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Macaronesia as a Fruitful Arena for Ecology, Evolution, and Conservation Biology

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Research in Macaronesia has led to substantial advances in ecology, evolution and conservation biology. We review the scientific developments achieved in this region, and outline promising research avenues enhancing conservation. Some of these discoveries indicate that the Macaronesian flora and fauna are composed of rather young lineages, not Tertiary relicts, predominantly of European origin. Macaronesia also seems to be an important source region for back-colonisation of continental fringe regions on both sides of the Atlantic. This group of archipelagos (Azores, Madeira, Selvagens, Canary Islands, and Cabo Verde) has been crucial to learn about the particularities of macroecological patterns and interaction networks on islands, providing evidence for the development of the General Dynamic Model of oceanic island biogeography and subsequent updates. However, in addition to exceptionally high richness of endemic species, Macaronesia is also home to a growing number of threatened species, along with invasive alien plants and animals. Several innovative conservation and management actions are in place to protect its biodiversity from these and other drivers of global change. The Macaronesian Islands are a well-suited field of study for island ecology and evolution research, mostly due to its special geological layout with 40 islands grouped within five archipelagos differing in geological age, climate and isolation. A large amount of data is now available for several groups of organisms on and around many of these islands. However, continued efforts should be made toward compiling new information on their biodiversity, to pursue various fruitful research avenues and develop appropriate conservation management tools.

Keywords: alien species, biodiversity hotspot, biotic interactions, extinction, long distance dispersal, reverse colonisation, speciation, volcanic oceanic islands

INTRODUCTION

Oceanic islands have long fascinated biologists, as they provide insights that have been incorporated into a number of ecological and evolutionary theories. Today, research on island systems is in the spotlight, with exciting new developments (e.g., Santos et al., 2016; Patiño et al., 2017; Whittaker et al., 2017; Valente et al., 2020). Many of these advances stem from studies performed partially or entirely in Macaronesia (*sensu* Engler, 1914), a region located in the Northeast Atlantic Ocean formed by the volcanic archipelagos of the Azores, Madeira, Selvagens, Canary Islands, and Cabo Verde (**Figure 1**).

Macaronesia comprises 40 islands and islets larger than 1 km^2, covering a latitudinal range from 14.8°N to 39.7°N (**Figure 1** and **Table 1**) and extending over a distance of almost 3,000 km. This encompasses a strong climatic gradient from oceanic temperate climate in the Azores, to Mediterranean climate in Madeira, the Selvagens and Canary Islands, and warm arid climate in Cabo Verde (Fernández-Palacios, 2010). The geological age of the extant (emerged) islands and islets ranges from less than 35,000 years for Alegranza in the Canary Islands, to 25.7 million years (Ma) for Selvagem Grande. However, seamounts around Madeira and the Canary Islands are as old as 67 Ma (Gettysburg near Madeira), which indicates that Macaronesia is at least twice or three times older than its oldest emerged land (Fernández-Palacios et al., 2011; Ávila et al., 2016). Furthermore, these islands show contrasting levels of geographical isolation from the mainland, varying from 96 km off North Africa (Fuerteventura, Canary Islands) to more than 1,500 km (Flores, Azores) off the Iberian Peninsula (Fernández-Palacios, 2010; **Figure 1**). The boundaries of Macaronesia in the marine realm differ slightly, as Cabo Verde is described as pertaining to a different province, and the rest of the archipelagos are included in the Lusitanian province (Freitas et al., 2019).

The wide latitudinal, altitudinal, size, and climate variations of the Macaronesian islands are in part responsible for the diversity of habitats they host. These range from desert and semi-arid vegetation, typical for most of Cabo Verde and the driest areas of the Selvagens and Canary Islands, to the humid laurel and juniper forests characteristic of the Azores, Madeira, and the mid to high altitudes of the western and central Canary Islands (del Arco-Aguilar et al., 2010; Fernández-Palacios, 2010). In addition, there are unique lentic and lotic ecosystems (Hughes and Malmqvist, 2005), as well as important microhabitats like subterranean cavities and volcanic hot springs (see Pipan et al., 2010). Macaronesia also straddles a wide range of marine habitats, which support a rich and yet incompletely known marine biota (Moro et al., 2003; Tuya and Haroun, 2009; Cordeiro et al., 2015).

In general, endemism appears to be high in many taxonomic groups, particularly from the terrestrial realm, like vascular plants, land snails and arthropods (**Figure 2A** and ESM1 in **Supplementary Material**). Indeed, a truly remarkable data is the percentage of endemic terrestrial mollusc species, that reaches over 41% in Azores (potentially close to 91% once the colonisation status is assigned to all species; Frias Martins, A., pers. comm.) and Cabo Verde, over 84% in Madeira (Teixeira, D., pers. comm.), and over 94% in the Canary Islands. Despite its small area, the Selvagens host over 50 endemic species (over the 15% of the total number of native species), sharing other endemisms with different Macaronesian archipelagos (Fernández-Palacios, 2010). In the Canary Islands, the level of endemism reaches 66% in spiders (Cardoso et al., 2010), and 100% in reptiles (Loureiro et al., 2008; Arechavaleta et al., 2010;

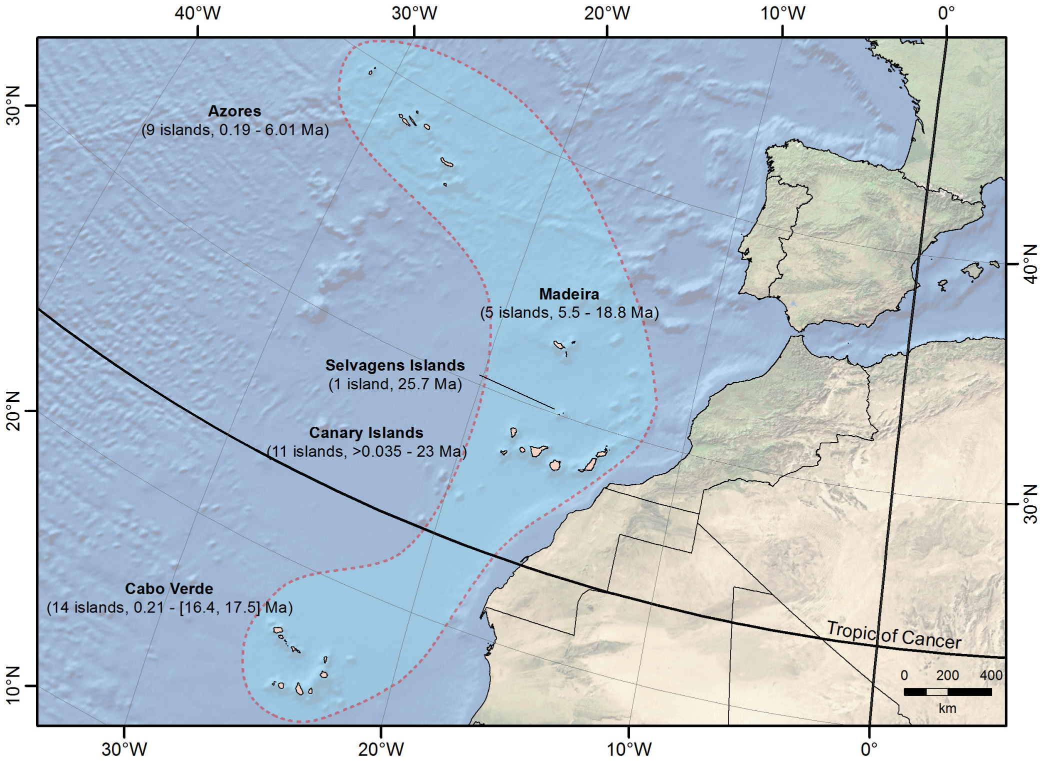

FIGURE 1 | Geographical location of the Macaronesian archipelagos, with indication of the number of islands and their geological age (only islets >1 km^2 were included; see **Table 1**).

Vasconcelos et al., 2013); within this context, almost 50% of the plant species of the Canary Islands are endemics (Reyes-Betancort et al., 2008), with over 70% of them being considered single-island endemics (Carine and Schaefer, 2010). Finally, this pattern of high endemicity is not so evident in marine ecosystems (**Figure 2B** and ESM1 in **Supplementary Material**), where for many groups, the number of endemic species does not even reach 6% of the archipelagic biodiversity (Freitas et al., 2019); the gastropods constitute the exception to this trend, particularly in Cabo Verde, where the number of endemic species represents over 44% of all native species (e.g., 86 *Conus* species inhabit this archipelago, being its majority endemic to Cabo Verde; Freitas et al., 2019).

Even though our knowledge of the flora and fauna of Macaronesia is still far from complete, the collective effort of systematists, ecologists, and biogeographers has resulted in the compilation of comprehensive data sets for species distributions (e.g., Arechavaleta et al., 2005; Borges et al., 2008, 2010; Arechavaleta et al., 2010; Romeiras et al., 2016a; Freitas et al., 2019), morphological traits (e.g., Schaefer et al., 2011; Whittaker et al., 2014; Henriques et al., 2017; Rigal et al., 2018; Macías-Hernández et al., 2020), ecological history and phylogenetic relationships (e.g., Emerson, 2002; Carine et al., 2010; Amorim et al., 2012; Caujapé-Castells et al., 2017), and species interactions (e.g., Dupont and Skov, 2004; Valido et al., 2004; Valido and Olesen, 2010; González-Castro et al., 2012). Nevertheless, despite the long-standing interest in Macaronesian biodiversity, our knowledge of the different archipelagos and taxa is still unbalanced, and the existing literature is rather heterogeneous (see Lobo and Borges, 2010; Romeiras et al., 2019). For example, the study of Cabo Verde's biota lags behind that of other Macaronesian archipelagos (Romeiras et al., 2020), which is probably associated with the fact that many endemic species only occur in habitats that are difficult to access, such as cliffs in the mountain areas (Neto et al., 2020). Certain taxonomic groups, like Platyhelminthes, Nematoda and Annelida, as well as the Bacillariophyta and Amoebozoa typical of freshwater habitats (but see Ritter et al., 2020; Gonçalves et al., 2021 for Madeira), are still poorly studied in most archipelagos (**Figure 2A** and ESM1 in **Supplementary Material**). Even in the case of terrestrial arthropods, a group that has been intensively studied in the last decades, species description is far from complete, with estimates indicating that a large number of species remains unknown (Lobo and Borges, 2010).

Human activity has drastically transformed Macaronesia (e.g., Borges et al., 2019), leading to profound changes in habitat diversity and community composition over a relatively short period of time (del Arco-Aguilar et al., 2010; Triantis et al., 2010; Illera et al., 2012; Boieiro et al., 2018). Although the documented European colonisation of Macaronesia only started about 600 years ago, increasing evidence points to much earlier human arrivals in some of the archipelagos (see Förster et al., 2009; Gabriel et al., 2015; Rull et al., 2017). However, it was not until Europeans started to settle on the islands that intense land transformation and introduction of alien species led to a more sudden and profound alteration in most native terrestrial

TABLE 1 | Main characteristics of the islands and islets larger than 1 km^2 included in the Macaronesian archipelagos of the Azores, Madeira, Selvagens, Canary Islands, and Cabo Verde (compiled from Geldmacher et al., 2001; Torres et al., 2002; Madeira et al., 2005; Azevedo and Portugal Ferreira, 2006; Holm et al., 2006; Ancochea et al., 2010; Dyhr and Holm, 2010; Madeira et al., 2010; Ramalho, 2011; Ancochea et al., 2012; van den Bogaard, 2013; Aranda et al., 2014; Johnson et al., 2014; Ancochea et al., 2015; Costa et al., 2015; Ramalho et al., 2015; Ávila et al., 2016 and references therein; Ramalho et al., 2017; Samrock et al., 2018; Marques et al., 2020; Cornu et al., 2021).

Archipelago/ Island	Latitude	Longitude	Area (km^2)	Distance from continent (km)	Distance from closest island (km)	Geological age of the oldest subaerial lavas (Ma)	Maximum altitude (m asl)
AZORES							
Corvo	39.6991	−31.1052	17	1,858	18	1.5	718
Flores	39.4419	−31.2025	143	1,864	18	2.16	913
Graciosa	39.0523	−28.0113	62	1,596	36	0.7	398
Terceira	38.7239	−27.2123	400	1,520	37	0.4	1,020
São Jorge	38.6372	−28.0292	246	1,584	18	1.85	1,067
Faial	38.5782	−28.7013	173	1,657	6	0.85	1,043
Pico	38.4695	−28.3336	436	1,610	6	0.19	2,351
São Miguel	37.7954	−25.4819	750	1,368	80	0.79	1,103
Santa Maria	36.9713	−25.0998	97	1,376	80	6.01	587
MADEIRA							
Porto Santo	33.0692	−16.3422	40	633	39	18.8	517
Ilhéu da Cal	33.0466	−16.3855	1.4	641	0.4	NA	178
Madeira	32.7463	−16.9991	740	639	24	7.0	1,850
Deserta Grande	32.5390	−16.5205	10	640	21	5.5	479
Bugio	32.4243	−16.4856	3	636	33.7	5.5	388
SELVAGENS							
Selvagem Grande	30.1453	−15.8656	3	374	18	25.7	153
CANARY ISLANDS							
Alegranza	29.4023	−13.5148	10	169	10	>0.035	289
Montaña Clara	29.2990	−13.5365	1	160	2	0.039	256
La Graciosa	29.2554	−13.5032	27.5	152	1	0.05	266
Lanzarote	29.0245	−13.6418	796	125	11	15.0	670
Lobos	28.7514	−13.8245	4	123	2	NA	122
La Palma	28.6899	−17.8583	729	414	57	1.7	2,425
Fuerteventura	28.4061	−14.0365	1,725	96	11	23.0	807
Tenerife	28.2911	−16.5563	2,058	286	28	12.0	3,718
La Gomera	28.1174	−17.2326	378	333	28	11.0	1,484
Gran Canaria	27.9548	−15.5932	1,532	195	61	15.0	1,950
El Hierro	27.7465	−18.0066	278	381	61	1.1	1,501
CABO VERDE							
Santo Antão	17.0565	−25.1701	779	834	13	7.57	1,979
São Vicente	16.8455	−24.9678	227	818	8	6.1	725
Santa Luzia	16.7663	−24.7452	35	797	8	7.0	351
Sal	16.7372	−22.9314	216	650	39	15.8	406
Branco	16.6543	−24.6682	2.8	792	7.6	6.0	327
Raso	16.6166	−24.5861	5.8	783	15.4	2.30	164
São Nicolau	16.5985	−24.2562	343	721	30	3.7	1,304
Boavista	16.0983	−22.8139	620	611	39	16.4–17.5	390
Maio	15.2180	−23.1606	269	614	26	11.9	436
Santiago	15.0837	−23.6248	991	634	26	2.39–2.87	1,392
Ilhéu de Cima	14.9731	−24.6330	1.5	772	8.2	NA	77
Ilhéu Grande	14.9655	−24.6768	3	777	6.7	NA	97
Fogo	14.9283	−24.3843	476	725	18	0.21	2,829
Brava	14.8515	−24.7055	64	716	18	0.5–1.99	976

Islands are ordered according to their North-South latitude. Latitude and longitude refers the centroid of the islands. NA indicates unavailable information on the geological age; when there is no concrete date for the emergence of an island, data on geological age was represented as an interval of the most probable values. Ma and asl indicate Millions of years and Above sea level, respectively.

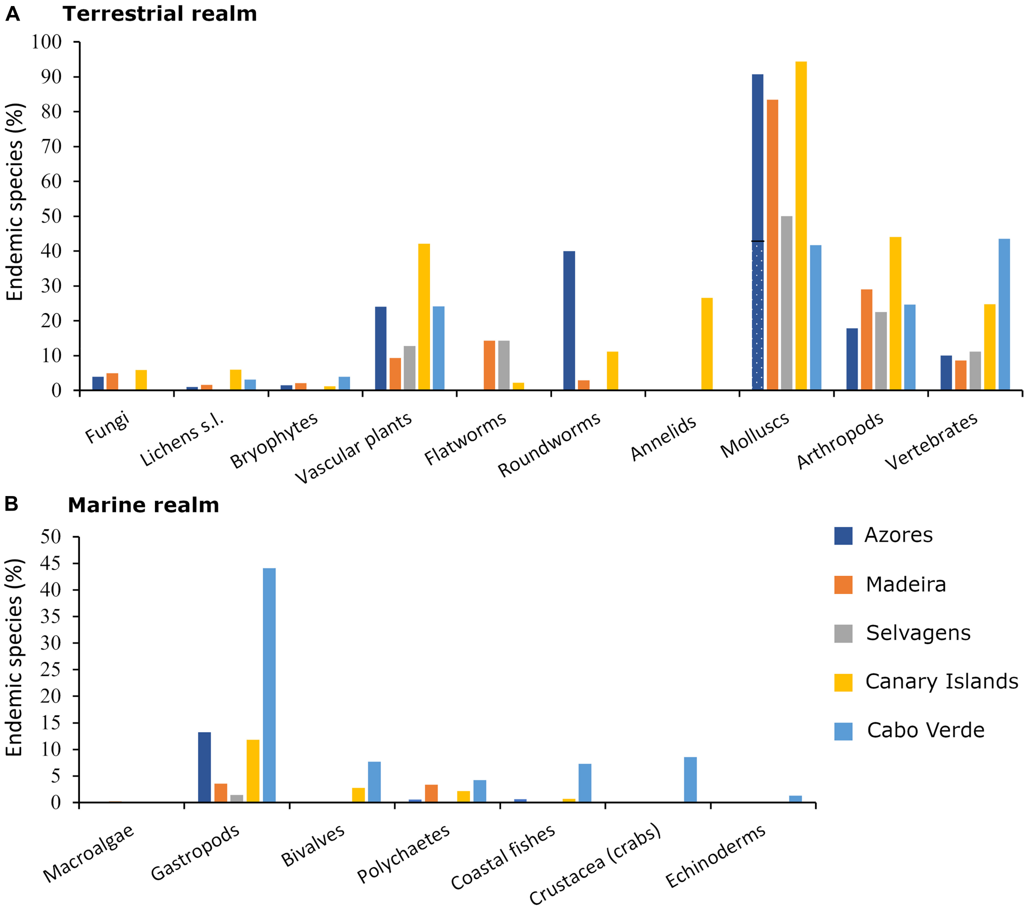

FIGURE 2 | Percentage of native species of several taxonomic groups that are endemic species of each Macaronesian archipelago (Azores, Madeira, Selvagens, Canary Islands, and Cabo Verde) at **(A)** the terrestrial and **(B)** the marine realms. Information on the terrestrial biota was extracted from Arechavaleta et al. (2005), Borges et al. (2008, 2010), Miralles et al. (2011), Vasconcelos et al. (2012b, 2020), and Biodiversity Data Bank of the Canary Islands (2021). Data on marine taxa was extracted from Freitas et al. (2019) and Neto et al. (2021a,b,c), and unpublished data from one of the authors (Ávila, S.P.) regarding bivalves. The proportion of the endemic species was calculated over the number of native species, which included those considered probably or possibly native. Only extant species and breeding birds were considered. Lichens s.l. includes lichenicolous fungi, Vascular plants include Spermatophyta, ferns, and fern allies, Arthropods include Tardigrada, and Crustacea only refers Brachyura (crabs). The dotted area in the bar of the Azorean Molluscs indicates the existence of some uncertainty regarding the proportion of endemic species (43–91%; Frias Martins, A., pers. comm). In the case of Madeira, we have considered 25 additional species that have recently been classified as native based on fossil evidence; Teixeira, D., pers. comm.). Diatoms and amoebae are not represented because of their incomplete information. Also, Platyhelminthes (flatworms) and Annelids show the same value in Madeira and Selvagens because the source literature does not discriminate between the two archipelagos. No data was reported for the Platyhelminthes, Nematoda (roundworms) and Annelida in Cabo Verde, and for Nematoda and crustaceans Brachyura (crabs) in Selvagens (see ESM1 in **Supplementary Material** for detailed information).

and aquatic ecosystems (Malmqvist et al., 1995; Triantis et al., 2010; Raposeiro et al., 2017; Lamelas-López et al., 2021). Marine ecosystems are also affected by similar anthropogenic pressures, mainly through overexploitation of biological resources (Martins et al., 2008, 2012) and increasing urbanisation of coastal areas (Cacabelos et al., 2016a,b; Martins et al., 2016). Climate change also represents a threat to Macaronesian diversity, as indicated by studies modelling the distribution of endemic and native bryophytes, vascular plants, and arthropods under different scenarios of climate change (Ferreira et al., 2016; Patiño et al., 2016).

The outstanding biodiversity of the Macaronesian archipelagos, together with the geographical, environmental and historical idiosyncrasies of their islands have fuelled a continuously increasing number of ecological, evolutionary, and conservation studies. Here, we review the most important findings of Macaronesian studies and identify further challenges in island biology that can be addressed in this insular system.

HISTORY AND ORIGIN

Young Lineages Instead of Tertiary Relicts

Macaronesia has primarily been defined as a biogeographical region based on its terrestrial flowering plant species. Engler (1879) suggested that the Macaronesian flora was mostly a relict of a formerly widespread subtropical flora covering southern Europe and North Africa during the Palaeogene and Neogene. Increasing evidence from dated phylogenies suggests that Macaronesian endemics are often much younger than the age of emergence of the islands they inhabit, casting doubts on Engler's hypothesis [e.g., vascular plants (Jones et al., 2014; Kondraskov et al., 2015), bryophytes (Patiño and Vanderpoorten, 2015), birds (Illera et al., 2012, 2016; Valente et al., 2017), spiders (Planas and Ribera, 2014), beetles (Emerson et al., 1999; Amorim et al., 2012), lichens (Sérusiaux et al., 2011), reptiles (Romeiras et al., 2019), and marine gastropods (Duda and Rolán, 2005; Baptista et al., 2019)]. Even the iconic Macaronesian laurel forest, long viewed as an assemblage of Tertiary relictual and palaeoendemic elements (see Fernández-Palacios et al., 2011) may be composed of mainly young and recent colonisers (Kondraskov et al., 2015). This pattern coincides with other archipelagos, for example New Caledonia, with a biota mainly formed by recent clades, despite being the oldest oceanic island in the world (Nattier et al., 2017). However, the complex geological dynamics of Macaronesia has led to the emergence and disappearance of several (palaeo-)islands (Fernández-Palacios et al., 2011), which could have served as stepping-stones and refugia for the persistence of older lineages, as in other archipelagos (Heads, 2010). Nevertheless, phylogenetic evidence for the persistence of "living fossils," whose origin predates their native islands, is extremely rare and limited to very few species (e.g., the moss *Hedenasiastrum percurrens*; Aigoin et al., 2009).

Long- and Short-Distance Dispersal in Macaronesia

The ancestors of most extant Macaronesian lineages had to overcome the long distances that separate the islands from the mainland. Accordingly, many Macaronesian plants (e.g., Patiño et al., 2013; García-Verdugo et al., 2019), lizards (Carranza et al., 2000) and marine molluscs (e.g., Ávila et al., 2012; Faria et al., 2017) show some adaptations to long distance dispersal (LDD). However, there is also evidence from the Azorean flora indicating that many plant species lack traits related to LDD (Heleno and Vargas, 2015), and that species ability to track its climatically suitable areas within an island is not strongly related with LDD syndromes (Leo et al., 2021). Notably, non-standard LDD mechanisms poorly evaluated in island systems have been described for Macaronesia. These include secondary seed dispersal mediated by predatory birds feeding on frugivorous birds and lizards, which carry seeds in their digestive system (Nogales et al., 2012; Padilla et al., 2012; Viana et al., 2016; but see Grant et al., 1975, regarding the Galápagos), and dispersal through mega-landslides (García-Olivares et al., 2017).

Colonisation and establishment of many plants is mediated by generalist seed dispersers. In the Canary Islands and Madeira, such a function is widely performed by frugivorous lizards (Sadek, 1981; Valido and Nogales, 1994; Nogales et al., 2016; Pinho et al., 2018), following a pattern common in many islands worldwide (Hervías-Parejo et al., 2019; Valido and Olesen, 2019). Lizard-plant interactions result in a relatively short-distance dispersal pattern of seed distribution, with the lizard *Gallotia stehlini* dispersing seeds over almost 100 m on Gran Canaria (Pérez-Méndez et al., 2016). In contrast, birds can disperse viable seeds over short and long distances within and between islands (Nogales et al., 2001; López-Darias and Nogales, 2016).

Macaronesia as Refugium and Source of Biodiversity for the Adjacent Mainland

Due to their buffered climate and larger sizes during glacial periods, oceanic islands were traditionally considered as sinks for continental terrestrial biotas (Wilson, 1961). However, a growing body of phylogenetic evidence suggests that islands also act as sources of continental diversity (Jønsson and Holt, 2015). Macaronesia has acted as both refugium (Vargas, 2007; Caujapé-Castells, 2011; Fernández-Palacios et al., 2011) and, at least to a certain extent, as a source of *de novo* species for neighboring continental regions (Patiño et al., 2015). Back-colonisation from islands to continental areas, from which the island ancestors originated ("boomerang events" *sensu* Caujapé-Castells, 2011), was first postulated by Ball and Hooker in 1878 for Macaronesia (Fernández-Palacios and Whittaker, 2020), and more than a century later was confirmed for the genera *Aeonium* (Mort et al., 2002) and *Convolvulus* (Carine et al., 2004). Further evidence derives from bryophytes and spermatophytes (e.g., Fernández-Mazuecos and Vargas, 2011; Hutsemékers et al., 2011), and beetles (Machado et al., 2017). Similar processes have later been described in New Zealand and New Caledonia (Condamine et al., 2017). The close proximity of some of the Macaronesian islands (Canary Islands and Cabo Verde) to their continental species pools, the changes in island surface area, isolation and predominant wind and ocean currents through time, together with the emergence of seamounts during glacial periods (Fernández-Palacios et al., 2011; Rijsdijk et al., 2014) may have allowed even greater connectivity between these landmasses in the past.

High or Reduced Genetic Diversity of Island Populations?

The few individuals that successfully arrive and colonise islands carry just a subset of the genetic variation in the parental continental populations (Frankham, 1997; Clegg, 2010). In Macaronesia, isolation after colonisation seems to have driven both genetic and phenotypic divergence in Berthelot's pipit (*Anthus berthelotii*), and not geographical distance or environmental differences (Spurgin et al., 2014). In contrast, Stuessy et al. (2012) suggested that genetic signatures of founder effects rarely persist over evolutionary time-scales in island plants. Indeed, a growing body of empirical evidence for Macaronesian bryophytes and angiosperms suggests that genetic diversity is often substantially higher than in the continental source populations (Fernández-Mazuecos and Vargas, 2011; Laenen et al., 2011; Desamoré et al., 2012; García-Verdugo et al., 2015; Patiño et al., 2015). Strikingly, the invasive house mouse (*Mus musculus domesticus*) in Madeira also follows this pattern. Evidence supports an initial introduction event about one millennium ago (Förster et al., 2009; Rando et al., 2014), with subsequent *in situ* genetic diversification that resulted in six chromosomal races distributed around the island (Britton-Davidian et al., 2000). This rapid diversification can be explained by meiotic drive due to a biased segregation of chromosomes to oocytes during female meiosis. The underlying biological mechanism involves differential centromere strength (a trait with natural variation among populations), predicting the direction of drive (Chmatal et al., 2014). This can result in the rapid fixation of distinct chromosomal combinations and, consequently, an increase in genetic diversity.

COMMUNITY ECOLOGY IN MACARONESIA

After arrival on islands, ecological processes act as major drivers of island community assembly, along with speciation and extinction events (**Figure 3**). MacArthur and Wilson (1963, 1967) highlighted the dynamic nature of the processes leading to community composition changes through time. Since not all species are equally likely to colonise islands, one general assumption is that island biotas are impoverished and taxonomically "imbalanced"—a phenomenon known as disharmony—when compared to adjacent mainland regions. As a consequence of this "vacant ecological space," some species might have the opportunity to broaden, or even shift their niche width through "ecological release" (Diamond, 1970). Prominent examples are the Azorean endemic bat *Nyctalus azoreum*, which exhibits the rare behaviour of being active during the day, probably due to the absence of avian competitors or predators (Moore, 1975; see Chua and Aziz, 2018, for a similar case in Malaysia). The Cabo Verde giant gecko *Tarentola gigas*, which preys on birds (Pinho et al., 2018) in the absence of mammalian top predators, is another example. Ecological release also occurs in different Macaronesian insect groups, in both terrestrial (Ribeiro et al., 2005; Stüben et al., 2010; Santos et al., 2011) and aquatic ecosystems (Raposeiro et al., 2012).

Mutualistic Interactions

Species interactions associated with pollination and seed-dispersal processes can influence large-scale biodiversity patterns. In insular systems, pollination networks commonly show distinctive and idiosyncratic ecological characteristics known as insular pollination syndromes (Valido and Olesen, 2010). For example, in the Canary Islands, generalist lizards and birds are important pollinators and seed dispersers (Valido et al., 2004; Valido and Olesen, 2010, 2019; Hernández-Teixidor et al., 2019), an uncommon behaviour in mainland systems (Olesen and Valido, 2003). Notably, Macaronesian pollinators tend to visit a wider range of plant species than their mainland relatives ("interaction release" *sensu* Traveset et al., 2015).

These particularities of island mutualistic networks suggest they may be notably vulnerable to similarly particular disturbances (see Heleno et al., 2013; Traveset et al., 2013 for Galápagos). González-Castro et al. (2012) compared the seed dispersal network structure of thermophilous woodland on Tenerife (Canary Islands) to mainland woodland and found that the lower number of species and greater specialisation on the island led to the prevalence of more symmetrical interactions, compared to the mainland. Also, Nogales et al. (2016) demonstrated that Canarian seed dispersal networks are highly nested (stable against disassembly) but weakly modular (the ensemble of species that interact more intensively), and therefore highly vulnerable to extinction cascades.

Alien Species

The introduction of alien species is one of the main threats to biodiversity in Macaronesia and worldwide. More than 70% of vascular plants and more than 50% of arthropod species in the Azores are aliens (Silva et al., 2008). Especially successful invaders in Macaronesia include the plants *Cenchrus* spp., *Hedychium gardnerianum, Pittosporum undulatum* and *Ulex europaeus*, as well as vertebrates like cats (*Felis sylvestris*), goats (*Capra hircus*), Corsican mouflons (*Ovis aries musimon*), Barbary sheep (*Ammotragus lervia*), rats (*Rattus rattus* and *R. norvegicus*), house mice (*Mus musculus domesticus)*, rabbits (*Oryctolagus cuniculus*), and Californian kingsnakes (*Lampropeltis californiae*). The spread of alien fish in the absence of native predators is an important threat to freshwater systems in Macaronesia (Ribeiro et al., 2009), impacting trophic cascades and ecosystem functioning (Skov et al., 2010; Buchaca et al., 2011; Raposeiro et al., 2017). A high number of alien species have been also reported in the marine realm of Macaronesia, with shipping as the most likely vector of these introductions (Chainho et al., 2015).

Schaefer et al. (2011) found that for the Azorean flora, alien species that are phylogenetically distant from native species are more likely to become invasive, corroborating Darwin's naturalisation hypothesis. Moreover, Padrón et al. (2009) and Picanço et al. (2017) showed that endemic and native super-generalist pollinators included new plant invaders in their set of food plants and thereby may help the establishment of alien and invasive plants. Indeed, alien bees pollinate most of the endemic Azorean flora (Weissmann et al., 2017). However, domestic honeybees (*Apis mellifera*) disrupt the structure and functionality of the plant-pollinator networks in Teide National Park (Tenerife, Canary Islands), reducing diversity and interaction links among wild pollinators, their hierarchical organisation, and the reproductive success of some endemic plants (Valido et al., 2002, 2019; Dupont et al., 2004). Also, alien arthropods added novel trait space in the Azores (Whittaker et al., 2014), and might play important roles in providing and maintaining some key ecosystem functions, particularly in anthropogenic systems such as cattle pastures (Rigal et al., 2018).

SPECIATION, DIVERSIFICATION, AND EXTINCTION IN MACARONESIA

Ecological opportunities on islands may foster diversification and speciation processes. New ecological opportunities are created when new habitats become available, such as subterranean environments that emerge as a consequence of present and/or past volcanic activity. For example, many phylogenetic and phylogeographical studies on endemic radiations of the Macaronesian arthropods include troglobiont species, such as

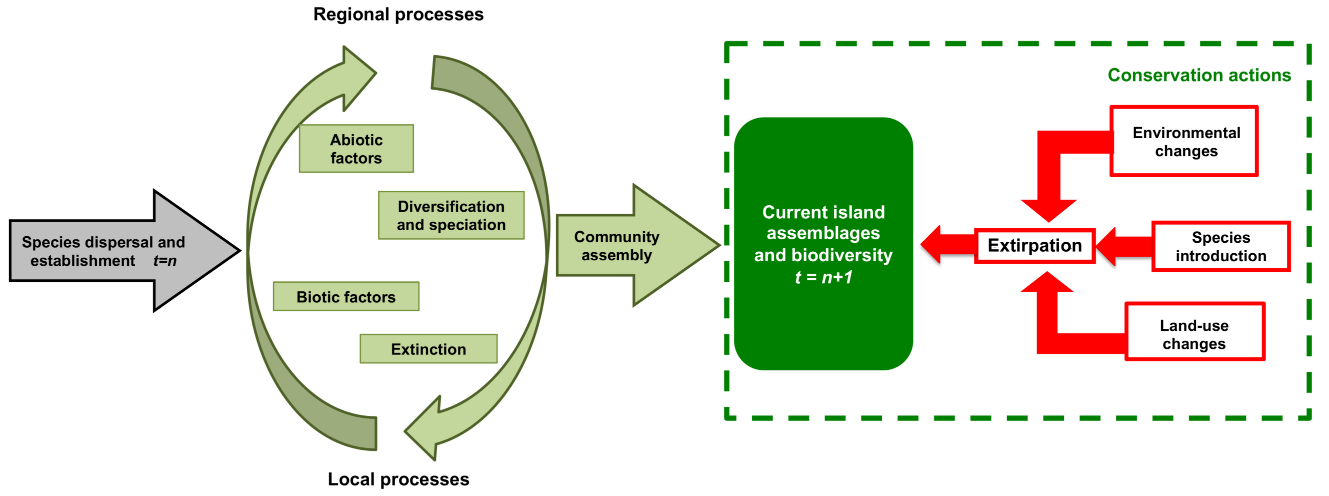

FIGURE 3 | Processes leading to community assembly in island biotas. The grey arrow represents dispersal from the species pool since historical times ($t = n$). Species able to colonise an island are subject to several processes and factors acting at the regional and local scales (some examples of these are indicated inside the two green arrows conforming a circle), which can lead to community assembly (large green arrow) and to the current biodiversity on islands (green box; $t = n + 1$). The extant island biodiversity is a result of speciation and diversification under regional and local abiotic constraints and biotic interactions. Current island assemblages and biodiversity are affected by anthropogenic disturbances such as environmental changes, species introductions and land-use changes (red arrows) that can lead to extirpation of species (red box), and are thus often targeted by conservation actions (green dashed box).

Dysdera spiders (Arnedo et al., 2007), *Palmorchestia* sandhoppers (Villacorta et al., 2008), *Trechus* ground beetles (Amorim, 2005; Contreras-Díaz et al., 2007), and *Laparocerus* weevils (Machado et al., 2017). Examples of radiations known to be adaptive are found among flowering plants (e.g., *Echium*—García-Maroto et al., 2009; *Aeonium*—Jorgensen and Olesen, 2001; Mort et al., 2001) and reptiles (e.g., *Gallotia*—Cox et al., 2010; *Tarentola*—Carranza et al., 2000; Vasconcelos et al., 2010). These taxa correspond to examples of diversification events associated with niche lability, in which closely related species present contrasting niches. Such niche differentiation can be reflected in current species distribution, as occurs in some plant clades in the Canary Islands, where closely related taxa present different climatic niches, particularly in allopatry (Steinbauer et al., 2016). However, not all diversification processes have arisen from changes in species niches; niche conservatism, which can be described as the tendency for ancestral niche and ecological characteristics to remain unchanged through time and space (Wiens and Graham, 2005), has also been an important speciation outcome in different taxa (e.g., *Helianthemum*—Albaladejo et al., 2021). Notably, the flora of the Azores is characterised by a limited incidence of adaptive radiations, contrasting with other Macaronesian archipelagos (Carine and Schaefer, 2010); the debate about the drivers of this pattern has pinpointed past climatic conditions, age, area and environmental homogeneity as the most plausible causes (Carine and Schaefer, 2010; Carine et al., 2012; Triantis et al., 2012).

Species interactions could also have fuelled species diversification in Macaronesia. By combining morphological data, radiocarbon dating, and molecular data, Rando et al. (2010) recovered an ecological interaction (resource competition) between sympatric extinct and extant finches of Tenerife for approximately 1 Ma. This interaction led to variations in bill size, as more famously known from the Galápagos finches (Grant and Grant, 2006). The presence on other Macaronesian islands of other extinct granivorous birds with significant variation in bill size suggests that character displacement between extinct and extant birds frequently occurred, to minimise competition for food (Rando et al., 2010).

The interaction between dispersal limitations and geological dynamics as drivers of diversification has attracted increased attention (Anderson et al., 2009; Fernández-Palacios et al., 2011; Rijsdijk et al., 2014; Ávila et al., 2015a). A history of massive landslides and their associated mega-tsunamis in Macaronesia allowed this question to be addressed at the within-island level (cf. Paris et al., 2018). Studies on endemic lizards and beetles point to an important role of these geological events in shaping the genetic structure of endemic lineages (Brown et al., 2006; García-Olivares et al., 2017) and, in combination with past climate oscillations, the community-wide diversification patterns across beetle species over a limited spatial scale (Salces-Castellano et al., 2020). Lava flows, that appear during volcanic activity, have led to population extirpation and the appearance of dispersal barriers, greatly affecting phylogeographic patterns and speciation (e.g., *Gallotia*—Bloor et al., 2008). The dynamics of sea-level changes, particularly those that occurred in the Quaternary, have affected island area, isolation and connectivity, which consequently influenced migration, extinction, and speciation, leaving an important imprint in current island richness, particularly of endemic species (Fernández-Palacios et al., 2011; Rijsdijk et al., 2014; Weigelt et al., 2016). As a consequence, Lanzarote and Fuerteventura, two islands that were connected in the Last Glacial Maximum (~18,000 years ago), share more insect and plant species than any other islands within the Canary Islands (Fernández-Palacios et al., 2011; Rijsdijk et al., 2014), and in Cabo Verde, only *Tarentola* spp. that occurred on islands connected during this period share haplotypes (Vasconcelos et al., 2010). Such dynamics also affected marine diversity, for example through its effects on sea-surface currents and dispersal routes (e.g., Ávila et al., 2009; Sousa et al., 2021), and on the characteristics of the intertidal zone (Ávila, 2013). Recent palaeocological studies have related marine ecological traits (e.g., the substrate where animals live) with extirpation/extinction trends, putting in evidence the impact of sea-level changes on insular shallow-water benthic marine communities (Ávila et al., 2009). Also, species range contractions and extensions (e.g., *Persististrombus* spp. and *Conus* spp., respectively; Meco et al., 2002; Ávila et al., 2015a, 2016) have been documented, and show the impact of climatic global changes associated with Pliocene climatic deterioration and the abrupt Pleistocene glacial/interglacial transitions (the so-called "Terminations") on species distributions.

Extinction in Macaronesia

Natural extinctions have been driven by ancient changes in climate and habitat. Oxygen isotope data suggest that most of the Pliocene marine fauna of the Azores became extinct 3.6–3.3 Ma ago as a result of glaciation (Ávila et al., 2015b, 2016; Santos et al., 2015). In addition, volcanism and geological catastrophes such as massive landslide events and mega-tsunamis, can also act as important drivers of island-wide natural extinction events (Anderson et al., 2009). However, human arrival has greatly impacted island biotas, accelerating species extinctions on islands (e.g., Triantis et al., 2010; Russell and Kueffer, 2019) to the point of influencing our understanding of basic evolutionary patterns (e.g., body size evolution toward dwarfism or gigantism on island species; Faurby and Svenning, 2016).

Canarian giant lizards (*Gallotia* spp., Lacertidae) underwent a strong defaunation process after human colonisation, with negative consequences on the seed dispersal distances and genetic variation of endemic plants, such as *Cneorum* (*Neochamaelea*) *pulverulentum* (Pérez-Méndez et al., 2018). Palaeobiological evidence also points to the extinction of several other species after human arrival, such as most flightless or weak-flying ground-nesting Canarian birds, as suggested by radiocarbon dating of bone collagen (Illera et al., 2016). In total, more than 20 endemic and many non-endemic vertebrate species that lived during the Upper Pleistocene-Holocene became extinct in Macaronesia, such as the iconic Cocteau's giant skink of Cabo Verde or the Macaronesian rails species (Vasconcelos et al., 2013; Alcover et al., 2015; Rando et al., 2020). Long-term fossil pollen and charcoal records have shown a decline in native plant diversity (possibly including some tree genera now absent as natives on Tenerife such as *Quercus* and *Carpinus*), introduction of non-native forest species (e.g., *Cryptomeria japonica* and *Pinus pinaster* in the Azores), and an increasing rate of fire occurrence after human arrival (de Nascimento et al., 2009, 2016; Gabriel et al., 2015; Rull et al., 2017). In the marine realm, the overexploitation of biological resources, such as the case of limpets, crustaceans and fishes, may also cause the extirpation of keystone species in coastal trophic chains (Navarro et al., 2005; Martins et al., 2008, 2010).

BIODIVERSITY PATTERNS AND MODELS

Species Distributions

Species abundance distributions (SADs), which are key descriptors of community structure, have been little investigated in island empirical studies (but see Ulrich and Zalewski, 2006, for lake islands, and Garcillán and Ezcurra, 2011, regarding Guadalupe Island, Baja California). In Macaronesia, Azorean arthropod communities are dominated by a few highly abundant single-island endemic species that may be assumed to be well adapted to specific island environmental conditions (Fattorini et al., 2016). These SADs of the Azorean arthropods follow a power law pattern when plotted according to sample size, which is similar to that observed for tropical tree SADs; this might indicate a general pattern in ecology (Borda-de-Água et al., 2017). Considered as one of the most general patterns in nature, the island species-area relationship (ISAR) has been widely studied using data from many archipelagos, namely those pertaining to Macaronesia (e.g., Cardoso et al., 2010; Santos et al., 2010; Aranda et al., 2013). Although the ISAR has mostly been studied in terrestrial systems, interest in evaluating it in marine and other aquatic systems is growing (Dawson, 2016). As an example in the marine realm, Tuya and Haroun (2009) found that intra-archipelago differences in species richness of Macaronesian macroalgae are largely related to variations in island perimeter (a proxy for island area).

The General Dynamic Model of Oceanic Island Biogeography

Islands are dynamic entities that have undergone climatic and geological changes through time. The General Dynamic Model of oceanic island biogeography (GDM; Whittaker et al., 2008; Borregaard et al., 2017) considers the effect of geological dynamics of oceanic islands on their diversity. The GDM has been intensively tested in Macaronesia, namely with arthropods (Borges and Hortal, 2009; Cardoso et al., 2010), reptiles (Vasconcelos et al., 2010), snails (Cameron et al., 2013), and bryophytes (Patiño et al., 2013; Aranda et al., 2014), and also in the sea (Ávila et al., 2018). While these evaluations show the potential of the GDM for predicting patterns of island species richness through time, they also pinpoint the need to account for island and taxon particularities when applying biogeographical models (see Borges and Hortal, 2009). The third component of the original theory of island biogeography, geographical isolation, was only recently included within the GDM framework, with Macaronesia (and Hawaii) being used as testing grounds (Patiño et al., 2013; Carvalho et al., 2015).

Recent studies on Macaronesian islands showed that the hump-shaped relationship between species richness and island geological age also holds for network interactions and genetic diversity, in which island age and dynamics act as regional drivers of plant-pollinator network complexity (see Trøjelsgaard et al., 2013 for an example in the Canary

Islands). Similarly, Vasconcelos et al. (2010) showed that volcanism and habitat diversity appear to be the main factors explaining the genetic diversity of *Tarentola* geckos in Cabo Verde, since they are both tightly linked with island ontogeny as postulated by the GDM. The importance of island age for explaining diversity patterns is also present in the marine realm. On a broader Atlantic archipelagos' context, Hachich et al. (2015) found a linear relationship between reef fish diversity and island age. More recently, Fernández-Palacios et al. (2016) developed a Glacial Sensitive Model (GSM) of oceanic island biogeography partially based on Macaronesian islands, which includes the role of glacial and interglacial periods in the GDM. Building on these models, Ávila et al. (2019) developed the Sea-Level Sensitive dynamic model (SLS) of marine island biogeography. This model offers predictions on how immigration, colonisation and *in situ* speciation rates affect marine biodiversity around oceanic islands.

NATURE CONSERVATION IN MACARONESIA

Several political, scientific and social initiatives toward improving conservation practices and public awareness have been established in Macaronesia. For example, the cost-effectiveness of conservation and governance policies can be improved by relying on island ecosystem-based management (Calado et al., 2016; Gil et al., 2016a), stakeholder engagement and public participation (Gil et al., 2011, 2016b), and funding to support and strengthen ecosystem functions and services delivery (e.g., Cruz et al., 2011; Fernandes et al., 2015). Hence, the last decade has witnessed the publication of important studies aiming to assist local and regional decision-making systems in moving toward more effective nature conservation planning and management policies in Macaronesia. Special attention has been given to "Natural Protected Areas" design and effectiveness (Vergílio et al., 2016; Gil et al., 2017). Several indices for the selection of priority areas for conservation have been developed based on Macaronesia (Gaspar et al., 2011; Borges et al., 2012; Cardoso et al., 2013). An innovative, cost-effective and replicable methodology has also been developed for protecting genetic diversity in reserves (Vasconcelos et al., 2012a). Furthermore, knowledge gathered in Macaronesia has been also used to propose several methodologies and standardised protocols for conservation assessment of endemic species (Borges et al., 2018). Identifying top-priority species is particularly useful for designing conservation strategies. However, applying IUCN criteria (IUCN Standards and Petitions Subcommittee, 2017) to oceanic islands may have serious shortcomings (Martín, 2009; Cardoso et al., 2011; González-Mancebo et al., 2012), leading, for example, to assigning species to higher threat categories (Romeiras et al., 2016a). Therefore, species risk tolerance should be adjusted within island systems (Romeiras et al., 2016b).

Macaronesia also served as the basis for developing successful innovative approaches for alien species management on islands, including prevention, early detection, eradication and control of invaders, as well as proper legislation. For instance, a list of the priority TOP 100 invasive alien species in Macaronesia has been compiled (Silva et al., 2008), based on their known impacts upon native and endemic biodiversity and the feasibility of successful control. Furthermore, the Canary Islands, Madeira and Selvagens have provided examples of successful eradication and control schemes for rabbits, cats, mice, and plants (e.g., Bell, 2001; Olivera et al., 2010). In the Azores, a regional programme to control invasive alien plants in sensitive areas has revealed the importance of maintenance to prevent alien regrowth (Costa et al., 2013).

Several initiatives and programmes have led to the successful restoration of different endemic and native species. One emblematic threatened species in Macaronesia is the Azorean endemic bullfinch (*Pyrrhula murina*), a species that has recovered through habitat restoration and removal of alien species ("LIFE Priolo" project; SPEA, 2006); such actions have led to positive impacts not only on the target species, but also on native plants, insects and birds (Heleno et al., 2010). The giant lizard *Gallotia simonyi* and the Raso lark *Alauda razae* are other threatened endemic species that have been the target of strong conservation actions, like breeding programmes and reintroductions in small islets and islands of the Canary Islands and Cabo Verde, respectively (Salvador, 2015; Brooke et al., 2020); recent innovative actions that will enhance future reintroductions of the giant lizards, include training procedures where individuals raised in captivity learn to avoid predators (Burunat-Pérez et al., 2018).

MACARONESIA AND FUTURE PROSPECTS IN ISLAND BIOLOGY

We have highlighted a large number of research questions addressed using Macaronesia as a natural laboratory. The comprehensive ecological and evolutionary datasets gathered so far in different studies have already proven essential for current understanding of island biology. Unfortunately, many extant and extinct species still remain undescribed and some environments underexplored (e.g., subterranean, marine), and thus our knowledge is far from complete in Macaronesia (Lobo and Borges, 2010). More efforts should be made toward gathering basic information on species taxonomy, distribution, abundance, evolution and ecology. Still, there are many research avenues to be explored (e.g., Santos et al., 2016; Patiño et al., 2017), and below we point out the importance of these archipelagos for pursuing them.

The proximity of some Macaronesian islands to the adjacent mainland provides a well-suited geological set-up for island-mainland comparisons, for instance to evaluate genetic diversity, gene-flow patterns and the importance of islands in generating mainland diversity. The genetic imprints of founder events and the impact of historical geological and climatic events (or their absence) can be tested with the increasing number of locally relevant population genetics and genomic datasets available, and applying approaches based on multitaxon comparisons that could help understand how much biotic interchange has occurred not only between islands and the mainland, but also between archipelagos (see e.g., Antonelli et al., 2018). Although ecological opportunities are considered as potential drivers of the remarkable radiations that occurred in the region, the degree to which isolation affects such speciation processes is still not entirely understood (Patiño et al., 2017). The combination of phylogenetic information and trait data that are increasingly becoming available in this region will allow understanding the processes behind niche evolution, particularly how labile and conserved ecological attributes, together with the availability of novel habitats, affect speciation and lineage diversification (see Edwards and Donoghue, 2013). The unique subterranean ecosystems and fossiliferous outcrops of Macaronesia are windows into past insular terrestrial and marine biotas, providing opportunities to evaluate the role of vacant ecological space, trait lability and isolation on diversification and speciation. Island-mainland comparisons can also be extended to different ecological questions, namely those related with the processes leading to community assembly and rarity (e.g., Santos et al., 2011; Borda-de-Água et al., 2017; Boieiro et al., 2018). Future research could therefore focus on comparing species-abundance distribution patterns between the two settings in order to understand the generality of such relationship (e.g., following, Borda-de-Água et al., 2017), or contrasting islands and mainland trait and phylogenetic diversity to ascertain which are the driving forces of community assembly (e.g., habitat filtering vs. competition; e.g., Santos et al., 2016). Another interesting and related topic is the study of the biodiversity-ecosystem functioning relationship; island-mainland comparisons can also be useful for understanding how systems with different species richness and trait diversity can provide the basic ecosystem services on which humans depend.

Research conducted in Macaronesia has been pivotal in understanding island mutualistic interactions. Further studies on interaction networks will shed new light onto how biotic interactions affect community assembly, immigration, and extinction on islands, and on how alien species become integrated into the receptive communities and impact species interactions. Further studies from other archipelagos will also confirm whether the network patterns found for the Macaronesian islands are general or rather idiosyncratic (first comparisons with the Galápagos suggest these patterns are not general). Evaluating how such patterns may have influenced colonisation/extinction dynamics or speciation rates are prominent avenues that might change our understanding of island biogeography (Nogales et al., 2016).

Some of the most pressing questions in current research agendas are linked to the impact of global change on biodiversity patterns and processes as well as on human well-being. Such efforts are devoted to developing management strategies that can safeguard biodiversity and ecosystem services (Butchart et al., 2010). The relatively well-known history of human settlement across the islands and associated land-use transformations aids in assessing the relative impacts of environmental (pre)historical, demographic, and socioeconomic changes on current island biodiversity (see for instance: Nogué et al., 2013, 2017, 2021; Norder et al., 2020). Alien species constitute one of the most important threats island biotas face (Russell and Kueffer, 2019). The simplified nature of island biotas might be essential for understanding how newly arrived species establish and affect existing species and ecosystems, and the implications of these novel species in conservation strategies. However, the precise impacts of novel native-alien interactions on island biodiversity and ecosystem functioning are still unclear (Patiño et al., 2017). Indeed, Lundgren et al. (2020) found that alien mammalian herbivores seem to have replaced some ecological functions that would otherwise be lost through the anthropogenic extinction of native species, a pattern that might not be extended to all island communities (e.g., Sobral et al., 2016). Long-term ecological data (see Van Leeuwen et al., 2005; Nogué et al., 2017) provide essential clues to disentangle the colonisation status of insular species and will contribute to progress in this research agenda.

CONCLUSION

Macaronesia has played a crucial role in the development of island biology. Research contributions in this region provide insights into ecological and evolutionary theories tested for other archipelagos (e.g., the General Dynamic Model of oceanic island biogeography, and its subsequent updates). Furthermore, political, scientific and social initiatives launched in Macaronesia to improve conservation practices and public awareness can be implemented in other regions, to assure the maintenance of biodiversity. However, knowledge of Macaronesia diversity is far from complete, and it is essential to continue gathering reliable data about species distribution to understand the relative importance of spatial, historical and ecological processes. Therefore, initiatives like long-term diversity studies need to be continued in Macaronesia, to obtain high quality data that will allow to widen knowledge of island biology in general.

DEDICATION

This article is dedicated to the memory of our co-author, Ana I. Neto. May she rest in peace.

AUTHOR CONTRIBUTIONS

MF led the manuscript writing, with significant contributions from AMCS, JP, SN, AT, PB, and HS. IRA led the subterranean biology group composed of PB, PC, PO, MA, and AM. RH led the marine biology group: AN, SÁ, and GM. AMCS led the community ecology group: JF-P, PB, and FR. PB led the biological conservation group composed of AG and RV. JP led the evolution group, comprising JCI, MR, HS, AVan, MA, and SG. MF led the freshwater biology group: PR and VG. AT led the plant-animal interaction and long-distance dispersal group: MN and AVal. MF led the biological invasion group: ML-D, LS, and MN. PB led the macroecology group, aided by PC. SN led the palaeobiology group: SÁ, JF-P, LN, and JR. All authors contributed to the drafts and gave final approval for publication.

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SUPPLEMENTARY MATERIAL

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