Chapter 1

The islands of Macaronesia

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Introduction: The oceanic islands ontogeny. Birth, growth and senescence

Ever since Alfred Russel Wallace (1881) real islands have been classified in three different categories: continental islands, continental fragments or microcontinents, and oceanic or volcanic islands (Whittaker & Fernández-Palacios, 2007). Oceanic islands, as the Macaronesian ones, share a volcanic origin and their more important biogeographical feature is their emersion devoted of life from the sea floor through the accumulation of magma after millions of years of volcanic activity. They have a very variable life span, ranging from a couple of days (Sabrina, Azores, 1811) to tens of millions of years (Selvagem Grande, 27 My) and different origins, such as volcanic arches developed above subduction zones (Small Antilles), volcanic buildings related to central oceanic ridge fences (Azores), intra-plate mantel plumes (Madeira, Canaries, Cape Verde). During their construction oceanic islands may reach important altitudes (Hawaii, 4,205 m) and sizes (Iceland, 103,000 km^2), although they are usually small (Fernández-Palacios & Martín Esquivel, 2001; Fernández-Palacios, 2004).

In the last decades a new impulse to the theoretical development of island biogeography and ecology has taken place, mainly due to the appearance of a set of works (Lomolino, 2000; Heaney, 2000) that have tried to complement MacArthur and Wilson (1967) Equilibrium Theory classical approach. This impulse has stressed the inclusion, besides the two main biogeographical processes considered by MacArthur and Wilson (immigration and extinction) of a third one, the speciation, without which any approach to understand the biological richness carried by continental fragments or oceanic islands can succeed. Furthermore, very recently a new impulse to this discipline has been given by Robert Whittaker and colleagues (Whittaker *et al*., 2007, 2008) with the modelling (including the age of the island together with its area and isolation) of the antique knowledge that hot spot oceanic islands, opposite to the stable continental islands and fragments, function as living beings that born, grow, age and disappear under the sea-level with time. Stuessy (2007) proposed the use of the term "island ontogeny" for the set of changes in geographic and biogeographic parameters that an oceanic island undergoes along its life.

Different life phases of a hot-spot originated oceanic island

The life of an oceanic island is constituted by a series of phases that go from its birth on the ocean floor to its disappearance under the sea level (Fig. 1). These are: a) *Birth and submarine construction phase*, b) *Emersion and aerial construction phase*; c) *Erosion and dismantling phase*, d) *Basal plain phase*; e) *Terminal disappearance phase* and f) *cut-summit seamount (guyot) phase*. (Fernández-Palacios & Whittaker, 2010).

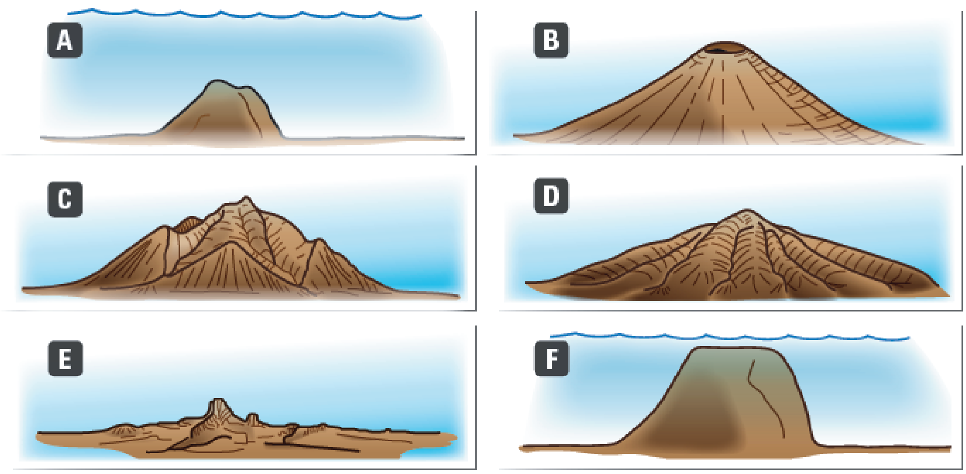

Figure 1. The six stages recognized in the volcanic island cycle: a) birth and submarine construction; b) emersion and aerial construction; c) erosion and dismantling dominant; d) reduction to a low-lying plain; e) terminal disappearance and f) guyot (flat-summit seamount) (Fernández-Palacios & Whittaker, 2010).

During the first and last phases the island is actually a seamount. The first phase is the longer lasting one and is usually not concluded, leading to seamounts that will never reach the sea surface. These never-emerged-seamounts do not show a flat summit, the more characteristic feature of a guyot (island emerged and later eroded to the sea level). Along the second phase, not necessarily long lasting, the island reaches its maximal area and altitude. Later destruction processes, such as erosion, gravitational land slides or subsidence, begin to work and they will progressively sink and dismantle the island, first to a roughed state where habitat diversity may attain its maximum value (Phase c), and later to a flat platform (Phase d) which will slowly disappear under the sea level (Phase e). Once under the sea level, erosion is not more functional and the former island, now seamount, will possess a flat summit (guyot), an unmistakable feature of its former insular nature (Phase f), and will last as seamount forever, unless its flat summit remains at a depth of 120 m or less, what will permit its periodic emersion during the glaciations.

The Macaronesian archipelagos

The name Macaronesia stems from the classic Greek words *makarios* (meaning happy) and *nessos* (meaning islands). The origin of this name is attributed to the British botanist Philip Barker Webb, although very likely he used it just thinking on Madeira, Salvages and the Canaries, the nucleus of the region (Stearn, 1973). Probably it was Engler (1879) the first author to include the Azores in the Macaronesian region, whereas it was not until 1961, when Dansereau (1961) included Cape Verde as well (Vanderpoorten *et al.,* 2007). So, today the Macaronesian region is widely considered to comprise those five volcanic archipelagos (Azores, Madeira, Salvages, Canaries and Cape Verde) located off the Iberian Peninsula and North Africa (Fig. 2).

The region (Table I) comprises 39 islands larger than 1 km^2 and more than one hundred islets and rocks that do not reach this size. It is distributed between 14.8º N (Brava, Cape Verde) and 39.7º N (Corvo, Azores), and between 13.4º W (Roque del Este, Canaries) and 30.9º W (Flores, Azores). The maximal distance within the region (2,812 km) separates Corvo from Brava. Fuerteventura is only 96 km away from the African coast (Stafford point, Western Sahara), whereas São Miguel lies 1,369 km away from Cabo da Roca in continental Portugal. On the other hand, Corvo lies just 1,930 km away from Cape Race in Newfoundland, Canada and Brava 2,812 km away from the Brazilian coast north to Natal.

The Salvages archipelago is the oldest one, with an age of 27 My (Selvagem Grande), whereas the Azores with 8 My (Santa Maria) is the youngest. Although all the islands share a common volcanic origin, only in three of the archipelagos (Azores, Canaries and Cape Verde) the volcanic activity is still present, with several eruptions within the last decades (Fernández-Palacios & Dias, 2001). The last volcanic eruption in Madeira is considered to have taken place some 25 Ky ago (Prada & Serralheiro, 2000), whereas in Salvages the last eruption was in the Pliocene (Geldmacher *et al*., 2005).

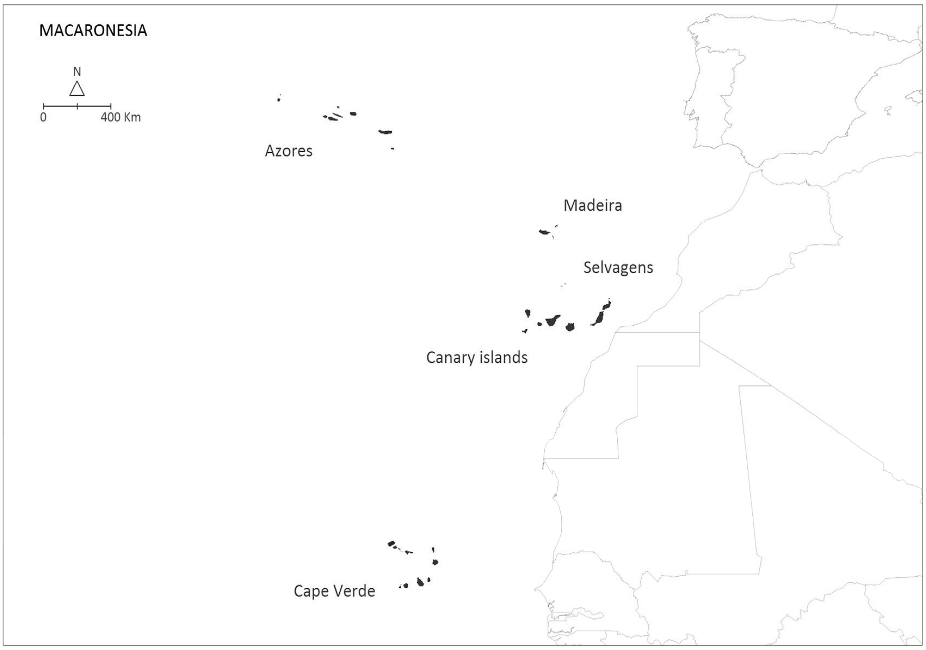

Figure 2. Map of the Macaronesian region (Author: Clara Gaspar).

Table I. Geographic parameters of the Macaronesian archipelagos.

Parameter	Azores	Madeira	Salvages	Canaries	Cape Verde	Macaronesia
Nº islands > 1km²	9	4	1	11	14	39
Area (km²)	2,764	815	4	7,445	4,033	15,061
Maximum elevation (m)	2,351 (Pico)	1,862 (Madeira)	163 (S. Grande)	3,718 (Tenerife)	2,835 (Fogo)	3,718
Continental isolation (km)	1,369 (São Miguel)	630 (P. Santo)	388 (S. Grande)	96 (Fuerteventura)	571 (Boavista)	96
Mean intra-archipelago isolation (km)	220	32	20	196	141	-
Age of the oldest emerged island (My)	8 (Sta. Maria)	14 (P. Santo)	27 (S. Grande)	21 (Fuerteventura)	16 (Sal)	27
Last volcanic eruption	1957 (Faial)	25 Ky BP (Madeira)	3.4 My BP (S. Grande)	1971 (La Palma)	1995 (Fogo)	1995
Latitude (º)	37- 40 N	33 N	30 N	27 - 29 N	15 - 17 N	40 - 15 N
Colonization date	1432 AD	1420 AD	-	ca. 2,500 BP	1456 AD	-
Human population (M)	0.25	0.35	-	2.2	0.45	3.2

Climate

The important latitudinal differences existing among the Macaronesian archipelagos (up to 25º among the Azores and Cape Verde) have as a consequence the existence of significant climatic differences among them (Table II). Whereas in Madeira and the Canaries - the Macaronesian core - a Mediterranean climate (fresh, humid winters and warm, dry summers) dominates, an oceanic temperate climate (cool, wet) prevails throughout the year in the Azores, and a warm, dry climate with tropical monsoon influence in summer is present in Cape Verde (de Nicolás *et al*., 1989).

Table II. Climatic data for several selected Macaronesian localities with representation of coastal (proximal and distal), mid-altitude and summit meteorological stations.

Locality	Latitude (N)	Longitude (W)	Altitude (m)	Rainfall (mm)	Temp. (º C)
Vila do Porto, Santa Maria	36º 58’	25º 10’	93	742	17.9
Santa Cruz, Flores	39º 27’	31º 08’	39	1,430	17.8
Achada das Furnas, São Miguel	37º 46’	25º 19’	550	1,730	13.2
Montanha do Pico, Pico	38º 28’	28º 24’	1,232	5,704	10.1
Airport, Porto Santo	33º 04’	16º 20’	93	353	19.0
Funchal, Madeira	32º 38’	16º 54’	58	641	18.7
Santo da Serra, Madeira	32º 43’	16º 49’	660	1,783	14.7
Bica da Cana, Madeira	32º 45’	17º 04’	1,560	2,966	9.3
Arrecife, Lanzarote	28º 57‘	13º 13’	10	139	20.2
Santa Cruz, La Palma	28º 44’	17º 46’	10	499	20.3
Pajonales, Gran Canaria	28º 00’	15º 39’	900	523	16.5
Izaña, Tenerife	28º 18’	16º 30’	2,367	514	9.7
Praia, Santiago	14º 55’	23º 31’	35	210	24.6
Mindelo, São Vicente	16º 53’	25º 00’	16	96	22.8
Vila Nova da Sintra, Brava	14º 52’	24º 43’	507	410	20.2
Monte Velha, Fogo	14º 57’	24º 21’	1,299	1,610	18.9

Three main rainfall gradients can be recognized throughout the region: i) a latitudinal (North to South) one with decreasing precipitations from the Azores to Cape Verde; ii) a longitudinal (East to West) gradient with increasing precipitations in all the archipelagos from the localities nearer to the continent towards those located farther, and iii) an altitudinal gradient of increasing precipitations in each specific island from the coast to the summit (de Nicolás *et al*., 1989).

Whereas on the Azores, the rain falls all over the year (with June and July as the driest months), on Madeira and the Canaries it occurs between the fall and the spring, with the summer remaining as a dry season. Finally, on Cape Verde there is, due to the tropical monsoon influence, a change in the precipitations pattern, with summer as the single wet station along the year. Temperatures follow as well the latitudinal (decreasing to the North) and the altitudinal (decreasing to the summits) gradients, but not the longitudinal gradient. Finally, Saharan dust influence is frequent on Cape Verde, infrequent on the Canaries and Madeira, and only exceptional on the Azores.

Macaronesia: a disputed biogeographical entity

Although for plant geographers Macaronesia is a stronger defined entity than for zoogeographers (but see Vanderpoorten *et al*., 2007), in general there is today an agreement about its nature of separate and well differentiated biogeographical region within the Holarctic Kingdom (Báez & Sánchez-Pinto, 1983; Santos-Guerra, 1990; Fernández-Palacios & Dias, 2001). However, their precise limits are still under controversy. For instance, for some authors (Báez & Sánchez-Pinto, 1983) Macaronesia is composed exclusively by the five already cited Atlantic archipelagos, whereas other authors include in the region a narrow strip of the African continental coast, the so called Atlantic Sahara, located between Agadir (Morocco) and Nouadhibou (Mauritania) (Sunding, 1979), or even the Algarve region in continental Portugal (Kunkel, 1993), due to their biotic affinities.

Nevertheless, the entity of Macaronesia as a single region has also been widely debated. Concerning to their floristic composition, the Azorean archipelago has clear Atlantic and Euro-Siberian affinities, whereas Madeira and the Canaries are clearly related to the Mediterranean realm. Finally, the Sudanian and tropical affinities of the Cape Verdean flora are important. Thus, many authors have restricted the use of the term Macaronesia only for the Madeiran (with Salvages) and the Canarian archipelagos, concept usually called as Central Macaronesia or the Macaronesian core, arguing that both the Azores and Cape Verde should be excluded from this region. The Azores are usually included in the Atlantic region of the Holarctic Kingdom (Lobin, 1982), whereas Cape Verde is incorporated either in the Saharo-

Sindian region of the Holarctic, or in the Sudanian region of the Palaeotropical (Aethiopical) Kingdom. Lüpnitz (1995) even goes further suggesting the elimination of the Macaronesia concept and the inclusion of Madeira within the Mediterranean region and the Canaries within the Saharo-Sindican region. Finally, for some authors the Macaronesian archipelagos are just an extrusion of the Mediterranean region within the Atlantic Ocean (Blondel & Aronson, 1999). Along this chapter I will consider the region as composed exclusively by the five mentioned archipelagos.

Brief description of the Macaronesian archipelagos

Azores

The Azorean archipelago is composed by nine volcanic islands, forming three well differentiated entities: the eastern (Santa Maria and São Miguel), the central (Terceira, Graciosa, São Jorge, Pico and Faial) and the western (Flores and Corvo) groups, located in the North Atlantic Ocean ca. 1,370 km off Lisboa (Fig. 3).

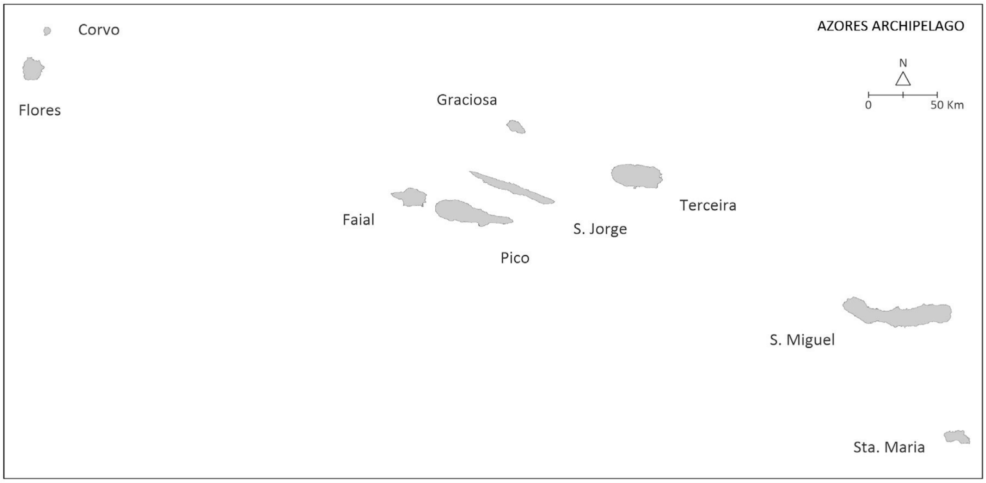

Figure 3. Map of the Azorean archipelago (Author: Clara Gaspar).

Located on both sides of the Central Atlantic Submarine Ridge, western and eastern extremes of the archipelago are actually drifting away. Santa Maria, its oldest island, is some 8 My old, and Pico, its youngest, just 0.25 My (França *et al*., 2005). Some 50 Ky ago the volcanic activity merged together the palaeoislands of Sete Cidades and Noreste-Povoação-Furnas to form today's São Miguel (Forjaz, 2002). Finally, in the last glaciation sea-level fall, Faial and Pico have merged together and some rocks (Formigas) and submarine banks (João Castro) emerged forming stepping-stones which enhanced intra-archipelago dispersal (Kämmer, 1982).

Affected by the Gulf Stream, the Azores have a very wet, mild climate, that coupled with the general low altitude of their islands (with the exception of Pico's peak, 2,351 m), has given rise to an ecologically homogeneous system, impoverished in species and with a relative scarce endemic level (Borges *et al.*, 2005). Its flora shows affinities with Atlantic and Boreal Europe (Juncaceae, Cyperaceae, *Sphagnum*) and with Madeira and the Canaries (*Ilex, Juniperus, Laurus, Myrica, Picconia, Prunus*, etc.) (Fernández-Palacios & Dias, 2001; Schäffer, 2003).

These islands were discovered by Portuguese sailors in AD 1432 and early colonized by Flemish settlers. Unfortunately their natural landscapes, where different forests types such as humid and hyperhumid laurel forest thrived, have been almost completely destroyed and substituted with pasturages and timber (mainly *Cryptomeria japonica*) plantations, existing today very few natural areas, all of them protected (Santana *et al*., 2006). Today, ca. 250.000 Azoreans live in the islands, supported by an agriculture, cattle and forest timber exploitation development model.

Madeira

The Madeiran archipelago (Fig. 4) comprises the islands of Madeira, Porto Santo and the Desertas (Ilhéu Chão, Deserta Grande and Bugio). Porto Santo (14 My) is the oldest island of the archipelago and is in an advanced destruction stage, whereas Madeira, which experienced its last volcanic activity some 25 ky ago (Prada & Serralheiro, 2000), is still high and full of cliffs and ravines, a feature that actually has served to enhance the good conservation stage of its nature.

During the last glaciation maximum, Madeira and the Desertas joined together forming a larger island. The archipelago is outstanding diverse in total (ca. 7450) and endemic (ca. 1300) species, among those as much as 980 endemic arthropods, 210 endemic molluscs and 154 endemic vascular plants (Borges *et al*., 2008). Furthermore, Madeira shares as well an important number of endemic species with the Canaries, the so called Canarian-Madeiran endemic elements, mainly related with the Laurisilva flora (Sziemer, 2000). Radiation processes have been important only in invertebrate genera, nine of them with more than 18 endemic taxa, such as *Laparocerus* weevils (34 sp.) *Sphaericus* beetles (28 sp.) or *Cylindroiulus* millipedes (28 sp.) (Borges *et al*., 2008).

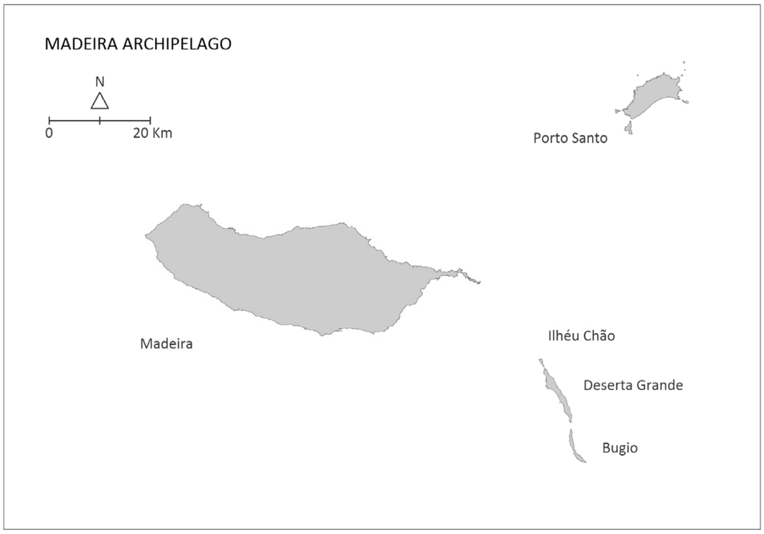

Figure 4. Map of the Madeiran archipelago (Author: Clara Gaspar).

The islands have been discovered by the Portuguese in 1418 AD (Vieira, 2001) and since then colonized. Today its main economical activity is the reception of mass tourism which to a great extent is rapidly deteriorating its outstanding nature. As much as 300.000 people inhabit today the archipelago, the big majority in southern Madeira.

Finally, the small Desertas archipelago, located off Maderia's São Lourenço tip, remains uninhabited by humans and protected within the Madeiran Natural Park.

Salvages

The Salvages archipelago (Fig. 5), composed by three uninhabited islets (Selvagem Grande, Selvagem Pequena and Ilhéu de Fora) and several rocks in an advanced destruction stage, is the smallest (4 km^2), lowest (163 m) and oldest (27 My) archipelago of Macaronesia. It is located some 175 km north to Tenerife (Canaries) and 255 km south of Bugio (Madeira). Although closer to the Canaries, this archipelago is administratively controlled by the Madeiran Government, which converted it and the surrounding sea waters in a natural park. Despite its minimum size this tiny archipelago harbours more than 50 endemic species, and many other Macaronesian endemisms shared either with Madeira, the Canaries or both (Borges *et al.*, 2008).

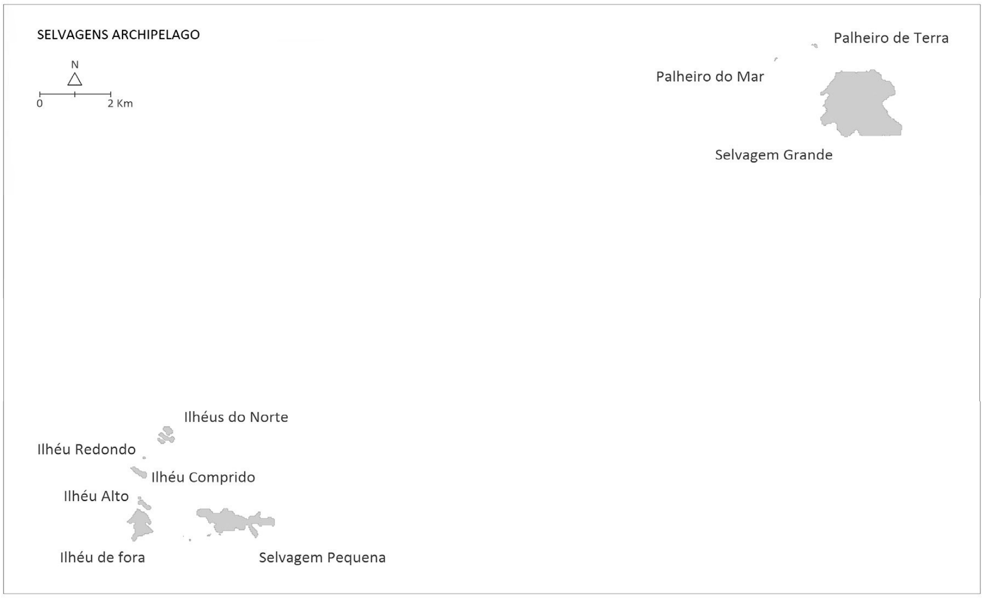

Figure 5. Map of the Salvages archipelago (Author: Clara Gaspar).

Canaries

The Canary archipelago (Fig. 6) is situated only 96 km off the hyper-arid coast of northwest Africa. Despite its age (21 My for Fuerteventura), the islands remain volcanically active, and over time have been subjected to intensive and at times catastrophic erosive and/or volcanic episodes. The Pleistocene glaciation cycles have reiteratively doubled and halved the archipelago area, with consequences as the fusion of nearby islands (Lanzarote, Fuerteventura and satellite islets) in a single landmass (today called Mahan), the emersion of several submarine banks, or the diminution of the distance to the African mainland (García Talavera, 1999), all of which facilitating dispersal processes. There are more than 12,500 terrestrial and 5,500 marine species in, or around, a land area of only 7,500 km^2, from which about 3,800 species and 113 genera are endemic (Izquierdo *et al*., 2004), being among them many examples of spectacular radiations of both invertebrates (*Laparocerus, Attalus, Dysdera, Napaeus, Hemicycla*, *Dolichoiulus*, etc.) and plants (*Aeonium, Argyranthemum, Cheirolophus, Echium, Limonium, Lotus, Pericallis, Sideritis, Sonchus,* etc.). The Canaries are affected by a Mediterranean-type climate and exhibit an outstanding ecosystem diversity, encompassing from the hot, dry semi-desert vegetation of the coastal lowlands, through the thermophilous woodlands, the laurel forest zone, to the Canarian pine forest and to the summit scrub.

Figure 6. Map of the Canarian archipelago (Author: Clara Gaspar).

Although the precise timing of human colonization from northwest Africa is uncertain, the sparse archaeological evidence suggests a date of around 2500 BP by the guanche people, an ethnic group related to the Berbers, which introduced in the Canaries goats, sheep and pigs, as well as cereals, and the use of fire for promoting the transformation of native forests. Hence, human modification of the ecology of these islands significantly predates written records (de Nascimento *et al.,* 2009). Castilian Conquest and settlement followed in the 15th century, and today more than 2 million people inhabit the islands, supported by an economical model based on mass tourism, which is destroying its unique natural heritage (Fernández-Palacios *et al.*, 2004; Fernández-Palacios & Whittaker, 2008).

Cape Verde

The Cape Verde archipelago (Fig. 7) comprises 14 volcanic islands and islets located ca. 570 km off Dakar (Senegal). The archipelago is divided into the two well defined groups, the windward (Santo Antão, São Vicente, Santa Luzia, Branco, Razo, São Nicolau, Boavista and Sal) and the leeward (Maio, Santiago, Fogo, Rombos Islets and Brava) chains. The oldest island, Sal, has been dated in 16 My old (Holm *et al.*, 2006), but the archipelago is still active as testified by the recent (1995) eruptions in the Fogo caldera. The glaciations sea-level minima had reiteratively joined the north-western islands group (Santo Antão, São Vicente, Santa Luzia, Branco, Razo and São Nicolau) in a single landmass (Kämmer, 1982).

Cape Verdean species-poor native flora (724 spp.) (Arechavaleta *et al.,* 2005) has both Macaronesian and tropical affinities (Santos-Guerra, 1999), with a low to moderate endemism level (65 spp.), where some examples of radiation (*Diplotaxis,* 8 spp., *Tornabenea*, 6 spp., *Lotus*, 5 spp. or *Limonium*, 5 spp.) are to acknowledge (Brochmann *et al*., 1997). A total of 2019 terrestrial animal species have been recorded from Cape Verde, 460 of which (22.7%) are endemics. This means a relatively poor diversity compared to the other archipelagos, but with a higher rate of endemisms, only inferior to the Canaries. This fauna includes few cases (*Cyphopterum*) of remarkable radiations among multiple-archipelagos monophyletic clades (see table VII), the rest being more related to tropical Africa than to Macaronesia, as indicate the insect genera *Oxycara*, *Dinas* or *Campylomma*, the *Mabuya* skinks and *Hemidactylus* geckos, and many other non-radiated genera. However, there are interesting cases of Cape Verde species derived from Canarian clades, as it has been stated using molecular data by Arnedo *et al.* (2001) for *Dysdera* spiders, and by Carranza *et al.* (2002) for *Tarentola* geckos.

Figure 7. Map of the Cape Verdean archipelago (Author: Clara Gaspar).

Discovered by Portuguese sailors in AD 1456, Cape Verde was early populated with mainland people imported as slaves for the slave markets or for working on the local plantations. Today, a population of ca. 400.000 people inhabited the archipelago, mainly dedicated to agriculture and goat herds, a development model that has strongly deforested the islands so that today natural landscapes are almost absent.

The existence of *Palaeomacaronesia*

In the last decades the improvements in the knowledge of the oceanic bathymetry, mainly after the use of multibeam technology, has allowed the discovery of several submarine chains and guyots located in the oceanic depths separating the Madeira and the Canaries from the Iberian Peninsula. Today we know that these seamounts have been created by the Palaeogene (64-25 My BP) activity of the same mantel-plume hot spots that have built much later (from the Miocene onwards) the extant islands (Geldmacher *et al.*, 2001, 2005) (Fig. 8). Two different hot spots have produced the Madeiran and the Canarian volcanic provinces (Table III), each of them with an array of already vanished and extant islands. Furthermore, a third volcanic hot spot within this region has built, hundreds of miles southwards, the former Saharan archipelago, located between the Canaries and Cape Verde (Geldmacher *et al.*, 2001). Undoubtedly both the existence of former islands and their later emersion as Pleistocene stepping stones, have played a major role in the shaping of nowadays Macaronesian biotas and communities.

Furthermore, the geo-chronological dating of those seamounts has allowed the reconstruction, although still with an important uncertainty, of their emersion sequence (Fernández-Palacios *et al.,* in press) and thus, of their past availability as targets for the colonization by propagules of the species participating in the former mainland communities. Actually, when these seamounts were still islands, they were located much closer to the Iberian Peninsula, and were affected by the existing East to West warm circum-equatorial marine current, which flew across the Tethys Sea, enhancing the colonization likelihood of these former islands from Iberia and North Africa.

Table III. Geographic and geologic parameters of selected Macaronesian seamounts and emerged islands. Geographic coordinates refers to the highest emerged point of the island. Island age data refer to the oldest and youngest known volcanic activity.Various sources.

Name	Location	Isolation to the nearest mainland (km)	Age (My)	Summit depth (-m) or altitude (+m)
Madeiran Volcanic Province				
Josephine	36º45'N 14º15'W	430 (Iberia)	?	-178
Ormonde	36º02'N 11º09'W	200 (Iberia)	67-65	-40
Gettysburg	36º31'N 11º34'W	240 (Iberia)	?	-63
Ampere	35º00'N 12º48'W	404 (Iberia)	31	-18
Coral Patch	34º56'N 11º57'W	300 (Iberia)	31	?
Unicorn	34º47'N 14º35'W	525 (Africa)	27	?
Seine	33º45'N 14º45'W	485 (Africa)	22	-152
Porto Santo	33º04'N 16º20'W	630 (África)	14-11	+516
Madeira-Desertas	32º44'N 16º55'W	650 (África)	5-0	+1862
Canarian Volcanic Province				
Lars	32º50'N 13º10'W	345 (Africa)	68	-900?
Anika	31º34'N 12º59'W	285 (Africa)	55	?
Nico	30º50'N 13º00'W	275 (Africa)	?	?
Last Minute	30º10'N 14º50'W	301 (Africa)	?	?
Salvages	30º09'N 15º52'W	388 (Africa)	26	-163
Dacia	31º15'N 13º45'W	355 (Africa)	47-9	-86
Conception	30º00'N 12º50'W	182 (Africa)	> 17	-140
Mahan	28º05'N 14º22'W	96 (Africa)	25-0	+807
Amanay	28º13'N 14º44'W	25 (to Mahan)	15	-25
Gran Canaria	27º57'N 15º36'W	196 (Africa)	15-0	+1949
La Gomera	28º06'N 17º15'W	333 (Africa)	12-3	+1487
Tenerife	28º16'N 16º38'W	284 (Africa)	11-0	+3718
La Palma	28º45'N 17º53'W	416 (Africa)	4-0	+2425
El Hierro	27º43'N 18º03'W	383 (Africa)	1-0	+1501

The oldest of these seamounts, Ormonde in the Madeiran volcanic province and Lars (also called Agadir seamount) in the Canarian volcanic province, are as old as 70 My (Geldmacher *et al*., 2001, 2005), dating back to the latest Cretaceous period, when the Tethys Sea was still open. This is to say that Palaeomacaronesia, as we can denominate these vanished archipelagos pre-dating today existing ones, is twice to three times as old as it was until now considered (Fig. 8).

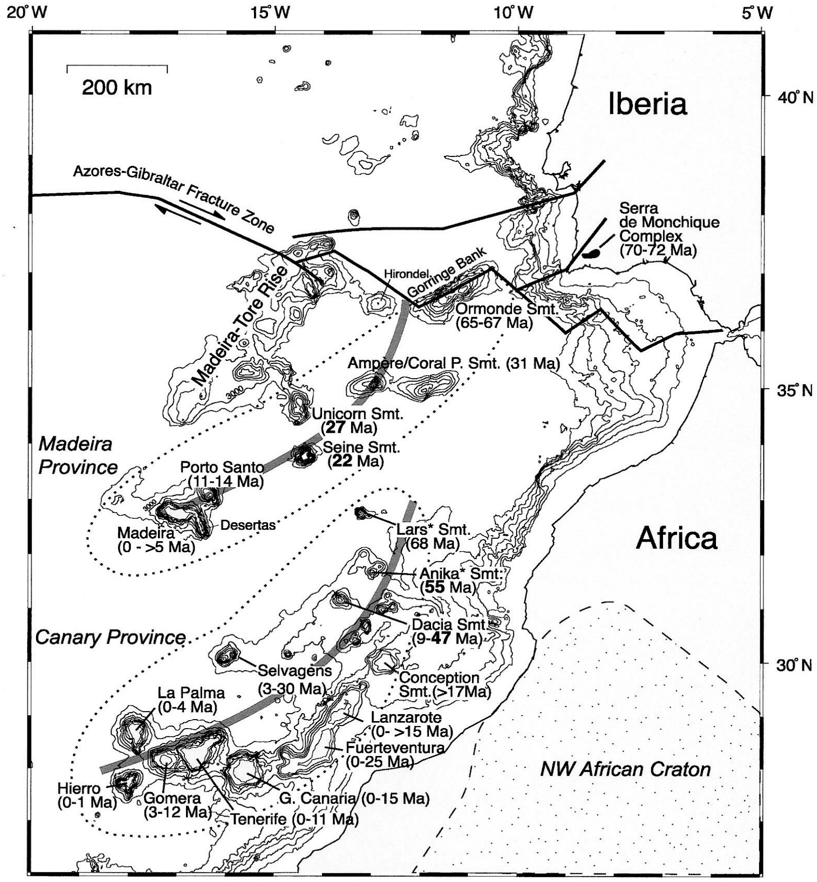

Figure 8. Bathymetry of the Madeiran and Canarian volcanic provinces, with the age of the seamounts and emerged islands. Source: Geldmacher *et al.*, 2005.

The island ontogeny exemplified in the Canarian archipelago

Volcanic islands are known to achieve important heights during their youth when the construction processes are still active, enabling them to contain different altitudinal disposed ecosystems. Nevertheless, in their senescence the erosion processes flatten the islands until their putative disappearance under the sea level (Whittaker *et al.*, 2007). The known geological ages of the islands basal shields forming the Palaeomacaronesian archipelago (Geldmacher *et al.*, 2001, 2005) enable us to consider as very likely the existence of several islands, representing different stages of their life cycle, simultaneously. The older islands were located closer to the Iberian Peninsula, while the younger ones were formed by the hot-spot activity some hundreds of km to the South West, due to the slight counter clockwise rotation of the African Plate (Geldmacher *et al.*, 2005).

The Canary Islands exemplify very well the different phases of the island ontogeny throughout the archipelago (Fig. 9). The initial phase, birth and submarine construction, is represented by “Las Hijas” seamount, recently discovered southwest from El Hierro, with a pike summit some 1,500 m above the ocean floor, but still 2,500 beneath the sea level (Rihm *et al.*, 1998), maybe constituting the next Canary Island to emerge. The emersion and subaerial construction phase is represented in the Canaries by La Palma, El Hierro and Tenerife. These islands achieve considerable heights especially when measured from the ocean floor (> 7000 m for the Teide Peak in Tenerife) and are still under construction as several eruptions in the last centuries have proved. These recent islands are also reiteratively affected by catastrophic land-slides (Canals *et al.*, 2000) due to the instability related with the huge amounts of volcanic material accumulated in a short period of time. The erosion phase is well represented by La Gomera and Gran Canaria, as well as by the Teno and Anaga massifs of Tenerife.

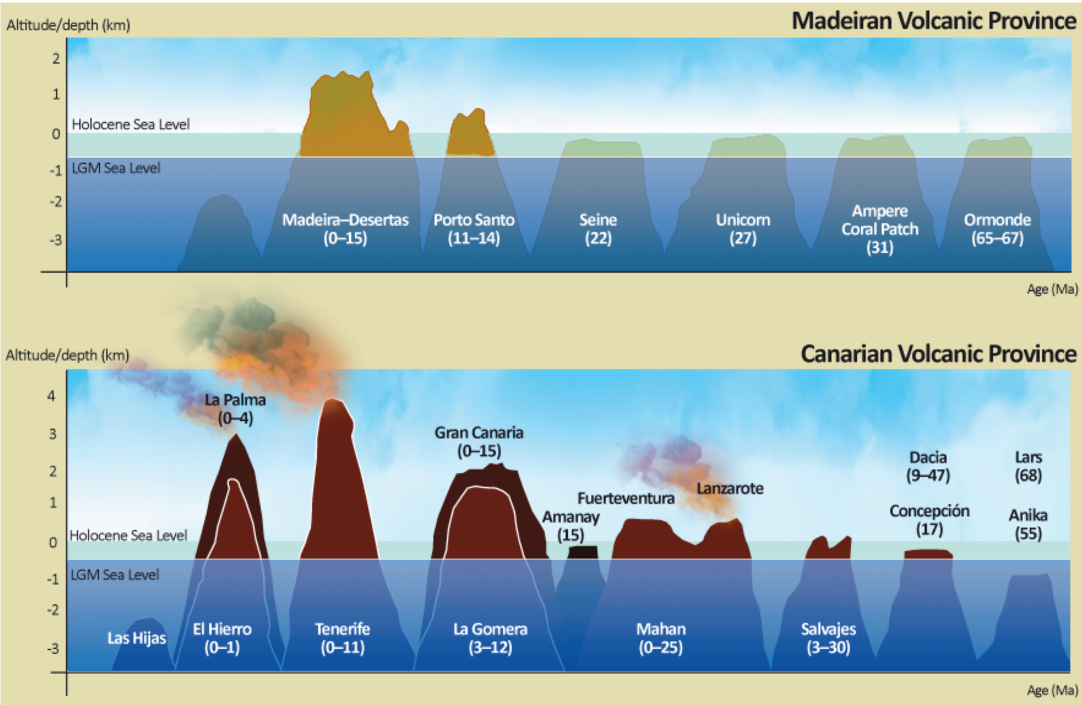

Figure 9. The different phases of the oceanic islands’ ontogeny exemplified with Madeira and the Canaries. Source: Fernández-Palacios *et al.*, 2011.

Those are old islands, that have been much larger and higher in the past, and today due to the prevalence of the destruction processes, the relief attains its maximum complexity. The basal plain stage is represented by Mahan, the Pleistocene island comprising Lanzarote, Fuerteventura and their surrounding islets. Although recent volcanic activity has taken place, Mahan is the rest of a former much larger and higher volcanic building. The terminal disappearance phase, is not existing in the Canaries, but is represented by Selvagem Pequena and Ilhéu de Fora (actually product of the same mantle hot spot that built the Canaries), which are very low islands hardly emerging over the ocean. The last phase, the guyot seamounts, is represented by Amanay, Conception and Dacia seamounts. As already stated, these guyots emerge with the sea regressions, given rise to the formation of biotic corridors that enhance the dispersal between the different Macaronesian archipelagos as well as between the archipelagos and the African and European mainland (Fernández-Palacios *et al.*, 2011).

The uniqueness of Macaronesian nature

Macaronesian biota

The Macaronesian region is worldwide known for its outstanding endemic biodiversity, without any doubt the highest of any other insular region within Europe, and comparable in endemism per area to the figures displayed in island show-cases such as Hawaii, Galápagos, New Zealand, New Caledonia or Madagascar. A thoroughly inventory of the Macaronesian terrestrial and marine biota has been recently finished and several checklists from all the archipelagos have been published in the last years (Izquierdo *et al*., 2004; Arechavaleta *et al*., 2005; Borges *et al*., 2005*,* 2008). The sum of the individual terrestrial biotas of all the Macaronesian archipelagos harbour more than 28,100 terrestrial species (not including bacteria, protozoa, as well as Azorean fungi and platyhelmints, and Cape Verdean nematodes, annelids and platyhelmints) in slightly more than 15,000 km^2 divided in 39 islands, less than Hawaiian archipelago area (Table IV). Nevertheless, this figure includes an undetermined number of species, either multiarchipelago endemisms (see Table V), native or introduced species that have been counted independently in each archipelago. This is to say that the real number of species in Macaronesia should be much lower than this, perhaps ca. 2,000 species lower. From them, ca. 5,930 species are endemic to the region (Martín-Esquível, 2010). The big majority of the Macaronesian endemisms belong to a single archipelago, although there is also an important element of Macaronesian endemic species occurring in more than one archipelago, especially the Canarian-Madeiran element, where many laurel forest species (palaeoendemics) are shared.

Table IV. Macaronesian archipelagos terrestrial biodiversity data, with endemic taxa in brackets (not including bacteria, protozoa, as well as Azorean fungi and platyhelmints, and Cape Verdean nematodes, annelids and platyhelmints). Sources: Izquierdo *et al*., 2004; Arechavaleta *et al*., 2005; Borges *et al*., 2005, 2008, 2009.

Archipelago	Azores	Madeira	Salvages	Canaries	Cape Verde
Fungi	No data	714 (36)	3 (0)	1634 (108)	62 (0)
Lichens	574 (12)	751 (12)	25 (0)	1307 (26)	260 (8)
Bryophytes	438 (9)	512 (11)	9 (0)	464 (10)	153 (6)
Pteridophytes	71 (7)	74 (8)	3 (0)	70 (3)	33 (1)
Spermatophytes	876 (61)	1118 (131)	102 (7)	2195 (636)	724 (64)
Arthropods	2227 (267)	3806 (935)	201 (44)	7410 (3085)	1915 (435)
Molluscs	111 (49)	294 (209)	8 (1)	267 (211)	39 (10)
Nematodes	80 (2)	63 (1)	0	200 (6)	No data
Annelids	21 (0)	36 (0)	0	66 (0)	No data
Platyhelmints	No data	7 (1)	0	51 (0)	No data
Vertebrates	69 (13)	58 (11)	10 (2)	184 (72)	65 (15)
Total	4467 (420)	7433 (1355)	361 (54)	13597 (4151)	3251 (540)

Macaronesia: a floristic crossroads

Macaronesia has long been regarded as a floristic crossroads (e.g. Hooker, 1866; Engler, 1879), where (i) 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), coexisting with (ii) 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), also alongside (iii) many native non-endemic species shared with North Africa and the Mediterranean (Medail & Quezel, 1999).

Despite constituting only an impoverished version of the original Tethyan-Tertiary Laurel forest, the Macaronesian laurel forest, is still rich in palaeoendemics, comprising around 40 Madeiran-Canarian species (Bramwell, 1976, 1985; Sunding, 1979). They include both geographic palaeoendemics (species or genera still extant in other parts of the world but vanished in the Mediterranean, as for instance, happened with *Persea, Ocotea* and *Clethra*) and taxonomic palaeoendemics (species or genera isolated within their clades due to 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 heath *Erica arborea*, which was already present in Madeira c. 2 Ma (Heer, 1855) and which appears to have colonized Macaronesia from the nearby continents at least twice (Désamoré *et al*., in press).

Recent phylogeographic analyses of both Macaronesian cryptogams (Aigoin *et al*., 2010; Vanderpoorten *et al*., 2007) and spermatophytes (Vargas, 2007) are supported of earlier work in highlighting the combined nature of the Macaronesian flora, with palaeoendemics coexisting with neoendemics. Such studies have also clearly demonstrated the role of Macaronesia as Pleistocene refugia for species that were later able to re-colonize Iberia or North Africa, as has happened 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, in press).

Radiation in Macaronesia

Macaronesia is home as well of important cases of phylogenetic radiation (different species deriving from a single founder event, what constitutes a monophyletic clade), that were originated either through adaptive radiation (the exploitation of different habitats within the same island) or vicariance (the exploitation of the same habitat within the same or in different islands). Such examples of explosive radiations can be easily found both in the animal as in the plant realms. Although usually the radiation is circumscribed to just one Macaronesian archipelago, with the Canaries clearly leading these statistics, there are several cases (see Table VI) where different archipelagos contribute with their own endemic species to the global picture of the clade.

Actually, one floristic monophyletic clade, the *Aeonium* group, include species distributed on the five Macaronesian archipelagos, each one with their own endemic species, all of them included in four different genera (*Aeonium, Greenovia, Aychrison* and *Monanthes*) of the

Crassulaceae family. This is also the case for one animal clade, the spider genus *Dysdera*, with endemic species on each of the archipelagos but has particularly radiated in the Canaries. Canary Islands are most probably the radiation center for this genus in Macaronesia, taking in consideration the results of molecular analyses on species from Cape Verde, Madeira and the Salvages (Arnedo *et al*., 2001, 2007; Macías *et al*., 2008) (Table VII).

Table V. Distribution among archipelagos of the Macaronesian plant endemic species. Sources: Izquierdo *et al*., 2004; Arechavaleta *et al*., 2005; Borges *et al*., 2005, 2008.

Endemic species number	Bryophytes	Pteridophytes	Spermatophytes	Total
Azores	9	7	61	77
Madeira	11	8	134	153
Salvages	-	-	7	7
Canaries	9	3	613	625
Cape Verde	6	1	65	72
Azores – Madeira	5	4	7	16
Madeira – Salvages	-	-	5	5
Madeira – Canaries	13	-	42	55
Salvages – Canaries	-	-	3	3
Canaries – Cape Verde	1	-	2	3
Azores – Madeira – Canaries	8	1	4	13
Madeira – Salvages – Canaries	-	-	6	6
Madeira – Canaries – Cape Verde	-	3	3	6
Salvages – Canaries – Cape Verde	-	-	1	1
Azores – Madeira – Canaries – CV	2	-	-	2
Madeira – Salvages – Canaries – CV	-	-	4	4
Single archipelago endemics	**35**	**19**	**880**	**934**
Multiple archipelago endemics	**29**	**8**	**73**	**110**
Macaronesia	**64**	**27**	**953**	**1,044**

This last fact implies the existence in the past not just of intra-archipelago dispersal events (needed for single-archipelago radiations), but of the much bizarre inter-archipelagos dispersals between islands that are separated by ca. 1,000 km of water gaps (for instance, Canaries ➔ Cape Verde, or Madeira ➔ Azores).

Table VI. Largest radiations in the Macaronesian archipelagos. Endemic genera in bold. *: Genera under taxonomic revision, on process of being splitted in single-archipelago endemic genera. Sources: Izquierdo *et al*., 2004; Arechavaleta *et al*., 2005; Borges *et al*., 2005, 2008; Alonso *et al*., 2006a, 2006b; Arnedo *et al.,* 2007; Machado, 2007, 2008.

Group	Azores	Madeira	Canaries	Cape Verde
Spermatophyta	*Agrostis (5)*	***Sinapidendron** (6)*	*Aeonium* clade *(52)*	*Diplotaxis (8)*
	Ammi (3)	*Sedum (4)*	*Sonchus* clade *(32)*	***Tornabenea** (6)*
	Carex (3)	*Helichrysum (4)*	*Sideritis (23)*	*Lotus (5)*
		***Musschia** (3)*	*Echium (23)*	*Limonium (5)*
		Lotus (3)	*Argyranthemum (19)*	*Echium (3)*
		Scrophularia (3)	*Limonium (19)*	
		Geranium (3)	*Lotus (17)*	
		Argyranthemum (3)	*Cheirolophus (15)*	
			Micromeria (15)	
Mollusca	*Oxychilus (13)*	*Leiostyla (34)*	*Napaeus (50)**	
	*Napaeus (7)**	***Caseolus** (27)*	***Hemicycla** (35)*	
	Leptaxis (7)	***Discula** (25)*	*Plutonia (21)**	
	*Plutonia (7)**	***Actinella** (22)*	***Canariella** (19)*	
	Leiostyla (4)	*Leptaxis (17)*	***Monilearia** (10)*	
		***Amphorella** (12)*	*Xerotricha (9)*	
		***Boettgeria** (9)*	*Ferussacia (8)*	
		***Geomitra** (9)*	*Discus (8)*	
		*Plutonia (8)**	***Cryptella** (6)*	
		***Craspedaria** (7)*		
Arthropoda	*Cixius (11)*	*Laparocerus (33)*	*Laparocerus (106)*	*Oxycara (16)*
	Trechus (9)	*Cylindroiulus (28)*	*Attalus (52)*	***Dinas** (11)*
	Tarphius (8)	*Sphaericus (26)*	*Dolichoiulus (46)*	*Apanteles (10)*
	Scoparia (4)	*Blastobasis (22)*	*Dysdera (47)*	*Megaselia (9)*
	Calathus (4)	*Tarphius (21)*	*Oecobius (33)*	*Peragallia (6)*
	Jaera (4)	*Geostiba (19)*	*Cardiophorus (33)*	*Cyphopterum (6)*
	Atheta (4)	*Acalles (17)*	*Tarphius (30)*	*Campylomma (5)*
	Clinocera (4)	*Trechus (19)*	*Acalles (29)*	*Melanagromyza (5)*
		Nesotes (16)	*Calathus (24)*	
		Chinacapsus (11)	*Cyphopterum (26)*	
		Torrenticola (10)	*Spermophorides (24)*	
		Caulotrupis (10)	*Hegeter (21)*	
Chordata			***Gallotia** (7)*	*Tarentola (5)*
			Tarentola (4)	*Mabuya (5)*

Table VII. Examples of some multiple-archipelagos monophyletic radiation events in Macaronesia. Sources: Izquierdo *et al*., 2004; Arechavaleta *et al*., 2005; Borges *et al*., 2005, 2008; Arnedo *et al.,* 2007; Machado, 2007, 2008.

Clade	Azores	Madeira	Salvages	Canaries	Cape Verde	Macaronesia
Fauna						
Laparocerus	0	33	1	106	-	140
Tarphius	8	19	-	30	-	57
Attalus	-	4	1	51	-	56
Dolichoiulus	3	3	1	46	3	56
Dysdera	1	4	1	47	2	53
Acalles	-	17	2	29	-	48
Sphaericus	1	26	2	14	2	45
Trechus	9	19	-	15	-	43
Nesotes	1	16	2	19	-	38
Cyphopterum	-	2	2	26	6	36
Porcellio	-	9	-	20	1	30
Asianidia	-	6	-	17	-	23
Flora						
Aeonium clade	1	5	1	52	1	60
Sonchus clade	-	3	-	32	1	36
Echium	-	2	-	23	3	28
Argyranthemum	-	3	1	19	-	23
Cheirolophus	-	1	-	15	-	16
Pericallis	1	1	-	12	-	14
Crambe	-	1	-	12	-	13

Sometimes Macaronesian clades have even been able to undergo retro-colonization, what is to say that species belonging to neoendemic Macaronesian clades have been able to colonize the Iberian peninsula or the African mainland, the probable source of the founder populations that originated those clades, resulting in the existence of Macaronesian-originated, Iberian or North-African neoendemisms (Caujapé, in press).

Macaronesian ecosystems

Although there are only a few fragments of the natural potential vegetation both in the Azores (where it has been almost substituted by conifer plantations and cattle rangelands) and in Cape Verde (where desertification and alien species introduction have completely transformed the landscapes), it is still possible to reconstruct their distribution. Despite the existence of a latitudinal difference of ca. 25º, Macaronesia shares to a certain degree a common biogeographic history, which emerged through the appearance of the similar biotic elements, with similar (vicariant) taxa, which have historically integrated to build close related ecosystems (Santos-Guerra, 1983), albeit with important differences in structure and function, mainly due to climatic reasons (Table VIII).

Table VIII. Distribution of Macaronesian main terrestrial ecosystems.

Ecosystem	Azores	Madeira	Salvages	Canaries	Cape Verde	Main floristic elements
Coastal desert scrub		X	X	X	X	*Euphorbia*
Thermophilous woodland		X		X	X	*Dracaena* *Sideroxylon* *Olea* *Juniperus turbinata*
Acacia woodland					X	*Faidherbia* *Zyzyphus*
Laurel forest	X	X		X		*Laurus* *Picconia* *Myrica* *Ilex*
Pine forest				X		*Pinus*
Summit heath	X	X				*Erica* *Calluna*
Summit scrub				X		*Spartocytisus* *Adenocarpus*
Summit meadow					X	*Cenchrus* *Hyparrhenia*
Lakes	X					*Littorella* *Potamogeton* *Lemna* *Juncus*
Bogs	X					*Sphagnum*
Lava fields	X			X	X	*Stereocaulon*

Absent from the Azores, too wet for its existence, but present in the rest of the archipelagos, the sub-desert succulent coastal scrub characterized by the dominance of endemic spurge shrubs (*Euphorbia piscatoria* in Madeira, *E. anachoreta* in Salvages, *E. balsamifera, E. obtusifolia, E. lamarckii* in the Canaries and *E. tukeyana* in Cape Verde) is the African aspect of the Macaronesian islands. Due to their low altitude it is actually the unique ecosystem existing in the Salvages, is well distributed on Cape Verde and the Canaries and only close to the sea in Madeira.

Directly above this scrub, but still absent from the Azores, an open thermophilous woodland exists, dominated by tree species of Mediterranean origin such as *Olea, Dracaena, Sideroxylon*, *Phoenix* (absent from Madeira), *Juniperus* (absent from Cape Verde) and *Pistacia* (absent from both of them) (Fernández-Palacios *et al*., 2008). Exclusive from Cape Verde, a special kind of woodland - the *Acacia (Faidherbia)* communities - highlights the important tropical affinities of these islands.

The largest support for the European Macaronesia (Azores, Madeira, Canaries) biotic relations is based on the existence in those archipelagos of the Atlantic laurel forest. This forest is actually an impoverished version of the Palaeotropical Laurisilva that occurred in Central and Southern Europe, as well as North Africa, from the Palaeocene until the late Pliocene glaciations (Barrón & Peyrot, 2006). The laurel forest is the main ecosystem from the Azores, extending from the coast to the summits of all islands, with the exception of the tallest Pico, and is well represented in the mid-altitudes of Madeira and the Canaries. It is a dense cloud forest, with a low canopy (5-10 m) in the Azores, but an important one (> 30 m) in Madeira and the Canaries. The dominant trees shared by the three archipelagos include genera such as *Picconia, Laurus, Ilex, Prunus* and *Myrica*, whereas *Juniperus brevifolia* is exclusive from Azores and *Apollonias, Persea* and *Ocotea* are restricted to Madeira and the Canaries (Santos, 1990; Capelo *et al*., 2007; Dias *et al*., 2007)

The more or less common scenario for Macaronesian coastal and mid-altitude ecosystems is absent when the summit ecosystems throughout the region are analyzed, mainly due to the peculiar summit climates and dispersal filters (islands summits are islands within islands). The summits of Pico (the single Azorean island high enough to trespass the laurel forest altitudinal distribution) and Madeira are characterized by a heath dominated by different Ericaceae species. Most of the high Canary islands (Gran Canaria, Tenerife, La Palma and El Hierro) present by contrast at the same altitudes an open, tall (> 30 m) pine forest, dominated by the palaeoendemic Canarian pine (*P. canariensis*). Only on La Palma and Tenerife the pine forest is substituted in height by a summit scrub characterized by endemic, cushion-like legumes (*Spartocytisus* and *Adenocarpus*). Finally, on the Cape Verde summits a grass (*Cenchrus, Hyparrhenia*) meadow dominates.

Whereas lakes and ponds are abundant in the Azores, by far the more humid system, the rest of the archipelagos lack them. Nevertheless, in Madeira this is only due to the absence of proper basins, because the water availability is high enough. The Canary Islands and Cape Verde although without lakes or ponds keep some permanent water fluxes where fresh water arthropods, including endemic species, may be found. On the other hand, with the exception of Madeira and Salvages (without Holocene volcanism), young volcanic terrain is abundant in all the archipelagos with several historical eruptions, some of them within the last years or decades, usually dominated in their first stages by the lichen *Stereocaulon vesubianum* (Table VIII).

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