 2015). With the exception of some allopatric taxa in specific genera, such as *Picconia* and *Prunus*, there was no, or very limited, diversification of these groups within Macaronesia. Besides the canopy trees, another important laurel forest element providing evidence for floristic relations among these three archipelagos are the understory ferns, with many species shared by the three archipelagos and the Iberian Peninsula (e.g. *Blechnum*, *Culcita*, *Davallia*, *Diplazium*, *Hymenophyllum*, *Polypodium*, *Polystichum*, *Vandenboschia*, and *Woodwardia*) (Fernández-Palacios *et al.*, 2017).

Recent palaeobotanical research offers new evidence of the relictual character of this vegetation type in Macaronesia. For instance, the revised floristic composition of the famous São Jorge fossils (Madeira) (Góis-Marques, Madeira & Menezes de Sequeira, 2018) resembles the current stink laurel (*Ocotea foetens*) forest, suggesting a warm and humid palaeoclimate and indicating that laurel forests were present in Macaronesia at least since the Gelasian (2.6–1.8 Ma), a time when the palaeotropical geofloral floristic component was almost extinct in Europe. The natural extinction of a Madeiran laurel forest dweller (*Eurya stigmosa*, Theaceae) was dated to 1.3 Ma, meaning that it was already relictual in Madeira, and pointing to a progressive empoverishment of the community (Góis-Marques *et al.*, 2019). Finally, *Erica* aff. *azorica* colonised Madeira before 1.3 Ma, from where it recolonized the European continent during the Quaternary glaciations, thus Macaronesia archipelagos acted as climatic refugia (Góis-Marques *et al.*, 2023).

Table 3. Macaronesian Rand Flora palaeoendemic lineages shared by two or three archipelagos (Pokorny *et al.*, 2015; Sanmartín *et al.*, 2016).

Lineage	Madeira	Canaries	Cabo Verde
Campylanthus		*salsoloides*	*glaber*
Dracaena	*draco*	*draco/tamaranae*	*caboverdeana*
Euphorbia	*piscatoria*	*aphylla*	*tuckeyana*
	anachoreta (Selvagens)	*atropurpurea*	
		berthelotii	
		bourgaeana	
		bravoana	
		lamarckii	
		regis-jubae	
Hypericum	*canariense*	*canariense*	
	grandifolium	*coadunatum/grandifolium/glandulosum*	
	glandulosum	*reflexum*	
Sideroxylon	*mirmulans*	*canariense*	*marginatum*

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Table 4. Macaronesian neoendemic lineages with presence in Azores and/or Cabo Verde. Several other shared candidate genera (such as *Asparagus*, *Erysimum*, *Forsskaolea*, *Kickxia*, *Lobularia*, *Paronychia*, *Phagnalon*, *Polycarpaea*, or *Pullicaria*) are not included because monophyly of these taxa has not been confirmed due to lack of phylogenetic studies.

Lineage	Azores	Madeira	Canaries	Cabo Verde	References
Aeonium alliance (59 spp.)	*Aichryson santamariensis*	*Ae. glandulosum* *Ae. glutinosum* *Aichryson villosum* *Aichryson dumosum* *Monanthes lowei* (Selvagens)	*Aeonium* (28 spp.) + *Aichryson* (10 spp.) + *Greenovia* (5 spp.) + *Monanthes* (9 spp.) = (52 spp.)	*Ae. gorgoneum*	Mort *et al.* (2002)
Artemisia (3 spp.)		*argentea*	*thuscula*	*gorgonum*	Tkach *et al.* (2007); Vitales *et al.* (2023)
Campylanthus (2 spp.)			*salsoloides*	*glaber*	Affenzeller *et al.* (2018)
Echium (30 spp.)		*nervosum* *candicans* *portosanctensis* (3 spp.)	*acanthocarpum* *aculeatum* *auberianum* *bethencourtii* *bonnetii* *brevirame* *callithyrsum* *decaisnei* *gentianoides* *giganteum* *handiense* *hierrense* *lancerottense* *leucophaeum* *onosmifolium* *perezii* *pininana* *simplex* *strictum* *sventenii* *triste* *virescens* *webbi* *wildpretii* (24 spp.)	*vulcanorum* *stenosiphon* *hypertropicum* (3 spp.)	Böhle *et al.* (1996); García Maroto *et al.* (2009)
Globularia (4 spp.)			*ascanii* *salicina* *sacrophylla*	*amygdalifolia*	Affenzeller *et al.* (2018)
Helianthemum sect. Helianthemum (16 spp.)			*aganae* *aguloi* *bramwelliorum* *broussonetii* *bystropogophyllum* *cirae* *gonzalezferreri*	*gorgoneum*	Albaladejo *et al.* (2021)

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Table 4. *(Cont.)*

Lineage	Azores	Madeira	Canaries	Cabo Verde	References
			inaguae *juliae* *linii* *teneriffae* *tholiforme* sp. nov. 1 sp. nov. 2 sp. nov. 3 (15 spp.)		
Lavandula (7 spp.)		*pinnata*	*bramwellii* *buchii* *canariensis* *minutolii* *pinnata* (5 spp.)	*coronopifolia* *rotundifolia*	Santos Rivilla *et al.* (2022)
Lotus sect. *Pedrosia* (31 spp.)	*azoricus* (1 sp.)	*argyrodes* *glaucus* *lancerottensis* *loweanus* *macranthus* *salvajensis* (6 spp.)	*arinagensis* *berthelotii* *callis-viridis* *campylocladus* *dumetorum* *emeroides* *eremiticus* *erythrohizus* *genistoides* *glaucus* *hillebrandii* *gomerythus* *holosericeus* *kunkelii* *lancerottensis* *leptophyllus* *maculatus* *mascaensis* *pyranthus* *sessilifolius* *spartioides* *tenellus* *sp. nov. 1* *sp. nov. 2* (24 spp.)		Jaén-Molina *et al.* (2021)

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Table 4. *(Cont.)*

Lineage	Azores	Madeira	Canaries	Cabo Verde	References
Limonium sect. *Jovibarba-Ctenostachys* (7 spp.)		*papillatum* (Selvagens) *pectinatum* var. *pectinatum* (Selvagens)	*papillatum* *pectinatum* var. *corculum* *pectinatum* var. *divaricatum* *pectinatum* var. *pectinatum pectinatum* var. *solandri*	*braunii* *brunneri* *jovi-barba* *lobinii sundingii*	Koutroumpa *et al.* (2021)
Nauplius (syn *Asteriscus*) (4 spp.)			*intermedius* *sericeum*	*daltonii* *smithii*	Francisco-Ortega *et al.* (2001)
Pericallis (16 spp.)	*malvifolia*	*aurita* *menezesii*	*appendiculata* *cruenta* *echinata* *lanata* *hadrosoma* *hansenii* *multiflora* *murrayi* *papyraceus* *steetzii* *tirmensis* *tussilaginis* *webbii* (13 spp.)		Jones *et al.* (2014)
Sonchus (34 spp.)		*fruticosus* *pinnatus* *ustulatus* *parathalassius*	18 *Sonchus* spp. + 11 spp. [*Atalanthus* (6 spp.), *Babcockia* (1 sp.), *Lactucosonchus* (2 spp.) *Chrysoprenanthes* (1 sp.), *Sventenia* (1 sp.)] = 29 spp.	*daltonii*	Kim *et al.* (1996)
Tolpis (16 spp.)	*azorica* *succulenta*	*macrorhiza* *succulenta*	*calderae* *coronopifiolia* *crassiuscula* *glabrescens* *laciniata* *lagopoda* *proustii* *santosi* *webbii* *sp. nov. 1* *sp. nov. 2* *sp. nov. 3* (12 spp.)	*farinulosa*	Mort *et al.* (2022)

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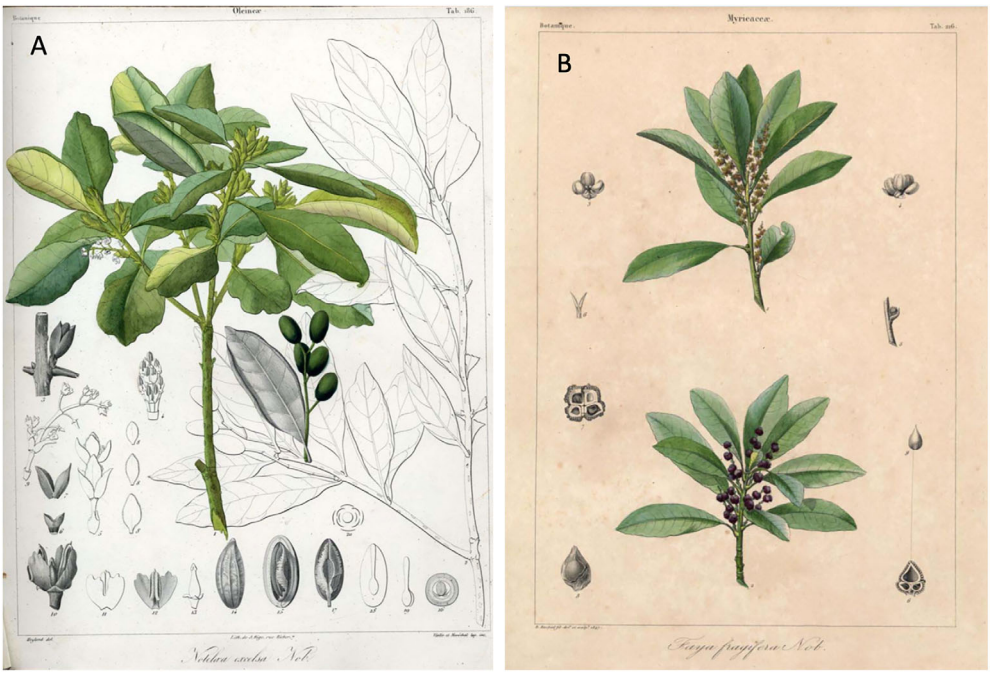

Fig. 4. Examples of Macaronesian flora representing the Palaeotropical-Tethyan Geoflora. (B) Plate of *Morella faya*. Source: Webb & Berthelot (1836–1850). (A) Plate of *Picconia excelsa*. Source: Webb & Berthelot (1836–1850).

When the Portuguese colonized Cabo Verde (*ca.* 1462 CE), there were no remains of such forest types, and there is no signal of such forests in the palaeoecological record (Castilla-Beltrán *et al.*, 2021*b*, 2023). We are not sure if this archipelago was too far south for frequent colonizations, or whether, if they happened, their signal was blurred by the aridification of the African Pliocene. Thus, the laurel forest constitutes a unifying floristic component of only the three northern archipelagos. Some authors have called these archipelagos Lauri-Macaronesia (Kunkel, 1993; Sánchez-Pinto, 2006) or Laurinesia (Fernández-Palacios *et al.*, 2024).

During the same period, or perhaps later, the three Macaronesian archipelagos located off the African coast (Madeira, Canaries and Cabo Verde) incorporated a distinct floristic component, called the African Rand Flora, a concept coined by the Swiss botanist Hermann Christ [1833–1933] (*Rand* means border in German), in order to highlight the peculiar current distribution of this vegetation type (Christ, 1910). Contrary to the laurel forest, the African Rand Flora is still extant, albeit very much fragmented, throughout the margins of Africa and the Arabian Peninsula, in places such as the coasts and lowlands of Maghreb, Horn of Africa, Yemen, Mozambique, South Africa and Namibia (Rivas-Goday & Esteve Chueca, 1964; Bramwell, 1985; Pokorny *et al.*, 2015; Sanmartín, Pokorny & Mairal, 2016). This Rand Flora is composed by a series of old, frequently monophyletic lineages that inhabit the thermophilous woodlands [*Dracaena* (Fig. 5A), *Hypericum*, *Sideroxylon*] or succulent scrub [e.g. *Camptoloma*, *Campylanthus*, *Euphorbia* sect. *Aphyllis* (Fig. 5B), *Kleinia*, *Justicia*, *Plocama*] of Madeira or the Canaries, and some of these (*Campylanthus*, *Dracaena*, *Euphorbia*, *Sideroxylon*) are also present in Cabo Verde (Table 3). At what point the Rand Flora floristic component began to colonize Macaronesia is still unknown. Anderson, Channing & Zamuner (2009) concluded, based on fossil evidence, that besides laurisilva and pine forest, thermophilous scrubland was already present on Gran Canaria before 3.9 Ma (Pliocene), implying an older arrival of the Rand Flora.

Following phylogenetic reconstructions (Durán *et al.*, 2020; Martín-Hernanz *et al.*, 2023), *Dracaena* has a stem age of about 12 Ma, but a crown age of only 2 Ma, so that it is an undetermined lineage with respect to the emergence of the Mediterranean-type climate (*ca.* 2.8 Ma). A similar lack of information with respect to colonization before or after the emergence of the Mediterranean-type climate, applies to other classical Rand Flora elements, such as *Gymnosporia* or *Hypericum* (Martín Hernanz *et al.*, 2023). By contrast, for *Sideroxylon* and *Chrysojasminum*, crown ages pre-date the onset of the Mediterranean climate, in accordance with predictions for Rand Flora taxa. However, probable extinctions both on the mainland (leading to an overestimated stem age) and the Canaries (underestimated crown age), the real colonization time of many such taxa could be anywhere between the current estimates of stem and crown ages (García-Verdugo, Caujapé-Castells & Sanmartín, 2019). Indeed, Pokorny *et al.* (2015) describe the Rand Flora as an example of biogeographical pseudocongruence, as the distinctive distribution patterns they share have arisen over a lengthy period, *via* different routes and mechanisms.

Palaeoecological research carried out recently in several Cabo Verdean islands (Castilla-Beltrán *et al.*, 2019, 2020,

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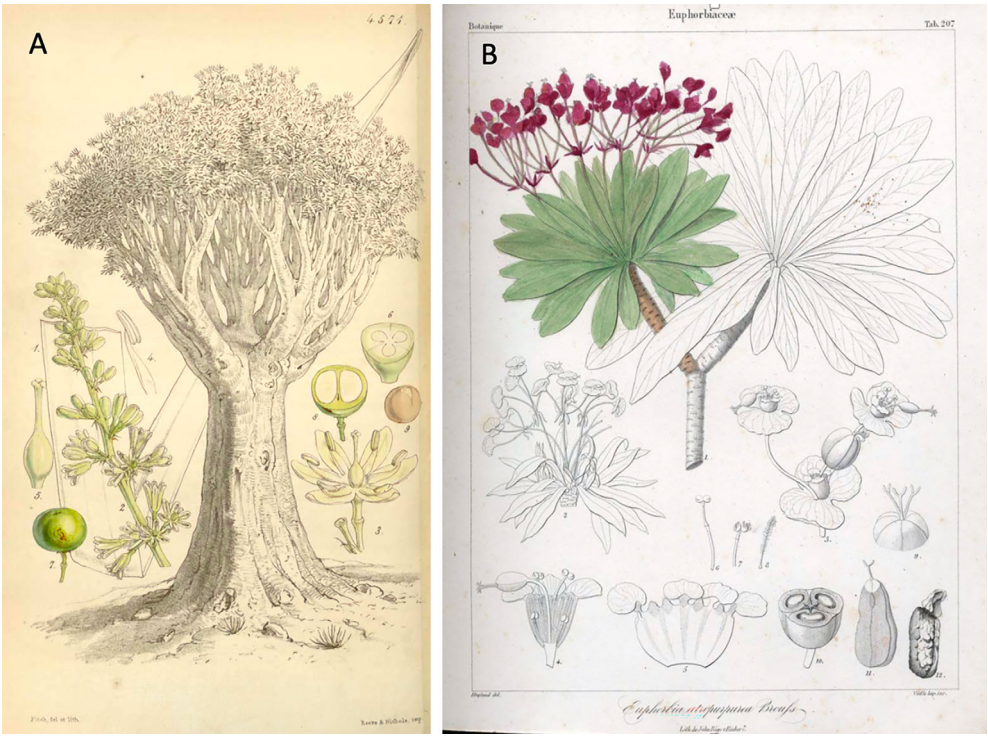

Fig. 5. Macaronesian endemics derived from the African Rand Flora. (A) Plate of *Dracaena draco*. Source: Hooker (1851). (B) Plate of *Euphorbia atropurpurea*. Source: Webb & Berthelot (1836–1850).

2021*a*, 2023) has confirmed the greater abundance of such Rand-Flora taxa before the Portuguese colonization of the islands. It is not known if elements of the Rand Flora were ever present in the Azores (maximum age of the oldest island <6 Ma), but this seems highly unlikely due to the isolation, latitude, geological youth, and wet climate of this archipelago. Notably, no traces of this vegetation type were found there from immediately before the Portuguese colonization of this archipelago (*ca.* 1420 CE; Connor *et al.*, 2012). Therefore, the Rand Flora should be considered a unifying floristic component exclusive to southern Macaronesia (i.e. Madeira, Canaries and Cabo Verde; Table 3), also designated Thermo-Macaronesia (Sánchez-Pinto, 2006) or Draconesia (Fernández-Palacios *et al.*, 2024).

With the exception of some lineages that arrived in the Miocene to Central Macaronesia (i.e. Canaries and Madeira), such as *Aeonium*, *Lavandula*, and *Ixanthus* in the early Miocene (18–16 Ma) or *Crambe*, *Echium*, *Lobularia*, *Ruta*, *Salvia* and *Sonchus* during the late Miocene (8–6 Ma), it is with the onset of the Pliocene (5–2.7 Ma) that a new floristic element of Mediterranean origin colonized these two archipelagos (Hooft van Huysduynen *et al.*, 2021; Martín-Hernanz *et al.*, 2023). Some representative genera are *Atractylis*, *Carlina*, *Convolvulus*, *Descurainia*, *Digitalis*, *Micromeria*, *Plantago* and *Sideritis*, which were followed especially after the onset of the Pleistocene (2.6 Ma–11.7 Ka) by *Argyranthemum*, *Artemisia* (Vitales *et al.*, 2023), *Asparagus* (with two different lineages), *Cheirolophus* (Vitales *et al.*, 2014), *Erysimum*, *Globularia*, *Gonospermum*, *Helianthemum* sect. *Helianthemum*, *Lotus*, *Ononis*, *Pericallis*, *Rubus*, *Silene*, etc. (Caujapé-Castells *et al.*, 2022; Martín-Hernanz *et al.*, 2023).

Many Mediterranean colonizers that gave rise to the neoendemic Macaronesian flora were herbaceous and constitute examples of insular secondary woodiness and concomitant radiation (Lens *et al.*, 2013; Zizka *et al.*, 2022), such as the *Aeonium* alliance (Fig. 6A), *Argyranthemum*, *Crambe*, *Cheirolophus*, *Echium*, *Limonium*, *Micromeria*, *Pericallis*, *Sideritis*, and the *Sonchus* alliance (Fig. 6B) among others, by which the Macaronesian flora is known worldwide. Although these lineages were at first restricted to Central Macaronesia, some expanded later to the more peripheral archipelagos. Colonizers of the Azores came mainly from Madeira [*Aeonium* alliance (Mort *et al.*, 2002), *Lotus* sect. *Pedrosia* (Jaén-Molina *et al.*, 2021), *Tolpis* (Mort *et al.*, 2022)] (Table 4), although *Pericallis* stems from the Canaries (Jones *et al.*, 2014), and colonizers of Cabo Verde came from the Canaries [*Aeonium* alliance (Mort *et al.*, 2002), *Echium* (Romeiras *et al.*, 2011), *Helianthemum* (Albaladejo *et al.*, 2021), *Lavandula* (Santos-Rivilla *et al.*, 2022), *Limonium* sect. *Jovibarba–Ctenostachys* (Koutroumpa *et al.*, 2021), *Nauplius* (Francisco-Ortega *et al.*, 2001), *Sonchus* alliance (Kim *et al.*, 1996), *Tolpis* (Mort *et al.*, 2022)] (Table 4). In the case of the Macaronesian *Tolpis* lineage, constituting 13 species with three others awaiting description, Mort *et al.* (2022) described a very interesting colonization route within Macaronesia. An Iberian colonist arrived to Madeira, from where the lineage jumped to the Azores, from there to the Canaries, and from the Canaries first to Africa and later to Cabo Verde. The situation for *Artemisia* is not yet resolved but it could have

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Fig. 6. Examples of Macaronesian neoendemics. (A) Plate of *Aeonium smithii*. Source: Sims (1818). (B) Plate of *Sonchus arboreus*. Source: Webb & Berthelot (1836–1850).

involved a colonization from the Canaries to Madeira (or *vice versa*) and to Cabo Verde, or independent colonizations from the mainland (Vitales *et al.*, 2023). This biogeographical colonization pattern has been called the "spring-board effect" (J. Price, J. Caujapé-Castells, C. García-Verdugo, R. Otto, M. Romeiras, M. Menezes de Sequeira & J.M. Fernández-Palacios, in preparation), and was a major driver of plant diversification in all Macaronesian archipelagos.

Besides herbaceous colonizers, several trees and shrubs of Mediterranean origin colonized the Canaries and Madeira (*Juniperus*, *Myrtus*, *Olea*, *Phoenix*, *Pistacia atlantica*, *P. lentiscus* (two lineages), *Phillyrea*), complementing the Rand Flora taxa already present in the midlands of these islands, and creating the complex vegetation mixture with different origins and colonization times that constitutes today's thermophilous woodlands (Castilla-Beltrán *et al.*, 2021*b*; Martín-Hernanz *et al.*, 2023; Fernández-Palacios *et al.*, 2024).

More recently, perhaps during the Late Pleistocene or even the Holocene, the last waves of natural colonization took place, much more related to the present climate and the availability of neighbouring, continental coastal and lowland populations, and thus, differentiated depending on the latitude of each receptor archipelago. For example, the Azores incorporated species of the Atlantic–Eurosiberian floristic component populating the Atlantic fringe of Europe, including Ericaceae such as *Calluna* or *Vaccinium*, besides many herbaceous species, but also species from NW Africa, such as *Ammi* which appears to have colonized these islands within this period (crown ages <1 Ma; Frankiewicz *et al.*, 2022) diversifying into three endemic species. In addition, a late Mediterranean wave mainly to Madeira and the Canaries also incorporated a non-endemic native component, including, for instance, *Bituminaria bituminosa* (García-Verdugo *et al.*, 2021), *Cistus monspeliensis* (Fernández-Mazuecos & Vargas, 2011) and *Erica arborea* (Desamoré *et al.*, 2011), among others.

Furthermore, a Saharo-Sindian floristic component characteristic of Saharan and Arabian deserts (Médail & Quézel, 2018) was incorporated recently into the flora of the Canaries and Cabo Verde, and to a lesser extent Madeira. Thus, the biogeographical affinities of the Atlantic–Sahara with Macaronesia are not negligible: 21% (121 spp.) of Atlantic–Saharan species are also found in the Canary Islands, and, of these, 15 species are Saharo-Macaronesian endemics (for instance, *Asteriscus schultzii*, *A. graveolens* subsp. *odorus*, *Limonium tuberculatum*, *Lotus arenarius*, *Ononis tournefortii* and *Pulicaria burchardii*) (Chatelain *et al.*, 2024). However, the majority of these non-endemic shared species are herbaceous (often annual) species which are quite widely distributed in Saharan Africa and in several ecoregions of Africa, and which therefore have a relatively low biogeographical value.

This last natural colonization wave brought to the archipelagos many species from the sub-desert steppe (*sensu* Lüpnitz, 1995*b*), which enriched the non-endemic native floristic contingent makeup of Macaronesia (e.g. *Artemisia reptans*, *Astydamia latifolia*, *Chenoleoides* (*Bassia*) *tomentosa*, *Gymnocarpos decander*, *Helianthemum canariense*, *Launaea*, *Lycium intricatum*, *Periploca*, *Salsola*, *Suaeda*, *Tamarix*, *Traganum moquinii*, *Zygophyllum*, etc.), and are well represented in the lower islands of both the Canaries (Lanzarote, Fuerteventura, Alegranza, La Graciosa) and, to a lesser extent, Cabo Verde (Sal, Boavista, Maio). Finally, Cabo Verde was colonized by the most vagile flora of the Sahel and tropical savannahs,

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including, besides many herbaceous species, woody taxa such as *Calotropis procera*, *Faidherbia albida* -syn. *Acacia caboverdeana*-, *Ficus sur*, *Ficus sycomorus*, *Tamarix senegalensis*, *Ziziphus mauritiana*, etc., that give this archipelago a distinctive Sahelian landscape (Neto *et al.*, 2020) (Fig. 3C).

VIII. CONCLUSIONS

(1) Despite the rejection of or scepticism towards Macaronesia as a biogeographical unit expressed in several studies, we consider that it holds some value in phytogeography. In particular, from the standpoint of vascular plant diversity, Macaronesia is robust enough to deserve the rank of independent floristic region within the Holarctic Realm, as for example, described in Takhtajan's (1986) regionalization.
(2) Based on the evidence assessed herein, and despite the singularity of the region's flora, including 46 endemic genera, we argue that the Macaronesian archipelagos share, to some extent, three different exclusive floristic components: the Palaeotropical-Tethyan endemic laurisilva lineages; the Macaronesian Rand Flora palaeoendemic lineages; and the Macaronesian neoendemic lineages. These floristic components originated in different time periods from diverse geographical sources, and are today nonexistent or extremely fragmented in their ancestral territories.
(3) Although the two archipelagos at the geographical extremes of the region, the Azores and Cabo Verde, barely share any of the main floristic components discussed herein, they are connected independently to the Central Macaronesian archipelagos (Madeira and the Canaries). Furthermore, Azores and Cabo Verde contribute substantially to the diversity of the Macaronesian neoendemic floristic component (J.P Price, J. Caujapé-Castells, C. García-Verdugo, R. Otto, M. Romeiras, M. Menezes de Sequeira & J.M. Fernández-Palacios, in preparation).
(4) The adscription of the African coastal enclave to the Macaronesian biogeographical region should be the subject of further studies, especially considering the importance of Macaronesian retrocolonization events (boomerangs) in this area. These include *Aeonium korneliuslemsii*, *Dracaena draco* ssp. *ajgal*, *Lotus assakensis* and *Sonchus bourgauei*, and some animals (e.g. in the genus *Laperocerus*), highlighting the importance of this region as a climatic refugium and dispersal centre.
(5) While we recognize that the concept of a Macaronesian biogeographical region does not have much application beyond the realm of vascular plant geobotany, we find that the geobotanical data demonstrate the prescience of Philip Barker Webb coining this term *ca.* 175 years ago.

IX. ACKNOWLEDGEMENTS

This review is dedicated to David Bramwell (24/11/1942–20/01/2022).

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(*Received 22 September 2023; revised 29 May 2024; accepted 4 June 2024; published online 18 June 2024*)

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