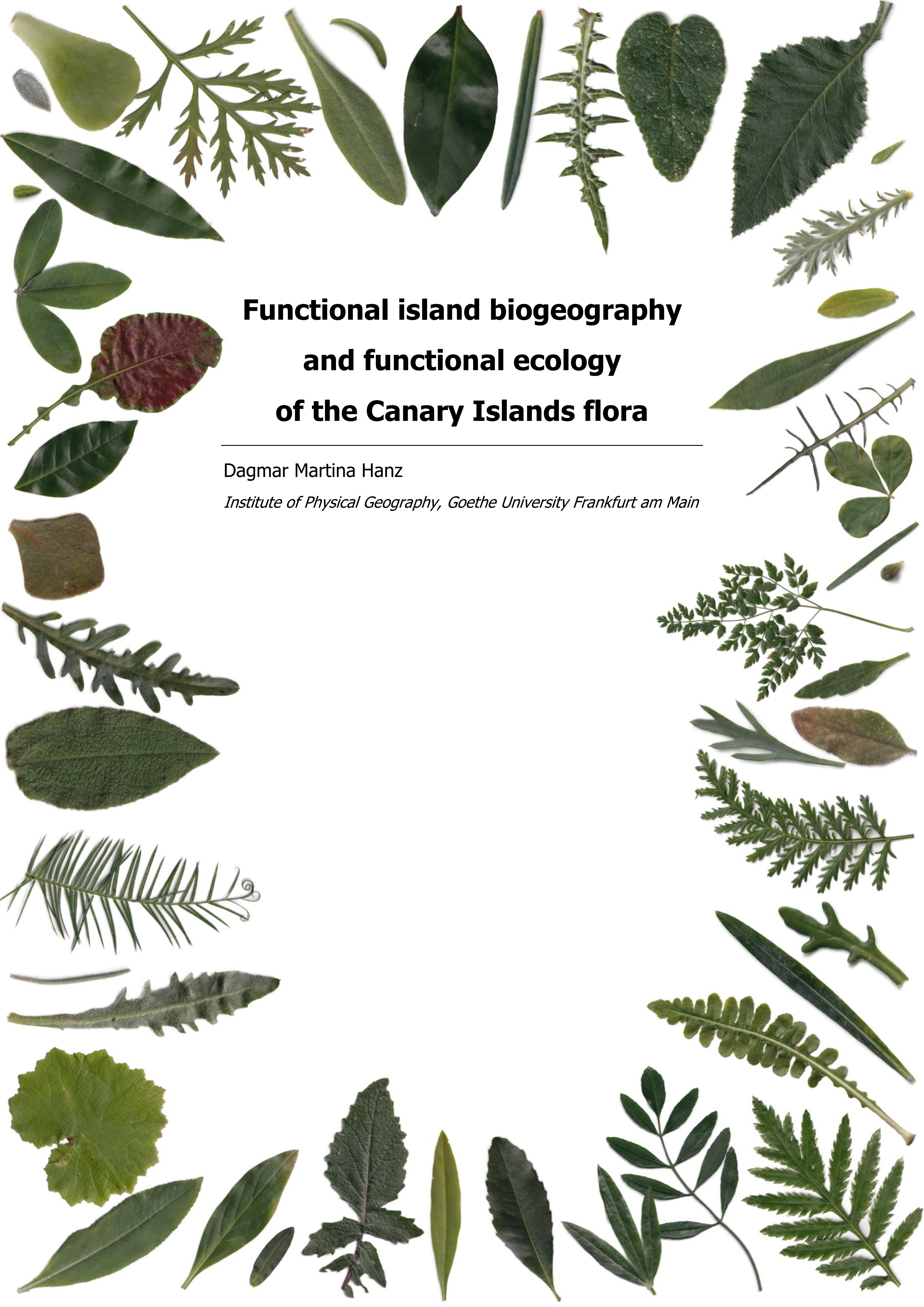

Functional island biogeography and functional ecology of the Canary Islands flora

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Functional island biogeography and functional ecology of the Canary Islands flora

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Chapter 1

Introduction

Left photo: Blooming *Aeonium appendiculatum* in the Barranco de Guarimiar on La Gomera, Canary Islands (own photo).

1.1 Functional island biogeography

Functional island biogeography studies eco-evolutionary processes in space and time in island biota using trait-based approaches (Ottaviani *et al.*, 2020; Schrader *et al.*, 2021). Functional traits can potentially inform us about the processes by which island life assembles as they indicate how species respond to the environment, interact with other species and influence ecosystem functions (Violle *et al.*, 2007; Cadotte *et al.*, 2015). Islands represent appropriate study systems to investigate patterns in functional traits and functional trait diversity as they generally offer extensive environmental gradients over a small spatial scale at different degrees of isolation (Whittaker & Fernández-Palacios, 2007). However, even though research of functional traits on islands promises novel insights into species assembly processes, few studies have investigated island biota on a functional level so far (e.g. Whittaker *et al.*, 2014; Zhao *et al.*, 2020; Kraemer *et al.*, 2022). Hence, in this dissertation, I tackle key questions in functional island biogeography concerning i) the establishment and succession of species, ii) the evolutionary shifts in traits and trait syndromes, and iii) the threat of species by global change (Patiño *et al.*, 2017; Ottaviani *et al.*, 2020; Schrader *et al.*, 2021). **Chapters 2, 3 and 4** address the effect of island isolation, heterogeneity, age and climate on trait composition and divergence. Moreover, **Chapters 2 and 3** focus on whether adaptive island radiations expand the functional trait space of endemic plant species. **Chapter 2** further assesses how the trait diversity of the native flora differs from the trait diversity of alien species. In **Chapter 4**, research on intraspecific variation in island plants is implemented, and **Chapter 5** dissects the use of scientific floras as sources for trait data. Lastly, **Chapter 6** discusses the potential impacts of climate change on the trait composition of island plants. All research questions of this dissertation aim to unravel biogeographical, ecological and evolutionary drivers that have shaped the functional trait composition of oceanic island floras to better understand and conserve the unique and vulnerable island life.

1.2 Oceanic islands as vulnerable biodiversity hotspots

Islands have been fundamental for developing biogeographical, ecological and evolutionary theories for centuries (Figure 1.1; Darwin, 1859; MacArthur & Wilson, 1967; Carlquist, 1974; Whittaker *et al.*, 2008). Islands comprise 6.7% of the Earth's land area (Sayre *et al.*, 2019) but harbour up to 20% of all terrestrial species and thereby contribute disproportionally to global biodiversity (Kier *et al.*, 2009). Particularly oceanic islands (i.e. islands that have never been connected to a continent) act as evolutionary motors through their isolation, environmental heterogeneity and sequential emergence (Whittaker & Fernández-Palacios, 2007). They harbour native species which initially colonised from the mainland and overcame strong dispersal and environmental filters, as well as endemic species that have evolved from native species and, in parts, strikingly radiated into island lineages (Baldwin & Sanderson, 1998; Losos & Ricklefs, 2009). Moreover, Palearctic oceanic islands have acted as climate refugia in the past, particularly during the Pleistocene, ensuring the persistence of specific paleoendemic taxa (Cronk, 1997; Fernández-Palacios *et al.*, 2011). Hence, oceanic islands are characterised by their (relict) endemic species richness and their uniquely unbalanced composition of taxonomic and functional groups (Carlquist, 1974; Taylor *et al.*, 2019; König *et al.*, 2021).

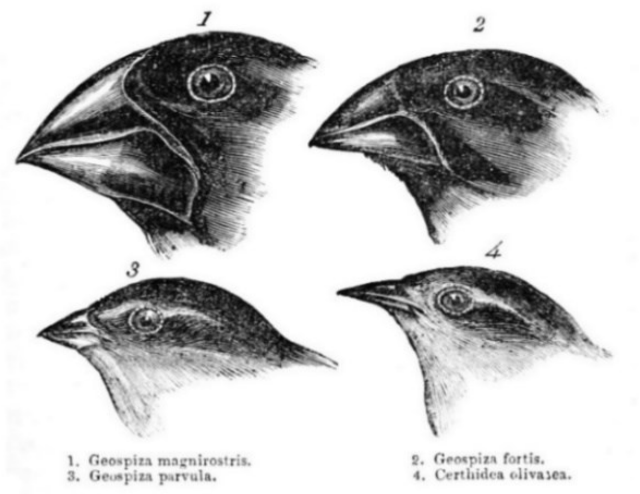

Figure 1.1 Sketches of 'Darwin's finches' (Geospizinae) by Charles Darwin. The sketches were drawn during his stay on the Galápgagos Islands (Darwin, 1859). These passerine birds are the most prominent example of evolutionary radiation on oceanic island archipelagos.

Even though islands are biodiversity cradles, island biota's extinction rates are disproportionally high (Fernández-Palacios *et al.*, 2021). Today, 50% of all recognised threatened species worldwide are island biota, primarily endangered by habitat loss, resource exploitation, invasive species and climate change (Figure 1.2; Fernández-Palacios *et al.*, 2021). Inherent characteristics, such as small population sizes, low habitat availability and low genetic variation, cause endemic island species to be particularly vulnerable (Frankham *et al.*, 2002). Moreover, island endemic species are often characterised by specific trait characteristics ('island syndromes'), which can reinforce their vulnerability (Fernández-Palacios *et al.*, 2021). Plants' most prominent examples of island syndromes include altered dispersal ability (Carlquist, 1974; Burns, 2019), insular woodiness (Darwin, 1859; Carlquist, 1974; Lens *et al.*, 2013; Burns, 2019) and morphological gigantism and dwarfism (Biddick *et al.*, 2019; Burns, 2019). The inherent vulnerability and the unprecedented loss of island biota lead to the conclusion that extensive research is needed to elucidate island species' conservation potential to prevent further biodiversity loss.

Figure 1.2 a) *Isoplexis sceptrum*, an endangered plant species endemic to northern Madeira (own photo). The species occurs in fewer than five locations on the island. **b)** *Phelsuma inexpectata* is a critically endangered gecko endemic to the highly fragmented coastal areas in Manapany-Les-Baines and St.-Joseph on Réunion (own photo).

1.3 Alien species on oceanic islands

Besides endemic and non-endemic native species, islands harbour alien species. For centuries humans have intentionally or unintentionally introduced alien species to islands worldwide (Dawson *et al.*, 2017; Seebens *et al.*, 2017). Some alien species become established through regular reproduction, and a subset of those species become invasive due to the ability to spread over long geographic distances (Richardson *et al.*, 2000; Pyšek *et al.*, 2004). Another, more anthropocentric, definition declares those species as invasive that harm the economy, environment or health of human beings (IUCN, 2000). On islands, alien species have been disproportionally introduced (van Kleunen *et al.*, 2015), posing direct and indirect risks to native species and the functioning of ecosystems (Pyšek *et al.*, 2020). Even though alien species increase the extinction risk of island biota, their extent and negative impact are expected to expand due to rising import volumes and human mobility (Seebens *et al.*, 2017). The success of alien species has been notably attributed to trait differences between native and alien species (*limiting similarity hypothesis*; Hutchinson, 1959; MacArthur & Levins, 1967) and vacant niches on islands (Elton, 1958). However, the concept of trait similarity has also received attention, suggesting that alien species succeed due to their pre-adaptation to the local environment (*environmental filtering hypothesis*; Keddy, 1992; Cornwell *et al.*, 2006). Hence, the establishment success of alien species on islands might be predicted by how alien species compare to native species. Comparing trait characteristics of endemic, non-endemic native, and alien species could offer novel mechanistic insights into the processes influencing island biodiversity patterns.

1.4 The relevance of functional traits

Analysing functional traits, i.e. measurable characteristics that strongly influence a species' fitness (McGill *et al.*, 2006), is a promising avenue in island biogeographic research (Patiño *et al.*, 2017; Ottaviani *et al.*, 2020; Schrader *et al.*, 2021), and can offer a cross-taxonomic insight into ecological processes (Díaz *et al.*, 2016). On continents, functional trait-based studies on plants have provided novel insights into global drivers of growth height (Moles *et al.*, 2009), the wood economic spectrum (Chave *et al.*, 2009), leaf size and the leaf economic spectrum (Wright *et al.*, 2004, 2017), the flower economic spectrum (Roddy *et al.*, 2021) and seed size (Moles *et al.*, 2006). The knowledge gained about trait-trait correlations and trade-offs has helped to unravel how environmental factors influence functional trait patterns of species (Ordoñez *et al.*, 2009). Moreover, functional traits have been used to calculate functional diversity, i.e. the diversity and distribution of functional traits in a species assemblage, on continents (Díaz & Cabido, 2001; Bruelheide *et al.*, 2018). However, the results of continental studies might not converge to islands as island plants tend to have distinct taxonomic and functional compositions from continents due to the effect of insularity (Figure 1.3; Carlquist, 1974; Burns, 2019; Taylor *et al.*, 2019). Understanding the ecological processes that drive functional trait patterns on islands is particularly important considering island biota's disproportional extinction rates. With the extinction of species, functions that a species fulfils in an ecosystem can be irretrievably lost (Petchey & Gaston, 2002). The loss of species' functions can have cascading effects on interaction networks, potentially influencing entire trophic chains and ecosystem functions (Díaz & Cabido, 2001;

Cadotte *et al.*, 2011; Schleuning *et al.*, 2016). Despite the imminent threat of island biota, functional trait-based studies of island biogeography are scarce and often restricted to particular taxonomic groups and geographic areas. Hence, research studies using comprehensive trait data across large spatial and temporal scales are needed to better understand island biota's functional peculiarities.

Figure 1.3 The habit of **a)** *Sonchus oleraceus*, a herbaceous continental species (photo: Boris Gaberščček), and **b)** *Sonchus fruticosus*, a woody Madeira endemic species (own photo). S. *fruticosus* belongs to the woody *Sonchus* alliance, a paradigm of island woodiness, which illustrates that results from trait-based studies on continents might not converge to islands.

1.5 Functional trait evolution of oceanic island floras

Island endemic species have evolved in isolation and bear the potential to shift functionally from their ancestors (Burns, 2019). Functional shifts are commonly attributed to cladogenesis and, to a lesser extent, to anagenesis (Emerson & Gillespie, 2008; Rundell & Price, 2009). Cladogenesis is defined as the speciation of independent lineages via lineage splitting from a single ancestor (Stuessy *et al.*, 1990) and is often connected to adaptive radiation (Stuessy *et al.*, 2006). Anagenesis is the gradual evolution of a single lineage through time (Stuessy *et al.*, 2006). So far, it has been proposed that cladogenesis is high on environmentally heterogeneous oceanic islands (such as Hawaii and the Canary Islands; Stuessy *et al.*, 2006) due to the availability of ecological opportunities (i.e. empty niches; Gillespie & Baldwin, 2009). A prominent example of cladogenesis and adaptive radiation are the lobelioids (Givnish *et al.*, 2009) in Hawaii and the *Echium* alliance (Böhle *et al.*, 1996) in the Canary Islands. However, it remains elusive whether cladogenetic species have functionally diverged by occupying unexplored regions of niche space on oceanic islands (sensu MacArthur, 1965). Similarly, it has not been explored whether anagenetic species have functionally converged and are more densely packed in niche space (sensu Klopfer & MacArthur, 1961). Moreover, it is unclear whether the lower species richness on islands compared to the mainland (Whittaker & Fernández-Palacios, 2007; Kreft *et al.*, 2008) results in weaker inter-specific competition (Schluter, 1988) and consequently reduces the overall selective pressure of trait divergence in endemic species. Hence, the link between *in situ* speciation, species traits and the environment has not been elucidated yet. A comprehensive cross-taxonomic study of endemic and non-endemic species (i.e. species that have not evolved *in situ*) is needed to understand how the environment influences trait evolution on oceanic islands.

1.6 Plant functional traits and the oceanic island environment

The *Theory of Island Biogeography* states that island isolation and area highly influence life on oceanic islands (MacArthur & Wilson, 1967). Immigration, speciation and extinction are affected by these parameters so that larger and less isolated islands harbour more species whereas small and more isolated islands obtain fewer colonising species. MacArthur & Wilson (1967) have developed this theory under the assumption that colonisation and extinction reach an equilibrium, but did not consider that island area is transient over geological timescales (Whittaker *et al.*, 2008). Island area changes over an island's ontogeny from low environmental heterogeneity at a very young age, over a peak in heterogeneity at mid-age, to a small and homogenous environment when islands become eroded (Whittaker *et al.*, 2008). Hence, immigration, speciation and extinction dynamically change the diversity of island biota throughout an island's ontogeny (*General Dynamic Model*; Whittaker *et al.*, 2008). Even though the *General Dynamic Model* and the *Equilibrium Theory of Island Biogeography* are essential for understanding species assemblage processes, these theories assume species are functionally equivalent. However, functional traits of plants are expected to play a vital role in immigration, speciation and extinction on islands (Schrader *et al.*, 2021). Immigration success should decrease with increasing isolation and depend on colonisers' ability to disperse over long distances (MacArthur & Wilson, 1967; Weigelt & Kreft, 2013). Hence, species characterised by functional traits that lower the settling velocity of diaspores are more likely to colonise isolated oceanic islands (Venable & Brown, 1988; Greene & Johnson, 1993; Thomson *et al.*, 2011). Moreover, speciation rates should be higher in geographically isolated and topographically complex areas that potentially limit gene flow between populations (Herrera & Bazaga, 2008; Losos & Ricklefs, 2009; Marques *et al.*, 2019). Topographically complex areas also offer a greater range of resources and more distinct habitats and climates for speciation (Keppel *et al.*, 2016; Barajas-Barbosa *et al.*, 2020). However, the *species-area relationship* predicts that the amount of species inhibits species' diversification in topographically complex areas because the virtual area of single habitats is reduced (Allouche *et al.*, 2012; Triantis *et al.*, 2012). Speciation rates should also be higher on mid-aged islands, as environmental heterogeneity usually peaks when islands have formed rugged landscapes, but long-term erosion does not yet prevail (Steinbauer *et al.*, 2013; Barajas-Barbosa *et al.*, 2020). Hence, the evolution of functional traits on islands should be tightly linked to island biogeographical variables. However, so far, the combined impact of island isolation, area and age on the functional trait composition of island floras has not been assessed (but for area–functional trait relationships, see Whittaker *et al.*, 2014).

Some oceanic islands are characterised by highly heterogeneous environments over short geographic distances and reveal an extensive gradient of temperature and water availability, particularly if the islands coincide with orographic precipitation regimes (Kier *et al.*, 2009; Weigelt *et al.*, 2013; Garzón-Machado *et al.*, 2014). This environmental heterogeneity potentially bears highly diverse functional trait compositions in species assemblages (Ordoñez *et al.*, 2009; Bjorkman *et al.*, 2018; Bruelheide *et al.*, 2018). Notably, climate is a well-known driver of functional trait variation and is primarily attributed to environmental filtering by the physiological constraints of biota (Spasojevic *et al.*, 2014).

The *environmental filtering hypothesis* states that only species with specific functional adaptations can survive under intense environmental pressure (Cornwell *et al.*, 2006; Cornwell & Ackerly, 2009; Laliberté *et al.*, 2013b), i.e. species with water-efficient traits in arid environments. This filtering mechanism suggests a functional trait convergence between species under unfavourable environmental conditions. However, unfavourable environments are also expected to increase intraspecific trait variation due to increased expression in genetic variability under stress (Hoffmann & Merilä, 1999). In contrast, resource-rich environments might offer many functional niches facilitating functional specialisations through competition (Mason *et al.*, 2011; Laliberté *et al.*, 2013b; Schellenberger Costa *et al.*, 2018a). However, climate could also shape functional trait variation in island floras due to the functional adaptation of species to the distinct climate they radiated in (Borregaard *et al.*, 2016). In fact, island endemics are abundant in marginal habitats (Fernández-Palacios *et al.*, 2021) and high-elevation environments (Steinbauer *et al.*, 2016b), usually expected to be shaped by environmental filtering processes. Even though climatic drivers of functional traits are well established on continents, it is unclear whether island floras respond functionally similar to climatic gradients due to their *in situ* speciation and potential *per se* functional specialisation.

In contrast to native island biota, alien species on islands have not undergone *in situ* speciation or a dispersal filtering and should not respond strongly to island biogeographical variables. Most alien species have been introduced by humans to easily accessible areas at lower elevations on oceanic islands (e.g. harbours and airports), typically associated with arid climatic conditions (Pauchard *et al.*, 2009). Hence, alien species richness is usually highest at lower elevations and decreases unidirectional with distance from the source of introduction. The concept of *directional ecological filtering* stresses that particularly alien species with narrow environmental niches are selectively filtered out along this gradient with the result that alien specialists are underrepresented under harsh environmental conditions in high elevation habitats (Alexander *et al.*, 2011). The filtering of alien plants on islands is most prominently driven by precipitation (Irl *et al.*, 2021), indicating that functional trait combinations of alien species are expected to be more diverse in arid species assemblages. However, whether alien plants are functionally filtered by the island environment and how functional trait patterns of aliens relate to those of native island plants remains to be tested.

1.7 Functional trait variation in island plants

A change in functional trait composition cannot only be caused by species turnover but also by intraspecific trait variability or a hybrid of these factors (De Bello *et al.*, 2011; Lepš *et al.*, 2011). In fact, intraspecific trait variation is vital for species to be able to respond to a changing environment (Norberg *et al.*, 2001; Björklund *et al.*, 2009; Lepš *et al.*, 2011). However, most studies assume that across species assemblages, turnover is prevalent over intraspecific trait variation, ignoring a possible trait and niche overlap between species (e.g. Keddy, 1992; Weiher *et al.*, 1998; Kraft *et al.*, 2015). Studies that have analysed species turnover and intraspecific variation across species assemblages do not agree on the ratio of species turnover to intraspecific variation (Albert *et al.*, 2010; Messier *et al.*, 2010; De Bello *et al.*, 2011; Violle *et al.*, 2012). Oceanic island floras could offer new insights into the relevance and drivers of intraspecific variation as they harbour species of different evolutionary origins. For endemic species that have undergone *in situ* speciation, species turnover could be more relevant in response to the environment because *in situ* speciation is expected to result in specialised adaptations to local environmental conditions (Carlquist, 1974; Burns, 2019). However, for non-endemic species, which are characterised by a larger genetic pool and higher associated phenotypic plasticity (Alexander & Edwards, 2010), intraspecific variation could be more relevant in response to environmental variation.

1.8 Accessibility and quality of trait data for oceanic island floras

The need to systematically describe and functionally classify plant species goes back to Theophrastus (ca. 300 B.C.). In his Enquiry into Plants (*Historia Plantarum*), Theophrastus classified plants primarily based on height and woodiness (Figure 1.4; Morton, 1981). Since then, many more detailed functional classifications have been developed to find general patterns and drivers of biodiversity through time and space (e.g. Raunkiær, 1934; Weiher *et al.*, 1999; McGill *et al.*, 2006) so that the demand for plant trait data has vastly risen (Kattge *et al.*, 2020). However, direct trait measurements in the field or under experimental conditions demand high cost and time and are often unavailable. Global plant trait databases offer information about various functional traits, making them more accessible to researchers worldwide (Kleyer *et al.*, 2008; Kattge *et al.*, 2020; Weigelt *et al.*, 2020). Nevertheless, global trait databases are highly biased, and many species and regions are underrepresented, particularly oceanic island floras. Due to this bias in global trait databases, scientific floras have further been used to answer diverse ecological questions (e.g. Whittaker *et al.*, 2000; Hawkes, 2007; Kissling *et al.*, 2008, 2010). Scientific floras offer a potential source for representative and complete trait data across large spatial and taxonomic scales (König *et al.*, 2019). Hence, using scientific floras could potentially answer novel trait-based research questions in island biogeography, but their reliability has yet to be assessed.

Figure 1.4 From Theophrastus to modern scientific floras: **a)** The cover of an illustrated version of *Historia Plantarum* by Theophrastus (1644) and **b)** the cover of an up-to-date scientific flora for the Canary Islands by Muer *et al.* (2016).

1.9 Impact of climate change on oceanic island floras and their functional traits

Due to their inherent vulnerability, extinction risks are much higher for island biota than for continental species and are further exacerbated by anthropogenic activities (Fernández-Palacios *et al.*, 2021). Besides habitat loss, resource overexploitation and invasive species, climate change is one of the leading anthropogenic threats to biodiversity on islands (Bellard *et al.*, 2012). The Intergovernmental Panel on Climate Change (IPCC) projections expect an increase in temperature and alterations in precipitation patterns by the end of the 21st century (IPCC, 2021). The most prevalent response of biota to climate change is spatial redistribution (Pecl *et al.*, 2017). However, area is limited on islands, and a latitudinal migration is mostly impossible (Gillespie *et al.*, 2008). Hence, species are forced to shift their elevational range, but this might only be possible on more complex and highly elevated islands (Harter *et al.*, 2015). Moreover, due to their evolution in isolation, island biota is often adapted to specific environmental conditions leaving them with narrow realised ecological niches (Thuiller *et al.*, 2005; Fortini *et al.*, 2013). Hence, the ongoing climate change is expected to exacerbate the already high vulnerability of island biota (Gillespie *et al.*, 2008; Fortini *et al.*, 2013), especially of single-island endemic species, which are often characterised by small population sizes and low habitat availability.

Most climate change studies on islands have focused on changes in taxonomic and phylogenetic diversity (Harter *et al.*, 2015; Veron *et al.*, 2019). However, climate change might have even more severe impacts on the functional composition of island floras. A prominent example of functional adaptation to insular environments, in particular climate, is insular woodiness. Insular woody species have been shown to have evolved from herbaceous ancestors under drought stress to avoid hydraulic dysfunction (Lens *et al.*, 2013; Dória *et al.*, 2018; Hooft van Huysduynen *et al.*, 2021; Zizka *et al.*, 2022). However, rapid climate change might pose an increased risk to insular woody species as woodiness is correlated with plant longevity and longer generation times (Smith & Donoghue, 2008; Givnish, 2010). Hence, a time lag in the response of woody plants to climate change can be expected (Kissling *et al.*, 2010). The example of insular woodiness demonstrates that a trait-based framework to predict the extinction risk of island biota and species most susceptible to extinction is urgently needed. In fact, future projections of functional trait changes can enable the assessment of potential consequences of different scenarios of future climate change to emphasize the urgency of climate change mitigation. However, research on the impact of environmental conditions and changes in environmental conditions on functional traits is often unavailable, particularly for oceanic islands.

1.10 The Canary Islands as a model system for trait-based studies

The Canary Islands (Spain) are, without a doubt, one of nature's excellent laboratories. The archipelago offers a wide range of geological and climatical gradients combined with defined boundaries that have brought forward an evolutionary and ecological unique flora. This distinct combination of abiotic characteristics makes the flora of the Canary Islands ideal for studying biogeographical research questions on plant functional traits.

Geography and Geology

The Canary Islands are an active volcanic archipelago located off the north-western coast of Africa (Figure 1.5). The archipelago consists of seven major islands: Fuerteventura, Lanzarote, Gran Canaria, Tenerife, La Gomera, La Palma and El Hierro. The easternmost islands (Fuerteventura and Lanzarote) are approximately 100 km off the African coast, whereas the westernmost island (El Hierro) is about 600 km off the African coast. Mount Teide reaches the maximum elevation of the archipelago on Tenerife at 3,718 m above sea level (m a.s.l from here on; Figure 1.6a). The lowest islands are Fuerteventura and Lanzarote (highest peak = 807 m a.s.l.). The Canary Islands are independent units, except for Lanzarote and Fuerteventura, which were united as the paleo-island "Mahan".

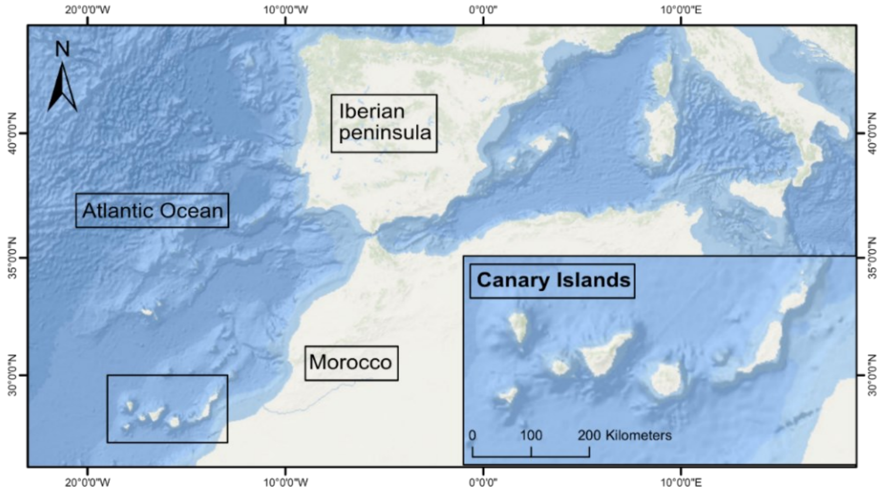

Figure 1.5 The Canary Islands are situated in the Atlantic Ocean off the north-western coast of Africa. Source of map: Esri, Garmin, GEBCO, NOAANGDC, and other contributors.

Due to the dynamic nature of oceanic archipelagos, each island consists older eroded and younger terrain, leading to great environmental heterogeneity (Barajas-Barbosa *et al.*, 2020), particularly on emerging islands like La Palma and Tenerife. On these islands, erosive valley structures (*barrancos*) and steep coastal cliffs mix with softer geomorphological features, such as lava fields (Figure 1.6b). Even though the Canary Islands are up to 23 Myr old, all islands, except for La Gomera, are volcanically active and display different phases of island ontogeny (Fernández-Palacios *et al.*, 2011; van den Bogaard, 2013). Lanzarote, Tenerife, and La Palma had historical eruptions (i.e. during the past 500 years), with the last volcanic eruption having occurred on La Palma from September to December 2021.

Climate

The Canary Islands are characterised by a Subtropical-Mediterranean climate (del Arco Aguilar *et al.*, 2010). The average temperature decreases gradually from the inframediterranean zone (18-22°C), over the thermo- and mesomediterranean zone (11-18°C) up to the supra- and oromediterranean zone (4-11°C) (Figure 1.6c; del Arco Aguilar *et al.*, 2010). The five higher islands (>1450 m) are influenced by rain shadow effects from the NE trade winds so that the amount of precipitation differs eminently between the northern and southern sections of these islands (Figure 4b). Due to a cloud layer formation ("sea of clouds"), the north-eastern flanks of these islands receive humidification via fog rain. Within the higher islands, humidity varies from an arid coast, through moderately temperate mountainous areas up to (sub-)alpine climate zones above the cloud layer (Figure 1.6d; del Arco Aguilar *et al.*, 2010). Fuerteventura and Lanzarote are lower than the NE trade winds, with the result that cloud layers cannot be formed, and less environmental variation is exhibited. The formation of cloud layers can be disrupted by Saharan weather in which dry and hot African wind and atmospheric dust haze ("calima") cause temperature to increase and relative humidity to massively decrease (del Arco Aguilar *et al.*, 2010).

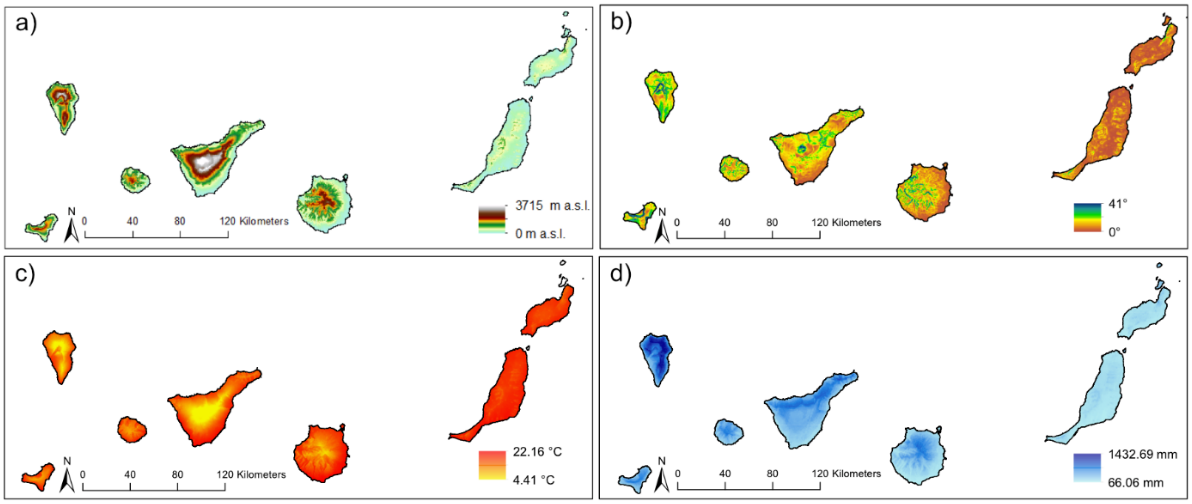

Figure 1.6 a) Elevation, **b)** slope, **c)** mean annual temperature and **d)** annual precipitation across the Canary Islands. The digital elevation model was provided by Cartográfica de Canarias (GRAFCAN). The climatic variables were interpolated by Irl *et al.*, (2020) on a 500 m x 500 m grid cell scale from a dense net of climate measurements (n = 155 for temperature and n = 305 for precipitation) provided by the Agencia Estatal de Meterología (AEMET).

Vegetation

The Canary Island flora comprises about 2,400 species, of which about 60% is considered native, c. 42% of the native flora endemic, and 40% alien (Beierkuhnlein *et al.*, 2021). Many species in the infra- and thermomediterranean zone, like *Aeonium*, *Euphorbia balsamifera* and *Euphorbia canariensis*, are associated with the xerophilous Rand Flora (del Arco Aguilar *et al.*, 2010). Trees like *Apollonias barbujana*, *Laurus azorica*, *Persea indica* and *Ocotea foetens* and ferns of the laurel forests are remnants of the evergreen broad-leaved forests that were once widespread in the Pliocene but retreated to the Canary Islands which offered climate refuge in the Pleistocene (Fernández-Palacios *et al.*, 2011; but see Kondraskov *et al.*, 2015). However, most of the native flora of the Canary Islands is of Mediterranean origin, like the non-endemic native *Pistacia lentiscus* or endemics such as *Echium* spp., *Sonchus* spp., *Micromeria* spp., Sideritis spp. or *Teline* spp. (Carine *et al.*, 2010). Many widely diversified genera derive from a single colonizing ancestor and result from spectacular adaptive radiations, e.g. *Aeonium*, *Argyranthemum*, *Echium*, *Micromeria*, *Sonchus* and *Tolpis* (Figure 1.7; Schenk, 2021). Alien species have been introduced to the Canary Islands since the arrival of European settlers in the 15th century. They include many American plants like *Opuntia* spp., *Ageratina* spp., and *Agave* spp.

Figure 1.7 Some species of the genus *Aeonium* illustrating the spectacular *in-situ* radiations on the Canary Islands (own photos). Row-wise from left to right: *Aeonium nobile*, *Aeonium canariense* subsp. *christii*, *Aeonium diplocyclum*, *Aeonium spathulatum*, *Aeonium appendiculatum*, *Aeonium saundersii*, *Aeonium davidbramwelii*, *Aeonium lindleyi*, *Aeonium sedifolium*, *Aeonium arboretum*, *Aeonium goochiae*, *Aeonium gomerense*.

The vegetation of the Canary Islands displays a marked zonal distribution into elevational belts (Fernández-Palacios & Nicolás, 1995; del Arco Aguilar *et al.*, 2010). These belts are unevenly distributed as the northern slopes give rise to a humid zone with its own vegetation type, the laurel forest. In general, six major terrestrial vegetation types can be distinguished: coastal *Euphorbia* scrub and shrublands, thermo-sclerophyllous woodlands, laurel forest, pine forest, summit scrub and Teide violet community (Figure 1.8; del Arco Aguilar *et al.*, 2010). Rock communities, specifically rich in endemic species, can be found throughout the elevational belts. However, the natural plant communities have been changed drastically by intense landscape alterations and the introduction of alien species since the prehistoric human settlement of the "Guanches" but especially since European settlers arrived in the Canary Islands (del Arco Aguilar *et al.*, 2010; de Nascimento *et al.*, 2020). Hence, a network of protected natural areas, including four National Parks, has been constituted for the conservation of nature in the Canary Islands.

Figure 1.8 Collage of the six major vegetation types of the Canary Islands after del Arco Aguilar *et al.*, (2010; own photos). The *Euphorbia* scrub and shrublands are succulent communities of the lower zone. Characteristic species are, e.g. *Euphorbia balsamifera* and *Euphorbia canariensis*. The thermo-sclerophyllous woodland of the insular midlands is characterised by *Juniperus turbinata* but also includes *Phoenix canariensis* palm communities. The laurel forest (*laurisilva*) is characteristic of the north-eastern midlands, which are influenced by trade-wind clouds. The most prominent tree species of the laurel forest is *Laurus novocanariensis*. The Canary pine forest grows above the cloud zone in the north and above the thermo-sclerophyllous woodland in the south. It is characterised by *Pinus canariensis*. The summit scrub occurs on La Palma and Tenerife above 2,000 m a.s.l. by legume scrubs, such as *Adenocarpus viscosus*. The Teide violet community grows above 2,700 m a.s.l. on the slopes of Mount Teide, Tenerife and is named after *Viola cheiranthifolia*.

1.11 Research goal and questions

This dissertation aimed to evaluate the patterns and drivers of functional plant traits on oceanic islands, using the Canary Islands' flora as a model system. For this, the influence of ecological, climatic, and biogeographical factors on functional plant traits on islands were considered. To achieve this goal, five main research questions (Figure 1.9), which fit within the framework of the proposed fundamental questions in island biology (Patiño *et al.*, 2017) and functional island biogeography (Ottaviani *et al.*, 2020; Schrader *et al.*, 2021), were developed. The first question (**Chapter 2**) examines how climatic and biogeographical factors drive the functional diversity of entire oceanic island floras. The second question (**Chapter 3**) is directed towards rare climates and whether they yield trait distinctiveness in oceanic island floras. The third question (**Chapter 4**) addresses the differences and similarities of island endemic and non-endemic species in terms of their inter- and intraspecific trait variation. The fourth question (**Chapter 5**) explores whether scientific floras can be alternative or additional sources for trait data in areas with poor data availability, i.e. oceanic islands. Finally, the fifth question (**Chapter 6**) aims to answer how climate change might impact the functional trait composition of native species on oceanic islands in the future. To answer these questions, new concepts were developed by combining trait-based approaches with island biogeography theories. I have structured my dissertation into five research articles, of which I am the first author of three (Hanz *et al.*, 2022a,b, in preparation) and two of which I am the second author (Cutts *et al.*, 2021; Cutts *et al.*, in review).

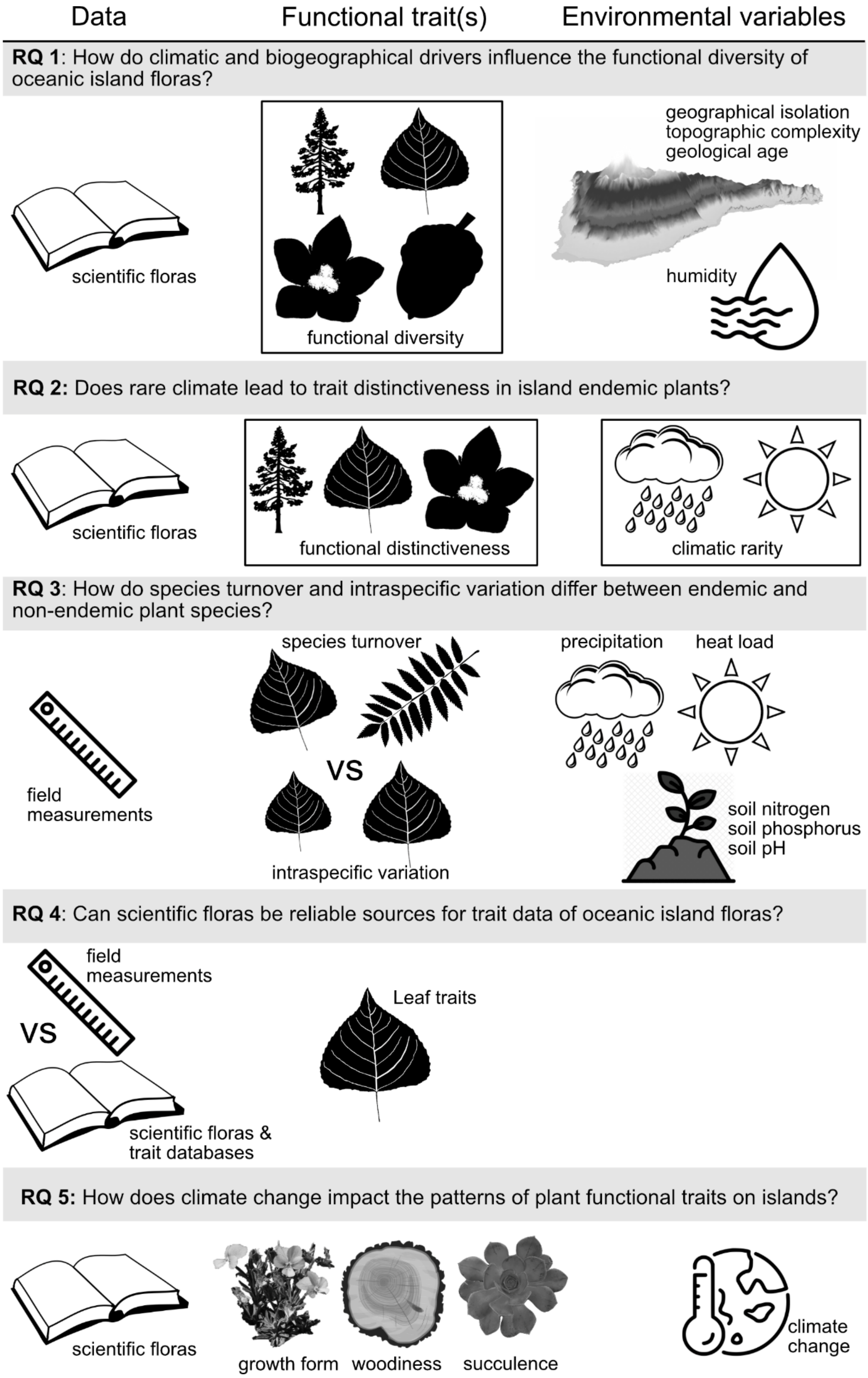

Figure 1.9 Schematic representation of the dissertation. I developed five main research questions to study plant functional trait patterns on the Canary Islands. (1) How do climatic and biogeographical drivers influence the functional diversity of oceanic island floras? (2) How does rare climate lead to trait distinctiveness in island endemic plants? (3) How do species turnover and intraspecific variation differ between endemic and non-endemic plant species? (4) Can scientific floras be reliable sources for trait data of oceanic island floras? (5) How does climate change impact the patterns of plant functional traits on islands? Trait silhouettes were retrieved from phylopic.org.

RQ 1: How do climatic and biogeographical drivers influence the functional diversity of oceanic island floras?

Classic island biogeography theories predict how species richness changes across various environmental gradients, given that species are functionally equivalent (MacArthur & Wilson, 1967; Whittaker *et al.*, 2008). However, species can possess distinct or redundant functional roles in an assemblage (Díaz & Cabido, 2001; Kattge *et al.*, 2020). To assess how species of different evolutionary origins functionally respond to environmental gradients, we analysed the functional diversity of endemic, non-endemic native and alien plant species assemblages on the Canary Islands and related the resulting patterns to climatic and island biogeographical gradients (**Chapter 2**; Hanz *et al.*, 2022b). First, we predicted that decreasing resource availability decreases the functional diversity of endemic and non-endemic native species assemblages due to environmental filtering (Spasojevic *et al.*, 2014). Based on island biogeographical theory, we further predicted a positive relationship between functional diversity and geographical isolation for endemic assemblages and a negative relationship for non-endemic assemblages. Our hypothesis is based on the theory that endemic species might have predominantly radiated in geographically isolated areas (Steinbauer *et al.*, 2012). In contrast, non-endemic native species had a greater probability of dispersal into less-isolated areas (MacArthur & Wilson, 1967; Weigelt & Kreft, 2013). Moreover, we hypothesised that endemic and non-endemic species assemblages have a hump-shaped relationship with topographic complexity and geological age. Topographic complex areas offer more habitats for species to radiate (Keppel *et al.*, 2016; Barajas-Barbosa *et al.*, 2020) but can also limit species diversification as the effective area of habitats is reduced with increasing complexity of an area (Allouche *et al.*, 2012). Additionally, it has been shown that young and old soils are depleted of nutrients (Lambers *et al.*, 2008; Laliberté *et al.*, 2013a), indicating that island age can filter plant functional compositions. We predicted a strong relationship of functional diversity patterns with elevation and climate for alien species assemblages due to directional ecological filtering (Alexander *et al.*, 2011) by water availability (Irl *et al.*, 2021).

RQ 2: Does rare climate lead to trait distinctiveness in island endemic plants?

Island endemic species are often associated with unique and distinct adaptations to the environments they evolved in (Carlquist, 1974; Burns, 2019). However, it is unclear whether these environments have brought forward species that are functionally distinct from their colonising ancestors. In this study, we used plant trait data to quantify functional distinctiveness for endemic and non-endemic species in the Canary Islands (**Chapter 3**; Cutts *et al.*, in review). Then, we linked species' functional distinctiveness to the mean climatic rarity of each species range. Because climate is known to influence trait distinctiveness (Raphael *et al.*, 2007), we expected that endemic species, which occur in climatically rare habitats, have become functionally distinct. We established our hypothesis under the premise that endemic species have adapted to their environment during speciation. Due to a lack of *in situ* speciation in non-endemic species, we did not expect to see a link between functional distinctiveness and climatic rarity within this floristic group.

RQ 3: How do species turnover and intraspecific variation differ between endemic and non-endemic plant species?

Trait variation in species communities can occur as species turnover and intraspecific variation and can influence plant assemblage dynamics to different extents (De Bello *et al.*, 2011; Lepš *et al.*, 2011). However, so far, it remains unclear how species turnover and intraspecific variation influence total trait variation. To assess how community assemblage patterns differ between endemic and non-endemic species in terms of species turnover and intraspecific trait variation, we established sampling sites along a directional environmental gradient on the oceanic island La Palma, Canary Islands (**Chapter 4**; Hanz *et al.*, 2022a). Within these sites, we recorded species abundances and measured traits for 1,223 plant individuals of 43 species. First, we hypothesized that trait variation in endemic assemblages mainly depends on species turnover, not intraspecific variation, due to the *in situ* speciation of endemics. Second, we hypothesized that species turnover and intraspecific variation decrease with limited resource availability in endemic and non-endemic plant assemblages due to environmental filtering.

RQ 4: Can scientific floras be reliable sources for trait data of oceanic island floras?

The demand for trait data is increasingly popular in ecology and biogeography as trait-based approaches can help to find general patterns and drivers of biodiversity and ecosystem functions (Díaz *et al.*, 2016; Bruelheide *et al.*, 2018). However, collecting quantitative trait data often relies on extensive fieldwork which may result in limited or biased data collection. Therefore, we tested whether trait information from scientific floras and global plant trait databases is as reliable as trait values measured in the field (**Chapter 5**; Cutts *et al.*, 2021). We used the Canary Islands as a study system because of the islands' evolutionary and ecological unique flora, and because of the rarity of trait-based research on islands (Ottaviani *et al.*, 2020; Schrader *et al.*, 2021). We specifically focused on leaf traits in our analyses as leaves fulfil core functions, such as carbon acquisition and transpiration (Press, 1999). We anticipated that leaf area, approximated by using leaf length and width, strongly correlates with field-measured leaf area. Moreover, we estimated that specific leaf area, estimated using leaf thickness, strongly correlates with field-measured specific leaf area.

RQ 5: How does climate change impact the patterns of plant functional traits on islands?

Climate change is one of the main threats to the unique biodiversity on islands (Bellard *et al.*, 2012). Therefore, it is important to mitigate climate change and to conduct suitable conservation measures. For this reason, we need to understand how climate change might impact functional trait patterns of endemic and non-endemic species on islands. In this study, we conducted species distribution models for current and future climatic conditions using occurrences of endemic and non-endemic native plant species on the Canary Islands (**Chapter 6**; Hanz *et al.*, in preparation). Subsequently, we calculated the relative difference in potential climatic suitable area for each species and analysed whether species with specific functional traits are more vulnerable to climate change, and particularly drought increase, than species with other sets of functional traits. We hypothesised that there is an overall reduction in potential climatic suitable area for island plants, but we expected a below-average climate change-related reduction for insular woody and succulent species due to the water use efficiency of these traits (Schenk *et al.*, 2008; Hoffman *et al.*, 2009; Lens *et al.*, 2016; Dória *et al.*, 2018).

Chapter 2

Climatic and biogeographical drivers of functional diversity in the flora of the Canary Islands

Dagmar M. Hanz, Vanessa Cutts, Martha Paola Barajas-Barbosa, Adam C. Algar, Carl Beierkuhnlein, José María Fernández-Palacios, Richard Field, Holger Kreft, Manuel J. Steinbauer, Patrick Weigelt & Severin D.H. Irl - *Global Ecology and Biogeography* 2022; 31: 1313-1331

Abstract

Aim: Functional traits can help us to elucidate biogeographical and ecological processes driving assemblage structure. We analysed the functional diversity of plant species of different evolutionary origins across an island archipelago, along environmental gradients and across geological age, to assess functional aspects of island biogeographical theory.

Location: Canary Islands, Spain.

Major taxa studied: Spermatophytes.

Time period: Present day.

Methods: We collected data for four traits (plant height, leaf length, flower length and fruit length) associated with resource acquisition, competitive ability, reproduction and dispersal ability of 893 endemic, non-endemic native and alien plant species (*c*. 43% of the Canary Island flora) from the literature. Linking these traits to species occurrences and composition across a 500 m × 500 m grid, we calculated functional diversity for endemic, non-endemic native and alien assemblages using multidimensional functional hypervolumes and related the resulting patterns to climatic (humidity) and island biogeographical (geographical isolation, topographic complexity and geological age) gradients.

Results: Trait space of endemic and non-endemic native species overlapped considerably, and alien species added novel trait combinations, expanding the overall functional space of the Canary Islands. We found that functional diversity of endemic plant assemblages was highest in geographically isolated and humid grid cells. Functional diversity of non-endemic native assemblages was highest in less isolated and humid grid cells. In contrast, functional diversity of alien assemblages was highest in arid ecosystems. Topographic complexity and geological age had only a subordinate effect on functional diversity across floristic groups.

Main conclusions: We found that endemic and non-endemic native island species possess similar traits, whereas alien species tend to expand functional space in ecosystems where they have been introduced. The spatial distribution of the functional diversity of floristic groups is very distinct across environmental gradients, indicating that species assemblages of different evolutionary origins thrive functionally in dissimilar habitats.

Left photo: View of Tenerife from the Mirador de El Bailadero on La Gomera (Canary Islands; own photo). Shrubs of the La Gomera endemic *Echium acanthocarpum* frame the view.

2.1 Introduction

Functional traits determine species' responses to the environment and can be used to assess meaningful variation of species assemblages through time and space (Díaz & Cabido, 2001; Kattge *et al.*, 2020). In fact, functional traits help to understand not only how environmental processes have influenced species' ecological strategies but can also inform about how evolutionary conditions have led to adaptation and specialisation of species, especially in oceanic archipelagos (Whittaker *et al.*, 2014). However, studies on the functional diversity of oceanic island floras that apply island biogeographic theory (e.g. MacArthur & Wilson, 1967; Whittaker *et al.*, 2008) are lacking, but hold the promise to answer fundamental questions on how spatial and ecological processes drive functional diversity patterns within insular systems and on how functional diversity patterns compare between islands (Patiño *et al.*, 2017; Ottaviani *et al.*, 2020; Schrader *et al.*, 2021).

Functional diversity, i.e. the trait variability in a species assemblage, can be quantified as the multidimensional trait volume that is occupied by a species assemblage (Blonder *et al.*, 2014; Blonder, 2018). On the one hand, expansion of an assemblage's functional trait volume with increasing species richness may indicate the exploitation of novel regions of niche space (MacArthur, 1965). On the other hand, if the niche space of an assemblage becomes more densely packed as species richness increases, it suggests finer specialisation or greater overlap of ecological niches (Klopfer & MacArthur, 1961; Pigot *et al.*, 2016). Thus, measuring functional diversity may help to better understand fundamental ecological strategies of species of different origins (e.g. endemic, non-endemic native, and alien).

The floras of oceanic islands are comparatively species poor, disharmonic and rich in endemics (Kreft *et al.*, 2008; Kier *et al.*, 2009; Taylor *et al.*, 2019). Oceanic islands harbour species that have colonised from the mainland, overcoming strong dispersal filters, and eventually evolved or even diversified into endemic species (Stuessy *et al.*, 2006). This evolution in isolation may have led to a high trait differentiation in native island species, making some islands hotspots of functional diversity (García-Verdugo *et al.*, 2020). However, an isolated evolution and small distributions have left endemic species on islands particularly vulnerable to habitat loss, climate change, and biological invasions through alien species that have been introduced intentionally or unintentionally by humans (Veron *et al.*, 2019; Fernández-Palacios *et al.*, 2021; Macinnis-Ng *et al.*, 2021). Because of the high, possibly unique, trait diversity on oceanic islands and its inherent vulnerability, it is important to understand how endemic, non-endemic native, and alien species are distributed in space and what their adaptations to island environments are.

Oceanic islands, and in particular islands of volcanic origin, are often distinguished by highly heterogeneous environments with distinct orographic precipitation regimes over short geographic distances (Kier *et al.*, 2009; Weigelt *et al.*, 2013). Water availability is a well-known driver of functional diversity and species richness (Wright *et al.*, 2004; Poorter *et al.*, 2010). Under arid conditions, functional diversity tends to be low as functional traits are subject to strong environmental filtering through physiological constraints (Spasojevic *et al.*, 2014). Hence, only species with specific functional traits might be adapted to survive strong environmental pressure (Cornwell & Ackerly, 2009). In particular, leaves and flowers are energetically costly for plants when water availability is limited (Roddy, 2019). Thus, dry environments should select species with water-efficient traits, such as smaller statures, leaves, and flowers (Moles *et al.*, 2009; Wright *et al.*, 2017; Kuppler & Kotowska, 2021). However, other mechanisms, such as the limiting similarity of coexisting species (Cornwell & Ackerly, 2009), can shape the distribution of trait values. In contrast, the distribution of alien species on oceanic islands is mainly determined by their pathway of introduction (Pauchard *et al.*, 2009). Alien species decline from low elevations, where they have been predominantly introduced, to high elevations due to directional ecological filtering (i.e. progressive dropping out of species with narrow ecological niches; Alexander *et al.*, 2011) via water availability (Irl *et al.*, 2021). On many highly elevated trade wind islands, water availability increases from the coast up to the orographic cloud layer (Garzón-Machado *et al.*, 2014) and, consequently, alien species with broad climatic niches should be more prevalent under arid conditions as species with narrow climatic niches tend to be selectively filtered out along a humidity gradient (Alexander *et al.*, 2011; Irl *et al.*, 2021).

Island biogeographic models predict that diversity of species assemblages on oceanic islands vary in relation to isolation, area and island age as a result of immigration, speciation and extinction (MacArthur & Wilson, 1967; Whittaker *et al.*, 2008; Schrader *et al.*, 2021). The models suggest that isolated areas are less diverse in species due to reduced dispersal probability with greater distance to the mainland, influencing the chance of colonisation (MacArthur & Wilson, 1967; Weigelt & Kreft, 2013). In contrast, less-isolated areas receive continuous arrival of propagules, increasing assemblage diversity (Brown & Kodric-Brown, 1977). Moreover, dispersal probability depends on plant height and diaspore size as tall and small-seeded species can disperse their diaspores further due to their lower settling velocity (Venable & Brown, 1988; Greene & Johnson, 1993; Thomson *et al.*, 2011). Hence, it can be expected that plant height and diaspore size of colonisers, i.e. non-endemic native species, is more similar in isolated habitats as primarily species with similar trait combinations might reach those habitats. Functional diversity of endemic species should increase with isolation relative to species richness as speciation rates should be higher where colonising assemblages are disharmonic (König *et al.*, 2021). Geographically isolated areas on oceanic islands can limit gene flow with mainland populations and offer greater ecological opportunity for exploitation of resources; this tends to enhance endemic species diversity (Whittaker & Fernández-Palacios, 2007; Steinbauer *et al.*, 2012). Hence, adaptive speciation may be more important in isolated habitats than non-adaptive speciation (e.g. genetic drift; (Losos & Ricklefs, 2009; Marques *et al.*, 2019). Potentially, alien species could profit from unoccupied niches as well, but unidirectional expansion from the sources of anthropogenic introduction might prevent them from reaching more isolated sites through directional ecological filtering (Alexander *et al.*, 2011; Irl *et al.*, 2021).

Similarly, topography can act as a dispersal barrier between populations, potentially leading to in situ speciation (Irl *et al.*, 2015; Otto *et al.*, 2016). Hence, topographic complexity might favour local adaptations by reducing genetic swamping (i.e. genetic homogenisation through hybridisation;

Herrera & Bazaga, 2008), possibly leading to an increase of functional diversity. Moreover, it has been shown that topography predicts habitat diversity (Keppel *et al.*, 2016; Barajas-Barbosa *et al.*, 2020), which can have vital implications for species richness–area relationships on islands (Hortal *et al.*, 2009). However, at small spatial scales an area–heterogeneity trade-off could prevent native assemblages from diversifying in very complex environments as the effective area of individual habitats is reduced, especially for species with narrow niches (Allouche *et al.*, 2012). As flat environments have low habitat diversity and topographically complex environments have limited effective area per habitat, functional diversity of native assemblages may have a unimodal relationship with topographic complexity. Alien species are more likely to be subject to directional ecological filtering since human introduction to easily accessible areas might have so far impeded colonisation of topographically complex areas on oceanic islands (Alexander *et al.*, 2011; Steinbauer *et al.*, 2017).

We further expect plant species to be more functionally diverse relative to species richness in environments with a heterogeneous geological structure. For instance, it has been shown that geological heterogeneity is highest at an intermediate geological age when soils have already formed and erosion does not yet prevail (Lambers *et al.*, 2008; Mueller-Dombois & Boehmer, 2013). Moreover, both poorly developed, young soils from recent volcanic eruptions and highly weathered older soils, which have been above sea level and have not been glaciated for millions of years, are poor in nutrients and may act as an ecological filter on functional properties of plants (Lambers *et al.*, 2008; Laliberté *et al.*, 2013a). Hence, we expect species assemblages in early and late successional stages to be functionally less diverse relative to species richness due to lower geological heterogeneity and nutrient depletion on very young as well as old sites.

In this study, we analyse how the functional diversity of endemic, non-endemic native and alien assemblages change across ecological gradients, using a 500 m x 500 m gridded distribution dataset for the flora of the Canary Islands (Figure 2.1a–d). First, we analyse how the functional diversity of these assemblages, relative to species richness, changes with humidity. We test the prediction that environmental filtering results in an increase of functional diversity with increasing humidity for endemic and non-endemic native assemblages (Figure 2.1a). For alien assemblages, we expect the pattern to be the opposite, due to the introduction of alien species to arid coastal environments and the subsequent directional ecological filtering (Figure 2.1a). Second, we analyse whether the mechanisms invoked by classic island biogeographic theory predict variation in functional diversity relative to species richness. Based on theory, we expect a positive relationship between functional diversity and geographical isolation for endemic assemblages and a negative relationship for non-endemic native and alien assemblages (Figure 2.1b). We further expect a hump-shaped relationship with topographic complexity for endemic and non-endemic native assemblages, and a negative relationship for alien assemblages (Figure 2.1c). Finally, we expect a hump-shaped relationship between functional diversity and geological age for endemic, non-endemic native and alien assemblages (Figure 2.1d).

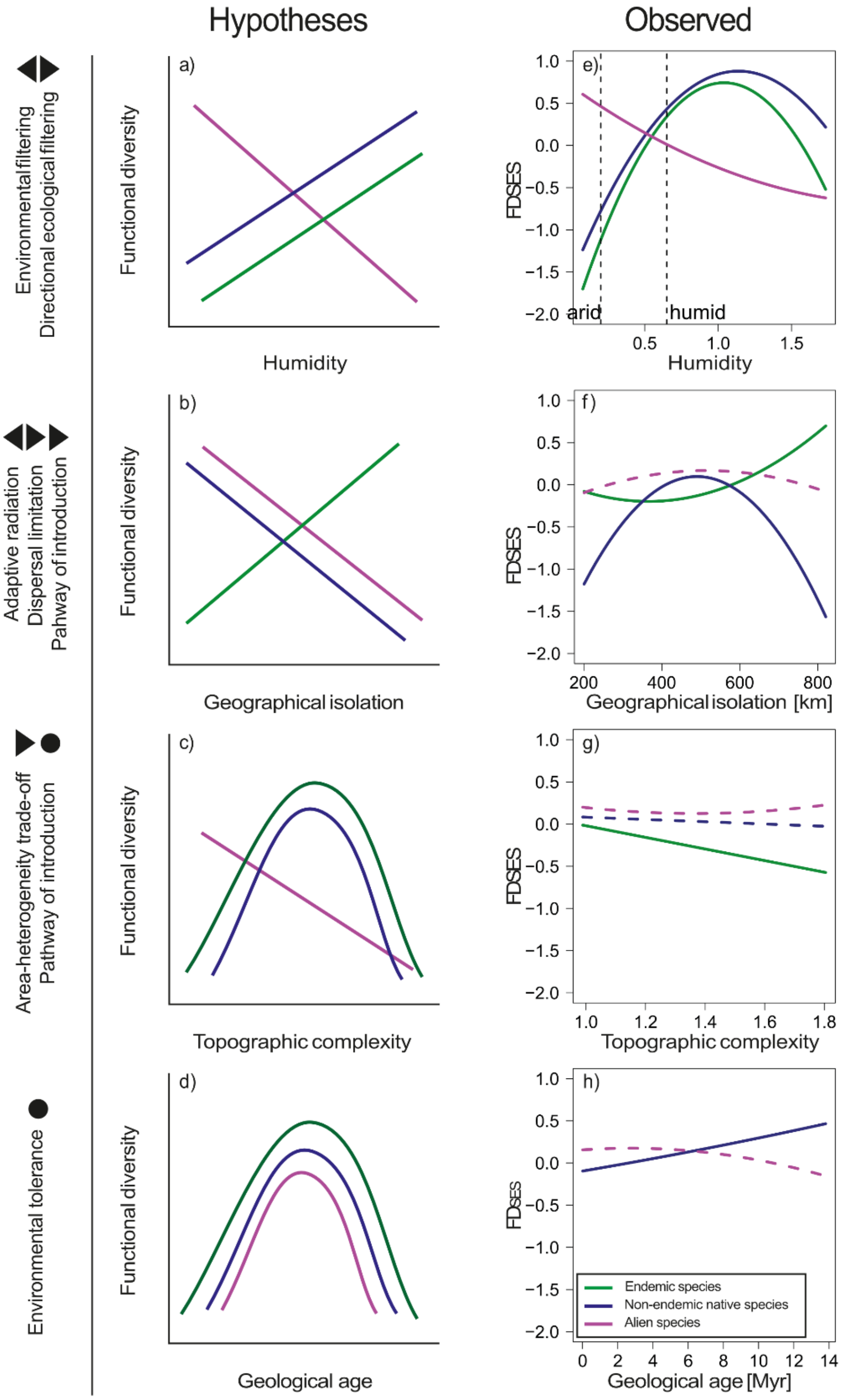

Figure 2.1 a-d) Hypothesised and **e-h)** observed relationships of standardised effect sizes of functional diversity (FD_{SES}) for endemic (green), non-endemic native (blue) and alien (violet) plant species assemblages, based on 500 m x500 m grid cells (n = 3,065) across the Canary Islands, along humidity, geographical isolation, topographic complexity and geological age gradients. Functional diversity is based on four functional traits (plant height, leaf length, flower length and fruit length) of 347 endemic, 306 non-endemic native and 240 alien plant species. Lines show the trends of the models given in Table 2.2 and Figure 2.4). The mechanisms that we based our hypotheses on are indicated on the left-hand side of the figure. Triangles either indicate a hypothesised increase or decrease of FD_{SES} along the respective environmental gradient. Circles indicate a hypothesised unimodal relationship of FD_{SES} along the respective environmental gradient.

2.2 Methods

2.2.1 Study area

We tested our hypotheses using the Flora of the Canary Islands (excluding Fuerteventura and Lanzarote due to underrepresented species occurrence data from very limited sampling; Figure 2.2). The Canary Islands are an active volcanic archipelago characterised by a Subtropical-Mediterranean climate regime (del Arco Aguilar *et al.*, 2010). The islands are under the influence of the NE trade winds and rain shadow effects cause humidity to differ greatly between northern and southern parts of the islands, with the north-eastern flank of the islands receiving the highest precipitation. Within islands, humidity varies greatly, from a dry and warm coast, through moderately temperate mountainous zones up to dry and cool conditions at high elevations (del Arco Aguilar *et al.*, 2010; Table 2.1). The high-elevation alpine ecosystems of La Palma and Tenerife are the most environmentally isolated, as the closest area with comparable climate is in the Atlas Mountains of Morocco, whereas the coastal climate across the archipelago is similar to the climate of the nearby north-western coast of Africa (Table 2.1). Due to high volcanic activity, each island is composed of older eroded terrain units and younger parts, leading to great variation in topographic complexity, especially on emerging islands such as La Palma and Tenerife (Table 2.1). Recent volcanic activity on El Hierro, La Palma and Tenerife further underlines the hotspot origin of the Canary Islands, where the islands have emerged successively and allow the observation of different phases of island ontogeny (Fernández-Palacios *et al.*, 2011; Table 2.1).

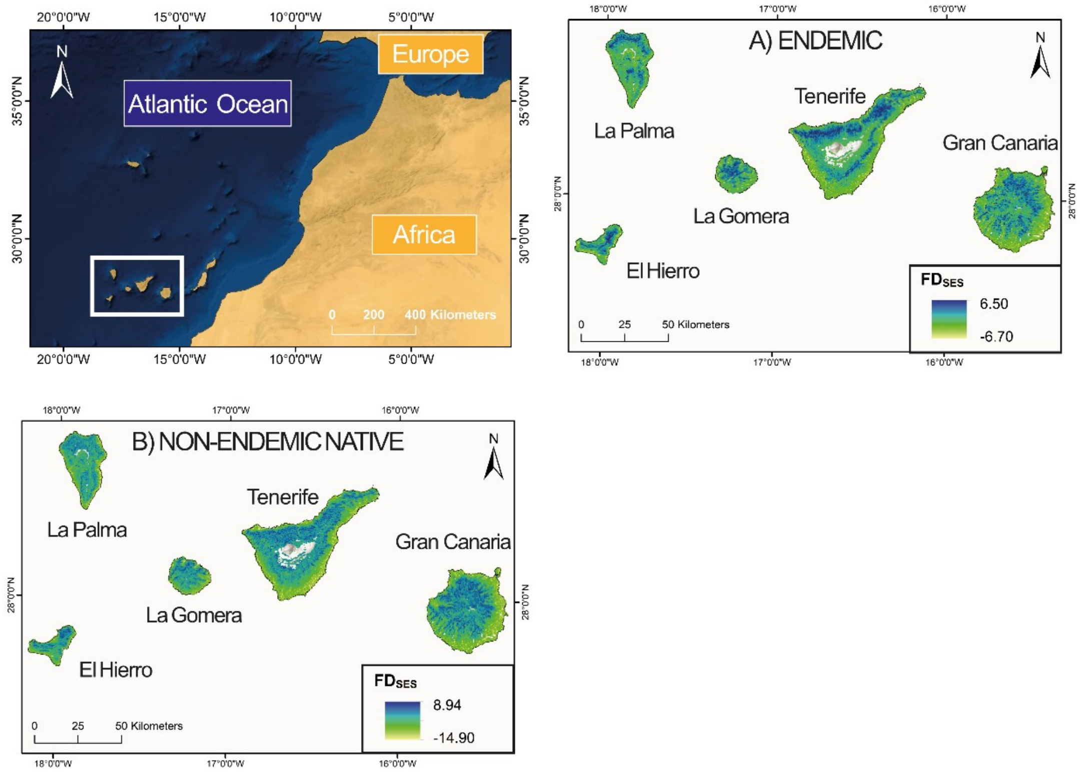

Figure 2.2. Map of the spatial distribution of modelled standardised effect size of functional diversity (FD_{SES}) values per 500 m x 500 m across the five studied Canary Islands for **a)** endemic, **b)** non-endemic native assemblages. Source of general map: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/ Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community.

Table 2.1. Climatic and biogeographic information for the five analysed Canary Islands (excluding Lanzarote, Fuerteventura and the Teide violet community, a vegetation unit between 2,400 and 3,500 m elevation on Mount Teide).

Island	**Humidity index**	**Geographical isolation (km)**	**Topographic complexity**	**Geological age**	**Species analysed (*n*)**	**Endemic (%)**	**Non-endemic native (%)**	**Alien (%)**
Gran Canaria	0.1–1.0	200.5–648.4	1.0–1.8	6 kyr–13.8 Myr	547	28	46	26
Tenerife	0.1–1.2	288.3–752.4	1.0–2.0	6 kyr–13.8 Myr	699	31	40	29
La Gomera	0.2–0.9	335.4–715.9	1.0–1.6	4.5–8.5 Myr	456	27	47	26
La Palma	0.2–2.1	421.4–886.1	1.0–2.1	6 kyr–4.5 Myr	483	27	46	27
El Hierro	0.1–0.9	383.2–778.7	1.0–1.8	6 kyr–0.5 Myr	343	26	56	18
All islands	0.1–2.1	200.5–886.1	1.0–2.1	6 kyr–13.8 Myr	893	39	34	27

Note: Humidity was quantified as mean annual precipitation in relation to mean annual potential evapotranspiration per grid cell. Geographical isolation was quantified as the distance of a grid cell to the nearest terrestrial area on the continent that has a mean annual temperature within 1°C. Topographic complexity per grid cell was estimated by calculating the ratio between 3D and 2D surface area. We derived mean geological age per grid cell from a continuous digital geological map of Spain (scale 1:50,000; Bellido Mulas *et al.*, 2020). Also given is the number of analysed species per island and the respective percentage of endemic, non-endemic native and alien plant species.

The native flora of the Canary Islands is considered to be mostly of Mediterranean origin (Carine *et al.*, 2010). Since the prehistoric human settlement and especially since the arrival of European settlers in the fifteenth century, the Canary Islands have been subject to intense landscape alterations and introduction of alien plants (del Arco Aguilar *et al.*, 2010; de Nascimento *et al.*, 2020). Human pressure decreases with elevation as large villages and agricultural settings are located mainly near the coast and human population density becomes low above 1,000 m (Arévalo *et al.*, 2005). Currently, the Canary Island flora encompasses about 2,000 species, of which roughly a third of the species are endemic, non-endemic native and alien species, respectively (Arechavaleta *et al.*, 2010).

2.2.2 Species occurrences and species distribution model

We collected occurrence data from Atlantis 3.3, an open-access database for all seed plant species in a raster of 500 m x 500 m grid cells covering El Hierro, La Palma, La Gomera, Tenerife and Gran Canaria (www.biodiversidadcanarias.es/biota). Atlantis provides presence-only information with better coverage for endemic species and flowering plants than other plant taxa (Steinbauer *et al.*, 2016b). Therefore, we additionally interpolated species' occurrences using species distribution models (SDMs; Calabrese *et al.*, 2014) which were parameterised following Irl *et al.*, (2020; see Appendix S2.1 in supporting information). To check whether using modelled species distributions created an artificial relationship between the predictor variables and functional diversity, we performed all statistical analyses separately with the modelled data and the original occurrence data. Furthermore, we excluded every grid cell that had less than half of the cell covered by land mass to account for low species occurrences based on grid cell area.

2.2.3 Morphological trait data

We collected data on four functional morphological traits that reflect fundamental ecological strategies of plants and relate to the different axes of the leaf-height-seed scheme defined by Westoby (1998):

plant height, leaf length, flower length and fruit length. Morphological trait data of the respective plant species were collected from literature sources, measured on digitised plant specimens and extracted from species' descriptions (for further information, see Appendix S2.2). We collected data on maximum trait values from floras as the expected maximum at maturity reflects responses of species' fitness to environmental gradients (Violle *et al.*, 2007) and has better data coverage throughout the literature. Recent work shows that trait data from plant identification books are comparable to measured trait data in the Canary Islands (Cutts *et al.*, 2021).

For our analyses we focused on the following traits:

1. Plant height is a crucial part of plant ecological strategy as it affects a plant's ability to compete for light resources (Falster & Westoby, 2003) and is correlated with several life-history traits, such as seed mass and longevity (Moles & Leishman, 2008). Plant height is limited by water availability as leaves need to be supplied with water without risking a xylem embolism (hydraulic limitation hypothesis; Ryan *et al.*, 2006; Moles *et al.*, 2009). Furthermore, plant height is more positively associated with species' seed dispersal distance than seed mass (Thomson *et al.*, 2011) and relates to the competitive ability of species (Gaudet & Keddy, 1988).
2. Leaf length is highly correlated with leaf area, independent of leaf shape (Shi *et al.*, 2019; Cutts *et al.*, 2021). Leaf size has important consequences for the energy and water balance of plants (Parkhurst & Loucks, 1972). Smaller leaves are more water-efficient as they cool down more quickly and maintain lower leaf temperatures (Leigh *et al.*, 2017). Larger leaves with a less efficient energy exchange capacity are more beneficial in humid habitats as they have higher photosynthetic capacities while being able to provide enough water for sufficient transpirational cooling (Parkhurst & Loucks, 1972). For stem-photosynthesising succulents (e.g. *Opuntia robusta*) the ephemeral leaf length was collected.
3. Flower length is also important for the energy and water balance of plants as flower petals can transpire significant amounts of water (Roddy *et al.*, 2016; Roddy, 2019). Hence, flower length, which can affect pollinator attraction (Thompson, 2001), declines on average with water deficit (Paušič *et al.*, 2019; Kuppler & Kotowska, 2021). For Poaceae, spikelet length was considered as the functional analogue to single flower length. For Asteraceae, ligule length was considered as the functional analogue to single flower length.
4. Fruit length is relevant for the dispersal strategy of plants. Fruit size is positively correlated with seed size (Wheelwright, 1993; Muñoz *et al.*, 2017) and can inform about the plants' dispersal probability and seedling survival (Muñoz *et al.*, 2017). In long-term isolated habitats, plants tend to have larger seeds to increase their establishment and persistence but also to decrease their dispersal ability (Rossetto & Kooyman, 2005).

We were able to collect complete trait and occurrence data for 893 species in total (347 endemics, 306 non-endemic natives and 240 aliens). Plant height, leaf length, flower length and fruit length were standardised by subtracting the column means from their corresponding columns and by dividing the (centred) columns by their standard deviations before functional diversity calculations. The four traits were only slightly correlated (Pearson’s r < 0.33 in all cases).

2.2.4 Environmental and biogeographical variables

For each grid cell, monthly mean temperature was used to calculate potential evapotranspiration according to the Thornthwaite equation (Thornthwaite, 1948). Subsequently, we calculated the humidity index after UNEP (1992). The humidity index is useful as it classifies the type of climate in relation to water availability by considering temperature, precipitation, sunshine hours and relative humidity (UNEP, 1992). Hence, the humidity index is considered a reliable source of potential water availability at various scales (Asadi Zarch *et al.*, 2015). Humidity index ranged approximately from 0.07 (arid) to 2.05 (humid) across the five islands (Table 2.1; see Appendix S2.3, Figure S2.3.1a).

We further calculated geographical isolation per grid cell based on the distance to climatically similar land mass (Weigelt & Kreft, 2013). Specifically, geographical isolation was quantified as the distance of a grid cell to the nearest terrestrial area on the continent that has a mean annual temperature within 1°C, following Steinbauer *et al.* (2016). Geographical isolation of the island grid cells ranged from 196.5 km to 885 km to the closest continental grid cell with similar environmental conditions (Table 2.1; see Appendix S2.3, Figure S2.3.1b).

We calculated topographic complexity per grid cell as it relates to the rate of elevational change in response to changes in location (Amatulli *et al.*, 2018) and can therefore act as a surrogate for habitat heterogeneity (Irl *et al.*, 2015). We estimated topographic complexity per grid cell by using a moving window approach that calculates the surface area for a cell based on slope information from a specified set of smaller grid cells (after Jenness, 2004). Topographic complexity ranged from 1 (flat) to 2.17 (high complexity; Table 2.1; see Appendix S2.3, Figure S2.3.1c).

Furthermore, we calculated geological age per grid cell as it represents a proxy for plant nutrient availability (Lambers *et al.*, 2008; Laliberté *et al.*, 2013a) which is known to affect functional diversity (Lambers *et al.*, 2011). Poorly developed, very young soils result from recent volcanic eruptions, whereas ancient, highly weathered soils have been above sea level and have not been glaciated for millions of years. Nitrogen is generally absent from soil parent material and enters ecosystems via nitrogen fixation, phosphorus is derived from rock weathering and declines as soils age (ecosystem regression; Lambers *et al.*, 2008; Laliberté *et al.*, 2013a; Mueller-Dombois & Boehmer, 2013). We calculated geological age as the mean age of the geological time period that we assigned to each grid cell of the Canary Islands based on a geological map (Bellido Mulas *et al.*, 2020). Mean geological age per grid cell ranged from 6 ka to 13.8 Ma (Table 2.1; see Appendix S2.3, Figure S2.3.1d).

For further analyses we ln-transformed the topographic complexity index to approximate normality and subsequently centred and scaled all environmental variables, yielding estimates in standard deviation units per grid cell. After standardisation we calculated correlation coefficients (Pearson’s *r*) between the environmental variables, as well as elevation (see Appendix S2.3, Table S2.3.1).

Humidity was highly correlated with geographical isolation (Pearson's $r = 0.80$, $p < 0.001$) and elevation (Pearson's $r = 0.72$, $p < 0.001$).

2.2.5 Functional diversity of oceanic islands

We calculated functional diversity using all traits to determine how ecological strategies vary between endemics, non-endemic natives and aliens (here also referred to as floristic groups), and whether we can establish if climate gradients and evolutionary processes can explain patterns of functional diversity across the Canary Islands. We used a hypervolume algorithm for calculating the overall functional diversity for each floristic group using the 'hypervolume' R package (Blonder *et al.*, 2014). We prefer this to other functional diversity metrics (e.g. functional richness) because it recognises clusters or holes in occurrence datasets within trait space (Blonder *et al.*, 2014). Finally, we calculated the pairwise overlap between functional diversity values of floristic groups (2x shared volume/ summed volume). Using the same methodological approach, we also calculated occurrence-based and SDM-derived functional diversity per grid cell for each floristic group separately. To ensure that we did not over- or underestimate functional diversity, we excluded grid cells with < 10 species (Blonder *et al.*, 2014) for occurrence-based and SDM-derived assemblage models. We constructed functional diversity by building a Gaussian kernel density estimate on an adaptive grid of 100 random points wrapping around each original data point. We used a fixed kernel density estimate bandwidth of 0.5 standard deviations to make functional diversity calculations comparable across analyses (Lamanna *et al.*, 2014). We used a quantile threshold which ensured that 95 percent of the estimated probability density is enclosed by the chosen boundary (Blonder *et al.*, 2014). To ensure that we did not estimate hypervolumes into negative trait space, we calculated the intersection between a hypothetical box hypervolume that we defined by the range of our trait data and the calculated hypervolumes with the function *hypervolume_set* ('hypervolume' R package; Blonder *et al.*, 2014).

To ensure that our results are not sensitive to species richness, we compared the functional diversity values of every floristic group to null-model expectations (for relationships between functional diversity and species richness see Appendix S2.4). Therefore, we calculated values from 10 sets of randomised assemblages created with the 'quasiswapcount' algorithm ('vegan' package; Oksanen *et al.*, 2020), based on the species pool within each island (i.e. all species observed in any grid cell in each island). This algorithm retains row and column sums and thus constrains species richness of grid cells. We computed the standardised effect size (FD_{SES}) for functional diversity as follows: FD_{SES} = (FD – mean randomised FD)/ SD of randomised FD). FD_{SES} <0 indicate functional clustering (FD lower than expected for a given species richness), FD_{SES} >0 suggest functional over-dispersion (FD higher than expected for a given species richness), and FD_{SES} ≈0 indicate a random functional structure.

2.2.6 Phylogenetic signal at the genus assemblage level

As the floristic groups could be phylogenetically structured (e.g. a high proportion of Crassulaceae in the endemic group), we tested for phylogenetic non-independence in our data. Ignoring a phylogenetic signal and treating species as independent could result in pseudoreplication (Felsenstein, 1985). Hence, we extracted phylogenies of the species in the dataset of a recently published supertree of seed plants (Smith & Brown, 2018). Because the phylogenetic tree contains many polytomies at the species level, we pruned the rooted tree to the genus-level for each floristic group using the ‘ape’ package in R (Paradis & Schliep, 2019; see Appendix S2.5, Figure S2.5.4). Subsequently, we measured Blomberg’s K statistic of phylogenetic signal for each analysed trait within every floristic group using the ‘picante’ package in R (Kembel *et al.*, 2010). The K statistic is a measure of phylogenetic signal that compares the observed signal in a trait to the signal under a Brownian motion model of trait evolution on a phylogeny (Blomberg *et al.*, 2003). K values closer to zero correspond to a random or convergent pattern of evolution, while K values greater than 1 indicate strong phylogenetic signal and conservatism of traits (Kembel *et al.*, 2010).

To analyse the influence of phylogenetic history on assemblage functional diversity, we calculated phylogenetic diversity for endemic, non-endemic native and alien assemblages based on occurrence and modelled data in the analysed grid cells. This approach allowed us to assess the degree of correlation between phylogenetic and functional diversity (termed phylogenetic signal at the metacommunity level sensu Pillar & Duarte, 2010). Phylogenetic diversity was calculated as Faith’s PD, which is defined as the total branch length of a tree including all species in a grid cell (‘picante’ R package; Kembel *et al.*, 2010). To test whether functional diversity was correlated with phylogenetic diversity, we computed correlation coefficients (Pearson’s r) for each floristic group using occurrence-based and modelled data. A strong correlation is expected when assemblages that are more similar in terms of phylogenetic structure are also similar regarding their average trait values.

2.2.7 Statistical analyses

We ran generalised linear regression models (GLMs) to test the relationship between FD_{SES} and environmental variables for occurrence-based and modelled endemic, non-endemic native and alien assemblages across all grid cells. We tested for quadratic relationships ($y \sim x + x^2$) of all explanatory variables as traits do not necessarily change linearly along environmental gradients. We first ran an initial full model including all four environmental variables but excluding elevation due to collinearity with humidity and geographical isolation. We further ran additional models that excluded either humidity or geographical isolation due to collinearity. Subsequently, we chose a model selection procedure, based on minimising the Akaike Information Criterion (AIC; Burnham & Anderson, 2002). We performed AIC model selection using the function dredge in the R package MuMIn (Barton, 2020) to obtain the overall best model. Because spatial autocorrelation was present in the model residuals analysed here, we performed spatial autoregressive (SAR) models using the same explanatory variables selected for the GLMs. We implemented error-dependence models with weighted neighbourhood structure as they accounted best for the spatial structure in the analysed data set (Dormann *et al.*, 2007). We selected a threshold distance of 500 m by examining correlograms. Spatial statistics were performed using the ‘spatialreg’ package in R (Bivand *et al.*, 2013). The explained variation of the models was quantified using Nagelkerke’s R^2. Spatial Moran’s I correlograms for the response variable as well as for the GLM and SAR residuals are provided in the supporting information (Figure S2.6.5). All analyses were performed using R version 3.6.2 (R Core Team, 2021).

2.3 Results

Some alien species had trait values outside the range of traits of endemic and non-endemic native species and expanded the Canary Islands' trait space within all trait dimensions. Around 27% of the functional trait space of alien species is shared by endemic species, around 28% of the functional trait space of aliens is shared by non-endemic-native species. Functional diversity of endemic and non-endemic native species showed a great overlap in all trait dimensions (hypervolume overlap = 72%; Figure 2.3).

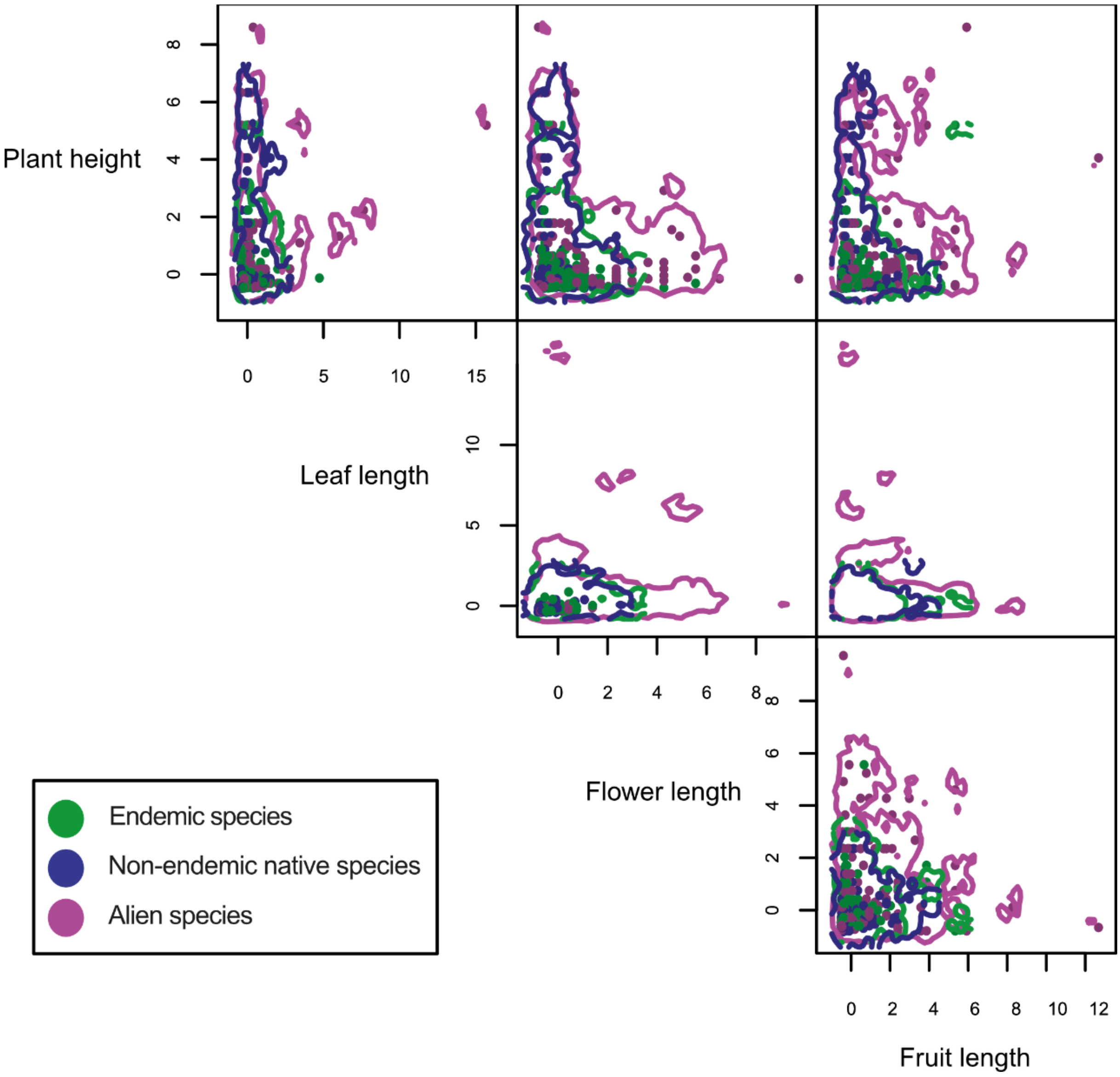

Figure 2.3. Estimated four-dimensional hypervolumes for endemic (green; n = 347), non-endemic native (blue; n = 306) and alien seed plant species (violet; n = 240) on the Canary Islands. The coloured points represent the different plant species and the coloured lines reflect the areas filled by random points sampled from the inferred hypervolume. Endemic species overlap non-endemic native species by 72%. Endemic species overlap alien species by 27% and non-endemic species overlap alien species by 28%.

On a grid cell scale, occurrence-based FD_{SES} of endemic and non-endemic assemblages had a unimodal relationship with humidity, whereas occurrence-based FD_{SES} of alien assemblages decreased with increasing humidity (Table 2.2, Figure 2.1e, Figure 2.4). With increasing geographical isolation, occurrence-based FD_{SES} of endemic assemblages increased. Occurrence-based FD_{SES} of non-endemic native assemblages had a non-significant hump-shaped relationship with geographical isolation and occurrence-based FD_{SES} of alien assemblages had a unimodal relationship with geographical isolation (Table 2.2, Figure 2.1f, Figure 2.4). Occurrence-based FD_{SES} of endemic assemblages decreased with topographic complexity, and non-endemic native assemblages showed a non-significant decrease with topographic complexity. Occurrence-based FD_{SES} of alien assemblages had a non-significant u-shaped relationship with topographic complexity (Table 2.2, Figure 2.1g, Figure 2.4). Geological age was not included in the most parsimonious model of endemic assemblages. With increasing geological age, occurrence-based FD_{SES} of non-endemic native assemblages linearly increased, whereas occurrence-based FD_{SES} of alien assemblages decreased non-significantly (Table 2.2, Figure 2.1h, Figure 2.4). Hence, functional diversity of endemic assemblages was highest on the more humid and isolated north-eastern slopes in less topographically complex habitats. Similarly, functional diversity of non-endemic native assemblages was highest in habitats with intermediate humidity and isolation in the older islands. In contrast, functional diversity of alien assemblages was highest at arid sites at the coasts across all islands. Humidity had the overall strongest explanatory power for functional diversity (Figure 2.4).

Table 2.2. Explained variation of generalised linear models (GLM) and spatial autoregressive (SAR) models analysing the combined effect of humidity, geographical isolation, topographic complexity and geological age on FD_{SES} of endemic, non-endemic native and alien seed plant assemblages based on 500 m x 500 m grid cells across the Canary Islands. FD_{SES} is based on four functional traits (plant height, leaf length, flower length and fruit length) and was calculated for grid cells with occurrence-based data (n = 3,065). Percentage of total deviance explained (% dev.), Akaike Information Criterion (AIC) and Moran's I are given. Model coefficients of SARs are given in Figure 2.4.

Floristic group	**GLM**			**SAR**		
	% dev.	**AIC**	**Moran's I**	**% dev.**	**AIC**	**Moran's I**
Endemic	27.3	9772.8	0.56	53.2	8427.2	-0.08
Non-endemic native	20.1	10868	0.68	60.6	8706.3	-0.10
Alien	7.6	10394	0.62	48.8	8591	-0.09

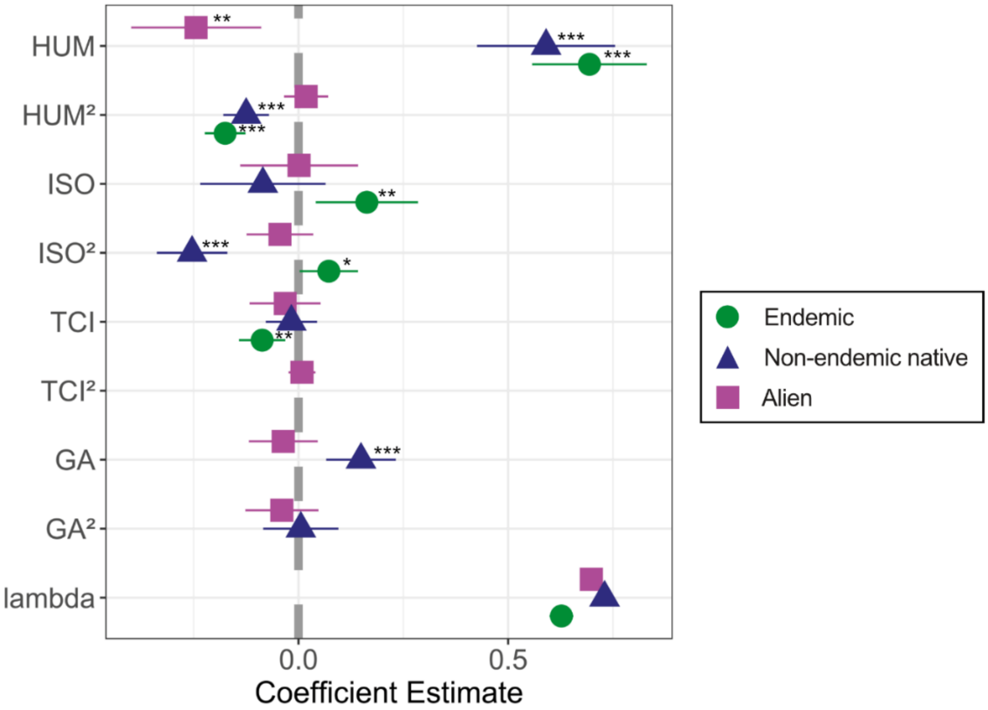

Figure 2.4. Multi-predictor spatial autoregressive models of humidity (HUM), geographical isolation (ISO), topographic complexity index (TCI), geological age (GA) on the occurrence-based FD_{SES} of endemic (n = 347 species), non-endemic native (n = 306 species) and alien plant assemblages (n = 240 species) on the Canary Islands. Functional diversity is based on four functional traits (plant height, leaf length, flower length and fruit length) and was calculated for occurrence-based data (n = 3,065) based on 500 m x 500 m grid cells. Shown are the respective best models according to a model comparison approach. Standardised estimates are provided for each predictor. Error bars represent confidence intervals of the coefficient estimates. Asterisks denote statistical significance (*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$).

In the models excluding humidity, geographical isolation had a stronger explanatory power for functional diversity of endemic, non-endemic native and alien assemblages (see Appendix S2.6, Table S2.6.2, Figure S2.6.6). However, overall model fit according to AIC and explained variance was better for the models that included all environmental variables as compared to models that accounted for collinearity (ΔAIC endemic = 5.9/87.3; ΔAIC non-endemic native = 29.7/41.8; ΔAIC alien = 6.3/7.9).

FD_{SES} patterns of the modelled data were broadly consistent with the occurrence-based FD_{SES} models (see Appendix S2.6, Table S2.6.3, Figure S2.6.7 and S2.6.8). However, contrary to the occurrence-based data, modelled FD_{SES} of alien assemblages showed a convex relationship with geographical isolation. This indicates that our results using species distribution models might have created an artificial relationship between functional diversity of alien assemblages and the analysed predictor variables. Therefore, modelled FD_{SES} values were only used for graphical illustration of endemic and non-endemic assemblages (see Figure 2.2) and not further discussed in this study.

SARs were selected over GLMs as they consistently improved model fit. According to the R², accounting for spatial structure increased the explained variation between 41% (for alien assemblages) and 26% (for endemic assemblages; Table 2.2; see Appendix S2.6, Table S2.6.3 for modelled FD_{SES}).

Blomberg’s *K* statistic of phylogenetic signal revealed that endemic and alien genera showed a significant phylogenetic signal for plant height (endemic: $K = 2.57$, $p < 0.001$; alien: $K = 1.90$, $p < 0.001$; see Appendix S2.6, Table S2.6.4). This indicates that within endemic and alien genera close relatives were more likely to have a similar plant height than would be expected by chance. There was a significant random (to intermediate) pattern in trait evolution for leaf length (endemic: $K = 0.58$, $p < 0.05$; non-endemic native: $K = 0.26$, $p < 0.05$) and fruit length (endemic: $K = 0.81$, $p < 0.05$; non-endemic native: $K = 0.25$, $p < 0.05$; alien: $K = 0.43$, $p < 0.001$). Blomberg’s *K* did not show any statistical significance in flower length for across the floristic groups.

Occurrence-based FD_{SES} had a slightly positive correlation with phylogenetic diversity of endemic and non-endemic native assemblages (endemics: Pearson’s $r = 0.23$, $p < 0.001$; non-endemic natives: Pearson’s $r = 0.25$, $p < 0.001$; see Appendix S2.6, Figure S2.6.9a, b). For alien assemblages, occurrence-based FD_{SES} had a slightly negative correlation with phylogenetic diversity (Pearson’s $r = -0.05$, $p = 0.003$; see Appendix S2.6, Figure S2.6.9c).

2.4 Discussion

Our study demonstrates that the functional traits of endemic and non-endemic native plant species on the Canary Islands are very similar to each other, whereas alien species possess novel trait combinations, suggesting differential effects of environmental filtering and human introduction pathways on these different floristic groups. On a 0.25 km² grid cell scale, functional diversity of endemic assemblages is highest under humid and isolated conditions, and functional diversity of non-endemic native assemblages is highest under humid conditions. In contrast, functional diversity of alien assemblages is highest in dry environments where most alien species have been introduced. These findings highlight the importance of functional traits for understanding the composition of island assemblages.

2.4.1 Functional trait space of floristic groups

The high overlap of trait space between endemic and non-endemic native species suggests a packing of niche space rather than an exploitation of new functional strategies. This is consistent with studies that have shown that high species richness is associated with denser occupation of functional trait space, which can either arise through very fine morphological specialisations or overlap in resource use (Klopfer & MacArthur, 1961; Pigot *et al.*, 2016). However, there are also species which do not follow this pattern, such as *Phoenix canariensis*, a Canary Island endemic palm tree. It clearly extends the occupied trait space through its large plant height and long fronds. Further, we show that alien species both expanded the overall trait space and overlapped in trait composition with endemic and non-endemic native species. This suggests that alien species were able to exploit novel regions of functional niche space (MacArthur, 1965) as well as use similar resources as native species (Klopfer & MacArthur, 1961). However, as the observed patterns represent roughly ~43 % of the Canary Island flora, they might be dependent on the particular species considered.

2.4.2 Functional diversity of endemic and non-endemic native plant assemblages

Our results indicate that humidity and geographical isolation may be important factors driving functional diversity patterns in native assemblages on the Canary Islands. However, due to their high collinearity with each other, and with elevation, we cannot clearly disentangle their effects on functional diversity. On the Canary Islands, humidity is highest at intermediate elevation on more isolated islands (i.e. in the laurel forest on La Palma) and lowest at the coast on islands closer to the continent (i.e. in the succulent shrub on Gran Canaria). Indeed, we found overlap in explained variation between humidity and geographical isolation, especially in endemic assemblages. Hence, the functional clustering in coastal habitats could be attributed to environmental filtering via humidity. According to the 'physiological tolerance hypothesis', environments with higher water availability permit a wider range of functional strategies (Spasojevic *et al.*, 2014), while species that occur in habitats with extreme environmental conditions often tend to have specific and similar adaptations (Cornwell & Ackerly, 2009). For example, when water resources are limited, plants have to reduce their transpiration rates (Gates, 1965) and therefore develop small leaves (Poorter *et al.*, 2010; Peppe *et al.*, 2011; Spasojevic *et al.*, 2014; Wright *et al.*, 2017) and small flowers (Paušič *et al.*, 2019; Kuppler & Kotowska, 2021). In contrast, laurel forests are dominated by mild climate and continual humidity that might have offered ecological opportunity for niche differentiation (Rundell & Price, 2009). However, competition could have led to functional divergence and hence increased functional diversity in humid habitats as well (MacArthur & Levins, 1967; Spasojevic & Suding, 2012). Taller plants with larger leaves, flowers and fruits have a higher competitive vigour and could be able to increase partitioning within the assemblages. Moreover, functional diversity could even be facilitated by tall, large-leaved and large-flowered species through a reduction of evaporative losses for smaller, functionally distinct, species through light interception (Callaway *et al.*, 2002; Spasojevic & Suding, 2012).

Functional diversity increased with increasing geographical isolation in endemic assemblages and had a hump-shaped relationship with non-endemic native assemblages. In endemic plant species, isolation may select against dispersal ability by increasing fruit and seed size to reduce dispersal into the sea (Rossetto & Kooyman, 2005; Kavanagh & Burns, 2014). Larger seeds have increased nutrient reserves and thus a highly competitive vigour during establishment (Thompson *et al.*, 1993; Moles & Westoby, 2004). To decrease competitive interaction with large-seeded species, endemic species might diverge in trait values (MacArthur & Levins, 1967), leading to greater functional diversity with greater isolation. Moreover, isolation can limit gene flow between species which drives ecological opportunity and may foster adaptive speciation in endemic summit scrub and rock communities of the Canary Islands (Fernández-Palacios *et al.*, 2021). Responses of non-endemic native functional diversity to isolation could be influenced by the dispersal mode of species. Species with wind and unassisted dispersal have smaller diaspores than species with animal dispersers (Leishman *et al.*, 1995). Moreover, dispersal limitation via plant height could have driven the decrease of functional diversity in highly isolated habitats in non-endemic native species (Thomson *et al.*, 2011). Hence, establishment of functionally diverse, non-endemic native assemblages at intermediate isolation appears to have been dependent on disharmonic diaspore size and plant height. However, our results need to be interpreted with caution as our metric of isolation considers distance to climatically suitable mainland and ignores other factors such as wind and ocean currents as well as climatically similar areas on other islands as possible modifiers to these distances (Price, 2004; Muñoz *et al.*, 2017). Moreover, studies on edaphic islands have shown that target effect (i.e. indicating the increased probability of a larger island to be colonised than a smaller island given the same isolation) might play a key role in determining plant diversity patterns (Mendez-Castro *et al.*, 2021; Conti *et al.*, 2022). Ignoring these additional isolation metrics might lead to an under- or overestimation of geographic isolation and its relationship with functional diversity. Nonetheless, despite its limitations climatic similarity has previously been shown to be an adequate measure of geographical isolation (Weigelt & Kreft, 2013).

Functional diversity of endemic and non-endemic assemblages decreased with topographic complexity. The observed pattern could be an indication of a trade-off between topographic complexity and the amount of area available for species (Allouche *et al.*, 2012). With very high topographic complexity, the amount of effective area available for species should decrease, thereby increasing the likelihood of stochastic extinctions in species with a narrow niche (Allouche *et al.*, 2012). The area–heterogeneity trade-off seems to be more important for endemic species than for non-endemic species, suggesting that non-endemic species might have wider niches in topographically complex habitats. Moreover, very high topographic complexity facilitates the isolation of small populations that may diverge to new endemic allopatric species, augmenting the species number but not the functional diversity (Badgley *et al.*, 2017). However, we must be careful with the interpretation of these results. Species which occur in very steep sites rarely get reported and therefore information on species assemblages in topographically complex sites is limited and could possibly over- or underestimate the functional diversity of plant assemblages.

Our results indicate that geological age has no relationship with functional diversity of endemic assemblages. This indicates that soil age does not act as an ecological filter on the functional diversity of endemic assemblages. Surprisingly, non-endemic native species assemblages seem to be functionally different from endemic assemblages in nutrient-deficient sites. This suggests that non-endemic native species have functional properties to grow on older volcanic sites where destructive processes, which cause nutrient depletion and soil homogenisation, dominate (Lambers *et al.*, 2008; Laliberté *et al.*, 2013a; Mueller-Dombois & Boehmer, 2013). However, the explained variation of the models is low, and the results should be interpreted with caution. Further, our measurement of geological age was approximate and might not be precise enough to reflect mechanisms of soil development on plant functional diversity.

2.4.3 Functional diversity of alien plant assemblages

Alien assemblages show a decrease of functional diversity with increasing humidity, geographical isolation and geological age, as well as an increase of functional diversity with increasing topographic complexity. This mostly contrasts with the relationships of endemic and non-endemic native assemblages. This could be due to a direct negative effect of native functional diversity through biotic resistance. If native assemblages are functionally diverse, it is more likely that they have overlapping resource requirements with alien species and are therefore able to outcompete them (Funk *et al.*, 2008; but see Galland *et al.*, 2019). For instance, the laurel forest is thought to be ecologically resistant to invasion through light interception in the understorey, highly competitive pressure for nutrients from tree roots, and the effect of allelopathy from laurel leaf-litter on alien species (Bermúdez *et al.*, 2007). Nevertheless, there is evidence that even this stable ecosystem can be invaded by an alien tree (Devkota *et al.*, 2020). We also expect the analysed predictor variables to be negatively correlated with anthropogenic activity (for patterns of alien species richness on Tenerife and La Palma, see Irl *et al.*, 2021). Hence, the observed relationship for alien species might also be influenced by a subsequent directional filtering proceeding from sources of anthropogenic introduction (Irl *et al.*, 2021). This indicates that so far only a functional subset of alien species with wide environmental tolerances has been able to invade habitats separated from the source pool by a steep environmental gradient.

2.4.4 Spatial structure and phylogenetic non-independence

Although we find relationships with environment and isolation, we need to consider that spatial autocorrelation and phylogenetic non-independence have influenced the observed patterns. Spatial structure accounted for a large part of the explained variation in some of the regression models. For alien assemblages, this could indicate a non-equilibrium distribution due to their recent island-specific introductions. Further, the analysed environmental variables are spatially aggregated on the Canary Islands. For example, very humid environments exist on La Palma but we do not find these conditions on other islands. Therefore, we can only analyse the relationship between functional diversity and highly humid environments within La Palma, and the relationship might be influenced by the phylogenetic non-independence of (single-island) endemic species.

At the assemblage level we could detect a significant but low to moderate correlation between functional and phylogenetic diversity for the three floristic groups. These results imply that the differences in functional diversity between the floristic groups at least partly reflect trait conservatism (Blomberg *et al.*, 2003). However, applying a correction for non-independence has been shown to lead to an unintended ‘over-correction’ (Ricklefs & Starck, 1996; but see Rohle, 2006) and is likely not feasible using a pruned tree with polytomies, as is the case for the tree used in this study. We conclude that even though our results might be partly influenced by phylogenetic non-independence, they nevertheless point to important relationships between functional diversity and the environment that inform us about the drivers of species assemblages on oceanic islands.

2.5 Conclusion

Our study indicates that endemic species do not substantially differ, functionally, from the more widespread non-endemic native species group. Both groups have adapted to the island environment over long time periods, although much longer for endemic than for non-endemic native species. However, functional diversity of endemic and non-endemic native plant assemblages is distributed differently along environmental and island biogeographical gradients, indicating the importance of climate and ecological opportunity for the evolution of plant form and function. In contrast, alien species tend to be functionally dissimilar to endemic and non-endemic native species, and their assemblages show great functional diversity in semi-arid and less isolated ecosystems, which are the main gateway for anthropogenic introduction. Furthermore, the strong connection between functional diversity of endemic and non-endemic native assemblages with climatic conditions suggests that current ongoing climate change might alter patterns of plant functional diversity on the Canary Islands. However, we are aware that the choice of traits and environment are highly relevant for the results of a trait-based study (Bernard-Verdier *et al.*, 2012; Carvajal *et al.*, 2019; Ottaviani *et al.*, 2020). Our study did not analyse leaf or flower economics data (e.g. ratio of leaf or flower area to dry mass), regenerative traits (e.g. seed mass) or below-ground traits (e.g. specific root length), which should be considered in future studies (if the data become available) to better link trait functions to hypotheses concerning water-use efficiency. Particularly, functional diversity patterns in different growth form types should be analysed in future studies as growth form can have important implications for community assembly across climatic and biogeographic gradients (Irl *et al.*, 2020; Schrader *et al.*, 2020). Moreover, further analyses with entire floras and from other islands, archipelagos or mountainous regions on continents, and with other taxonomic groups, are needed to test the wider generality of our results in the context of functional island biogeography, and to understand the importance of functional diversity for the establishment and diversification of native and alien plant species in space and time.

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Data availability statement

All morphological trait data are deposited on DRYAD (https://doi.org/10.5061/dryad.wdbrv 15r1). The data provided include the full list of species names, trait data and the respective references.

Supporting information

Appendix S2.1

Details on species distribution models

We interpolated species' occurrences using species distribution models (SDMs; Calabrese *et al.*, 2014) which were parameterised following Irl *et al.* (2020). SDMs were implemented using generalised linear models with a binomial distribution, logit-link function, and polynomial terms of second-order, but did not include interaction terms among explanatory variables ($y \sim x + x^2$). Potential explanatory variables were elevation, aspect (calculated as the cosines of the radian measure (aspect north) and the sines of the radian measure (aspect east)) and slope. We chose these variables to reduce potential circularity problems associated with using variables later used to test the hypotheses.

Stepwise variable selection in both directions (i.e. forward and backward) was applied using the Akaike Information Criterion. Pseudo-absence points were generated by random selection of grid cells that were not occupied by the species. If possible, we selected as many pseudo-absence points as there were presences for each species. Models were trained using occurrence records from the Canary Islands; species occurrences on islands where species are naturally absent were not included. Species with fewer than 25 occurrences (294 species, ~ 15 %) in the database were excluded from the analysis. The trained GLMs were validated using 10-fold cross-validation to avoid over-fitting when using small sample sizes. For each species, a probability of occurrence in each 500 m × 500 m grid cell was assigned by the SDM. For model validation, all presence and pseudo-absence points were split into training and testing data samples with a ratio of 80:20 percent using random stratified sampling. Predicted probability values that were greater than the species' prevalence (proportion of presences relative to the number of grid cells) were categorised as "present". Those values that were smaller than the species' prevalence were categorised as "absent" (Cramer, 2003). To check whether using modelled species distributions created an artificial relationship between the predictor variables and functional diversity, we performed all statistical analyses with the original occurrence data and the modelled species distribution data.

Appendix S2.2

Morphological trait data collection

We collected data on four functional morphological traits that reflect fundamental ecological strategies of plants. Morphological trait data of the respective plant species were collected from literature sources (Hohenester & Welß, 1993; Eggli, 2002; Muer *et al.*, 2016; Schönfelder & Schönfelder, 2018a,b), extracted from the GIFT database (Weigelt *et al.*, 2020), measured on digitised plant specimens stored on JSTOR (www.plants.jstor.org) or GBIF (www.gbif.org) and extracted from species' descriptions (Sprague & Hutchinson, 1914; Bramwell, 1972, 1975, 1995a,b; Hansen, 1972; Stearn, 1972; de Paz, 1973, 1977; Wildpret de la Torre, 1973; Humphries, 1976; La Serna, 1980; La Serna & Wildpret de la Torre, 1980; del Arco Aguilar & Acebes Ginovés, 1981; de Paz & Hernriquez, 1981; Halliday, 1986; Mendoza-Heuer, 1987; Galván & Guerra, 1988; Kilian, 1988; Liu, 1989; Boyce, 1994; Scholz & Böcker, 1996; Marrero *et al.*, 1998; Pedrola-Monfort & Caujapé Castells, 1998; Nogales *et al.*, 1999; del Arco Aguilar, 2000; Scholz *et al.*, 2000; Valcárcel *et al.*, 2001; Baudet, 2002; Gaisberg & Wagenitz, 2002; Marrero & Navarro, 2003; Montelongo *et al.*, 2003; Upson & Andrews, 2003; Chaisongkram & Chantaranotha, 2006; Kyncl *et al.*, 2006; Sandral *et al.*, 2006; Alamo *et al.*, 2007; Marrero, 2008, 2013; Prina & Martínez-Laborde, 2008; Rodríguez *et al.*, 2010; Verloove, 2010; Baudet *et al.*, 2013; Gonzáles *et al.*, 2013; Santos Guerra, 2014; Vitales *et al.*, 2014; Wood *et al.*, 2015; Negrin-Sosa & de Paz). We collected data on maximum trait values as the maximum better reflects mature species' fitness and has better data coverage throughout the literature. This is a valid approach as recent studies show that trait data from plant determination books are comparable to measured trait data (Cutts *et al.*, 2021).

Appendix S2.3

Calculation of environmental variables

Monthly mean temperature and monthly total precipitation were interpolated on a 500 m x 500 m grid cell scale from a dense net of climate measurements (n = 155 for temperature and n = 305 for precipitation) provided by the Agencia Estatal de Meteorología (AEMET). Climate interpolation included spatial variables, elevation, aspect, slope, rain shadow effects and precipitation increases caused by orographic lift of air masses (assuming northerly wind directions from 020°) as well as cloud cover (Platnick *et al.*, 2015) as explanatory variables in a multiple regression (for temperature) and a boosted regression tree model (for precipitation;(Irl *et al.*, 2020). In the Teide violet communities above 2,400 m a.s.l. (del Arco Aguilar *et al.*, 2010) we can find cold and dry environments which are very rare and different from the environmental conditions that are found elsewhere in the Canary Islands. Hence, we removed grid cells over 2,400 m a.s.l. to avoid spatial autocorrelation and approximate an even distribution of grid cells along the remaining environmental gradient. This has only a minor effect on our analyses as alien species mainly do not occur at higher elevations and can hence not be compared to endemic and non-endemic native species there. Monthly mean temperature was used to calculate potential evapotranspiration according to the Thornthwaite equation (Thornthwaite, 1948) using the 'SPEI' package in R (Beguería & Vicente-Serrano, 2017). Subsequently, we calculated the Humidity Index after UNEP (1992) which is given by:

$$Humidity\ index = \frac{\sum_{i}^{12} \frac{P_i}{PET_i}}{12},$$

where P is the monthly mean precipitation and PET the monthly potential evapotranspiration. The Humidity index is useful as it classifies the type of climate in relation to water availability (UNEP, 1992). Humidity index ranged approximately from 0.07 (arid) to 2.05 (humid) across the five islands (Table 2.1; Figure S2.3.1a).

We further calculated geographical isolation per grid cell based on the distance to climatically similar land mass (Weigelt & Kreft, 2013). Geographical isolation was quantified as the distance of a grid cell to the nearest terrestrial area on the continent that has a mean annual temperature within 1°C, following Steinbauer *et al.* (2016). Only the focal grid cell and grid cells beyond the archipelago were used in this calculation because endemism is defined at the archipelago level. Mean annual temperature for the continent was obtained from 1 km x 1 km resolution CHELSA data (Karger *et al.*, 2017). Processing of spatial data was done using the R package 'raster' (Hijmans, 2019). Geographical isolation of the island grid cells ranged from 196.5 km to 885 km to the closest continental grid cell with similar environmental conditions (Table 2.1; Figure S2.3.1b).

We calculated topographic complexity per grid cell as it relates to the rate of elevational change in response to changes in location (Amatulli *et al.*, 2018) and can therefore act as a surrogate for habitat heterogeneity (Irl *et al.*, 2015). We estimated topographic complexity per grid cell by using a moving window approach that calculates the surface area for a cell based on slope information from a specified set of smaller grid cells (in this study 20 x 20 grid cells; after Jenness (2004):

$$Topographic\ complexity\ index\ = \frac{\sum_{500mx500m} \left(\frac{Area_{25mx25m}}{cos\,(Slope_{25mx25m}\,)}\right)}{Area_{500mx500m}},$$

where $Area_{25mx25m}$ is the area per grid cell from a 25 m x 25 m digital elevation model (DEM; GRAFCAN (2019), $Slope_{25mx25m}$ the slope (in radians) of each grid cell from the same DEM in degrees, and $Area_{500mx500m}$ the area per grid cell from a 500 m x 500 m DEM containing all grid cells form the 25 m x 25 m DEM. Topographic complexity ranged from 1 (flat) to 2.17 (high complexity; Table 2.1; Figure S2.3.1c).

Furthermore, we calculated geological age per grid cell as it represents a proxy for plant nutrient availability (Lambers *et al.*, 2008) which is known to generate functional diversity (Lambers *et al.*, 2011). We derived geological age per grid cell from a continuous digital geological map of Spain (scale 1:50,000; Bellido Mulas *et al.*, 2020). We calculated geological age as the mean age of the geological time period that we assigned to each grid cell of the Canary Islands based on the geological map. Mean geological age per grid cell ranged from 6 ka to 13.8 Ma (Table 2.1; Figure S2.3.1d).

For further analyses we ln-transformed the humidity and topographic complexity index to approximate normality and subsequently centred and scaled all environmental variables, yielding estimates in standard deviation units per grid cell. After standardisation, we calculated correlation coefficients (Pearson's *r*) between the environmental variables, as well as elevation (Table S2.3.1).

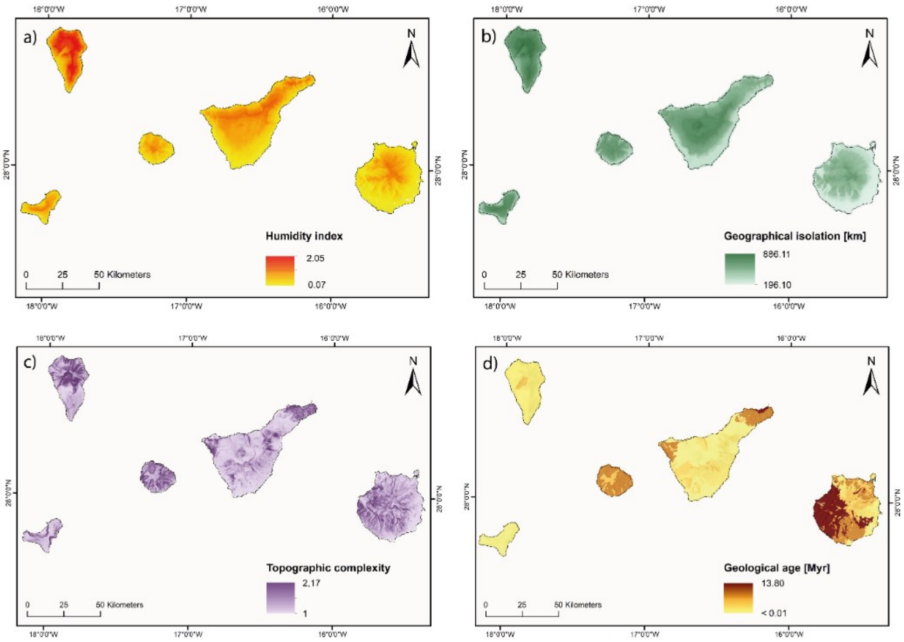


Figure S2.3.1. Climatic and biogeographic variables across the Canary Islands. a) Humidity was quantified as mean annual precipitation in relation to mean annual potential evapotranspiration per grid cell, b) geographical isolation was quantified as the distance of a grid cell to the nearest terrestrial area on the continent that has a mean annual temperature within 1°C, c) topographic complexity per grid cell was estimated by calculating the ratio between 3D and 2D surface area, e) geological age per grid cell was derived from a continuous digital geological map of Spain (scale 1:50,000; Bellido Mulas *et al.*, 2020).

Table S2.3.1. Pearson's correlation coefficient between humidity, geographical isolation, topographic complexity and geological age on the Canary Islands based on 500 m x 500 m grid cells. Coefficients given in black are based on observed FD_{SES} grid cells (n = 3,065), coefficients given in grey are based on modelled FD_{SES} grid cells (n = 17,095).

	Log – Humidity	**Geographical isolation**	**Log – Topographic complexity**	**Geological age**	**Elevation**
Log - Humidity	-	0.891	0.244	-0.291	0.781
Geographical isolation	0.804	-	0.296	-0.302	0.784
Log – Topographic complexity	0.191	0.379	-	0.371	0.210
Geological age	-0.198	-0.128	0.418	-	-0.129
Elevation	0.720	0.723	0.189	-0.045	-

Appendix S2.4

Functional diversity and species richness of the Canary Islands

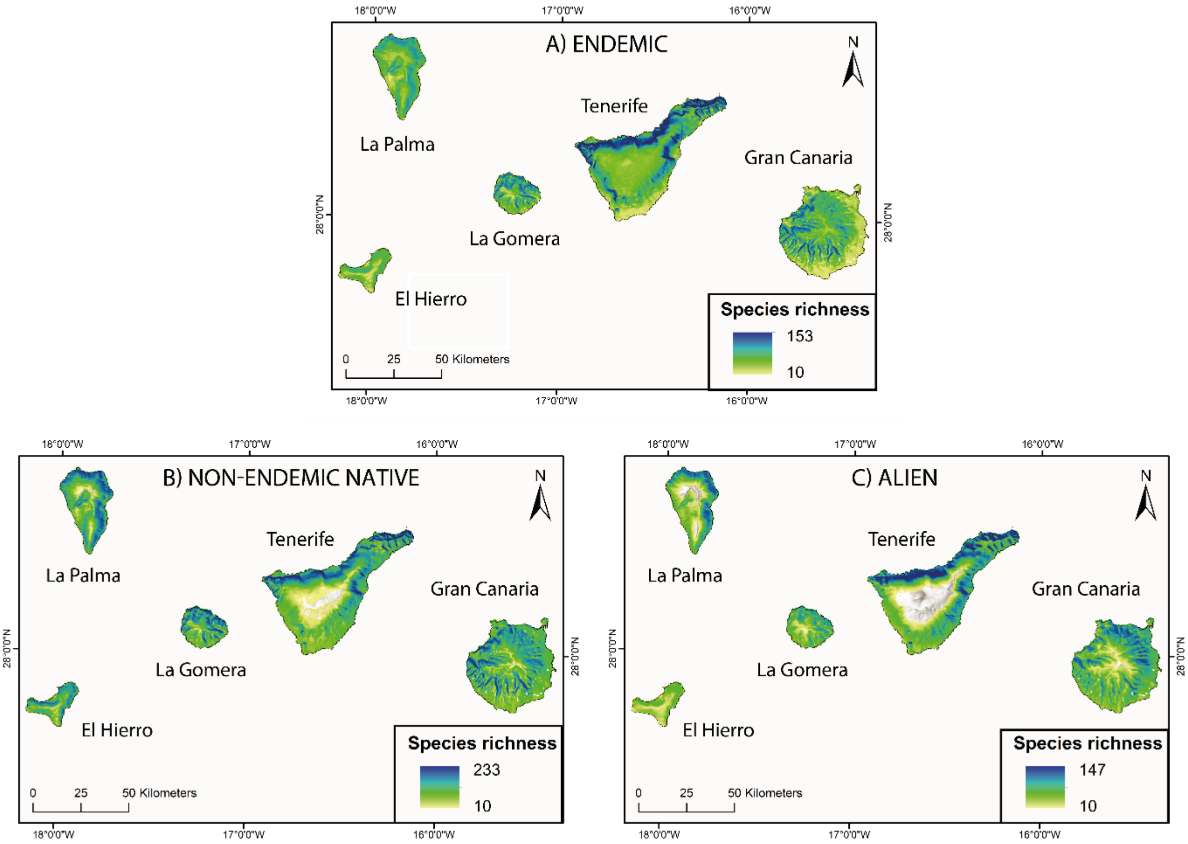


Figure S2.4.2. Map of modelled plant species richness per 500 m x 500 m across the Canary Islands for **a)** endemic, **b)** non-endemic native and c) alien assemblages (> 10 species).

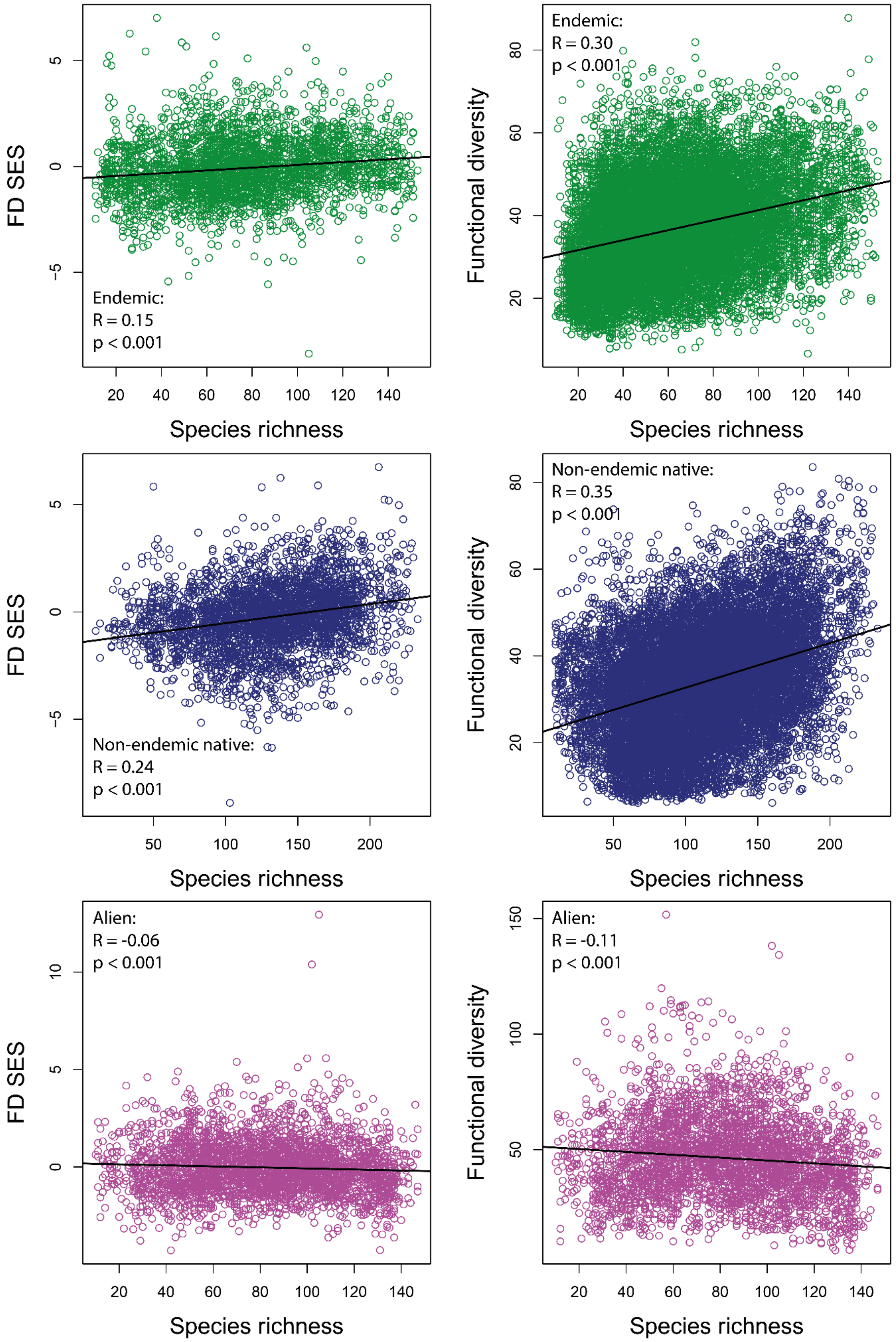
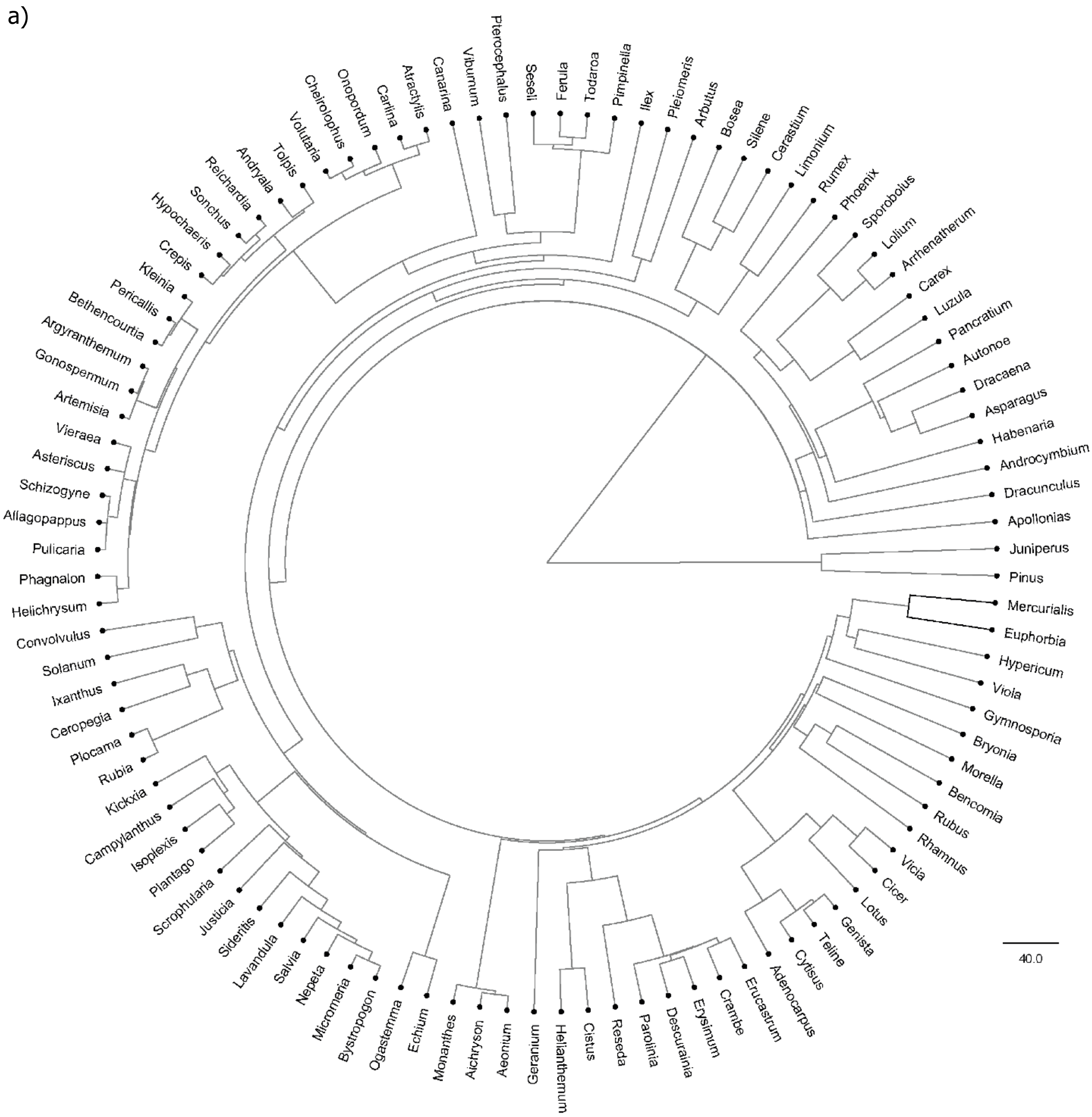


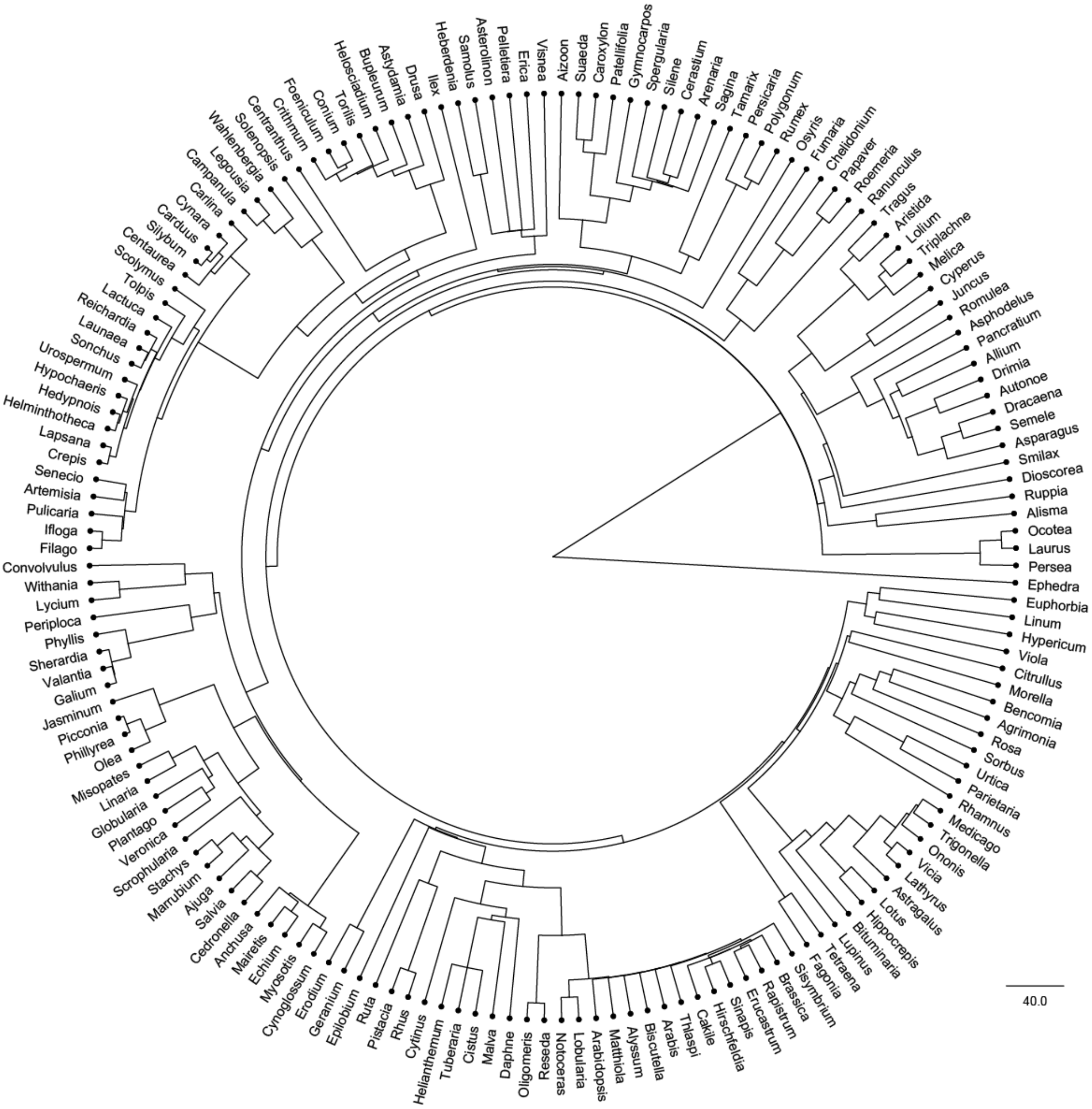
Figure S2.4.3. Pearson's correlation between **a-c)** species richness and FD_{SES} and **d-f)** species richness and functional diversity based on 500 m x 500 m grid cells for observed endemic (n = 3,065), non-endemic (n = 3,063) and alien (n = 3,056) species assemblages. R is Pearson's correlation coefficient and p indicates the statistical significance. Simple linear regression lines are depicted on the graphs for a clearer visualisation of the trends.

Appendix S2.5

Phylogenetic signal at the genus- and assemblage level



b)


Convolvulus
Withania
Lycium
Periploca
Phyllis
Sherardia
Valantia
Galium
Jasminum
Picconia
Phillyrea
Olea
Misopates
Linaria
Globularia
Plantago
Veronica
Scrophularia
Stachys
Marrubium
Ajuga
Salvia
Cedronella
Anchusa
Mairetis
Echium
Myosotis
Cynoglossum
Erodium
Geranium
Epilobium
Ruta
Pistacia
Rhus
Cytinus
Helianthemum
Tuberaria
Cistus
Malva
Daphne
Oligomeris
Reseda
Notoceras
Lobularia
Arabidopsis
Matthiola
Alyssum
Biscutella
Arabis
Thlaspi
Cakile
Hirschfeldia
Sinapis
Erucastrum
Rapistrum
Brassica
Sisymbrium
Fagonia
Tetraena
Lupinus
Bituminaria
Hippocrepis
Lotus
Astragalus
Lathyrus
Vicia
Ononis
Trigonella
Medicago
Rhamnus
Parietaria
Urtica
Sorbus
Rosa
Agrimonia
Bencomia
Morella
Citrullus
Viola
Hypericum
Linum
Euphorbia
Ephedra
Persea
Laurus
Ocotea
Alisma
Ruppia
Dioscorea
Smilax
Asparagus
Semele
Dracaena
Autonoe
Drimia
Allium
Pancratium
Asphodelus
Romulea
Juncus
Cyperus
Melica
Triplachne
Lolium
Aristida
Tragus
Ranunculus
Roemeria
Papaver
Chelidonium
Fumaria
Osyris
Rumex
Polygonum
Persicaria
Tamarix
Sagina
Arenaria
Cerastium
Silene
Spergularia
Gymnocarpos
Patellifolia
Caroxylon
Suaeda
Aizoon
Visnea
Erica
Pelletiera
Asterolinon
Samolus
Heberdenia
Ilex
Drusa
Astydamia
Bupleurum
Helosciadium
Torilis
Conium
Foeniculum
Crithmum
Centranthus
Solenopsis
Wahlenbergia
Legousia
Campanula
Carlina
Cynara
Carduus
Silybum
Centaurea
Scolymus
Tolpis
Lactuca
Reichardia
Launaea
Sonchus
Urospermum
Hypochaeris
Hedypnois
Helminthotheca
Lapsana
Crepis
Senecio
Artemisia
Pulicaria
Ifloga
Filago
40.0

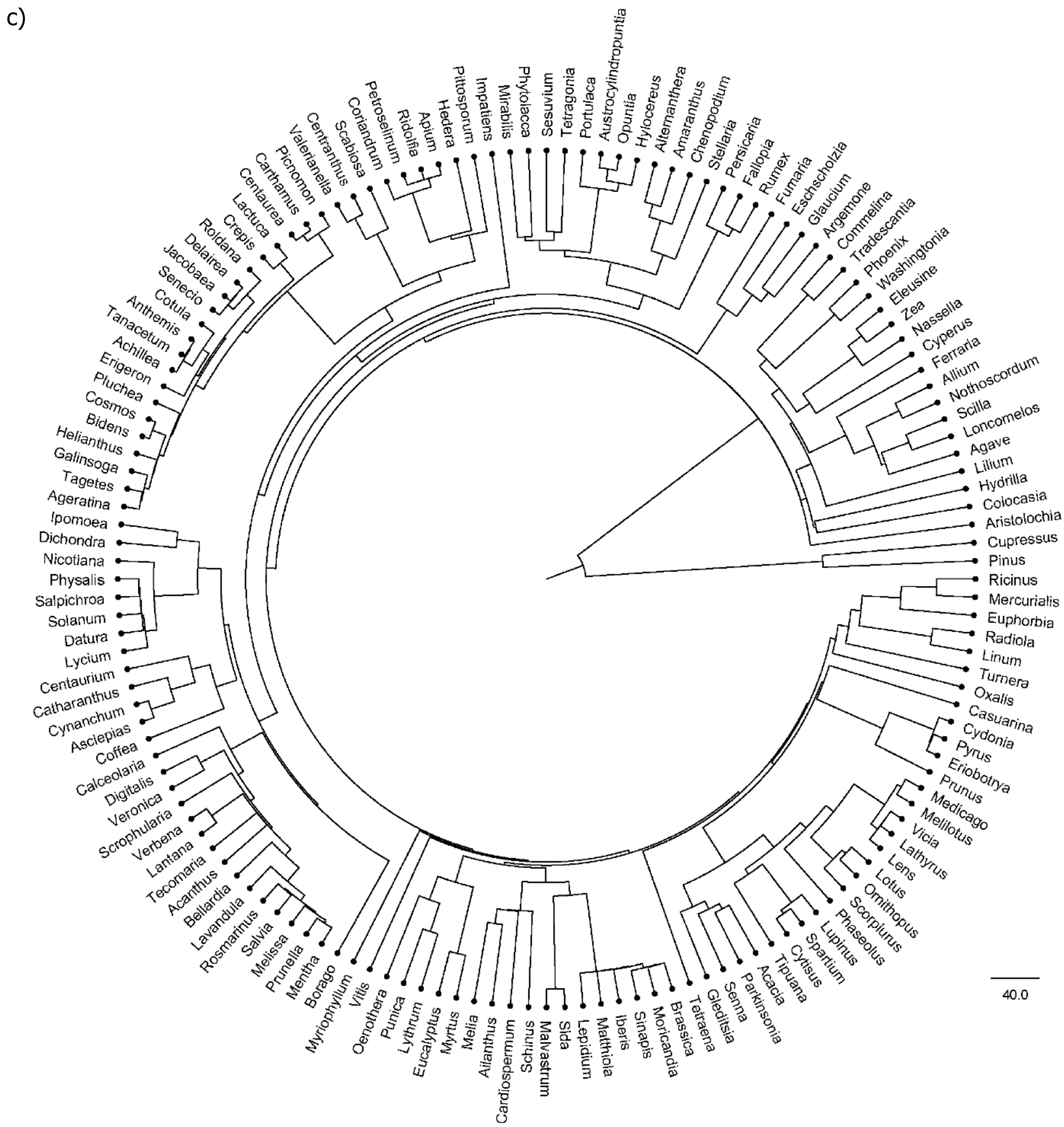


Figure S2.5.4. Phylogenetic tree of **a)** 103 endemic, **b)** 166 non-endemic native and **c)** 147 alien plant genera of the Canary Islands. The trees were pruned from the global seed plant phylogeny from Smith & Brown (2018).

Appendix S2.6

Results of models accounting for collinearity and of models using modelled species occurrence data

Table S2.6.2. Explained variation of generalised linear models (GLM) and spatial autoregressive (SAR) models analysing the combined effect of **a)** humidity, topographic complexity and geological age and **b)** geographical isolation, topographic complexity and geological age on FD_{SES} of endemic, non-endemic native and alien seed plant assemblages based on 500 m x 500 m grid cells across the Canary Islands. FD_{SES} is based on four functional traits (plant height, leaf length, flower length and fruit length) and was calculated for grid cells with occurrence-based data (n = 3,065). Percentage of total deviance explained (% dev.), Akaike Information Criterion (AIC) and Moran's I are given. Model coefficients of SEMs are given in Figure S6.6.

a)	GLM			SAR		
	% dev.	AIC	Moran's I	% dev.	AIC	Moran's I
Endemic	26.1	9818.1	0.57	53.1	8433.1	-0.08
Non-endemic native	18.3	10928	0.68	60.2	8736	-0.10
Alien	6.6	10418	0.63	48.8	8584.7	-0.09
b)	GLM			SAR		
	% dev.	AIC	Moran's I	% dev.	AIC	Moran's I
Endemic	18.9	10105	0.60	51.8	8514.5	-0.09
Non-endemic native	12.6	11134	0.71	60.0	8748.1	-0.11
Alien	3.4	10524	0.64	48.6	8598.9	-0.09

Table S2.6.3. Explained variation of generalised linear models (GLM) and spatial autoregressive (SAR) models analysing the combined effect of humidity, geographical isolation, topographic complexity and geological age on FD_{SES} of endemic, non-endemic native and alien seed plant assemblages based on 500 m x 500 m grid cells across the Canary Islands. FD_{SES} is based on four functional traits (plant height, leaf length, flower length and fruit length) and was calculated for grid cells with modelled data (n = 17,094). Percentage of total deviance explained (% dev.), Akaike Information Criterion (AIC) and Moran's I are given. Model coefficients of SEMs are given in Figure S6.7.

	GLM			SAR		
	% dev.	AIC	Moran's I	% dev.	AIC	Moran's I
Endemic	34.6	52114	0.48	54.9	45767	-0.09
Non-endemic native	50.7	59856	0.52	68.1	52406	-0.10
Alien	39.4	57818	0.54	61.8	49948	-0.10

Table S2.6.4. Phylogenetic signal in the trait variation of endemic, non-endemic native and alien seed plants of the Canary Islands, using Blomberg's *K* statistic. n is the number of genera with trait data represented in the given phylogeny. Asterisks indicate statistical significance (*p < 0.05, **p < 0.01, ***p < 0.001).

	Genus level		
	Endemic (n = 103) *K*	**Non-endemic native (n = 166) *K***	**Alien (n = 147) *K***
Plant height	2.568***	0.370***	1.902***
Leaf length	0.584*	0.258*	0.345
Flower length	0.201	0.210	0.173
Fruit length	0.814*	0.248*	0.426***

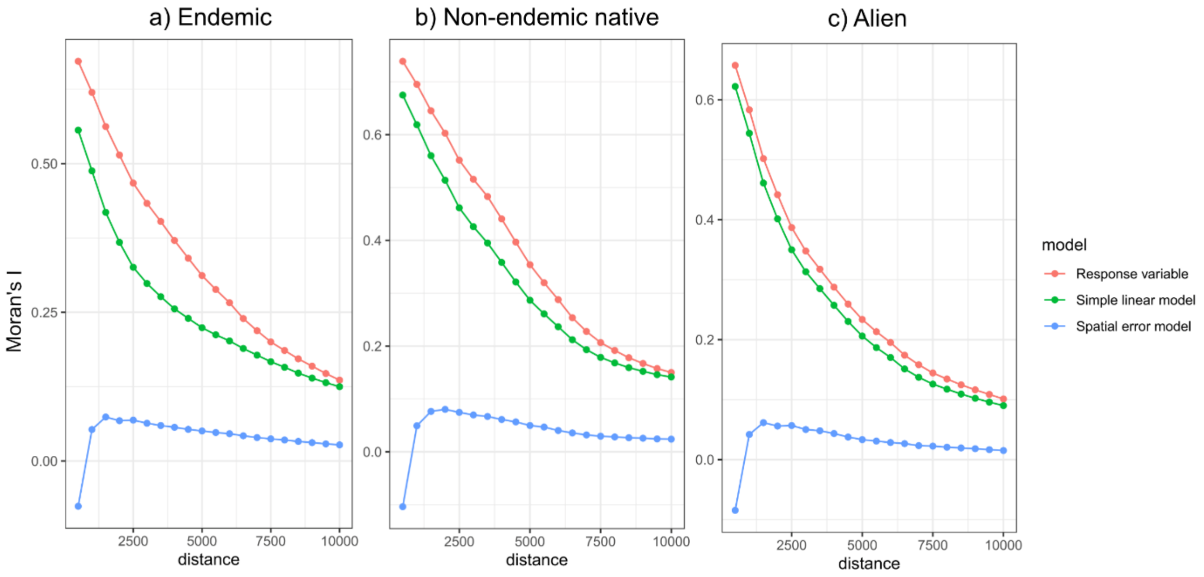


Figure 2.6.5 Correlogram of the response variable (functional diversity), the simple linear model and the spatial error model analysing the relationship between functional diversity and humidity, geographical isolation, topographic complexity and geological age in **a)** endemic, **b)** non-endemic native and **c)** alien plant species assemblages on the Canary Islands.

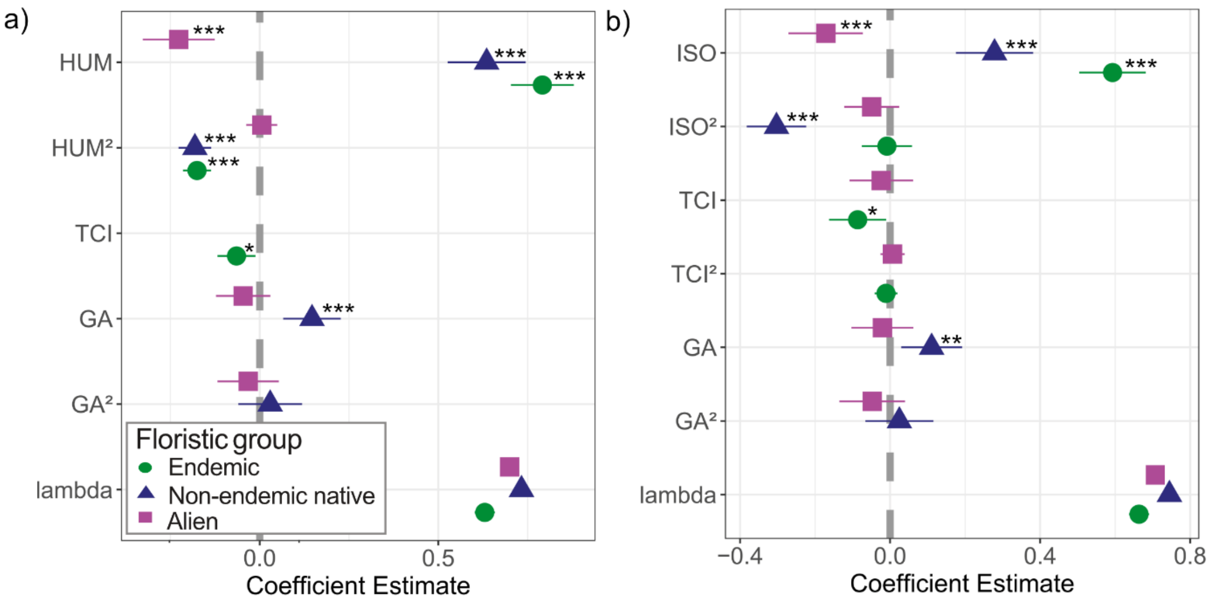


Figure S2.6.6. Multi-predictor spatial autoregressive models of **a)** humidity (HUM), topographic complexity (TCI) and geological age (GA) and **b)** geographical isolation (ISO) topographic complexity (TCI) and geological age (GA) on modelled FD_{SES} of endemic (n = 313 species), non-endemic native (n = 291 species) and alien plant species assemblages (n = 216 species) on the Canary Islands. FD_{SES} is based on four functional traits (plant height, leaf length, flower length and fruit length) and was calculated for occurrence-based data based on 500 m x 500 m grid cells (n = 3,065). Shown are the respective best models according to a model comparison approach. Standardised estimates are provided for each predictor. Error bars represent confidence intervals of the coefficient estimates. Asterisks denote statistical significance (*** p < 0.001; ** p < 0.01; * p < 0.05).

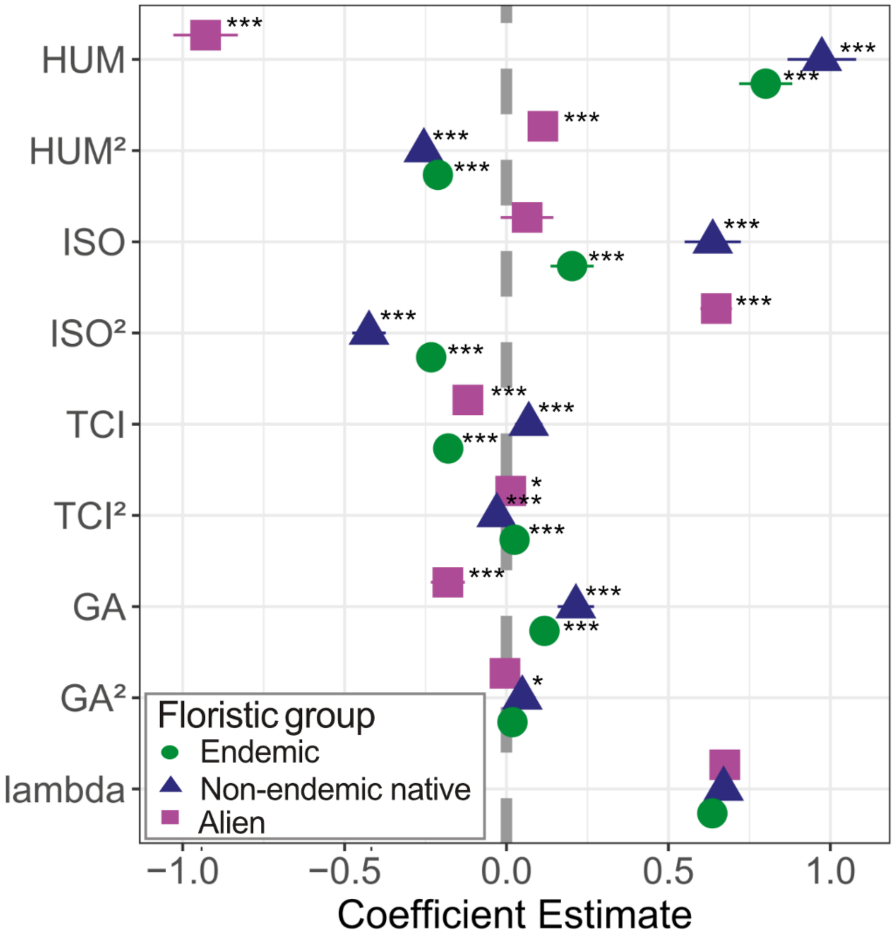


Figure S2.6.7. Multi-predictor spatial autoregressive models of humidity (HUM), geographical isolation (ISO), topographic complexity (TCI) and geological age (GA) on modelled FD_{SES} of endemic (n = 313 species), non-endemic native (n = 291 species) and alien plant species assemblages (n = 216 species) on the Canary Islands. FD_{SES} is based on four functional traits (plant height, leaf length, flower length and fruit length) and was calculated for modelled data based on 500 m x 500 m grid cells (n = 17,094). Shown are the respective best models according to a model comparison approach. Standardised estimates are provided for each predictor. Error bars represent confidence intervals of the coefficient estimates. Asterisks denote statistical significance (*** p < 0.001; ** p < 0.01; * p < 0.05).

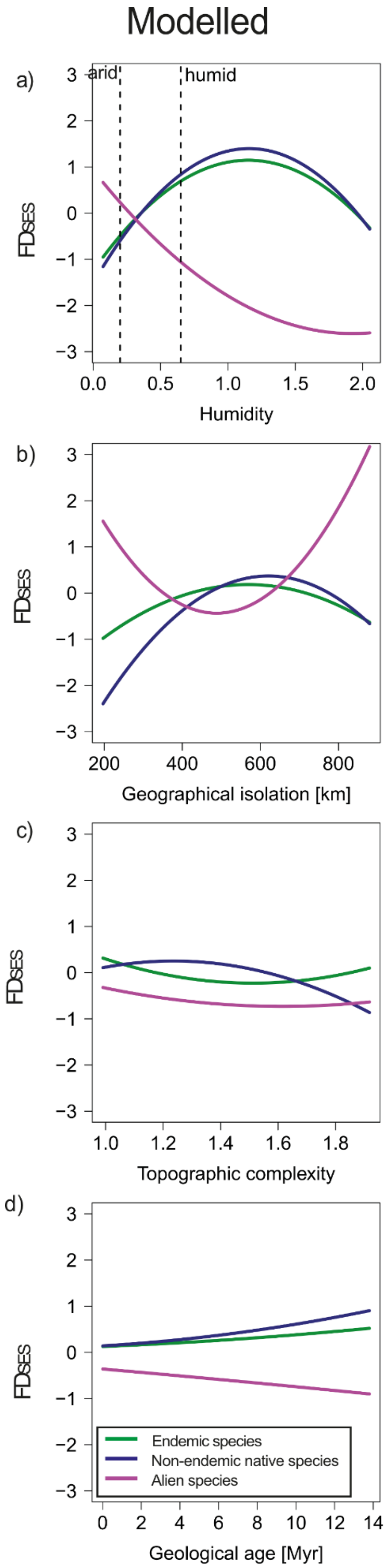


Figure S2.6.8. Modelled FD_{SES} of plant assemblages based on 500 m x 500 m grid cells (n = 17,094) along **a)** humidity, **b)** geographical isolation, **c)** topographic complexity and **d)** geological age gradients across the Canary Islands. Functional diversity is based on four functional traits (growth height, leaf length, flower length and fruit length) of 313 endemic, 291 non-endemic native and 216 alien plant species. Lines show the trends of the models given in Figure S2.6.7 and Table S2.6.3.

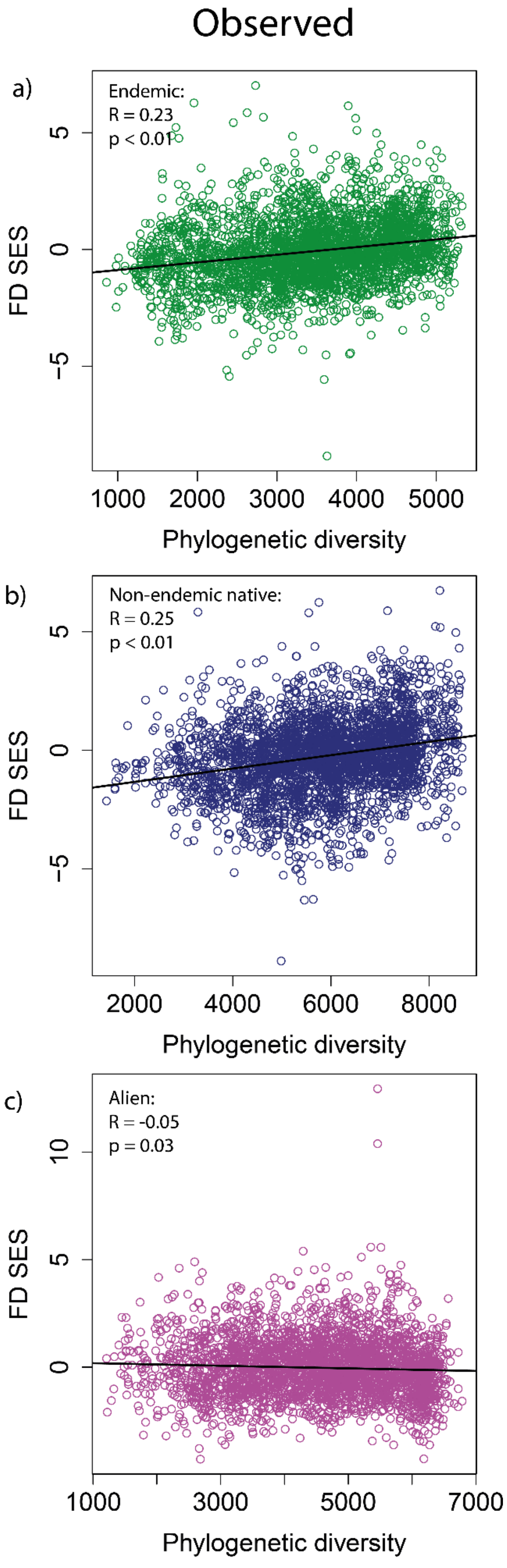


Figure S2.6.9. Pearson's correlation between FD_{SES} and phylogenetic diversity based on 500 m x 500 m grid cells for observed **a)** endemic (n = 3,065), **b)** non-endemic (n = 3,063) and **c)** alien (n = 3,056) species assemblages. R is Pearson's correlation coefficient and p indicates the statistical significance. Simple linear regression lines are depicted on the graphs for a clearer visualisation of the trends.

Chapter 3

Links to rare climates do not translate into distinct traits for island endemics

Vanessa Cutts, **Dagmar M. Hanz**, Martha Paola Barajas-Barbosa, Franziska Schrodt, Manuel Steinbauer, Carl Beierkuhnlein, Pierre Denelle, José Maria Fernández-Palacios, Pierre Gaüzère, Matthias Grenié, Severin D. H. Irl, Nathan Kraft, Holger Kreft, Brian Maitner, François Munoz, Willfried Thuiller, Cyrille Violle, Patrick Weigelt, Richard Field & Adam Algar - *Ecology Letters* (in review)

Abstract

Current models in island biogeography treat species as though they are functionally equivalent, focussing primarily on species richness. Thus, the functional composition of island biotas in relation to island biogeographic variables remains largely unknown. Using plant trait data (plant height, leaf area, flower length) for 895 species in the Canary Islands, we quantified functional trait distinctiveness for endemic and non-endemic species and linked it to the mean climatic rarity of each species' range. We did this for each island in the archipelago, relating functional trait distinctiveness and climatic rarity to island age. Endemics showed a link to climatically rare habitats that is consistent with island geological change through time; however functional trait distinctiveness did not differ between endemics and non-endemics and remained constant with island age. Thus, there is no link between trait distinctiveness and occupancy of rare climates, at least for the traits measured here.

Left photo: Ice-covered *Adenocarpus viscosus* subsp. *spartioides* growing on the Roque de los Muchachos, La Palma (Canary Islands; own photo). *A. viscosus* subsp. *spartioides* is a legume scrub and endemic to the summit of La Palma.

3.1 Introduction

Islands have been highly influential to theoretical developments in ecology and evolution (Darwin & Wallace, 1858; MacArthur & Wilson, 1967; Carlquist, 1974; Whittaker *et al.*, 2008). The isolated nature of islands coupled with high levels of in situ speciation means islands harbour high proportions of endemic species and contribute substantially to global biodiversity (Kier *et al.*, 2009). Current models in island biogeography use island area, age and isolation to predict changes in species richness (MacArthur & Wilson, 1967; Whittaker *et al.*, 2008). However, focusing on species richness treats species as though they are functionally equivalent (Schrader *et al.*, 2021). Indeed, many researchers have pointed out the importance of incorporating functional trait-based approaches into island biogeography (Borregaard *et al.*, 2016; Santos *et al.*, 2016; Patiño *et al.*, 2017; Ottaviani *et al.*, 2020; Schrader *et al.*, 2021), yet studies in functional island biogeography remain limited due to the lack of comprehensive trait data for endemic species (but see Weigelt *et al.*, 2020; Hanz *et al.*, 2022b). Thus, the reasons why functional traits vary within and across islands remain unknown.

In a set of species, some traits are more distinct than others. Functional trait distinctiveness (herein functional distinctiveness) is a relatively recent index that measures how distinct species traits are in relation to a given set of species (e.g. a community, an island biota, a regional species pool, Violle *et al.*, 2017). Assessing patterns of trait distinctiveness of endemic and non-endemic species on islands may shed light on the ecological, evolutionary and biogeographic processes that influence the composition of island biotas. However, the trait distinctiveness of endemic species relative to non-endemic native species, and the mechanisms that drive species distinctiveness within islands, are not straightforward to elucidate.

Due to strong dispersal and environmental filters, island biotas are often a non-random subset of the continental source pool with certain phylogenetic groups being under- or over- represented (Carlquist, 1974; König *et al.*, 2021). Evolutionary processes on islands therefore occur from an already biased set of species. Endemic species evolving through in situ speciation are commonly associated with adaptive radiations (Carlquist, 1974; Schluter, 2000; Stuessy *et al.*, 2006), where trait divergence is high but genetic differentiation is low. Thus, a number of distinct characteristics, often referred to as island syndromes (Burns, 2019), are typical for island species—a well-known example being the evolution of secondary woodiness in plants (Lens *et al.*, 2013a). Given the unique circumstances under which island biotas are shaped and the distinctive qualities of island endemic species, we might expect to see distinct combinations of functional traits (Keppel *et al.*, 2018; Veron *et al.*, 2019; Ottaviani *et al.*, 2020; Hanz *et al.*, 2022b). On the other hand, much of the speciation on islands is a result of allopatric speciation, which is non-adaptive (Stuessy *et al.*, 2006); therefore, we might expect the traits of endemics to change very little following in situ evolution. Comparing trait composition of endemic species with non-endemic species (which have not undergone local adaptation to the same extent) could provide insight into the processes influencing trait evolution on islands.

Islands vary in their climatic heterogeneity, often as a function of age. This heterogeneity plays a key role in determining species' composition and evolutionary outcomes on islands (Irl *et al.*, 2015;

Carvajal-Endara *et al.*, 2017; Taylor *et al.*, 2019). Thus, the links between species traits and climate likely influence species distinctiveness (Raphael *et al.*, 2007). Species radiating into empty niches may become specialised to spatially scarce habitats (Gaston, 1994). Recent evidence from the Canary Islands shows that evolutionary successful lineages (including many endemics) are abundant in marginal habitats (Fernández-Palacios *et al.*, 2021) and many island endemics are associated with rare environments at high elevations (Steinbauer *et al.*, 2016b). If species traits have adapted to these once-empty niches, then trait distinctiveness should be linked to climate rarity. On the other hand, if species utilise generalist strategies to occupy a broad array of environmental conditions, the relationship between trait distinctiveness and climatic rarity may be weak. We also cannot discount the role of stochastic processes: allopatric divergence and genetic drift could create scenarios where species traits are not explicitly linked to their environment via adaptive processes. Thus, the question that remains unanswered is: by occupying rare climates, do endemic species evolve distinct traits?

Ecological and evolutionary outcomes on oceanic islands are influenced by island area, isolation and heterogeneity (Simpson, 1953; MacArthur & Wilson, 1967; Schluter, 2000). These island features are not static but change through time (see Figure 3.1a). The General Dynamic Model (GDM; Whittaker *et al.*, 2008) proposes how changes in these parameters influence immigration, speciation and extinction over the course of an island's geological development (from emergence to subsidence). Furthermore, the GDM postulates that species diversity is related to topographic heterogeneity, predicting a unimodal relationship through time. Here, we use the GDM's framework to make predictions for the functional rarity dynamics of endemic species on oceanic islands, specifically the relationships between functional distinctiveness, climate rarity and endemism. We test three competing hypotheses: 1) the endemic specialisation hypothesis, 2) the endemic expansion hypothesis and 3) the endemic release hypothesis (Figure 3.1), which we outline below. For each hypothesis, we predict how the functional distinctiveness and climatic rarity of endemics and non-endemics change through island ontogeny.

The **endemic specialisation hypothesis** relies on the taxon cycle concept (Wilson, 1961). Species colonising islands become established in the closest habitats, which are often coastal, followed by niche differentiation and speciation associated with inland expansion, with the resulting endemic species characterised by increased specialisation as they speciate into climatically rare, montane habitats (Ricklefs & Cox, 1972, 1978; Ricklefs & Bermingham, 1999). This may lead to the evolution of many distinct species that support new functions (Borregaard *et al.*, 2016). As islands age, high-elevation environments are lost to erosion and submergence, leading to the extinction of endemic species. Thus, we expect trait distinctiveness of endemics to follow a hump-shaped relationship (Figure 3.1, H1). For non-endemic native species, we expect the opposite relationship for functional distinctiveness, in part because rarity is relative, but also because the distinctiveness of endemics may enhance the colonising success of immigrating species by reducing competition (Darwin, 1859; Strauss *et al.*, 2006; Park *et al.*, 2020). Many non-endemics are subject to continued gene flow, increasing the genetic variation, and potentially phenotypic variation of the non- endemic pool. In this case, we expect non-endemics to become less distinct over time as they are widespread, occupying in both rare and common climates. Functional distinctiveness of endemics and non-endemics collapse as islands reach old age.

The **endemic expansion hypothesis** begins similarly to the previous hypothesis: endemic species initially speciate through inland expansion into rarer habitats (hence the small hump in Figure 3.1, H2). However, this is followed by expansion across habitat zones – based on the idea that populations of established endemics can undergo multiple expansions (Ricklefs & Bermingham, 1999), and that they are not doomed to continued range-restriction and specialisation. Therefore, this hypothesis predicts that endemics occupy rare climates in the youngest islands, but quickly spread to occupy both rare and common habitats. Under this scenario, immigrating non-endemic species become less competitive (e.g. due to counter- adaptations Ricklefs & Cox, 1972) and so the colonising space for incoming non-endemics becomes progressively smaller. Thus, in contrast to the previous hypothesis, non-endemics are more distinct relative to the endemics.

Both the endemic specialisation and the endemic expansion hypotheses predict that trait distinctiveness tracks climatic rarity, in that species with distinct traits occur in climatically rare habitats, while species with common traits occur in climatically common habitats. In contrast, our final hypothesis, the **endemic release hypothesis**, predicts no relationship between climatic rarity and functional distinctiveness (Figure 3.1, H3). This suggests endemic species evolve non-adaptively through geographic isolation alone, as they spread inland and to higher elevations (Steinbauer *et al.*, 2016b). Lower species richness on islands compared to the mainland (Whittaker & Fernández-Palacios, 2007; Kreft *et al.*, 2008) could result in weak inter-specific competition (Schluter, 1988), reducing the selective pressure to occupy and adapt to rare climates and resulting in little trait change (or a very long lag behind the shift into rare climates).

We tested these hypotheses for endemic and non-endemic native (NEN) plants on the Canary Islands. Because part of our aim was to compare between different islands, we divided the endemic group into single-island endemics (SIEs) and multi-island endemics (MIEs). For each group, we used plant functional trait data and climatic variables to estimate functional distinctiveness and climatic rarity, respectively, and tested whether differences between the endemic groups differ within and between islands of different ages, as predicted by our hypotheses. To summarise the main findings, the rarity of the climate influences endemic and non-endemic species differently, but no clear signal in their traits could be found.

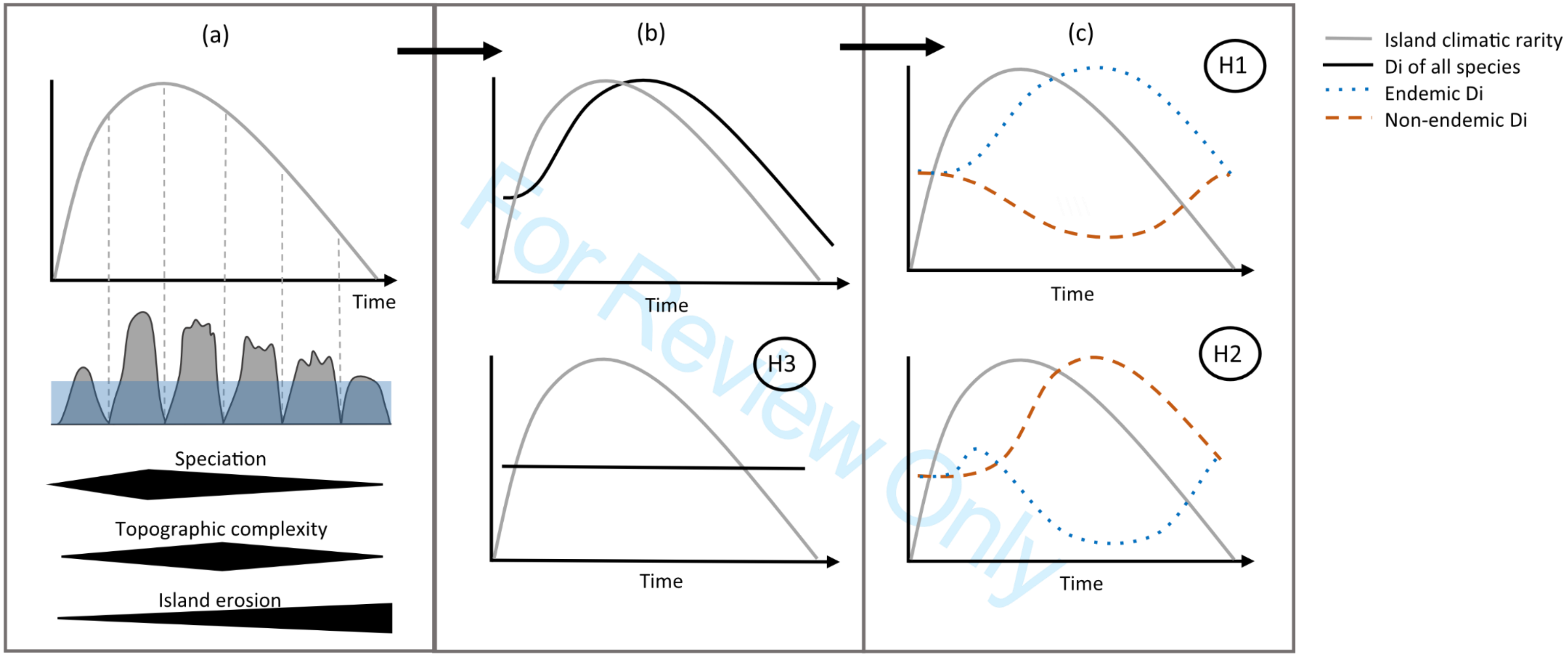


Figure 3.1 Different scenarios of how functional trait distinctiveness (D_i) changes with respect to climatic through island ontogeny: a workflow of our hypotheses. Panel **a)** shows how we expect climatic rarity to change as islands age. Beneath the graph is a schematic diagram: the shaded humps represent islands at different stages in their geological evolution, the black bars represent the variation in speciation, topographic complexity and island erosion through time (Whittaker *et al.*, 2008, 2017; Borregaard *et al.*, 2016). This island ontogeny is what is considered on the x-axis of all plots. Panel **b)** shows two alternative scenarios for D_i: the top graph shows D_i tracking climatic rarity, the bottom graph shows no change in D_i with island ontogeny. In the instance that D_i does track climatic rarity, panel **c)** shows how this may play out differently for endemic and non-endemic species. H1) The endemic specialisation hypothesis. H2) The endemic swamping hypothesis. H3) The endemic release hypothesis. Note that D_i is relative.

3.2 Methods

3.2.1 Study area

The Canary Islands (Spain) are an active volcanic archipelago consisting of seven major islands (Figure 3.2) and four islets. The climate is of subtropical Mediterranean-type, which varies quite drastically within islands, particularly in the young and middle-aged islands due to the north-eastern trade winds and topographic variation generating a precipitation gradient from the northeast to the south west slopes (del Arco Aguilar *et al.*, 2010). In contrast, the eastern islands of Fuerteventura and Lanzarote are much lower in elevationand relatively uniform in climate. The strong climatic gradients and high environmental heterogeneity (Barajas-Barbosa *et al.*, 2020), particularly on the younger islands, have generated considerable ecosystem diversity, which manifests as habitat zones in the form of elevational belts from the coast to the mountaintops (Fernández-Palacios & Nicolás, 1995; del Arco Aguilar *et al.*, 2010). Approximately one third of the Canarian plant species are endemic to the archipelago, one third native non-endemic, and one third introduced (Arechavaleta *et al.*, 2010). Several of the plant lineages are thought to have undergone adaptive radiations, including *Aeonium*, *Argyranthemum*, *Cistus*, *Echium*, *Micromeria*, *Sonchus* and *Tolpis* (Schenk, 2021).

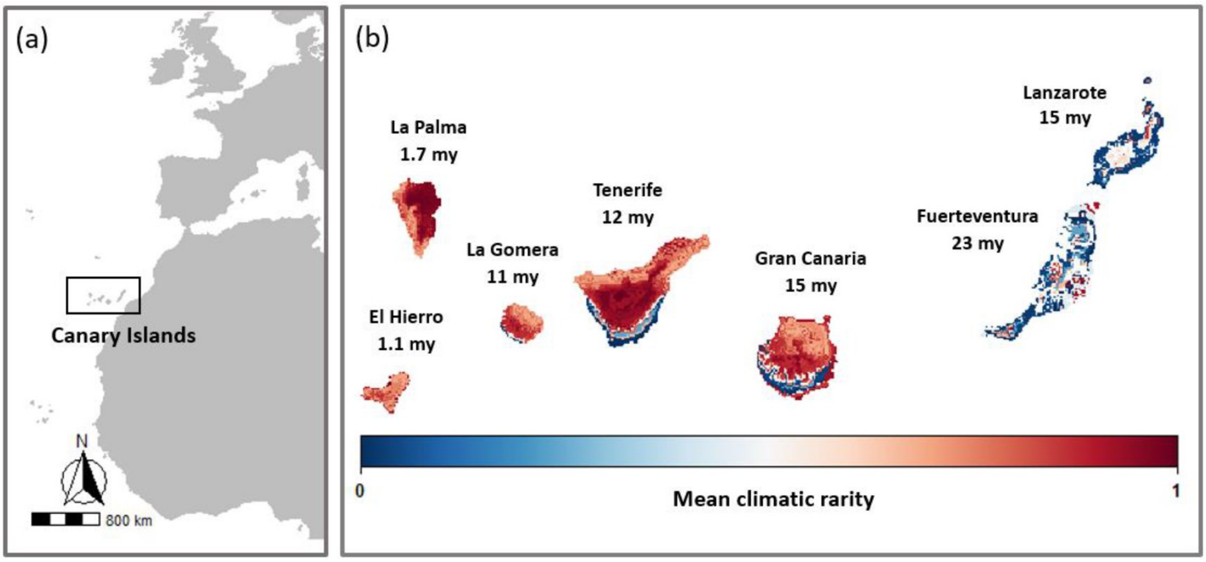


Figure 3.2 a) Map of the location of the Canary Islands. **b)** Map of the Canary Islands. Colour gradient indicates the climatic rarity index for 500x500m grid cells (before it is aggregated by species). Climatic rarity is scaled between 0 and 1 with values closer to 1 indicating a rare climate. This is calculated at the archipelago level, thus the values for each grid cell indicate the rarity of that cell relative to all other cells in the archipelago. Islands are labelled with their approximate ages (van den Bogaard, 2013), my = million years. Areas of white space appear where grid cells have missing data.

3.2.2 Trait data

We used three plant traits: maximum plant height, maximum leaf area and maximum flower length. Plant height is a commonly used measure of plant size. It determines a plant's ability to compete for light sources and has important consequences for seed dispersal (Westoby *et al.*, 2002; Muller-Landau *et al.*, 2008). Leaf area is a measure of leaf size. Leaves play a large role in carbon acquisition and transpiration, as well as being important for the interception of light and CO_2 (Press, 1999). Flower length is a proxy for flower size. Flower petals are important for energy balance and transpiration (von

Arx *et al.*, 2012; Harrap & Rands, 2022). All three traits show relationships with environmental variables, including temperature and precipitation (Moles *et al.*, 2009; Paušič *et al.*, 2019; Dong *et al.*, 2020). We used maximum trait values as they reflect the species fitness response to environmental gradients and generally have better data coverage.

Data were sourced from the literature (Bramwell & Bramwell, 1974; Hohenester & Welß, 1993; Eggli, 2002; Muer *et al.*, 2016; Schönfelder & Schönfelder, 2018b,a), online herbarium specimens from GBIF (www.gbif.org) and JSTOR (www.plants.jstor.org), and species descriptions (see Hanz *et al.*, 2022b). We used maximum leaf length and leaf width values to calculate maximum leaf area using the following formula:

$$LA = \frac{LL \times LW \times \pi}{2}$$

where LA = leaf area, LL = leaf length, LW = leaf width. Leaf length and leaf width can accurately estimate leaf area (Kraft *et al.*, 2008; Pandey & Singh, 2011; Shi *et al.*, 2019; Cutts *et al.*, 2021).

The current plant checklist for the Canary Islands places species into six categories: definitely native (including endemics), probably native, possibly native, probably introduced, introduced non-invasive and introduced invasive (Arechavaleta *et al.*, 2010). We only include species that are in the first three of these categories (i.e. excluding introduced species). We used principal components analysis to visualise where endemics and non-endemics sit in Canary Island trait space.

Plant trait data are scarce for the Canary Islands, with many species missing from online and literature sources (Beierkuhnlein *et al.*, 2021; Cutts *et al.*, 2021), which is why we are limited to the aforementioned traits. However, trait choice can strongly influence results (Zhu *et al.*, 2017; Mouillot *et al.*, 2021) because the position of a species in trait space relative to other species might change depending on the traits chosen. To understand the impact of our choice of traits, we also examine an expanded set of traits for Tenerife species (sufficient data on additional traits were not available for other islands). In addition to the three traits mentioned above, we have field measurements for the following traits for Tenerife species: specific leaf area (SLA), stem specific density (SSD) and leaf dry matter content (LDMC). See supporting information (Appendix S3.1) for trait measurement protocols.

3.2.3 Species occurrence data

In order to estimate the mean climatic conditions within each species' range, we used species occurrence data from Atlantis 3.1 (www.biodiversidadcanarias.es/biota), a governmental, open-access database with occurrence data of Canary Islands species. The data are presence-only, at a resolution of 500x500m, and are not exhaustive, but are particularly good for endemic species, for which there has been long-term sampling. For more information see Steinbauer *et al.* (2016a), which provides a review of the data quality. We updated the species presence data and taxonomy using the most recent checklist for Canary Island plants—FloCan (Beierkuhnlein *et al.*, 2021). During this process, we ended up with duplicates of two species: *Arenaria serpyllifolia* was measured twice under different names and *Serapias mascaensis* was included as both a species and a subspecies. In both instances, we removed the smaller of the two as we focus exclusively on maximum trait values.

3.2.4 Rarity indices

We calculated functional distinctiveness (D_i) and climatic rarity at the archipelago scale (i.e. rarity of any one grid cell relative to all the grid cells in the archipelago) and for each individual island (i.e. rarity of any one grid cell relative to all the grid cells in the focal island).

a) *Functional distinctiveness*

D_i measures the mean functional distance to all other species in the community (Violle *et al.*, 2017). We calculated Di using a Euclidean distance matrix of the three (maximum plant height, maximum leaf area, maximum flower length, see results section). We used the following equation:

$$D_i = \frac{\sum_{j=1,i\neq j}^{N} d_{ij}}{N-1}$$

Where N is the number of species, d_{ij} is the distance in trait space between species i and j (Grenié *et al.*, 2017; Violle *et al.*, 2017). All three traits were log-transformed. There were five instances where a species had a zero value for leaf area because they do not possess leaves (e.g. *Euphorbia canariensis*). This creates an issue when transforming the data. We did not want to remove these species as they represent rare trait values, so we replaced the zeros with an arbitrary value that is less than the minimum value for all the other species. As the minimum value for leaf area was 2.36mm, we replaced the zeros with a value of 0.5mm. D_i was scaled between 0 and 1 using the following formula: (x–min(x)) ÷ (max(x) – min(x)).

b) *Climatic rarity*

We computed climatic rarity following Irl *et al.* (2015). Mean annual precipitation and mean annual temperature were interpolated, at a resolution of 500x500m to match the occurrence data, using data obtained from meteorological stations on the Canary Islands, provided by Agencia Estatal de Meteorología (see Irl *et al.*, 2015). Precipitation was log-transformed because ecologically meaningful variation among smaller values is underemphasised when using the raw data, which are strongly right-skewed. Climatic rarity was calculated as follows. Firstly, temperature and precipitation variables were divided into equal sized bins. We trialled using 10, 20 and 30 bins. We report the results using 20 bins as this produced slightly higher R^2 values, thus explaining more of the variance (but see Appendix S3.2 for results from 10 or 30 bins). Next, each grid cell was assigned a temperature and precipitation bin. The combination of these bins was used as a climatic rarity index. The climatic rarity index is the number of cells that each climate occurs in; for example, if a grid cell shared its particular temperature-precipitation combination with 10 other grid cells, the climatic rarity value for those cells would be 10. The climate rarity index was reverse-coded (by subtracting the maximum value and adding one) and scaled between zero and one so that high values represented very rare climates for ease of comparison with D_i. To obtain a climatic rarity value for each species, we took the mean climatic rarity value of all the grid cells where the focal species was present. Thus, this index was centred on the species, not the geographic location. The index was calculated for the entire archipelago (archipelago-level climatic rarity) and separately for each island (island-level climatic rarity).

3.2.5 Statistical analysis

To compare D_i and climatic rarity between endemism groups and between islands, we conducted phylogenetically corrected ANOVAs using the 'caper' and 'phytools' packages in R (Revell, 2012; Orme *et al.*, 2018; R Core Team, 2021). The phyANOVA() function is simulation-based and conducts posthoc comparisons of means between groups. We set the number of simulations to 10,000 and used Bonferroni correction for pairwise comparisons. Phylogenetic information for the Canary Island species was obtained by pruning a mega seed plant phylogeny (Smith & Brown, 2018). The resulting tree contained polytomies at the species level with 25% of the nodes unresolved. Unresolved trees can underestimate phylogenetic diversity (Swenson, 2009), so we randomly resolved the phylogeny prior to analysis (Appendix S3.5). Many of the species in our data occurred on multiple islands, which created multiple observations for the same species. This led to computational difficulties when preparing the data for the phylogenetic ANOVA, as the comparative.data() function in the caper package cannot handle duplicate species. To troubleshoot this, we added the duplicates to the phylogeny as sister species, with branch lengths of 0.001 (Grenié *et al.*, 2017). To visualise the relationship of D_i and climatic rarity with island age, we plotted line graphs using ranked ages (Figure 3.6).

3.3 Results

Overall, we collected trait, climate and phylogenetic data for 895 native species (271 SIE, 205 MIE, 419 NEN; Table 3.1), representing approximately 87% of the SIEs, 90% of MIEs and 50% of non-endemic natives from the Canary Islands. Fuerteventura and Lanzarote naturally have very few SIEs, so their sample sizes are small.

Correlations between traits were significant but weak: plant height–leaf area $r = 0.35$, $p < 0.001$; plant height–flower length $r = 0.10$, $p < 0.001$; leaf area–flower length $r = 0.26$, $p < 0.001$. Principal components analysis revealed that the species groups strongly overlap in Canary Island trait space, with the endemic species nested within the non-endemic natives, which occupied the core and the periphery (Figure 3.3).

D_i and climatic rarity did not correlate overall ($r = -0.009$, $p = 0.77$), nor did they correlate within each endemism group (SIE $r = 0.02$, $p = 0.69$; MIE $r = -0.16$, $p = 0.81$; NEN $r = 0.03$, $p = 0.60$) or within each island (El Hierro $r = 0.06$, $p = 0.26$; La Palma $r = 0.09$, $p = 0.05$; La Gomera $r = 0.06$, $p = 0.23$; Tenerife $r = 0.04$, $p = 0.32$; Gran Canaria $r = 0.04$, $p = 0.35$; Lanzarote $r = -0.01$, $p = 0.85$; Fuerteventura $r = 0.05$, $p = 0.33$).

Table 3.1 Number of species with complete data, which includes all three traits (max plant height, max leaf area, max flower length), climatic rarity and phylogenetic data. Our sample size as a percentage of the total number of species present is indicated in brackets. SIE = single island endemic, MIE = multi-island endemic, NEN = non-endemic native. Note that (except for SIEs) many of the species occur on multiple islands, so that adding the island figures surpasses the archipelagic total.

	SIE	**MIE**	**NEN**
El Hierro	12	98	245
La Palma	34	137	281
La Gomera	30	127	273
Tenerife	104	177	386
Gran Canaria	71	125	350
Fuerteventura	8	56	268
Lanzarote	12	46	240
Total	271 (87 %)	205 (90 %)	420 (50 %)

3.3.1 Functional distinctiveness

A phylogenetic ANOVA revealed no significant difference in D_i between the endemism groups ($F = 14.17$, $p = 0.24$, $R^2 = 0.03$; Figure 3.4). However, pairwise comparisons showed a significant difference between SIEs and MIEs, with MIEs being more distinct ($p = 0.005$). For between-islands comparisons of D_i (Figure 3.5), a phylogenetic ANOVA indicated no significant difference for SIEs ($F = 1.85$, $p = 0.11$, $R^2 = 0.04$) or MIEs ($F = 0.40$, $p = 0.54$, $R^2 = 0.003$), and a significant effect for NENs ($F = 4.40$, $p = 0.005$, $R^2 = 0.01$). Pairwise comparisons revealed some differences for NENs, with D_i decreasing in Lanzarote and Fuerteventura, but no pairwise differences were found between islands for SIEs or MIEs (Figure 3.5). In all cases, the proportion of variance in functional distinctiveness explained by endemism class or island was small.

3.3.2 Climatic rarity

Climatic rarity varied across the archipelago (Figure 3.2b). There was a noticeable difference between the five high-elevation islands in the west, which possess more rare climates, and the two older islands (Fuerteventura and Lanzarote) in the east, which contain very few areas of rare climate. Within islands, rare climates tend to be found at areas of high elevation or high topographic complexity, and high humidity (Figure 3.2b). Climate space is shown in Figure 3, where it appears endemic species are occupying a wider range of climates, including cold and dry climates, compared to non-endemics.

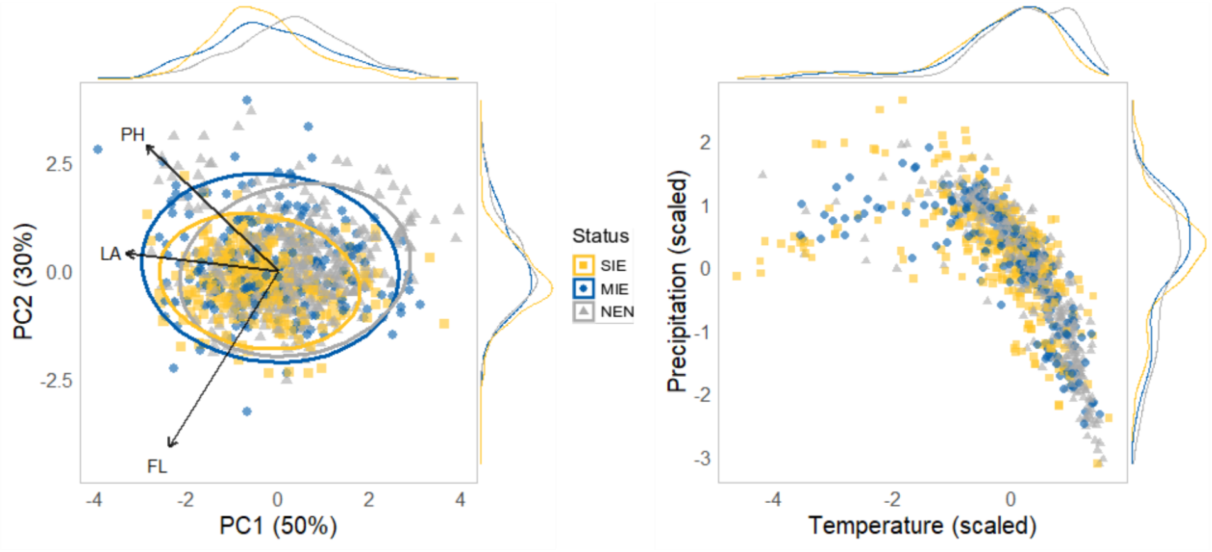


Figure 3.3 Left: Functional trait space represented using principal component analysis for the Canary Islands based on three traits: maximum plant height (PH), maximum leaf area (LA) and maximum flower length (FL), Ellipses show 95% confidence. Right: Position of species in climate space (mean annual temperature and precipitation). Precipitation is log-transformed. At the top and left of each graph, marginal density distribution plots are shown for each endemism group. SIE = single island endemic, MIE = multi-island endemic, NEN = non-endemic native.

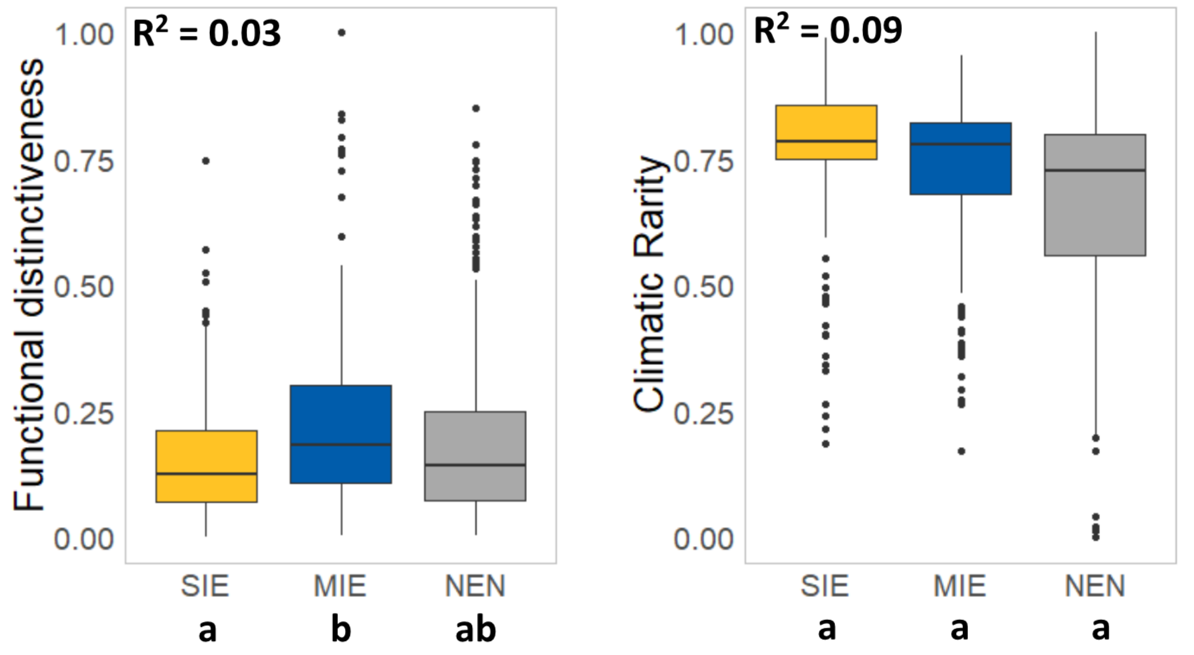


Figure 3.4 Functional distinctiveness and climatic rarity for each endemism group across the entire Canary archipelago. Differing letters indicate pairwise significant differences between groups (p<0.05). SIE = single island endemic, MIE = multi-island endemic, NEN = non-endemic native.

Endemism increases with climatic rarity: endemics were found in rarer climates compared to non-endemics, with SIEs occupying the rarest climates (F = 42.13, p = 0.02, R^2 = 0.09). However, pairwise comparisons showed no significant differences between pairs of groups (SIE–MIE: p = 0.27; SIE–NEN: p = 0.06; MIE–NEN: p = 0.13; Figure 3.4). Comparing between islands revealed a strong pattern for SIEs (F = 145.41, $p < 0.001$, R^2 = 0.75): they are found in very rare climates in the young and middle-aged islands (El Hierro, La Palma and La Gomera), for which there were no pairwise differences, but are found in progressively less rare climates as the islands increase in age. MIEs show a similar, but much less pronounced pattern across islands (F = 56.98, $p < 0.001$, $R^2 = 0.31$), and the pattern for NENs is similar but weak (F = 27.61, $p < 0.001$, $R^2 = 0.08$). See Figure 3.5 for pairwise difference across islands and supporting information for ANOVA tables and pairwise P values (Appendix S3.3).

3.3.3 Assessing the impact of trait choice using Tenerife data

We used data from the island of Tenerife to investigate the impact of our choice of traits by calculating D_i (at the Tenerife scale) using an expanded set of traits. The two measures of D_i (3-trait and 6-trait) showed a strong positive correlation ($r = 0.79$, $p < 0.001$) and in both cases, functional distinctiveness showed a similar pattern in relation to endemicity. Again, principal components analysis revealed a nested pattern, but this pattern was much clearer when using the expanded set of traits. These results are shown in supporting information (Appendix S3.4).

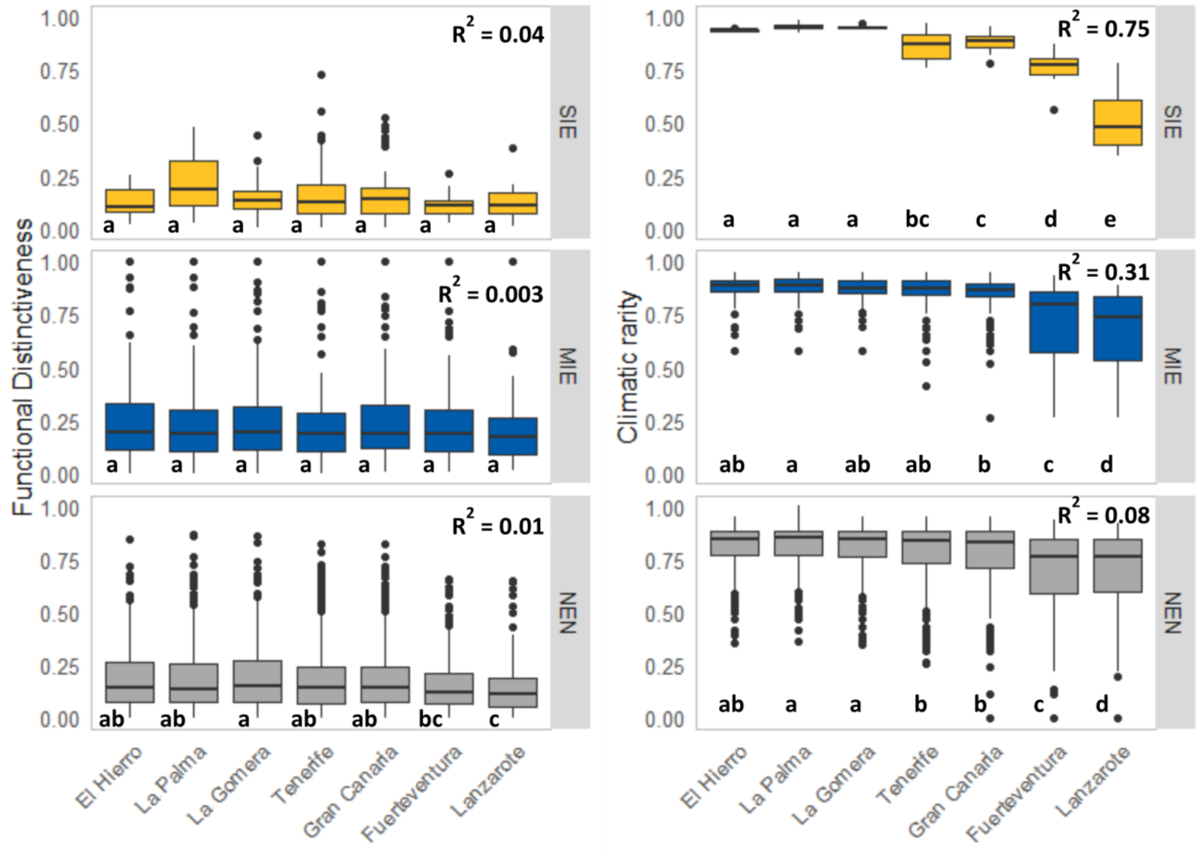


Figure 3.5 Functional distinctiveness and climatic rarity for each island. Differing letters indicate pairwise significant differences between groups (p<0.05). SIE = single island endemic, MIE = multi- island endemic, NEN = non-endemic native.

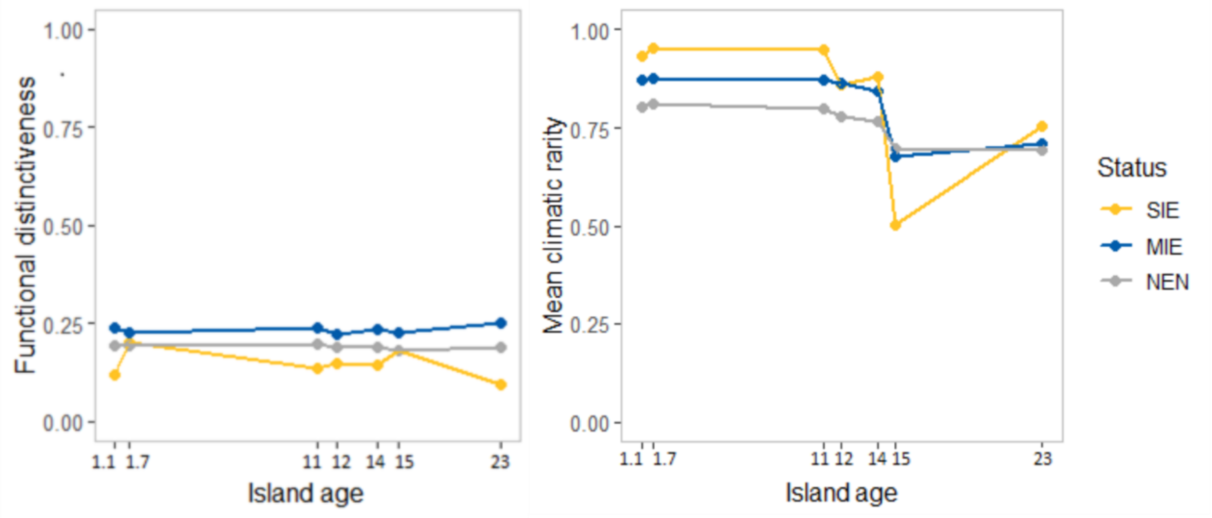


Figure 3.6 Line graphs representing functional distinctiveness and climatic rarity (of the species) with increasing island age (million years old). Island ages are obtained from van den Bogaard (2013). Points correspond to mean values for each island. SIE = single island endemic, MIE = multi-island endemic, NEN = non-endemic native.

3.4 Discussion

The General Dynamic Model posits that the geological evolution of an island influences the evolution of species and that species richness can be linked to island age (Whittaker *et al.*, 2008). In this study, we investigated how this translates to species traits, specifically examining functional distinctiveness of endemic and non-endemic species, and how they relate to the rarity of the climate where species occur. We tested three hypotheses to explain the relationship between functional distinctiveness, climatic rarity and endemism: 1) the endemic specialisation hypothesis, 2) the endemic expansion hypothesis and 3) the endemic release hypothesis.

All species showed a decline in the occupancy of rare climates with increasing island age, but no concordant pattern is seen for functional distinctiveness, which remains constant through time and does not differ between endemism groups. The lack of relationship between functional distinctiveness and climatic rarity rejects the endemic specialisation and the endemic expansion hypotheses, which both expect functional distinctiveness to relate to climatic rarity and for there to be marked differences in functional distinctiveness between endemic and non-endemic species. Therefore, our results most closely align with the endemic release hypothesis, which predicts no relationship between climatic rarity and functional distinctiveness and no trend of functional distinctiveness with island age.

One of the main premises of the GDM is that topographic heterogeneity will be maximised on middle-aged islands, coinciding with the availability of empty niche space (Whittaker *et al.*, 2008). More recent work has shown environmental heterogeneity and species richness to peak early during island ontogeny (Steinbauer *et al.*, 2013; Barajas-Barbosa *et al.*, 2020). Here, we found that endemics, particularly single-island endemics, are already occupying rare climates in the younger islands, with the decline beginning at middle-age (La Gomera- Tenerife), suggesting a very early peak in the diversity of available niche space and coinciding with changes in elevation (Borregaard *et al.*, 2016). In older islands, there are fewer opportunities to occupy rare climates, as topographic heterogeneity decreases as a result of erosion and subsidence. Non-endemics occupied rare climates similarly through time, with a small decline in climatic rarity in the oldest islands. Thus, endemic species appear to be more closely linked to the rarity of the climate than non-endemics.

Evolution on islands is typified by high rates of trait diversification following ecological opportunity (Carlquist, 1974; Jorgensen & Olesen, 2001; Givnish *et al.*, 2009; Losos & Ricklefs, 2009) and island endemics are often used as examples of adaptive radiations (Schluter, 2000; Schenk, 2021). Despite occupying rarer climates, we found that endemics are no more distinct in their traits than non-endemic natives. We would expect species with distinct traits to occupy the peripheries of trait space but our results show considerable overlap of the species groups, with single-island endemics being slightly more clustered in the centre. This may be indicative of specialisation and niche packing (Hanz *et al.*, 2022b), particularly considering that endemics occupy a wide range of climate space overall (Pigot *et al.*, 2016). Therefore, it is possible that endemics are experiencing selection without it driving them into novel areas of trait space. In fact, diversifying lineages may decrease trait distinctiveness by producing more similar species.

Allopatric speciation is maximised in middle-aged islands when topography and climate are highly dissected (Whittaker *et al.*, 2008). Non-adaptive processes commonly drive evolution on islands but have often received less attention (Simões *et al.*, 2016) and the imprint of this in functional trait space is less easy to predict or interpret. Within-island allopatry and relaxed competition on islands may lessen selective pressure, allowing genetic drift to become a more prominent evolutionary process (Stuessy *et al.*, 2006). Therefore, non- adaptive speciation might explain the lack of distinct traits for single-island endemics. It could be that there is a lag between climate shifts and trait divergence, particularly for species that have colonised more recently. Alternatively, environmental filtering may select species that already have relevant adaptations (Donoghue, 2008).

Trait choice can greatly influence the outcome of hypothesis tests (Zhu *et al.*, 2017; Mouillot *et al.*, 2021). Trait data are scarce for island endemics (Cutts *et al.*, 2021), and thus our choice of traits was limited. However, the traits we used – plant height, leaf area and flower length – have been linked to environmental conditions in terms of temperature and precipitation (Byars *et al.*, 2007; Guerin *et al.*, 2012; Givnish *et al.*, 2014; Tao *et al.*, 2016; Paušič *et al.*, 2019). Nevertheless, we used data for a broader suite of traits, available only for Tenerife, to determine whether expanding our trait set would fundamentally alter patterns of functional distinctiveness. The use of more traits did not affect the results in such a way that one would draw different conclusions—functional distinctiveness followed the same pattern with respect to endemism. Still, it is possible that even the Tenerife example did not capture the 'right' traits; the objection that the 'right' traits were not measured is, of course, an unfalsifiable hypothesis, and thus it is impossible to eliminate. However, a potential candidate set of traits for future investigation would be those linked to dispersal. Insularity has an effect on the composition of dispersal traits in islands (Gillespie *et al.*, 2012), and limited dispersal has been linked to lower speciation area thresholds, which could produce endemics, on islands (Kisel & Barraclough, 2010). Similarly, species that are able to disperse well enough to colonise areas with rare climates, such as montane habitats, but unable to maintain gene flow with populations in rarer climates, such as mountain-tops, may be more likely to specialise on these climates, creating a link between distinctiveness of dispersal traits and climatic rarity.

3.5 Concluding remarks

Endemic species on islands have fuelled the curiosity of generations of biologists because of their spectacular radiations and unique characteristics. However, trait evolution on islands remains a rather elusive subject. Some species demonstrate ecological shifts (e.g. Kim *et al.*, 1996), but whether these shifts are followed by trait divergence is less well understood and rigorous tests are lacking. We find that rare climate occupancy for island endemics is dynamic with increasing island age, yet we find no signal in the distinctiveness of their traits. The hypotheses we lay out here are simplistic and do not capture all the possible influences and stochastic processes that shape functional trait composition. Nevertheless, we see this as a practical step towards integrating functional traits into island theory and towards understanding the functional signature of island species.

Acknowledgements

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Data accessibility statement

If accepted, data supporting the results for this manuscript will be available on FigShare.

Supporting information

Appendix S3.1

Tenerife trait measurements

For Tenerife species, we measured the following traits in the field: leaf dry matter content (LDMC), specific leaf area (SLA), stem specific density (SSD). These were to be used in combination with maximum plant height, maximum leaf area and maximum flower length to assess the impact of our trait choice. We followed standardised protocols based on the handbook by Pérez-Harguindeguy *et al.* (2013). We aimed to measure these traits for five adult individuals per species, taking samples from different locations where possible to account for variation in climate. Leaf and stem samples were collected from adult plants. We collected 10-100 adult leaves per individual, depending on the species—for species with small leaves we collected up to 100 to obtain accurate mass measurements. Leaves were cut from the stem and the petiole was removed. Stem samples were taken from secondary stems where possible to minimise disturbance and cut to approximately 10 cm.

LDMC is the oven-dry mass of a leaf divided by its fresh mass. We weighed the fresh leaves for each individual, then the leaves were dried in an incubator at 80°C for at least 24 hours. Dried leaves weighed again.

SLA is the leaf area divided by its oven-dry mass. To calculate leaf area, up to 10 leaves per individual were scanned using an A4 scanner and leaf area calculated for each leaf using WinFOLIA software (version: 2016b Pro; Regent Instruments Inc., Québec, Canada, 2016).

SSD is the dry mass per unit of fresh stem volume. The exact volume of the stem was determined by measuring its exact length and diameter, which was measured at three points along the stem. To determine the dry mass, stems were dried in an incubator at 80°C for at least 24 hours and then weighed.

Appendix S3.2

Trialling different levels of precision for computing climatic rarity.

Climatic rarity was computed using binned data for temperature and precipitation. The size of the bins was determined by splitting the range of each variable up equally. For the results in the text, the range was divided by 20, and that result was used as a bin size. The workflow below shows how we got to this value for temperature and precipitation (precipitation is transformed prior).

Temperature: $\frac{\text{Max temp} - \text{min temp}}{20} = \frac{20.807 - 3.459}{20} = 0.867°\text{C}$

Precipitation: $\frac{\text{Max } \log(\text{precip}) - \min \log(\text{precip})}{20} = \frac{3.104 - 1.884}{20} = 0.061\text{mm}$

As this number is somewhat arbitrary, we also trialled using fewer divisions and more divisions, i.e. 10 and 30, which resulted in larger and smaller bin widths, respectively. R^2 values were slightly lower in both instances, thus we stuck with the middle bin width size in the main text. One of the models became non-significant when using a lager bin width—comparing climatic rarity between endemism groups (p-value is highlighted in grey). See the results below.

Table S3.2.1 Climatic rarity between endemism groups with larger bin widths (max-min)/10. Temp bin = 1.735°C; precipitation bin = 0.122mm.

	df	Sum sq	Mean sq	F	P	R^2
Endemism	2	1.249	0.625	25.523	0.098	0.05
Residual	893	21.858	0.024			
Island SIE		4.058	0.676	93.218	**0.000**	0.66
Residual		2.083	0.007			
Island MIE		3.388	0.565	54.929	**0.000**	0.3
Residual		7.986	0.010			
Island NEN		3.116	0.519	35.521	**0.000**	0.09
Residual		31.651	0.016			

Table S3.2.1 Climatic rarity between endemism groups with smaller bin widths (max-min)/30. Temp bin = 0.578 °C; precipitation bin = 0.041 mm.

	df	Sum sq	Mean sq	F	P	R^2
Endemism	2	1.808	0.904	42.264	**0.020**	0.086
Residual	893	19.098	0.021			
Island SIE		3.008	0.501	121.696	**0.000**	0.72
Residual		1.182	0.004			
Island MIE		3.186	0.531	56.260	**0.000**	0.3
Residual		7.333	0.009			
Island NEN		3.848	0.641	29.916	**0.000**	0.9
Residual		41.182	0.021			

Appendix S3.3

ANOVA tables between endemism groups

Table S3.3.1 We used phylogenetically corrected ANOVA's to compare functional distinctiveness and climatic rarity between endemism groups. Here, we repot the ANOVA tables.

	df	Sum sq	Mean sq	F	P	R^2
			Functional distinctiveness			
X	2	0.646	0.323	14.161	0.253	0.031
Residual	893	20.368	0.023			
			Climatic rarity			
X	2	2.208	1.104	42.039	**0.022**	0.086
Residual	893	23.452	0.026			

Table S3.3.2 We used phylogenetically corrected ANOVA's to compare functional distinctiveness and climatic rarity between endemism groups. Here, we repot the pairwise p-values from the posthoc comparisons.

		Functional distinctiveness	
	SIE	MIE	NEN
SIE	1.000	**0.007**	1.000
MIE	**0.007**	1.000	0.959
NEN	1.000	0.959	1.000
		Climatic rarity	
SIE	1.000	0.286	0.061
MIE	0.286	1.000	0.130
NEN	0.061	0.130	1.000

ANOVA tables and pairwise comparisons between islands

Table S3.3.3 We used phylogenetically corrected ANOVA's to compare functional distinctiveness between islands. Here, we repot the ANOVA tables. We conducted separate ANOVAS for single island endemics (SIE), multi-island endemics (MIE) and non-endemic natives (NEN).

	df	Sum sq	Mean sq	F	P	R^2
		Functional distinctiveness SIE				
X		0.149	0.025	1.924	0.050	0.04
Residual		3.594	0.013			
		Functional distinctiveness MIE				
X		0.081	0.014	0.404	0.505	0.003
Residual		25.846	0.033			
		Functional distinctiveness NEN				
X		0.669	0.112	4.524	**0.004**	0.01
Residual		46.981	0.025			

Table S3.3.4 We used phylogenetically corrected ANOVA's to compare functional distinctiveness between islands. Here, we repot the pairwise p-values from the posthoc comparisons between islands. The pairwise comparisons use the bonferroni correction.

			Functional distinctiveness SIE				
	EH	LP	LG	T	GC	F	L
EH	1.000	0.183	1.000	1.000	1.000	1.000	1.000
LP	0.183	1.000	0.498	0.137	0.233	0.485	0.445
LG	1.000	0.498	1.000	1.000	1.000	1.000	1.000
T	1.000	0.137	1.000	1.000	1.000	1.000	1.000
GC	1.000	0.233	1.000	1.000	1.000	1.000	1.000
F	1.000	0.485	1.000	1.000	1.000	1.000	1.000
L	1.000	0.445	1.000	1.000	1.000	1.000	1.000
			Functional distinctiveness MIE				
EH	1.000	1.000	1.000	1.000	1.000	1.000	1.000
LP	1.000	1.000	1.000	1.000	1.000	1.000	1.000
LG	1.000	1.000	1.000	0.897	1.000	1.000	1.000
T	1.000	1.000	0.897	1.000	1.000	1.000	1.000
GC	1.000	1.000	1.000	1.000	1.000	1.000	1.000
F	1.000	1.000	1.000	1.000	1.000	1.000	0.174
L	1.000	1.000	1.000	1.000	1.000	0.174	1.000
			Functional distinctiveness NEN				
EH	1.000	1.000	1.000	1.000	1.000	1.000	**0.015**
LP	1.000	1.000	1.000	1.000	1.000	**0.017**	**0.002**
LG	1.000	1.000	1.000	1.000	1.000	**0.002**	**0.002**
T	1.000	1.000	1.000	1.000	1.000	**0.015**	**0.002**
GC	1.000	1.000	1.000	1.000	1.000	**0.006**	**0.002**
F	1.000	**0.017**	**0.002**	**0.015**	**0.006**	1.000	**0.002**
L	**0.015**	**0.002**	**0.002**	**0.002**	**0.002**	**0.002**	1.000

Table S3.3.5 We used phylogenetically corrected ANOVA's to compare climatic rarity between islands. Here, we repot the ANOVA tables. We conducted separate ANOVAS for single island endemics (SIE), multi-island endemics (MIE) and non-endemic natives (NEN).

	df	**Sum sq**	**Mean sq**	**F**	**P**	**R^2**
			Climatic rarity SIE			
X		2.351	0.392	145.667	**0.000**	0.75
Residual		0.772	0.003			
			Climatic rarity MIE			
X		2.926	0.488	56.978	**0.000**	0.32
Residual		6.651	0.009			
			Climatic rarity NEN			
X		3.612	0.602	28.723	**0.000**	0.09
Residual		40.263	0.021			

Table S3.3.6 We used phylogenetically corrected ANOVA's to compare climatic rarity between islands. Here, we repot the pairwise p-values from the posthoc comparisons between islands. The pairwise comparisons use the bonferroni correction.

				Climatic rarity SIE			
	EH	LP	LG	T	GC	F	L
EH	1.000	1.000	1.000	**0.002**	**0.006**	**0.002**	**0.002**
LP	1.000	1.000	1.000	**0.002**	**0.002**	**0.002**	**0.002**
LG	1.000	1.000	1.000	**0.002**	**0.002**	**0.002**	**0.002**
T	**0.002**	**0.002**	**0.002**	1.000	**0.029**	**0.002**	**0.002**
GC	**0.006**	**0.002**	**0.002**	**0.029**	1.000	**0.002**	**0.002**
F	**0.002**	**0.002**	**0.002**	**0.002**	**0.002**	1.000	**0.002**
L	**0.002**	**0.002**	**0.002**	**0.002**	**0.002**	**0.002**	1.000
				Climatic rarity MIE			
EH	1.000	1.000	1.000	1.000	0.185	**0.002**	**0.002**
LP	1.000	1.000	1.000	0.972	**0.002**	**0.002**	**0.002**
LG	1.000	1.000	1.000	1.000	**0.002**	**0.002**	**0.002**
T	1.000	0.972	1.000	1.000	**0.015**	**0.002**	**0.002**
GC	0.185	**0.002**	**0.002**	**0.015**	1.000	**0.002**	**0.002**
F	**0.002**	**0.002**	**0.002**	**0.002**	**0.002**	1.000	**0.004**
L	**0.002**	**0.002**	**0.002**	**0.002**	**0.002**	**0.004**	1.000
				Climatic rarity NEN			
EH	1.000	1.000	1.000	1.000	0.838	**0.002**	**0.002**
LP	1.000	1.000	1.000	**0.002**	**0.002**	**0.002**	**0.002**
LG	1.000	1.000	1.000	0.055	**0.002**	**0.002**	**0.002**
T	1.000	**0.002**	0.055	1.000	1.000	**0.002**	**0.002**
GC	0.838	**0.002**	**0.002**	1.000	1.000	**0.002**	**0.002**
F	**0.002**	**0.002**	**0.002**	**0.002**	**0.002**	1.000	1.000
L	**0.002**	**0.002**	**0.002**	**0.002**	**0.002**	1.000	1.000

Appendix S3.4

Assessing the impact of trait choice using Tenerife data

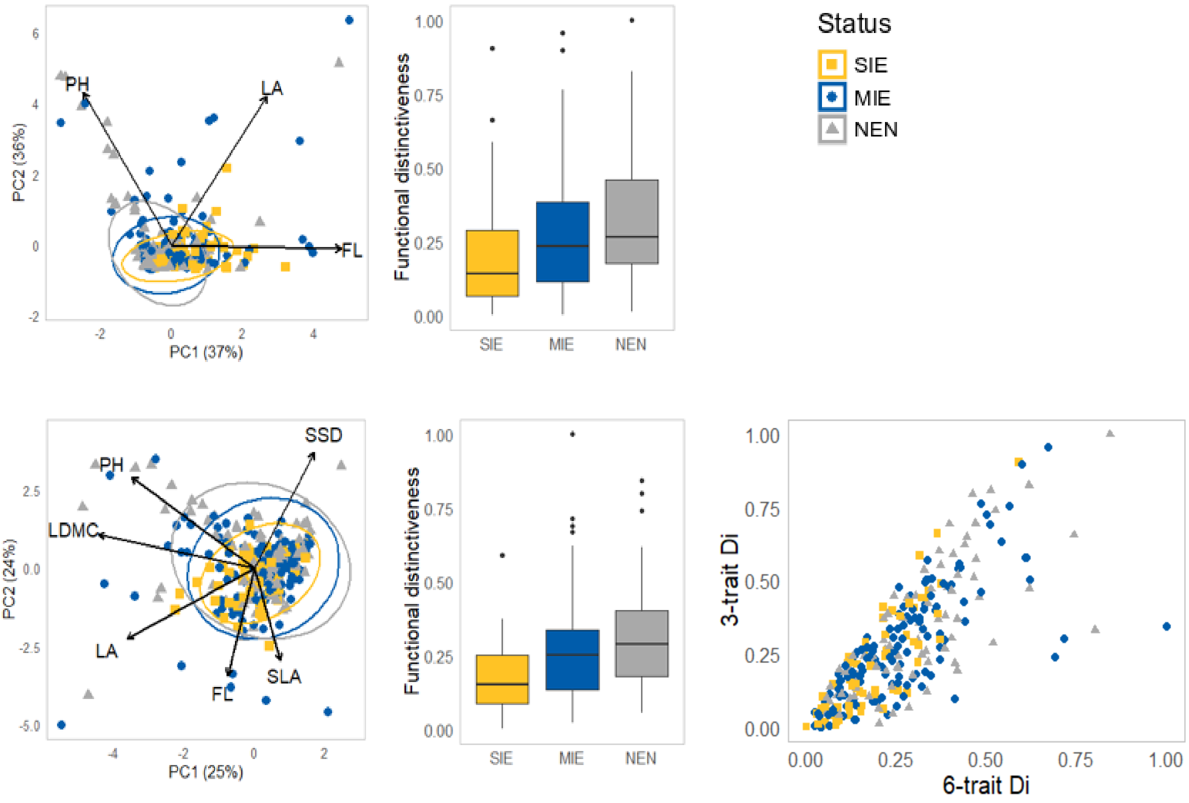

Figure S3.4.1 Functional trait space and functional distinctiveness for species groups on Tenerife: single-island endemics (SIE), multi-island endemics (MIE) and native non-endemics (NEN). Principal component analysis is used to represent trait space. Ellipses show the 95% confidence. We calculated functional distinctiveness using a Euclidean distance matrix. The top two figures show trait space and functional distinctiveness calculated using three traits: maximum plant height (PH), maximum leaf area (LA) and maximum flower length (FL). Data for these traits are available for all other islands in the Canaries. The bottom two graphs show trait space and functional distinctiveness calculated using three additional traits that are only available for Tenerife: specific leaf area (SLA), leaf dry matter content (LDMC), stem specific density (SSD). All traits were transformed to achieve normality. PH, LA, FL and SLA were log10-transformed. SSD and LDMC were square root-transformed. The bottom right graph shows a scatter plot for both measures of functional distinctiveness (D_i).

Appendix S3.5

Phylogenetic tree of all species included in the study

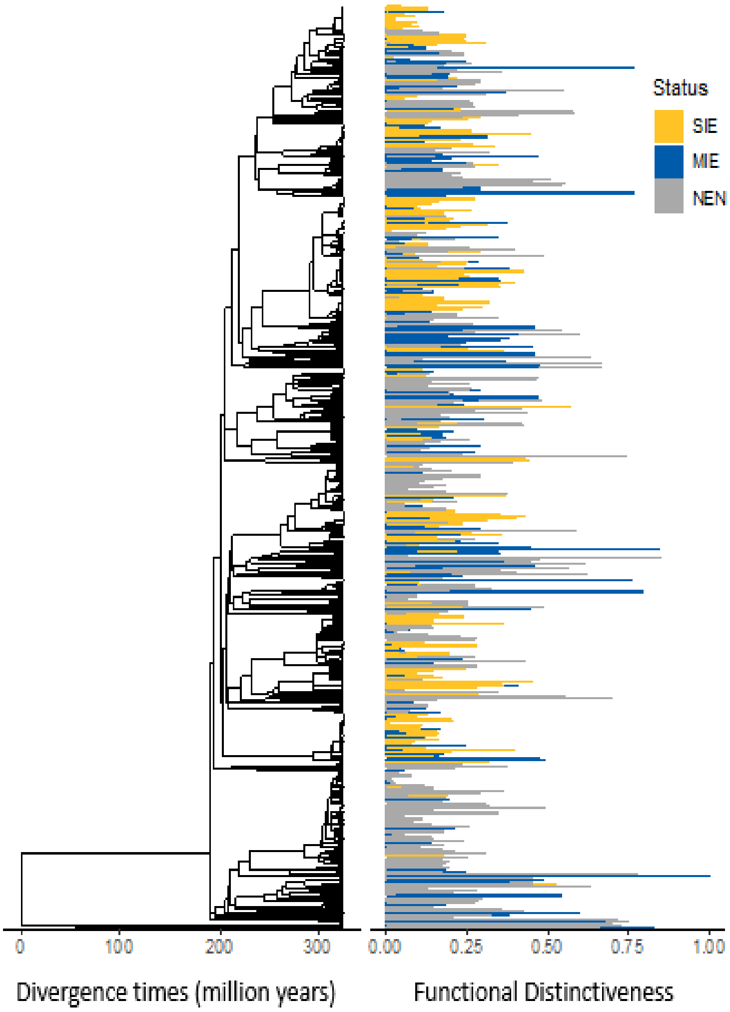

Figure S3.5.1 The phylogeny was obtained from Smith & Brown (2018). The bars in right panel show functional distinctiveness for each species, coloured by endemism status: single-island endemics (SIE), multi-island endemics (MIE) and native non-endemics (NEN). Higher values (longer bars) mean species are more distinct.

Chapter 4

High species turnover and low intraspecific trait variation in endemic and non-endemic plant species assemblages on an oceanic island

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Abstract

Questions: Both species turnover and intraspecific trait variation can affect plant assemblage dynamics along environmental gradients. Here, we asked how community assemblage patterns in relation to species turnover and intraspecific variation differ between endemic and non-endemic species. We hypothesized that endemic species show lower intraspecific variation than non-endemic species because they tend to have high rates of in situ speciation, whereas non-endemic species are expected to have a larger gene pool and higher phenotypic plasticity.

Location: La Palma, Canary Islands.

Methods: We established 44 sampling sites along a directional gradient of precipitation, heat load, soil nitrogen, phosphorus and pH. Along this gradient, we estimated species abundances and measured three traits (plant height, leaf area and leaf thickness) on perennial endemic and non-endemic plant species. In total, we recorded traits for 1,223 plant individuals of 43 species. Subsequently, we calculated community-weighted mean traits to measure the relative contribution of species turnover, intraspecific variation and their covariation along the analysed gradient.

Results: The contribution of intraspecific variation to total variation was similar in endemic and non-endemic assemblages. For plant height, intraspecific variation explained roughly as much variation as species turnover. For leaf area and leaf thickness, intraspecific variation explained almost no variation. Species turnover effects mainly drove trait responses along the environmental gradient, but intraspecific variation was important for responses in leaf area to precipitation.

Conclusions: Despite their distinct evolutionary history, endemic and non-endemic plant assemblages show similar patterns in species turnover and intraspecific variation. Our results indicate that species turnover is the main component of trait variation in the underlying study system. However, intraspecific variation can increase individual species' fitness in response to precipitation. Overall, our study challenges.

Left photo: *Canarina canariensis* population observed in Chamorga, Tenerife (own photo). *Canarina canariensis* is a herbaceous climber and native to the Canary Islands.

4.1 Introduction

Oceanic islands harbour a morphologically unique and endemic-rich flora that is often of high conservation concern (Fernández-Palacios *et al.*, 2021). Multiple studies have analysed the trait diversity (i.e. the extent of trait variation in a species assemblage) of oceanic island floras to determine their responses to abiotic conditions and stressors (Whittaker *et al.*, 2014; Ottaviani *et al.*, 2020; Schrader *et al.*, 2021). However, intraspecific trait variation has not yet been analysed thoroughly, even though it can have important implications for the fitness and survival of species (Des Roches et al., 2018), especially under changing environmental conditions (Norberg *et al.*, 2001; Björklund *et al.*, 2009). Assessing trait variation of endemic species might show isolation-driven adaptations to local environmental conditions resulting from their evolutionary history.

Trait variation occurs both as species turnover and intraspecific variation (De Bello *et al.*, 2011; Lepš *et al.*, 2011). Here, we refer to trait variation due to changes in species composition and abundance as species turnover and to trait variation due to within-species differences as intraspecific variation. Previous studies have found that species turnover is usually higher than intraspecific variation across terrestrial plant assemblages because it is a focal parameter of species coexistence due to differing degrees of trait and niche overlap between species (Messier *et al.*, 2010; De Bello *et al.*, 2011; Violle *et al.*, 2012). However, other studies have shown that intraspecific variation can be as extreme as trait variation between species in plant assemblages (Albert *et al.*, 2010). Hence, it remains unanswered to what extent species turnover and intraspecific variation contribute to total trait variation.

Oceanic islands are valuable to analyse trait variation because they harbour both endemic and non-endemic species. Endemic species have undergone an isolated evolution on islands through anagenetic or cladogenetic speciation (Stuessy *et al.*, 2006). In situ speciation often results in specific adaptations to local environmental conditions (Carlquist, 1974; Burns, 2019), possibly leading to high trait variation between species. Non-endemic species are either native and have colonized from the mainland by natural means or were (un-) intentionally introduced by humans. Because of their larger genetic pool and successful establishment in novel environments, non-endemic species are expected to have high phenotypic plasticity (i.e. trait variation for a given genotype in different environments; Alexander *et al.*, 2011; Davidson *et al.*, 2011), yielding substantial intraspecific variation (Bradshaw, 1965). Hence, we expect non-endemic species to show higher intraspecific variation, whereas we expect endemic species to show higher species turnover owing to local adaptations resulting from in situ speciation.

Across environmental gradients, plant traits can change because of species turnover and intraspecific variation (Ackerly, 2003; Cornwell & Ackerly, 2009). Most studies state that species turnover is the main driver of trait characteristics along gradients because abiotic conditions select species with adequate traits to survive in a given environment (Keddy, 1992; Weiher *et al.*, 1998; Kraft *et al.*, 2015). For example, dry and high-irradiation environments select species with water-efficient and temperature-regulative traits, such as smaller plant height, smaller leaf area and thicker leaves (Moles *et al.*, 2009; Poorter *et al.*, 2009; Wright *et al.*, 2017). Soil nutrient availability (notably nitrogen and phosphorus) can further affect plant trait values because of species turnover (Aerts & Chapin, 2000; Ordoñez *et al.*, 2009; Cadotte *et al.*, 2011). Nutrient-deficient soils lead to a shift from species associated with rapid resource acquisition to species associated with resource conservation (Aerts & Chapin, 2000; Díaz *et al.*, 2004; Ordoñez *et al.*, 2009). Furthermore, soil acidification can affect trait values due to species turnover because low pH requires plants species that efficiently acquire micronutrients or phosphorus from soils (Lambers *et al.*, 2008). Yet, most studies have ignored the role of intraspecific variation, even though it can also be important in driving trait characteristics along gradients (Lepš *et al.*, 2011). Simultaneously analysing how the relative contribution of species turnover and intraspecific variation change along climatic and soil gradients might help to redefine our understanding of community assemblage mechanisms.

In this study, we analyse species turnover and intraspecific variation in essential plant traits in endemic and non-endemic assemblages on the oceanic island of La Palma (Canary Islands, Spain). First, we hypothesize that trait variation mostly depends on species turnover rather than intraspecific variation in endemic assemblages compared with non-endemic assemblages. Second, we hypothesize that species turnover and intraspecific variation decrease with decreasing resource availability through selective filtering in plant species assemblages. However, it is not yet clear how the relative contributions of species turnover and intraspecific variation change along environmental gradients.

4.2 Methods

4.2.1 Study site and plot selection

We conducted our study on La Palma (Canary Islands, Spain) from March to April 2018. La Palma is an oceanic island located in the Atlantic Ocean, ca. 500 km off the coast of northwestern Africa. The island is characterized by northeasterly trade winds giving rise to a humid windward and a dry leeward side (Garzón-Machado *et al.*, 2014). This rainfall pattern can even be observed in the inframediterranean thermotype along the island's coast (hereafter referred to as coastal succulent scrub), where the ombrotypes range from arid in the southwest to upper-dry in the northeast (Garzón-Machado *et al.*, 2014). La Palma is a volcanic island made of basaltic rock. It can be divided geologically into the older northern part (ca. 2.0 Ma), where volcanic activity has ceased and erosive processes dominate, and the younger southern part, where subaerial volcanic ontogeny is ongoing (0.54 Ma to 2021; (Ancochea *et al.*, 1994; Carracedo *et al.*, 2001). The most common vegetation assemblage of the coastal succulent scrub, the Tabaibal-Cardonal vegetation, is characterized by focal species such as *Kleinia neriifolia*, different *Euphorbia* and *Echium ssp*. (del Arco Aguilar *et al.*, 2010). *Opuntia* and *Agave ssp*. are successful invaders within the Tabaibal-Cardonal vegetation as they are adapted to arid–dry conditions (del Arco Aguilar *et al.*, 2010). The Tabaibal-Cardonal vegetation represents a circum-insular ecosystem, in which the temperature is relatively constant and the species pool is endemic-rich.

We selected 44 study plots along the entire coastal succulent scrub at an elevation of ca. 100-200 m a.s.l. with a minimum distance of 700 m (Figure 4.1). At each point, we selected a 7 m ×

7 m plot by haphazardly throwing an object to determine the centre, on the condition that there was minimal evidence of human disturbance. Areas affected by recent volcanic eruptions, on which vegetation is poorly developed, were not taken into consideration. The study area covered strong variation in both climate and soil (Table 4.1). Hence, our study system is ideal for comparison of these factors and their influence on trait variation between species assemblages.

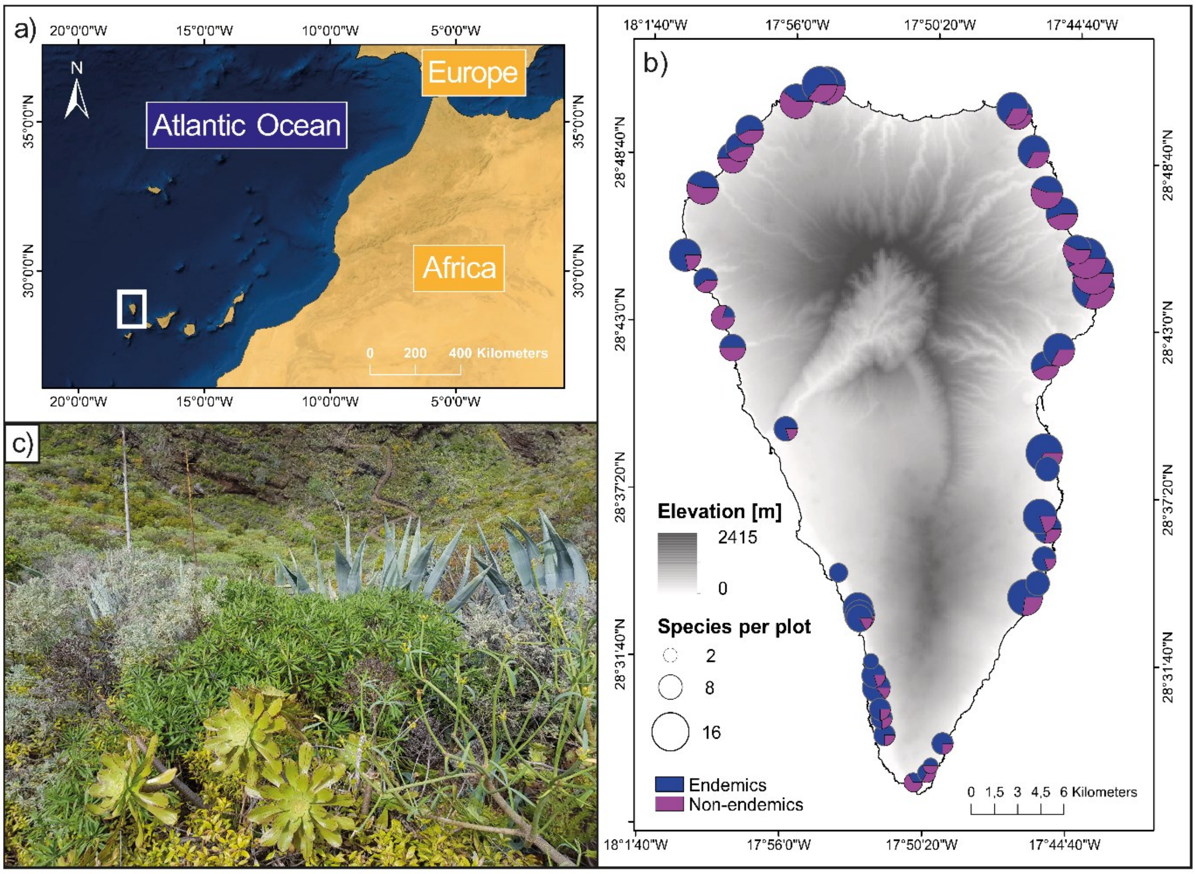


Figure 4.1 a) La Palma is the most northwestern island of the Canary Islands archipelago (white rectangle). **b)** Map of study sites, circles correspond to vegetation survey plots where trait data was collected (circle size = the number of species sampled in each plot; n = 44). The proportion of sampled endemic (blue) and non-endemic (purple) species is given for each plot. All plots were sampled at an elevation of approximately 100–200 m a.s.l. **c)** Typical vegetation assemblage of the Tabaibal-Cardonal consisting of endemic species (here: *Aeonium arboreum*, *Euphorbia lamarckii*, *Rubia fruticosa*) and non-endemic species (here: *Agave americana*, *Globularia salicina*, *Schizogyne sericea*).

4.2.2 Vegetation survey and plant trait measurements

We estimated the percentage coverage of every perennial plant individual visually in each plot to quantify species composition. For each perennial species within a plot, five individuals were chosen for trait sampling, if available. We measured three essential “soft” (i.e. easy to measure, sensu Hodgson *et al.*, 1999) morphological traits of perennial plant species that capture the essence of plant form and function. Overall, we recorded trait information for 1,223 individual plants of 43 species (27 endemic species and 16 non-endemic species; see supporting information, Table S4.1).

To determine maximum plant height, we measured the orthogonal distance from the upper boundary of the main photosynthetic tissues of plants to ground level (Pérez-Harguindeguy *et al.*, 2013). We estimated leaf area based on measurements of maximum leaf length and maximum leaf width using digital callipers. For simple-leaved species, we measured three young but fully developed (i.e. current growing season) and undamaged leaves (excluding petiole because it is of less importance for light interception compared with the leaf blade) per individual. For compound-leaved species, we measured one leaflet of three different leaves per individual. Subsequently, we averaged the three leaf measurements for each individual. We determined leaf length as the maximum distance from the base to the tip of the leaf and leaf width as the maximum distance from one side of the leaf to the other. Assuming an oval-shaped leaf, we approximated leaf area as the product of (leaf length × width × π)/2. For stem-photosynthesizing succulents (*Opuntia dillenii*, *Opuntia maxima* and *Euphorbia canariensis*), a leaf length of zero was determined. Leaf thickness was measured with digital callipers at an intermediate position between the tip and the base of the leaf, avoiding major veins. We measured leaf thickness on the same three leaves per individual we measured leaf area. We averaged the three measurements for each individual and determined a leaf thickness of zero for stem-photosynthesizing succulents (*O. dillenii*, *O. maxima* and *E. canariensis*).

4.2.3 Climate and soil variables

Interpolated data for mean annual temperature and annual precipitation were obtained from Irl *et al.*, (2020). We used mean annual temperature (range: 18.4–21.0°C) to analyse a possible effect of potential direct incident radiation on trait variation. Hence, we calculated the heat load index after (McCune & Keon, 2002) using the *spatialEco* package in R (Evans, 2021). The heat load index assumes that a slope with the afternoon sun shining on it will have a higher maximum temperature than an equivalent slope with the morning sun shining on it.

To measure soil nitrogen and phosphorus content, we collected one soil sample for each plot. Each sample consisted of a homogenized mixture of five subsamples collected in each corner and at the centre of the plot (from ca. 10 cm depth). The samples were passed through a 2-mm sieve and air-dried for 3 days. Soil pH was measured using a glass electrode in a soil/CaCl2 ratio of 1:2. We determined total N and C by dry combustion using a LECO TruSpec N auto analyser and a LECO RC-412, respectively (LECO Corporation). Phosphorus was determined following the CAL-Method described by (Schüller, 1969). We excluded soil carbon from the analyses because almost all plots had a carbon content of ca. 0%.

We ln-transformed nitrogen and phosphorus values to approximate normality, and subsequently centred and scaled all environmental variables, yielding estimates in SD units. After standardization, we calculated correlation coefficients (Pearson's *r*) between the environmental variables (Table S4.2).

Table 4.1 Mean, standard deviation and range of environmental variables included in regression analyses.

Variable	Unit	Mean	Standard deviation	Min	Max
Annual precipitation	mm	377.13	92.22	202.90	572.65
Heat load index		0.76	0.18	0.43	1.0
Soil nitrogen	%	23.47	15.33	0.70	95.00
Soil phosphorus	mg/100 g	6.02	19.37	0.30	202.56
Soil pH		6.21	0.79	4.44	7.85
Species richness (total)		9	3.46	2	16

4.2.4 Total variation, species turnover and intraspecific variation

To assess the contribution of species turnover and intraspecific variation to total variation in traits, we calculated community-weighted mean trait values for endemic and non-endemic species assemblages in each plot (because of the small number of non-endemic species in our study system and our focus on endemic species, we did not further differentiate between native and non-native species assemblages). To assess the relevance of species turnover and intraspecific trait variation on community-weighted mean traits, we calculated specific and fixed averages (Lepš *et al.*, 2011). Specific averages were calculated from the plot-specific trait values per species:

$$Specific\ average = \sum_{i=1}^{S} p_i x_{i\_plot}$$

where pi is the relative abundance of the ith species based on the cover in the plot, S is the number of species and xi_plot is the specific trait value of the ith species for the specific plot in which it was sampled. Fixed averages were calculated with trait values averaged over all plots within the gradient for each species. Fixed averages are therefore plot-independent, meaning that one species has one mean trait value regardless of the plot in which it is found. Subsequently, we calculated intraspecific variation as the difference between specific averages and fixed averages.

4.2.5 Statistical analyses

To summarize variation in plant species composition, we used Non-Metric Multidimensional Scaling (NMDS; Minchin, 1987). NMDS ordination was obtained using the "metaMDS" function in the R package *vegan* (Oksanen *et al.*, 2020) using Bray–Curtis dissimilarity on the matrix of species abundances across sites. To further examine the effects of the environmental gradients on plant species composition, we used vector fitting, as implemented in the "envfit" function (R package *vegan*; Oksanen *et al.*, 2020).

We performed partitioning of trait variation among plots to quantify how much variability can be accounted for by species turnover or intraspecific variability alone. The method is based on a sum of squares decomposition (De Bello *et al.*, 2011; Lepš *et al.*, 2011) and was calculated using the "decompCTRE" function in the R package *cati* (Taudiere & Violle, 2016). This function fits an ANOVA to each component (i.e. total variation, species turnover and intraspecific variation) and takes the total sum of squares as a measure of the total variability for the respective component. The decomposition of sum of squares can also be applied across ANOVAs to calculate their covariation. If the covariation between species turnover and intraspecific variation is positive, both effects reinforce each other. If the covariation between species turnover and intraspecific variation is negative, both effects oppose each other (e.g. when effects of large-leaved species are decreased by small-leaved individuals). Before analyses, we normalized leaf area and leaf thickness using an ln-transformation.

We further assessed responses in trait variation to climate, soil and species richness because changes in trait values can be driven by species turnover alone, by intraspecific variation alone or by both species turnover and intraspecific variation. We built multiple linear regression models for each plant trait, considering the specific averages (which include the effect of both species turnover and intraspecific variation) and fixed averages as the response variables, and the environmental variables (annual precipitation, heat load index, soil nitrogen, soil phosphorus, soil pH and species richness) as explanatory variables. We tested all models for quadratic relationships ($y \approx x + x^2$) because trait characteristics do not necessarily change linearly along environmental gradients. We first ran an initial full model for each trait (including all five environmental variables) and subsequently checked for spatial autocorrelation using Moran's I statistic. We could not detect spatial autocorrelation in any of the multiple regression models. Subsequently, we chose a model selection procedure, based on minimizing the AICc (Burnham & Anderson, 2002). We performed AICc model selection using the function "dredge" in the R package *MuMIn* (Barton, 2020) to obtain the overall best model. All analyses were performed using R (version 4.1.1, R Core Team, R Foundation for Statistical Computing, Vienna, AT).

4.3 Results

4.3.1 Species richness and species composition

Total species richness in the 44 plots ranged from 2 to 16, with an average of 9. Proportion of endemic species in assemblages ranged from 20% to 100%, with an average of 67%. Species composition varied across the analysed plots on La Palma. Species composition was significantly correlated with precipitation ($r^2 = 0.71$, $p < 0.001$), heat load index ($r^2 = 0.42$, $p < 0.001$), soil nitrogen ($r^2 = 0.17$, $p = 0.025$) and soil pH ($r^2 = 0.44$, $p < 0.001$). Soil phosphorus had no significant effect on species composition ($r^2 = 0.01$, $p = 0.910$; Figure 4.2).

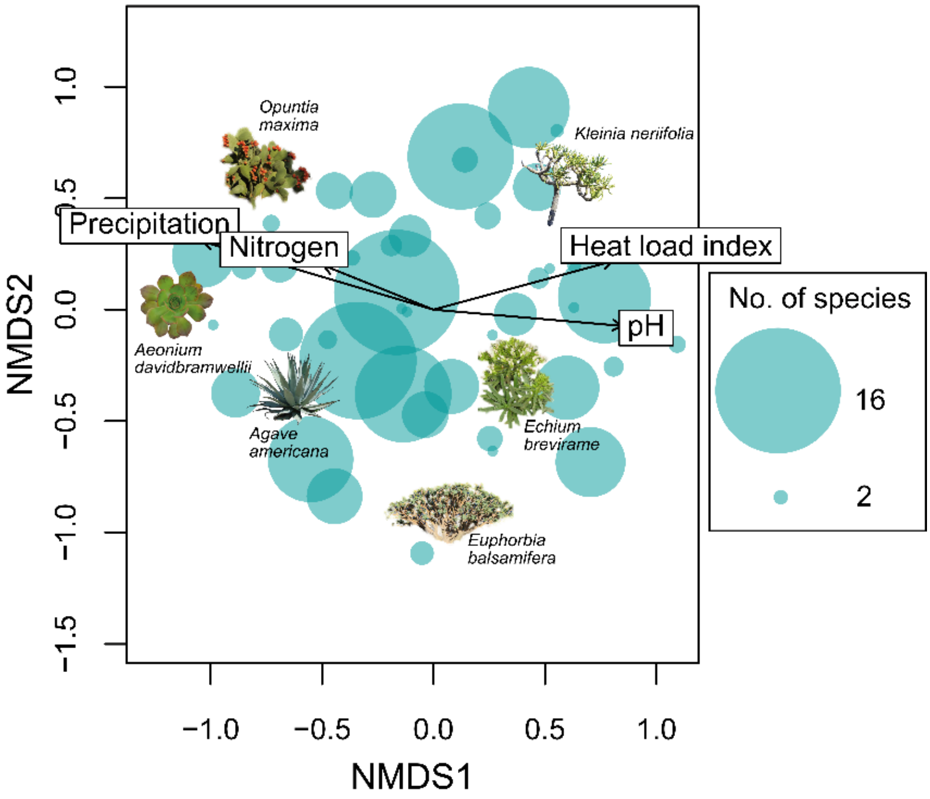


Figure 4.2 Non-Metric Multidimensional Scaling (NMDS) ordination of plant species assemblages in 44 plots in the coastal succulent scrub on La Palma, Canary Islands. Circle sizes illustrate total species richness in each plot. A Bray–Curtis similarity index on coverage data was used. Arrows represent the environmental variables that correlated significantly with the ordination ($p < 0.05$). The stress value was 0.16. Plant icons display the position of characteristic endemic (*Aeonium davidbramwellii*, *Echium brevirame*, *Euphorbia balsamifera*) and non-endemic (*Agave americana*, *Opuntia maxima*, *Kleinia neriifolia)* plant species.

4.3.2 Contribution of species turnover and intraspecific variation

The contribution of species turnover and intraspecific variation to total variation showed only minor discrepancies between endemic and non-endemic assemblages (Figure 4.3, Table S4.3). Species turnover accounted for most variation across almost all traits in endemic (plant height, 46%; leaf area, 98%; leaf thickness, 81%) and non-endemic assemblages (plant height, 33%; leaf area, 81%; leaf thickness, 89%). For plant height, intraspecific variation accounted for 31% of explained variation in endemic assemblages and 41% of explained variation in non-endemic assemblages. For leaf area and leaf thickness, intraspecific variation accounted for 18% and 28% of explained variation in endemic assemblages, and 7% and 6% of explained variation in non-endemic assemblages, respectively. We found positive covariation between species turnover and intraspecific variation for plant height in endemic assemblages, and for plant height, leaf area and leaf thickness in non-endemic assemblages. This indicates that plots dominated by species with high values for those traits also held individuals with comparatively high trait values for their species. Conversely, we found negative covariation between species turnover and intraspecific variation for leaf area and leaf thickness in endemic assemblages. This indicates that plots dominated by endemic species with high values for leaf area and leaf thickness held individuals with comparatively low trait values for their species.

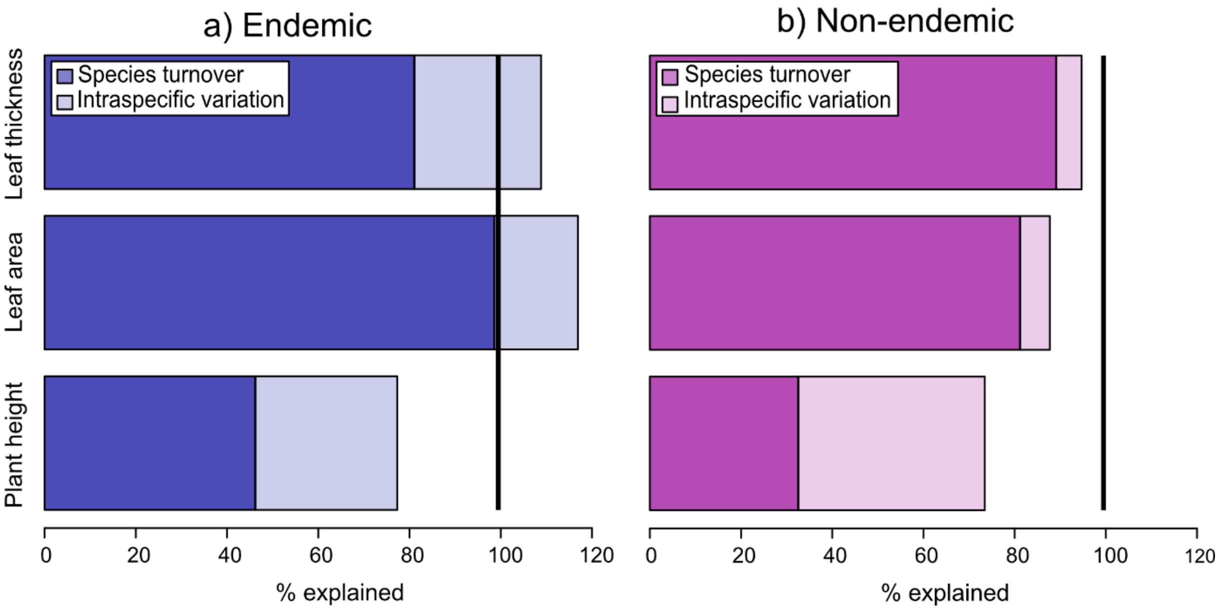


Figure 4.3 Decomposition of total variation in plant height, leaf area and leaf thickness for **a)** endemic (*n* = 44) and **b)** non-endemic (*n* = 41) assemblages. Dark areas on the bars correspond to species turnover and light areas to intraspecific variation effects. Vertical black lines denote total variation. The space between the end of the bar and the black line corresponds to the effect of covariation; if the line is to the right the bar, the covariation is positive, whereas if the line crosses the bar, the covariation is negative.

4.3.3 Variation in traits along environmental gradients

For plant height, specific averages increased significantly with increasing precipitation, and both specific and fixed averages increased with heat load index (Figure 4.4a). Also, fixed averages of plant height had a significant unimodal relationship with soil phosphorus (Figure 4.4a). For leaf area, specific averages increased significantly with increasing precipitation (Figure 4.4b). Both specific and fixed averages of leaf area had a significant U-shaped relationship with heat load index and increased significantly with soil phosphorus (Figure 4.4b). For leaf thickness, specific and fixed averages increased significantly with heat load index and had a significant U-shaped relationship with soil nitrogen (Figure 4.4c). The explained variation in the multiple regression models analysing specific averages was 27% for plant height, 51% for leaf area and 44% for leaf thickness. The explained variation in the multiple regression models analysing fixed averages was 18% for plant height, 41% for leaf area and 49% for leaf thickness (Table S4.4).

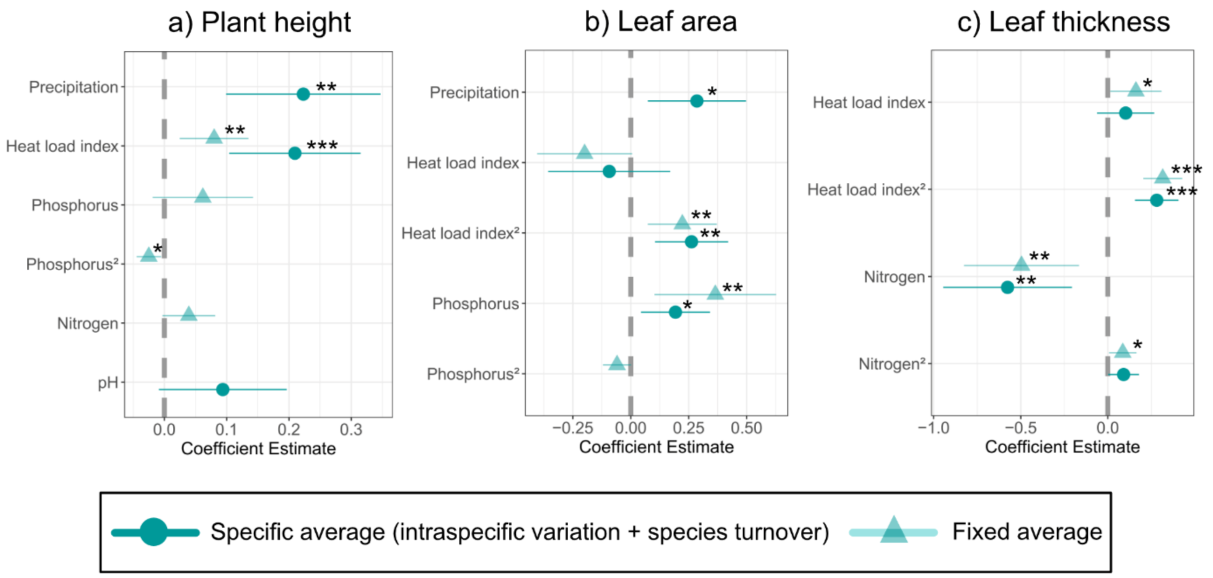


Figure 4.4 Multiple regression models of precipitation, heat load index, soil nitrogen, soil phosphorus and soil pH on specific averages and fixed averages of **a)** plant height, **b)** leaf area and **c)** leaf thickness in entire plant assemblages (*n* = 44) across the coastal succulent scrub of La Palma, Canary Islands. Circles denote the specific averages (species turnover and intraspecific variation); triangles denote fixed averages only. Standardized estimates are provided for each predictor. Error bars represent confidence intervals of the coefficient estimates. Asterisks denote statistical significance (***$p < 0.001$; **$p < 0.01$; *$p < 0.05$).

Specific and fixed average relationships of endemic and non-endemic assemblages with environmental variables were overall similar to those of entire assemblages. Adversely, fixed averages of leaf area decreased with species richness in endemic assemblages and specific averages of leaf area increased with species richness in non-endemic assemblages. Coefficient estimates and adjusted r^2-values are given in the supporting information (Figure S4.1–2, Table S4.4).

4.4 Discussion

Our study tests whether trait variation in endemic and non-endemic plant assemblages is related to species turnover (differences in species composition) and intraspecific variation, and what drives plant trait variation along multiple environmental gradients in the coastal succulent scrub of the island of La Palma. In contrast to our first hypothesis, we found that trait variation mostly relates to species turnover rather than intraspecific variation in both endemic and non-endemic assemblages. Following our second hypothesis, our study shows that total plant trait variation generally decreased with decreasing resource availability, mostly due to species turnover effects. The importance of intraspecific variation in driving trait responses depended on the environmental factor considered. Despite their distinct evolutionary history, trait variation for endemic and non-endemic assemblages on oceanic islands may be driven by similar mechanisms across strong climatic and edaphic gradients.

4.4.1 Similar contribution of species turnover and intraspecific variation

In most cases, species turnover was the main contributor to trait variation in both endemic and non-endemic plant assemblages on La Palma. However, we expected higher intraspecific variation in non-endemic species because of a larger gene pool and higher phenotypic plasticity. Indeed, we recorded few, but consistently occurring invasive species (*Agave americana*, *Opuntia dillenii*, *Opuntia maxima*) across the coastal succulent scrub, known to be plastic in their traits and diverse in their genetic composition (Alexander *et al.*, 2011; Davidson *et al.*, 2011). We expected high species turnover in endemic assemblages because species that have developed on the Canary Islands through adaptive radiation, such as species from the genera *Aeonium* and *Echium*, are known to have high morphological variation between species (Liu, 1989; Böhle *et al.*, 1996; Jorgensen & Olesen, 2001). Even though trait variation was driven primarily by species turnover, our results show that intraspecific variation in plant height made a relatively high contribution to total trait variation both in endemic and non-endemic assemblages. These results concur with previous studies showing that intraspecific variation has a relevant role in total trait variation in plant height (Jung *et al.*, 2010; Lepš *et al.*, 2011; Gross *et al.*, 2013). By contrast, leaf area and leaf thickness are less plastic and hence less variable within species (Wilson *et al.*, 1999; Roche *et al.*, 2004). However, we acknowledge that trait responses can be variable because they are dependent on functional trade-offs driven by biotic interactions (Callaway *et al.*, 2003) and the abiotic environment (Ackerly, 2003). Hence, the here observed species turnover effect in plant assemblages might be biased by our trait choice and the studied environment.

Intraspecific variation contributed to trait variation not only directly, but also through covariation with species turnover effects. Positive covariation occurred in traits of endemic and non-endemic assemblages, which is consistent with the expectation that species turnover and intraspecific trait responses should be in the same direction to increase individual plant fitness (Cornwell & Ackerly, 2009). However, we also found that intraspecific variation decreases total variation through negative covariation with species turnover in leaf area and leaf thickness of endemic assemblages. This indicates that within some individual plant species, trait characteristics showed opposing responses in comparison with responses among species trait characteristics (Kichenin *et al.*, 2013; Weemstra *et al.*, 2021). This response of species might be driven by trait divergence as a consequence of a reduction in niche overlap and heterospecific competition (Schluter, 2000; Ackerly *et al.*, 2006), which seems to be more pronounced in endemic than non-endemic species. This distinct pattern seems reasonable because endemic species are often associated with minor competitive ability due to their evolution in less-competitive environments (Fernández-Palacios *et al.*, 2021). Our results indicate that endemic and non-endemic assemblages underlie similar mechanisms shaping trait variation but might respond differently to competition because of their distinct evolutionary history.

4.4.2 Strong environmental filtering of trait characteristics due to species turnover

Specific and fixed averages showed similar responses to climatic and edaphic variables across all traits. This overlap indicates that species turnover is the most important contributor to total trait variation across the analysed gradients. However, intraspecific variation tended to play a substantial role in trait responses of endemic and non-endemic assemblages to precipitation. This result may reflect a wide variation in precipitation against more stable heat load and soil conditions. Most of the precipitation on La Palma falls between October and April, with extensive drought periods in summer (Garzón-Machado *et al.*, 2014). Environmental variation, such as precipitation seasonality, can promote adaptive phenotypic plasticity for plants to increase their fitness (Ghalambor *et al.*, 2007). Previous studies corroborate our results because they found that plant height and leaf area are highly responsive to precipitation within species and contribute strongly to total trait variation (Gross *et al.*, 2013; Jung *et al.*, 2014; but see Siefert *et al.*, 2014).

Fixed averages generally decreased with decreasing resource availability allocated by climate and soil. This result indicates that trait-mediated environmental filtering mainly occurred by changes in species composition of plant assemblages. Dry, highly irradiated and infertile environments can result in low trait values because plant species need to possess adequate traits to survive in such environments (Keddy, 1992; Weiher *et al.*, 1998; Kraft *et al.*, 2015). However, we found that plant height increased with heat load index, especially in endemic assemblages. This pattern could indicate that heat stress for plant height is less pronounced due to high isothermality (Moles *et al.*, 2009) in the succulent scrub on the Canary Islands. Large and thin leaves generally have a low water stress tolerance, whereas species with small and thick leaves are better suited for arid environments (Moles *et al.*, 2009; Poorter *et al.*, 2009; Wright *et al.*, 2017). In fact, the invasive species *O. dillenii* and *O. maxima*, as well as the endemic *Euphorbia canariensis*, are striking examples of convergent evolution and have analogously developed ephemeral leaves in which photosynthetic activities have been replaced by cladodes or photosynthesizing stems, respectively. Those species also use CAM photosynthesis, an adaptation of plants to increase water-use efficiency under arid conditions (Cushman, 2001). Moreover, trait averages responded mostly nonlinearly to soil nutrient availability. Nutrient-poor soils promote a shift from acquisitive to conservative strategies in species (Díaz *et al.*, 2004; Ordoñez *et al.*, 2009). Hence, species in nutrient-poor sites display small but thick leaves, which in theory translates into greater investment in leaf construction (but see Cutts *et al.*, 2021). However, this pattern is less clear for plant height, possibly because of the prevalent limitation of nitrogen in young soils (Lambers *et al.*, 2008). Surprisingly, soil acidity decreased leaf area in only endemic assemblages, even though it can limit nutrient uptake and therefore restrict growth (Gujas *et al.*, 2012). This pattern could be explained by the relatively narrow range of soil pH values captured in our study.

Interestingly, fixed averages of leaf area decreased with increasing species richness in endemic assemblages but increased in non-endemic assemblages. This indicates that small-leaved endemic species and large-leaved non-endemic species are more prominent in species-rich assemblages. Large-leaved species can outcompete other species because of light interception to lower vegetation layers (Parkhurst & Loucks, 1972). Hence, our results indicate that non-endemic species might have a competitive advantage over endemic species in comparatively species-rich assemblages owing to the dominance of large-leaved species.

4.5 Conclusions

Disproving our first hypothesis, we found that species turnover accounted for a considerable part of the total variation in plant height, leaf area and leaf thickness in endemic and non-endemic plant species assemblages. Hence, our results challenge the theory that intraspecific trait variation is important for the proliferation of non-endemic species. Concurring with our second hypothesis, we found that species turnover and intraspecific variation generally increased with resource availability. Moreover, we were able to show for the first time that intraspecific variation is more important than species turnover in response to limiting environmental factors, such as precipitation in an arid ecosystem. We conclude that non-endemic plant species can establish successfully in coastal environments despite low levels of intraspecific trait variation. However, plant species can establish higher intraspecific trait variation in response to seasonal environments, which could have important implications during a time of global change.

Acknowledgements

We would like to thank Dagmar Schneider and Doris Bergmann-Dörr for performing the soil sample analyses in the laboratory of the Institute of Physical Geography at the Goethe University Frankfurt. We would further like to thank Felix M. Medina from the Consejería de Medio Ambiente, Cabildo de La Palma, for advising us with his expert knowledge on the Canary Island flora during fieldwork. Open access funding enabled and organized by ProjektDEAL.

Data availability statement

All environmental and morphological data are available in the Supporting Information (see Hanz *et al.*, 2022a) and were submitted to the TRY Plant Trait Database (www.try-db.org) on 8 July 2021.

Supporting information

Table S4.1 List of endemic and non-endemic species sampled in all plots (n = 44) at the coastal succulent scrub of La Palma, Canary Islands. For each species the number of plots it occurred in, and the number of measured individuals is given.

Family	**Species**	**Floristic status**	**No. plots**	**No. individuals**
Agavaceae	*Agave americana*	non-endemic	1	40
Apiaceae	*Astydamia latifolia*	non-endemic	4	7
Asclepiadaceae	*Periploca laevigata*	non-endemic	21	34
Asteraceae	*Argyranthemum frutescens frutescens*	endemic	1	5
Asteraceae	*Artemisia thuscula*	endemic	9	2
Asteraceae	*Kleinia neriifolia*	endemic	33	5
Asteraceae	*Pericallis papyraceae*	endemic	1	5
Asteraceae	*Phagnalon saxatile*	non-endemic	3	34
Asteraceae	*Phagnalon umbelliforme*	endemic	7	5
Asteraceae	*Pulicaria viscosa*	non-endemic	1	8
Asteraceae	*Reichardia ligulata*	endemic	2	53
Asteraceae	*Schizogyne sericea*	non-endemic	20	7
Asteraceae	*Tolpis santosii*	endemic	1	96
Boraginaceae	*Ceballosia fruticosa fruticosa*	endemic	3	20
Boraginaceae	*Echium brevirame*	endemic	24	22
Brassicaceae	*Lobularia canariensis intermedia*	endemic	2	105
Brassicaceae	*Lobularia maritima*	non-endemic	1	1

Family	**Species**	**Floristic status**	**No. plots**	**No. individuals**
Cactaceae	*Opuntia dillenii*	non-endemic	11	21
Cactaceae	*Opuntia maxima*	non-endemic	9	12
Convollariaceae	*Asparagus umbellatus*	endemic	1	5
Crassulaceae	*Aeonium arboreum holochrysum*	endemic	10	8
Crassulaceae	*Aeonium canariense christii*	endemic	3	147
Crassulaceae	*Aeonium davidbramwellii*	endemic	8	90
Crassulaceae	*Aeonium goochiae*	endemic	1	10
Crassulaceae	*Aeonium hierrense*	endemic	1	16
Euphorbiaceae	*Euphorbia balsamifera*	non-endemic	4	8
Euphorbiaceae	*Euphorbia canariensis*	endemic	6	5
Euphorbiaceae	*Euphorbia lamarckii broussonetii*	endemic	25	43
Fabaceae	*Bituminaria bituminosa*	non-endemic	11	37
Fabaceae	*Retama rhodorhizoides*	endemic	13	25
Frankeniaceae	*Frankenia capitata*	endemic	5	1
Globulariaceae	*Globularia salicina*	non-endemic	4	87
Hypericaceae	*Hypericum canariense*	non-endemic	1	15
Lamiaceae	*Lavandula canariensis*	endemic	24	27
Lamiaceae	*Micromeria herpyllomorpha herpyllomorpha*	endemic	11	4
Oleaceae	*Jasminum odoratissimum*	non-endemic	2	6
Plumbaginaceae	*Limonium imbricatum*	endemic	2	32
Plumbaginaceae	*Limonium pectinatum*	endemic	4	10
Polygonaceae	*Rumex lunaria*	endemic	12	66
Rhamnaceae	*Rhamnus crenulata*	endemic	4	24
Rubiaceae	*Rubia fruticosa fruticosa*	non-endemic	18	3
Rutaceae	*Ruta pinnata*	endemic	1	70
Zygophyllaceae	*Fagonia cretica*	non-endemic	1	2

Table S4.2 Pearson's correlation coefficient between precipitation, heat load index, soil nitrogen, soil phosphorus and soil pH across plant assemblages (n = 44) along the coastal succulent scrub of La Palma, Canary Islands.

	Precipitation	**Heat load index**	**Soil nitrogen**	**Soil phosphorus**	**Soil pH**
Heat load index	-0.607	-	-	-	-
Soil nitrogen	0.225	-0.399	-	-	-
Soil phosphorus	-0.184	0.174	0.209	-	-
Soil pH	-0.590	0.344	-0.424	0.210	-
Species richness	0.454	-0.676	0.242	-0.141	-0.400

Table S4.3 Relative contribution of total variation in community-weighted mean trait values due to species turnover, intraspecific variation, and their covariation across **a)** endemic and **b)** non-endemic plant assemblages on La Palma, Canary Islands.

	a) Endemic			**b) Non-endemic**		
	Plant height	Leaf area	Leaf thickness	Plant height	Leaf area	Leaf thickness
Intraspecific variation	0.31	0.18	0.28	0.41	0.07	0.06
Species turnover	0.46	0.98	0.81	0.33	0.81	0.89
Covariation	0.23	-0.17	-0.09	0.27	0.12	0.05

Table S4.4 Small sample-size corrected Akaike Criterion (AICc) and explained variation (adjusted R^2) of multiple regression models analysing the effect of precipitation, heat load index, soil nitrogen, soil phosphorus and soil pH on specific and fixed averages in **a)** plant height, **b)** leaf area and **c)** leaf thickness of entire, endemic and non-endemic plant assemblages along the coastal succulent scrub of La Palma, Canary Islands.

	a) Plant height						**b) Leaf area**					
Models	**Entire**		**Endemic**		**Non-endemic**		**Entire**		**Endemic**		**Non-endemic**	
	AICc	R^2	AICc	R^2	AICc	R^2	AICc	R^2	AICc	R^2	AICc	R^2
Specific average	15.7	0.27	47.6	0.24	10.7	0.17	76.9	0.51	64.6	0.48	112.9	0.62
Fixed average	-31.0	0.18	9.0	0.14	-33.0	0.14	73.0	0.41	69.1	0.23	113.6	0.58

	c) Leaf thickness					
Models	**Entire**		**Endemic**		**Non-endemic**	
	AICc	R^2	AICc	R^2	AICc	R^2
Specific average	59.3	0.44	63.8	0.20	92.9	0.35
Fixed average	49.4	0.49	64.6	0.19	88.6	0.36

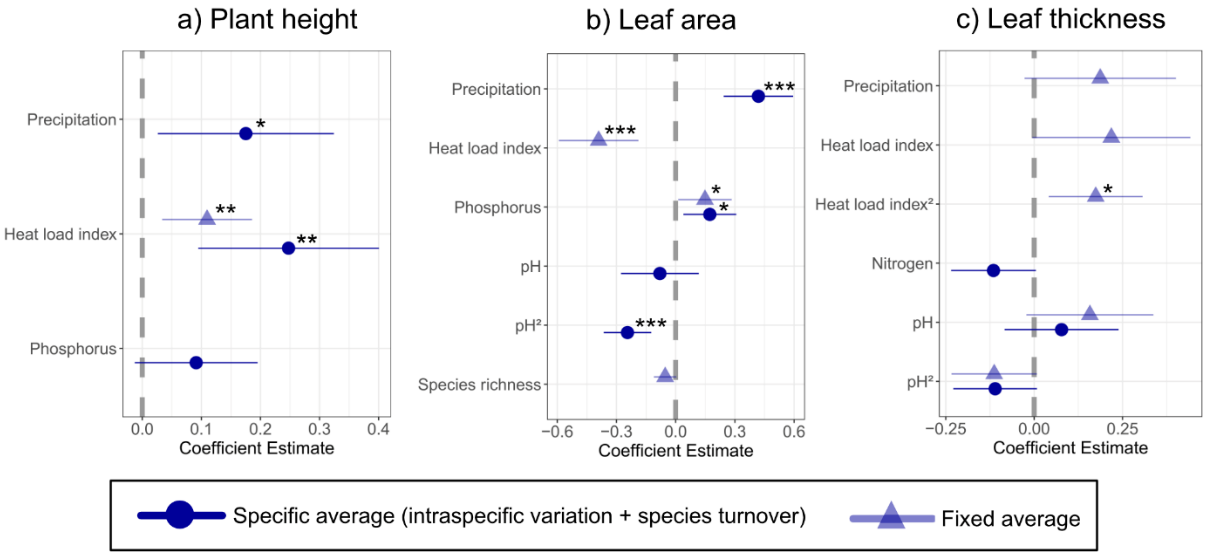


Figure S4.1 Multiple regression models of precipitation, heat load index, soil nitrogen, soil phosphorus and soil pH on specific averages and fixed averages of **a)** plant height, **b)** leaf area and **c)** leaf thickness in endemic plant assemblages (n = 44) at the coastal succulent scrub of La Palma, Canary Islands. Dark circles denote the specific averages (species turnover and intraspecific variation); light triangles denote fixed averages only. Standardized estimates are provided for each predictor. Error bars represent confidence intervals of the coefficient estimates. Asterisks denote statistical significance (*** p < 0.001; ** p < 0.01; * p < 0.05).

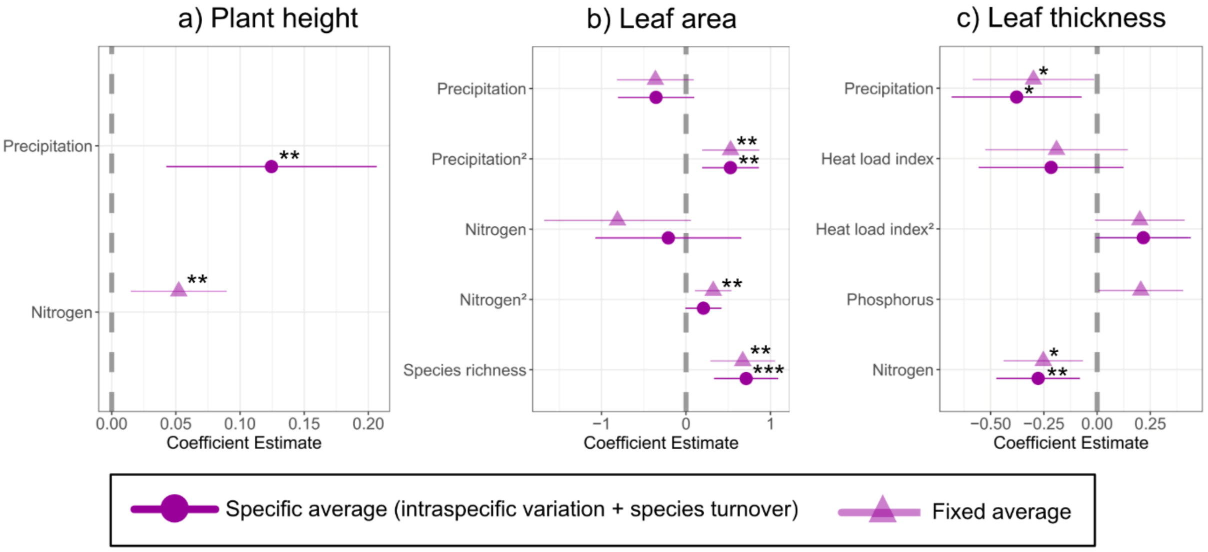
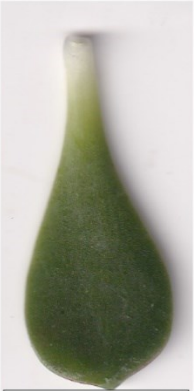


Figure S4.2 Multiple regression models of precipitation, heat load index, soil nitrogen, soil phosphorus and soil pH on specific averages and fixed averages of **a)** plant height, **b)** leaf area and **c)** leaf thickness in non-endemic plant assemblages (n = 44) at the coastal succulent scrub of La Palma, Canary Islands. Dark circles denote the specific averages (species turnover and intraspecific variation); light triangles denote fixed averages only. Standardized estimates are provided for each predictor. Error bars represent confidence intervals of the coefficient estimates. Asterisks denote statistical significance (*** p < 0.001; ** p < 0.01; * p < 0.05).

Aeonium canariense latifolium

Aeonium diplocyclum

Aeonium decorum



Aeonium gomerense

Aeonium castello-paivae

Aeonium appendiculatum

Aeonium nobile

Aeonium lindleyi viscatum

Aeonium saundersii

Aeonium goochiae

Aeonium davidbramwellii

1 cm

Chapter 5

Scientific floras can be reliable sources for some trait data in a system with poor coverage in global trait databases

Vanessa Cutts, **Dagmar M. Hanz**, Martha Paola Barajas-Barbosa, Adam C. Algar, Manuel J. Steinbauer, Severin D.H. Irl, Holger Kreft, Patrick Weigelt, Jose María Fernandez Palacios & Richard Field - *Journal of Vegetation Science* 2021; 32: e12996

Aim: Trait-based approaches are increasingly important in ecology and biogeography, but progress is often hampered by the availability of high-quality quantitative trait data collected in the field. Alternative sources of trait information include scientific floras and taxonomic monographs. Here we test the reliability and usefulness of trait data acquired from scientific floras against trait values measured in the field, and those in TRY, the most comprehensive global plant trait database.

Location: Tenerife and La Palma, Canary Islands, Spain.

Methods: We measured leaf area and specific leaf area (SLA) in the field for 451 native vascular plant species and compared them with equivalent trait data digitised from the most recent and comprehensive guide of the Canarian flora, and data sourced from TRY. We regressed the field-measured traits against their equivalents estimated from the literature and used the regression models from one island to predict the trait values on the other island.

Results: For leaf area, linear models showed good agreement between values from the scientific flora and those measured in the field ($r^2 = 0.86$). These models were spatially transferable across islands. In contrast, for SLA we found a weak relationship between field-measured values and the best estimates from the scientific flora ($r^2 = 0.11$). Insufficient data were available in the TRY database for our study area to calculate trait correlations with other data sources.

Conclusions: Scientific floras can act as useful data sources for quantitative plant trait data for some traits but not others, whilst the TRY database contains many traits, but is incomplete in species coverage for our study region, and oceanic islands in general.

Left photo: Leaf collage of different *Aeonium* specimen from La Palma and La Gomera (Canary Islands; own collage).

5.1 Introduction

Functional trait-based approaches in ecological research have, in recent years, enhanced our understanding of biodiversity and how traits relate to ecosystem functioning. Functional traits are morphological, physiological or phenological features of organisms, measurable at the individual level, that impact individual performance and fitness (Violle *et al.*, 2007). While the classification of species into functional groups has a long tradition (Raunkiær, 1934; Weiher *et al.*, 1999), the definition of a "trait" has shifted from a simple grouping towards a more quantitative categorisation, allowing more predictive science within ecology (McGill *et al.*, 2006). Trait-based approaches are now abundantly used to answer research questions across a variety of topics including community ecology (Mouillot *et al.*, 2013; Satdichanh *et al.*, 2015), species diversity gradients (Lamanna *et al.*, 2014; Whittaker *et al.*, 2014; Si *et al.*, 2017; Schellenberger Costa *et al.*, 2018b), responses to environmental change (Bjorkman *et al.*, 2018; Liu *et al.*, 2018; Winchell *et al.*, 2020), and niche dynamics (Reif *et al.*, 2016; Schellenberger Costa *et al.*, 2018b).

Functional traits have been particularly important in understanding the role of plant diversity in ecosystem functioning, and efforts have been made to identify trait–trait correlations and trade-offs to develop an economic spectrum for plant traits (Wright *et al.*, 2004; Chave *et al.*, 2009; Reich, 2014; Díaz *et al.*, 2016; Kong *et al.*, 2019; Shen *et al.*, 2019). This, in turn, has aided the quantification of trait–environment relationships to understand how abiotic factors influence functional characteristics (Ordoñez *et al.*, 2009; Bruelheide *et al.*, 2018). Recognising the importance of plant functional traits in ecology has increased the demand for plant trait data (Kattge *et al.*, 2020). However, acquiring such data is a challenge. The fundamental source of trait data is through the direct measurements of plant individuals, either in the field or under experimental conditions. A major disadvantage of these direct methods of data collection is their intensiveness — they require a significant amount of time, equipment and money. Even if resources are abundant, accessibility to field sites can be difficult and field work can be disrupted. This can lead to biased data collection, whereby field sites that are easier to access, such as those at low elevations or near roads, are preferentially chosen. As a result, the data may be limited in geographic or taxonomic coverage. Furthermore, measuring traits in the field can be destructive — collecting leaf and stem samples can be detrimental to an individual's survival. This is important to consider when studying rare or endangered species, for which non-destructive methods should be preferred (if acquiring a collection permit is even possible).

An alternative source for trait information is to rely on data that have been sampled in the past and made available via global databases (Kleyer *et al.*, 2008; Kattge *et al.*, 2020). This has benefited trait-based research by making plant trait data accessible to more researchers and it has allowed recent studies to examine plant trait variation across larger geographic and phylogenetic scales (e.g. Díaz *et al.*, 2016; Bjorkman *et al.*, 2018; Bruelheide *et al.*, 2018). For plants, the TRY database is the largest collection of plant functional traits and holds an impressive amount of trait records for almost 280,000 species (Kattge *et al.*, 2020). Despite efforts to update and improve trait databases, they are still incomplete (Schrodt *et al.*, 2015; Jetz *et al.*, 2016) and large taxonomic and geographic gaps remain.

These knowledge gaps are non-randomly distributed, such that some species and regions are underrepresented (Schrodt *et al.*, 2015; Jetz *et al.*, 2016; Cornwell *et al.*, 2019). There are also biases towards certain traits and trait values. Easily measured traits are more likely to be reported than those that are difficult, or require more resources, to measure. In addition, bias towards higher or lower trait values has been found for frequently measured traits in the TRY database (Sandel *et al.*, 2015), and certain trait values may go unreported (but see Scheffer *et al.*, 2015).

Outside of these databases, a wealth of information about plant form and function exists in the literature that is yet to be digitised. Information on plant species has been assembled and published in thousands of scientific floras (Floras hereafter) and taxonomic monographs for centuries. In fact, attempts to assemble botanical knowledge were made in ancient times and date as far back as AD 77 (see Pliny & Healey, 2004). Floras catalogue all known plant species in a given geographic region and represent some of the oldest collections of plant information in the botanical literature. They contain detailed taxonomic descriptions, keys, illustrations and sometimes distribution maps, geographical and ecological information that can be used for locating and identifying species (Frodin, 2001). Such detailed descriptions of plant morphology often systematically provide values for some traits. They may even include basic information on intraspecific variation, such as when maximum and minimum values are reported for a given trait, or when different values are reported for different regions.

Trait values extracted from Floras have the potential to be used for ecological purposes (Whittaker *et al.*, 2000; Hawkes, 2007; Kissling *et al.*, 2008, 2010), and there is a growing effort to mobilise and integrate them into global biodiversity databases (Weigelt *et al.*, 2020). Data from Floras and checklists provide highly representative and complete data from large regions, which is beneficial to macroecological research, but this data type is currently underutilised compared to fine-scale, high-resolution data, such as site-specific trait measurements (König *et al.*, 2019). Comparing data quality with systematically collected field data is necessary to understand how data from Floras can be successfully applied in trait-based research. Thus, the aim of our study is to compare trait data obtained via three different methods of collection: (a) Floras, where trait information is extracted from species descriptions and identification keys; (b) field work, where established quantitative plant traits are measured directly in the field, specific to the geographic location of interest; and (c) the TRY database, where a species list of the focal region is used to download data for the focal traits.

We use the islands of Tenerife and La Palma in the Canary Islands (Spain) as the study system, for which an up-to- date, comprehensive and modern Flora is available (Muer *et al.*, 2016). Oceanic islands are an appropriate study system for trait-based research (Ottaviani *et al.*, 2020) due to their spectacular radiations and disproportionately high numbers of endemic species (Stuessy *et al.*, 2006; Kier *et al.*, 2009). Island systems have the potential to answer fundamental questions in functional ecology (Patiño *et al.*, 2017) but the use of trait-based research on islands remains underexploited (Ottaviani *et al.*, 2020) and readily available trait data for island species are rare. Leaves are at the core of plant functional ecology due to their role in carbon acquisition and transpiration, which influences biochemical cycling and ecosystem functioning (Press, 1999). Thus, we specifically focus on two commonly used traits: leaf area and specific leaf area (SLA), for which precise measurements are not usually recorded in Floras. We estimate leaf area and SLA using simpler trait measurements recorded in Floras and evaluate how well these estimates reflect leaf area and SLA measured directly from specimens collected in the field. We expected that leaf area estimated using leaf length and leaf width would be strongly positively correlated with field-measured leaf area, and that SLA estimated using leaf thickness would be positively correlated with field-measured SLA. We also tested the ability of traits from Floras to predict field traits using independent data by using trait data from one island to predict trait values on another.

5.2 MethodsField data

We studied traits of native vascular plant species of the islands of Tenerife and La Palma, Canary Islands, Spain. The latest plant checklist of the Canary Islands classifies species into to six categories: definitely native (either endemic or not), probably native, possibly native, probably introduced, introduced non-invasive and introduced invasive (Arechavaleta *et al.*, 2010). We focused on species within the definitely native category only. Leaf traits were measured using standardised protocols for measurement of plant functional traits (Pérez-Harguindeguy *et al.*, 2013): leaf area is the one-sided area of a fresh adult leaf, and SLA is the leaf area divided by its dry mass. We aimed to measure these traits for five adult individuals per species but, due to logistical constraints and the rarity of certain species, this was not always possible. If sampling more than individual per species, we took samples from different locations across the islands where possible, to account for environmental variation in trait values. Species were sampled where botanical experts or the Flora indicated they were located. We collected between 10 and 100 adult leaves per individual, depending on the species: for most species we collected 10–20 leaves but for species with small leaves we collected up to 100 to accurately measure their mass. Where possible, we sampled leaves that were not in the shade. Leaves were cut from the stem and the petiole was removed. Up to 10 leaves were scanned per individual using an A4 scanner and leaf area calculated for each leaf using WinFOLIA software (version: 2016b Pro; Regent Instruments Inc., Québec, Canada, 2016) for Tenerife specimens and ImageJ software (version 1.52a; Schneider *et al.*, 2012) for La Palma specimens. We used the mean value for leaf area per species. The two software packages produced near-identical average values for leaf area per species (paired-t_{44} = 1.32, $p = 0.19$; Pearson's $r = 0.99$). The leaf samples were weighed, then oven-dried and weighed again to calculate both fresh mass and dry mass per leaf. For compound leaves, we kept the entire leaf intact for scanning. SLA was calculated by dividing the leaf area by its oven-dried mass (Pérez-Harguindeguy *et al.*, 2013). We calculated leaf dry matter content (LDMC) of a single leaf by dividing the oven-dry mass by its fresh mass.

5.2.2 Flora data

We sourced plant trait data from the most recent and comprehensive guide to the Canarian flora (Muer *et al.*, 2016). The information in the Flora is based on expert knowledge and contains species from all islands in the archipelago. These data were supplemented using other Floras to increase data coverage (Bramwell & Bramwell, 1974; Hohenester & Welß, 1993; Schönfelder & Schönfelder, 2018a).

In some instances, we recorded data for subspecies when the trait values were known to differ between subspecies found on different islands. This ensured the field and Flora data matched as precisely as possible, according to our aim throughout: that the data we obtained would be those typically used in trait-based research using the data source in question. We extracted the following leaf traits: leaf length, leaf width and leaf thickness (information on SLA was not provided). Maximum and minimum values were often reported for these traits, but we calculated and used the mean values. We used leaf length and leaf width to estimate leaf area using the following formula:

$$estimated\ LA = \frac{LL\ x\ LW\ x\ \pi}{2}$$

where LA = leaf area, LL = leaf length, LW = leaf width. This equation assumes elliptical-shaped leaves. SLA is normally calculated by dividing leaf area by its dry mass. Dry mass will depend on the volume and density of the leaf. In the absence of information on dry mass or leaf density, we cannot estimate SLA directly. However, it still may be possible to obtain a proxy for SLA in the absence of dry mass data if variation in volume has a greater influence. Given that leaf volume, LV = LA × Lth, where Lth is leaf thickness, then:

$$SLA = \frac{LA}{LV\ x\ LD}$$

where LD is leaf density (dry mass per unit volume; Poorter *et al.*, 2009). Thus, assuming invariant LD across species, SLA will vary as a function of Lth:

$$estimated\ SLA \sim \frac{1}{Lth}$$

Following this reasoning, we test whether SLA, measured in the field, can be estimated from the Lth values in the Flora. As a test-of- concept, we also test whether SLA varies with 1/Lth using only our field data. Lastly, leaf thickness has also been shown to correlate reasonably well with SLA × LDMC (Vile *et al.*, 2005). We tested this by regressing leaf thickness from the Flora with SLA × LDMC as calculated from field data.

5.2.3 TRY data

Species names in TRY, our species list and the Flora were resolved using the Taxonomic Name Resolution Service (Boyle *et al.*, 2013). We used the resolved species list to download the following traits from the freely available data: leaf length, leaf width, leaf thickness, leaf area and SLA. To ensure consistency with field data, TRY data were filtered to include only measurements from living adult individuals in their natural environments.

5.2.4 Statistical analyses

Simple linear regressions were carried out with field data as the dependent variable and Flora data as the independent variable. We removed *Kunkeliella retamoides* from the analysis —this species has tiny ephemeral leaves that are reduced to scales, making it difficult to define the functional equivalent of the leaf, which led to different definitions across data sources, and thus non-comparable values between field and Flora datasets. We regressed field-measured leaf area against Flora-estimated leaf area and field-measured SLA against Flora-estimated SLA. We also regressed field-measured leaf area and SLA against leaf length and leaf width obtained from the Flora to determine how well each measurement predicted leaf area and SLA by itself. Furthermore, to scrutinise our method of estimating SLA using Flora data, we regressed field-measured SLA with field-measured 1/Lth. We compared these models with a second set of models that included leaf type (simple vs compound) and leaf shape (broad-leaved vs needle-like) as interaction variables in order to determine if the regression slope differed between these groups (see Supporting Information). We also compared leaf thickness from field data and Flora data. All variables were loge-transformed to improve the residuals of the regressions. In addition, we compared trait values obtained from the Flora with those from TRY using Pearson's *r*.

Firstly, we looked at the relationships across all the data (La Palma + Tenerife). Secondly, we modelled La Palma data only and tested the predictions of this model against data from Tenerife (with field-measured leaf area from Tenerife as the dependant variable and predicted values from La Palma regressions as the independent variable). We also did the reverse, regressing observed values from La Palma against values predicted from Tenerife. We then compared the slope and intercept parameters of the observed vs predicted values against the 1:1 line (i.e. slope = 1, intercept = 0) using a one-sample t test to determine the spatial transferability of the models. All analyses were carried out in R (version 3.6.1, R Core Team, 2017).

5.3 Results

5.3.1 Data coverage

We measured traits for 451 definitely native species in the field (Table 5.1); 398 of these were measured on Tenerife and the remaining 53 on La Palma. From the Floras, we compiled a list of 554 definitely native species (including all 451 species sampled in the field) from La Palma and Tenerife that had values for at least one of our selected traits (most species came from Muer *et al.*, 2016). We found data for only 24 out of these 554 species in TRY, of which just five were endemic to the Canary Islands (Table 5.1). When considering individual traits, eight definitely native species had measurements for leaf area in TRY and 16 had measurements for SLA. Due to this low coverage of the TRY data, we were unable to conduct meaningful comparisons with the field and Flora data. Leaf thickness was scarcely reported in the Flora (only 4% of native species; Table 5.1) and only for species with clearly succulent leaves (to within 0.1 mm precision). Thus, our sample size for the regression of field-measured SLA with estimated SLA is very small (n = 18) and is not representative of all leaf types.

To maintain consistency among data sources, we focus primarily on definitely native species occurring on La Palma and Tenerife, as these were the species measured for the field data. However, for informative purposes, in Table 5.2 we also report Flora and TRY data for all species, including exotics, occurring across the entire Canary Island archipelago. We considered probably introduced, introduced non-invasive and introduced invasive as exotic species.

Table 5.1 Trait coverage for native species occurring on La Palma and/or Tenerife from each data source. Columns show the numbers (and percentages) of species that have a value for each trait in each data source, respectively; totals are the numbers of species with at least one measured trait. The percentage is in reference to the number of La Palma/Tenerife species recorded in the Flora.

	Flora (%)	**Field work (%)**	**TRY (%)**
Leaf length	267 (48)	-	8 (1.4)
Leaf width	215 (39)	-	8 (1.4)
Leaf thickness	22(4)	401 (72)	22 (4.0)
Leaf area	192 (35)	392 (71)	8 (1.4)
Specific leaf area	22(4)	384 (69)	16 (2.9)
Total no. of species	554 (100)	451 (81)	24 (4)

Table 5.2 Trait coverage for all Canary Island species in the Flora and in the TRY database. Columns show the total number (and percentage) of species that have a value for at least one measured trait. Numbers are shown for all species (which includes exotics) and for definitely native species. The percentages relate to the number of species recorded in the Flora of the relevant category (all or definitely native).

	Flora (%)		**TRY (%)**	
Trait	**All species**	**Definitely native**	**All species**	**Definitely native**
Leaf length	1,060 (47)	403 (47)	43 (2)	9 (1)
Leaf width	974 (44)	335 (39)	111 (5)	9 (1)
Leaf thickness	42 (2)	37 (4)	256 (11)	23 (3)
Leaf area	882 (39(	306 (35)	141 (6)	8 (1)
Specific leaf area	42 (2)	37 (4)	220 (10)	17 (2)
Total no. of species	2,237 (100)	865 (100)	270 (12)	24 3)

5.3.2 Linear regression

The relationship between field-measured leaf area and Flora-estimated leaf area was strong for the overall dataset (r^2 = 0.86, p < 0.001, df = 146; Figure 5.1), and when considering Tenerife (r^2 = 0.82, p < 0.001, df = 116) and La Palma (r^2 = 0.96, p < 0.001, df = 23) separately. This relationship did not differ between leaf groups (see supporting information, Table S5.2, Figure S5.1 and S5.2). Relationships between leaf area and leaf length or leaf width were also significant (leaf length: r^2 = 0.64, p < 0.001, df = 192; leaf width: r^2 = 0.69, p < 0.001, df = 162; Figure 5.1).

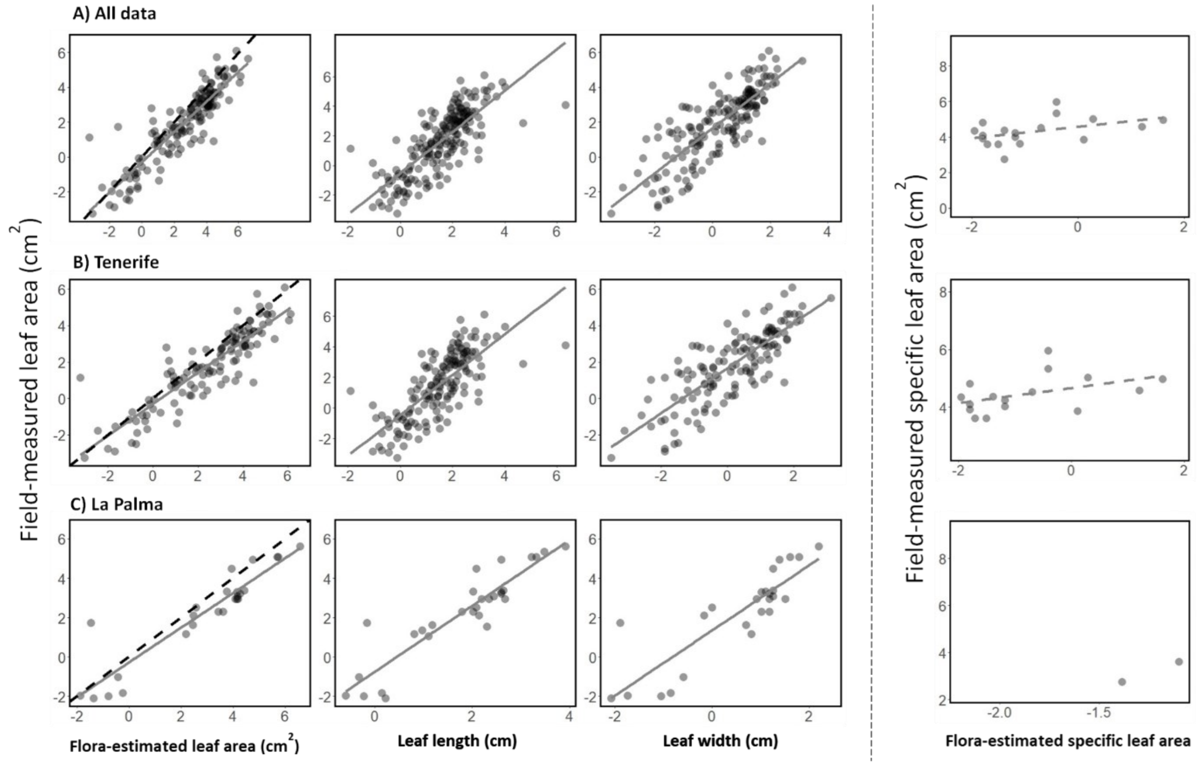


Figure 5.1 Scatter plots showing the relationship between field-measured leaf area (on the y-axis) and Flora traits (on the x-axis) for: **a)** all data; **b)** Tenerife only; and **c)** La Palma only. The grey lines are the linear regression models (grey dashed lines indicate a non-significant relationship). The black dashed lines are the 1:1 lines (not shown on the leaf length and leaf width graphs because the axes are on different scales). The left-hand panel shows relationships between field-measured SLA and Flora-estimated SLA. All axes are loge-transformed. See Table 5.4 for regression equations.

Field-measured SLA was not significantly correlated with estimated SLA for the overall dataset ($r^2 = 0.11$, $p = 0.17$, $df = 16$; Figure 5.2), neither was it when looking at Tenerife only ($r^2 = 0.20$, $p = 0.08$, $df = 14$). We did not analyse for La Palma only because not enough species from La Palma had trait values for leaf thickness and SLA. No significant relationship was found between SLA and either leaf length or leaf width for Tenerife or La Palma (Table 5.3). When testing this using only field data, we found the r^2 values to be extremely low ($df = 382$, $r^2 = 0.07$, $p < 0.001$; Table S5.1). The addition of leaf type and shape as interactions terms did not improve the regression model ($r^2 = 0.08$; Table S5.3; Figure S5.3 and S5.4). In addition, there was no relationship between leaf thickness and SLA × LDMC ($r^2 = 0.01$, $p = 0.71$, $df = 16$; Table S5.4). Leaf thickness measured from the field showed a reasonably strong and significant relationship with leaf thickness from the Flora ($df = 18$, $r^2 = 0.49$, $p < 0.001$). Due to the low sample size no further analysis was conducted using SLA. Correlations between Flora data and TRY data using all species (including exotics) showed a significant correlation for leaf area (Pearson's $r = 0.89$, $p < 0.001$, $df = 65$) and leaf width (Pearson's $r = 0.63$, $p < 0.001$, $df = 67$), but not for leaf length (Pearson's $r = -0.18$, $p = 0.31$, $df = 31$). This was due to an incorrect leaf length value (or incorrect units) for *Phoenix canariensis* in the TRY data (0.55 cm). When this species was removed, leaf length values correlated well (Pearson's $r = 0.64$, $p < 0.001$, $df = 30$). We could not make any further comparisons of traits among data sources

because, although the numbers in Tables 5.1 and 5.2 look promising, often trait values are not available for the same set of species.

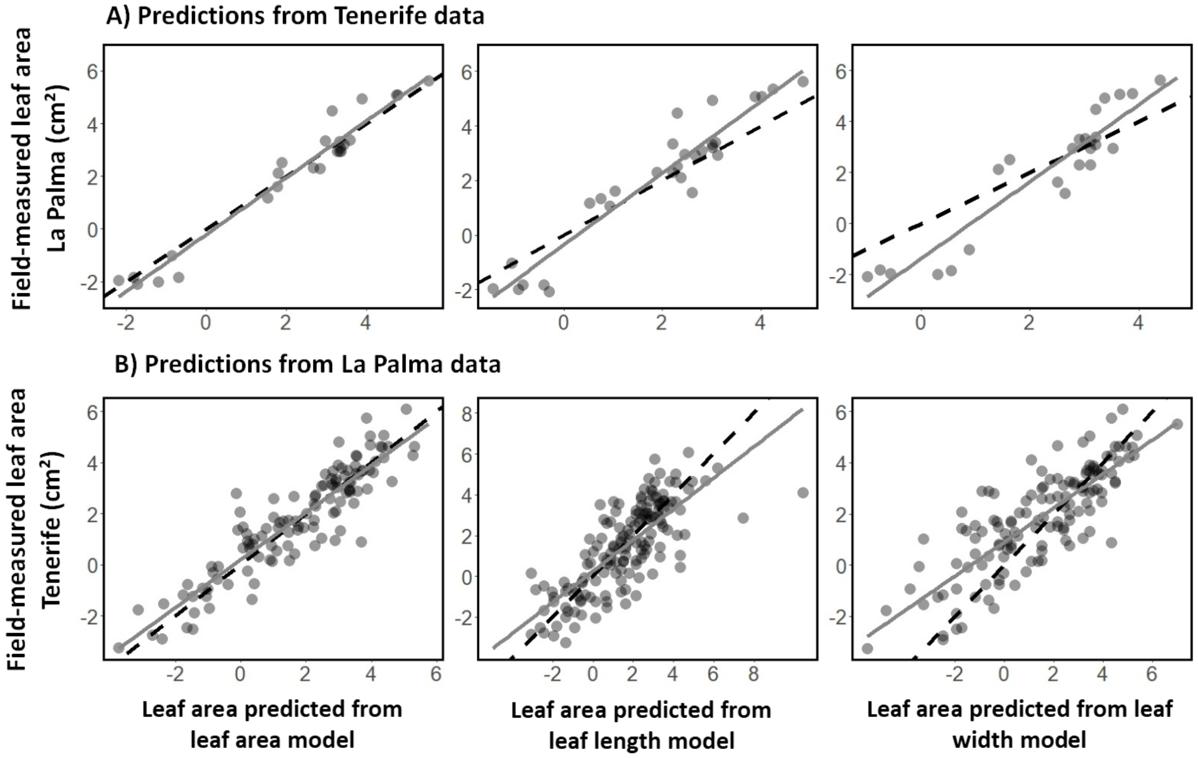


Figure 5.2. Scatter plots showing the observed vs predicted leaf area. Predictions (X-axes) are based on leaf area, leaf length and leaf width models. **a)** The observed La Palma data ($\log_e$ transformed) were regressed against predictions from Tenerife data, **b)** The observed Tenerife data ($\log_e$ transformed) were regressed against predictions based on La Palma data. Grey lines are the linear regression models; black dashed lines are the 1:1 lines. See Table 5.4 for regression equations.

Correlations between Flora data and TRY data using all species (including exotics) showed a significant correlation for leaf area (Pearson's $r = 0.89$, $p < 0.001$, $df = 65$) and leaf width (Pearson's $r = 0.63$, $p < 0.001$, $df = 67$), but not for leaf length (Pearson's $r = -0.18$, $p = 0.31$, $df = 31$). This was due to an incorrect leaf length value (or incorrect units) for *Phoenix canariensis* in the TRY data (0.55 cm). When this species was removed, leaf length values correlated well (Pearson's $r = 0.64$, $p < 0.001$, $df = 30$). We could not make any further comparisons of traits among data sources because, although the numbers in Tables 5.1 and 5.2 look promising, often trait values are not available for the same set of species.

Table 5.3. Univariate linear regressions with field-measured traits as the response variables (LA_{field} = field-measured leaf area, SLA_{field} = field-measured specific leaf area, Lth_{field} = field-measured leaf thickness) and Flora-measured traits as the explanatory variables (LA_{flora} = Flora-estimated leaf area, LL_{flora} = leaf length from Flora, LW_{flora} = leaf width from Flora, SLA_{flora} = Flora-estimated specific leaf area, Lth_{flora} = leaf thickness from Flora). $SLA_{field\text{-}est}$ = SLA estimated using 1/Lth from field data. All data were $\log_e$ transformed (except Lth_{field} and Lth_{flora}). SE = standard error.

	All Data					**Tenerife**					**La Palma**				
	df	Slope±SE	Intercept±SE	r^2	p	df	Slope±SE	Intercept±SE	r^2	p	df	Slope±SE	Intercept±SE	r^2	p
$LA_{field} \sim LA_{flora}$	146	0.93±0.03	-0.52±0.11	0.86	<0.001	116	0.91±0.04	-0.47±0.13	0.82	<0.001	23	0.99±0.04	-0.71±0.16	0.96	<0.001
$LA_{field} \sim LL_{flora}$	192	1.48±0.08	-0.71±0.16	0.64	<0.001	155	1.40±0.09	-0.61±0.18	0.59	<0.001	27	1.83±0.12	-1.61±0.25	0.90	<0.001
$LA_{field} \sim LW_{flora}$	162	1.34±0.07	1.58±0.09	0.69	<0.001	132	1.26±0.08	1.63±0.10	0.66	<0.001	23	1.90±0.15	1.09±0.19	0.87	<0.001
$SLA_{field} \sim SLA_{flora}$	16	0.32±0.29	4.58±0.21	0.20	0.06	14	0.26±0.14	4.66±0.19	0.20	0.08	-	-	-	-	-
$SLA_{field} \sim SLA_{field\text{-}est}$	382	0.25±0.05	4.56±0.07	0.07	<0.001	312	0.28±0.04	4.62±0.05	0.14	<0.001	50	0.41±0.23	4.10±0.32	0.06	0.09
$SLA_{field} \sim LL_{flora}$	189	-0.11±0.09	4.55±0.17	0.01	0.20	153	-0.09±0.05	5.01±0.09	0.02	0.08	27	0.23±0.18	1.63±0.38	0.06	0.20
$SLA_{field} \sim LW_{flora}$	161	-0.02±0.08	4.44±0.10	0.00	0.84	131	0.02±0.05	4.90±0.06	0.00	0.64	23	0.39±0.18	1.82±0.24	0.16	0.05
$Lth_{field} \sim Lth_{flora}$	18	0.48±0.11	1.07±0.48	0.49	<0.001	15	0.49±0.14	1.12±0.53	0.46	0.003	-	-	-	-	-

5.3.3 Cross-island predictions

We used the linear regression models to predict leaf area outside the geographical range of input data (i.e. the other island), using Flora data. We then correlated these predicted values with the observed values. All La Palma models successfully predicted leaf area on Tenerife; there was a strong positive relationship between the observed values on Tenerife and the predicted values from La Palma models based on Flora data (r^2 = 0.79). This was also true the other way around, i.e. observed values from La Palma vs predicted values from Tenerife models (r^2 = 0.85). Again, leaf width had a higher predictive power than leaf length (Table 5.4). For leaf area predictions on both La Palma and Tenerife, the slope and intercept were very close to, and not significantly different from, 1 and 0 respectively (i.e. the 1:1 line: Table 5.4; Figure 5.2). For leaf length, the slope differed significantly from 1 but the intercept did not differ from 0 for both islands. For leaf width, the slope and intercept differed significantly from 1 and 0 for both islands.

Table 5.4. Observed vs. predicted regressions for field-measured leaf area (LA), where Flora-estimated leaf area, leaf length and leaf width were used as explanatory variables. Predicted LA values from La Palma models were regressed against observed values from Tenerife (top) and vice versa (bottom). SE = standard error. All regressions were significant at P <0.001. 'Slope P' and 'Intercept P' are P-values from one-sample t-tests comparing slopes with 1 and intercepts with 0. All data were $\log_e$ transformed.

	df	**Slope±*SE***	**Slope *p***	**Intercept±SE**	**Intercept *p***	**r^2**
Tenerife observed LA vs predicted La Palma LA						
Flora-estimated leaf area	116	0.95±0.04	0.06	-0.19±0.10	0.07	0.82
Leaf length	155	0.76±0.05	<0.001	0.27±0.14	0.05	0.59
Leaf width	132	0.66±0.04	<0.001	0.91±0.12	<0.001	0.66
La Palma observed LA vs predicted Tenerife LA						
Flora-estimated leaf area	23	1.08±0.05	0.11	-0.21±0.15	0.17	0.96
Leaf length	27	1.31±0.08	<0.001	-0.35±0.21	0.10	0.90
Leaf width	23	1.51±0.12	<0.001	-1.37±0.33	<0.001	0.87

5.4 Discussion

We have demonstrated that a combination of easily obtained leaf parameters – leaf length and leaf width – can be used to estimate leaf area as a non-destructive alternative to field sampling. Furthermore, we were able to successfully predict independent field-measured data on leaf area across islands in the Canaries, indicating that the reliability of Floras as sources of trait data may be transferable to new regions.

Our estimates of leaf area correlated strongly with field-measured leaf area on both La Palma and Tenerife despite assuming an elliptical shape. Other studies using leaf length and width to estimate leaf area have found similar results (Kraft *et al.*, 2008; Pandey & Singh, 2011; Shi *et al.*, 2019). Accounting for the differences in leaf type (simple vs compound) and leaf shape (broad-leaved vs needle-like) did not improve our models. In fact, we find that the species that diverge furthest from the 1:1 line are a mix of species with simple or compound leaves. Thus, the variation in leaf type and leaf shape does not necessarily correspond to variations of leaf area (leaf shape probably relates more closely to leaf perimeter). Therefore, the additional variance in leaf area due to leaf shape that is not accounted for in the model (e.g. from compound or severely lobed leaves) does not have a sufficient effect on leaf area to render a parsimonious model uninformative.

To evaluate the performance of the leaf area model, we used it to make predictions on a different island. The success of the predictions could be driven by the climatic overlap between islands as leaf area is linked to climate and microclimate (Byars *et al.*, 2007; Peppe *et al.*, 2011; Guerin *et al.*, 2012; Sumida *et al.*, 2018). Also, the phylogenetic relatedness within the Canary Island flora means that many species occurring on different islands belong to the same genera and are morphologically similar, such as *Argyranthemum*, which might contribute to the strong predictive ability. Nonetheless, despite considerable overlap, the climates of Tenerife and La Palma are different in some areas – La Palma receives the highest levels of precipitation in the archipelago due the northeasterly trade winds, and is cooler and wetter than Tenerife in some places, whereas Tenerife, being taller, reaches lower temperatures than La Palma at its summits. Also, although many of the closely related species are morphologically similar, some genera have radiated into species that are morphologically quite different (Jorgensen & Olesen, 2001). Therefore, despite both environmental and trait differentiation, the model predicts well across islands. Whether or not this can be translated beyond the Canary Island archipelago is a subject for further study. Intraspecific trait differences could be present in native species occurring on both the islands and the continent and could potentially have an island-continental gradient.

Despite our expectation, and considering that SLA is a function of leaf thickness (Witkowski & Lamont, 1991; Pérez-Harguindeguy *et al.*, 2013), we only found a weak and non-significant relationship between field-measured SLA and Flora-estimated SLA. Accounting for differences between leaf groups only slightly improved these estimations. Perhaps a more complex model is required –assuming a constant volume to mass ratio for leaves is simplistic, because plants invest more or less in structural elements based on their ecological strategies (Westoby *et al.*, 2002). Therefore, accounting for different leaf strategies might reveal different relationships. However, Vendramini *et al.*, (2002) found a clear association between SLA and leaf thickness, but when accounting for leaf strategies (succulent, sclerophyllous and tender-leaved) this relationship disappeared. SLA is also a function of LDMC (Vile *et al.*, 2005), thus, future research could see how the relationship differs across different LDMC values. Our attempt to estimate SLA using leaf thickness from available Flora data was unsuccessful. Leaf thickness seems to be scarcely reported in Floras, perhaps due the difficulty of making precise measurements, resulting in little variation. Furthermore, it is possible that leaf thicknesses from Floras are obtained from dried herbarium specimens, which would not be comparable to measurements from fresh leaves. This might account for the unexplained variation in the relationship between field-measured leaf thickness and Flora leaf thickness. We therefore encourage researchers to continue reporting true values for SLA.

We have identified significant gaps in the TRY database for the Canary Islands –only 3% of the definitely native species in the Canary Islands had any trait data, of which only five species were endemic to the archipelago (representing only 1% of the endemic species). Trait data may be scarce for islands in general, due to the high proportion of endemic species. If island data are disproportionally underrepresented in the TRY database, this could hinder trait-based research in insular systems (Ottaviani *et al.*, 2020). The lack of data available for Canary Island endemics in TRY makes data available in the Flora all the more valuable \–many Canary Island endemics are extremely rare and some are critically endangered (e.g. *Lotus eremiticus*). As well as lacking species, the TRY database often also lacks simple morphological traits in favour of more complex ones that are assumed to be more informative about plant functions. For example, researchers may provide data for SLA, but not upload the measurements used to calculate this (leaf area and leaf dry mass), which are useful in their own right. Floras provide highly representative data that are currently underexploited in ecology and, although the trait data they contain are limited in precision, these data have been shown to represent a more complete and unbiased view of spatial variation in functional traits (König *et al.*, 2019). Thus, Floras provide complementary information to the data that are available in TRY.

In addition to the limitations of field data and TRY data, there are also clear limitations to using data from Floras. Firstly, the lack of standardised taxonomy across geographic regions is present, and probably reinforced, in Floras. However, applications are available to aid in resolving species lists once they have been digitised, for example the Taxonomic Name Resolution Service (Boyle *et al.*, 2013). Secondly, Floras lack standardised vocabulary and definitions for the traits they describe, though recent efforts to harmonise the terminology around plant characteristics might alleviate this (Hoehndorf *et al.*, 2016; Garnier *et al.*, 2017). Finally, it is not always clear whether the data from Floras were collected in a standardised way, due to a lack of transparency. The limitations referred to here have been addressed by recent efforts to collate trait and distribution data from Floras and checklists, where trait values are standardised by language, terminology and unit of measurement (Global Inventory of Floras and Traits [GIFT]; Weigelt *et al.*, 2020). This provides a standardised way of digitising and presenting the data in Floras and checklists worldwide.

A promising avenue for future research would be to evaluate digitalised herbarium specimens as a source of trait data. There are some clear advantages to using herbarium specimens to gather trait data, namely that the measurements are precise and the geographical/temporal origin of the specimens are known. However, there may be bias from using this type of data, whereby the most appealing specimens are collected. This may not accurately represent a species mean for a given trait.

5.5 Concluding remarks

We have demonstrated that Floras can provide some valuable data for the Canary Islands, whereas the TRY database currently cannot, a situation that we expect will affect other insular systems with high numbers of endemic species. This points towards a need for more field work to fill in gaps and reduce bias. However, due to the high cost and typically destructive nature of field sampling, it may not be feasible to sample rare and endangered species if we are to protect them. Thus, Floras remain an important resource in the emerging field of functional island biogeography, for which a lot of new data are required.

Acknowledgements

We would like to thank Félix Medina and Rüdiger Otto for their botanical expertise; Jana Alonso, Manuel Nogales, Nora Straßburger and Mercedes Vidal-Rodríguez for their assistance with lab and fieldwork; and Franziska Schrodt for her help with online data extraction and commenting on the final manuscript.

Data availability statement

Data will be available on FigShare by August 2021 (https://figshare.com/s/f2161 33811 b345c 322e7).

Supporting information

Table S5.1 Linear regressions with SLA (mm^2mg^{-1}) as the response variable and 1/leaf thickness (mm) as the explanatory variable using field data only. Both variables are $\log_e$ transformed. SE = standard error, df = degrees of freedom.

	df	Slope±SE	Intercept±SE	r^2	*p*
Intercept	382	0.26±0.05	4.56±0.07	0.07	<0.001
Tenerife	312	0.28±0.04	4.62±0.05	0.14	<0.001
La Palma	50	0.41±0.23	4.10±0.32	0.06	0.09

Table S5.2 Linear regressions with field-measured leaf area (cm^2) as the response variable and Flora-estimated leaf area (cm^2) as the explanatory variable. Both variables are $\log_e$ transformed. Leaf type (simple/compound) and leaf shape (broadleaf/needle-like) are included as interaction terms. r^2 = 0.87, *n* = 104.

	Estimate	SE	t values	*p*
Intercept	-0.74	1.23	-0.60	0.55
Leaf area	0.87	0.33	2.61	0.01
Leaf type Simple	0.15	1.25	0.12	0.91
Leaf shape Needle	0.11	0.28	0.39	0.70
Leaf area: Leaf type Simple	-0.15	0.29	-0.51	0.61
Leaf area: Leaf shape Needle	0.20	0.12	1.67	0.10

Table S5.3 Linear regressions with SLA (mm^2mg^{-1}) as the response variable and 1/leaf thickness (mm) as the explanatory variable using field data only. Both variables are $\log_e$ transformed. Leaf type (simple/compound) and leaf shape (broadleaf/needle-like) are included as interaction terms. SE = standard error. r^2 = 0.08, *n* = 237.

	Estimate	SE	T values	*p*
Intercept	4.95	0.55	8.93	0.00
SLA(1/Lth)	-0.10	0.36	-0.28	0.78
Leaf type Simple	-0.54	0.51	-1.06	0.29
Leaf shape Needle	0.02	0.26	0.07	0.95
SLA(1/Lth): Leaf type Simple	0.26	0.30	0.86	0.39
SLA(1/Lth): Leaf shape Needle	0.18	0.22	0.84	0.40

Table S5.4 Linear regressions with SLA (mm^2mg^{-1}) x LDMC ($mg\ g^{-1}$) from field data as the response variable and leaf thickness (mm) from Flora data. Both variables are $\log_e$ transformed. Regressions were carried out for all data and Tenerife separately. We did not have enough samples from La Palma to do a regression. SE = standard error, df = degrees of freedom.

	df	Slope±SE	Intercept±SE	r^2	p
All data	16	-0.22±0.59	5.11±0.78	0.01	0.71
Tenerife	14	0.11±0.14	5.68±0.18	0.04	0.43
La Palma	-	-	-	-	-

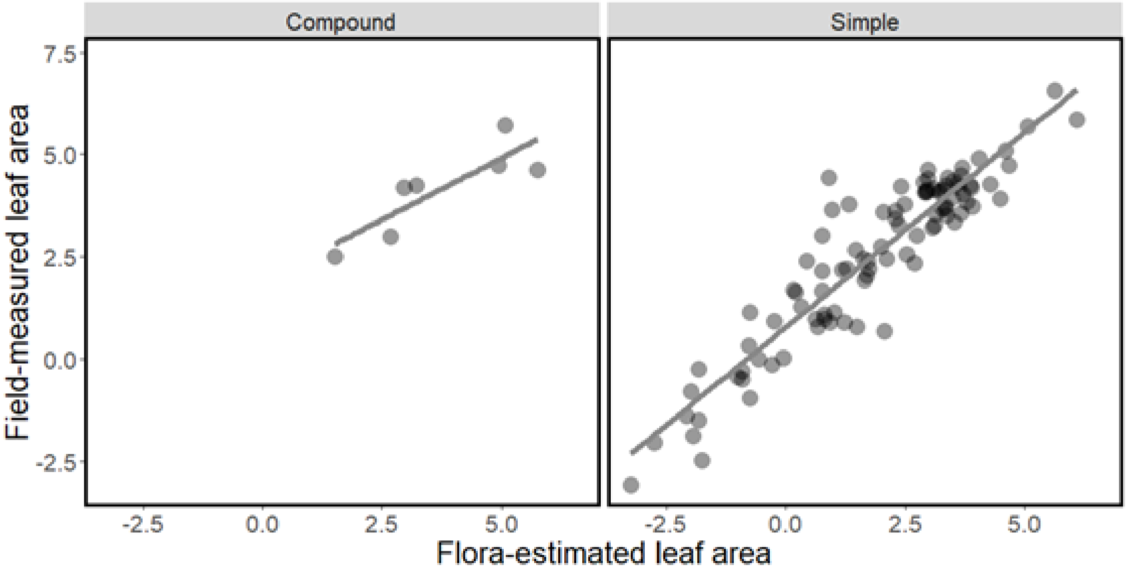


Figure S5.1 Scatter plots showing field-measured leaf area on the Y-axis and Flora-estimated leaf area on the X-axis for compound leaves and simple leaves. Solid lines indicate a significant relationship.

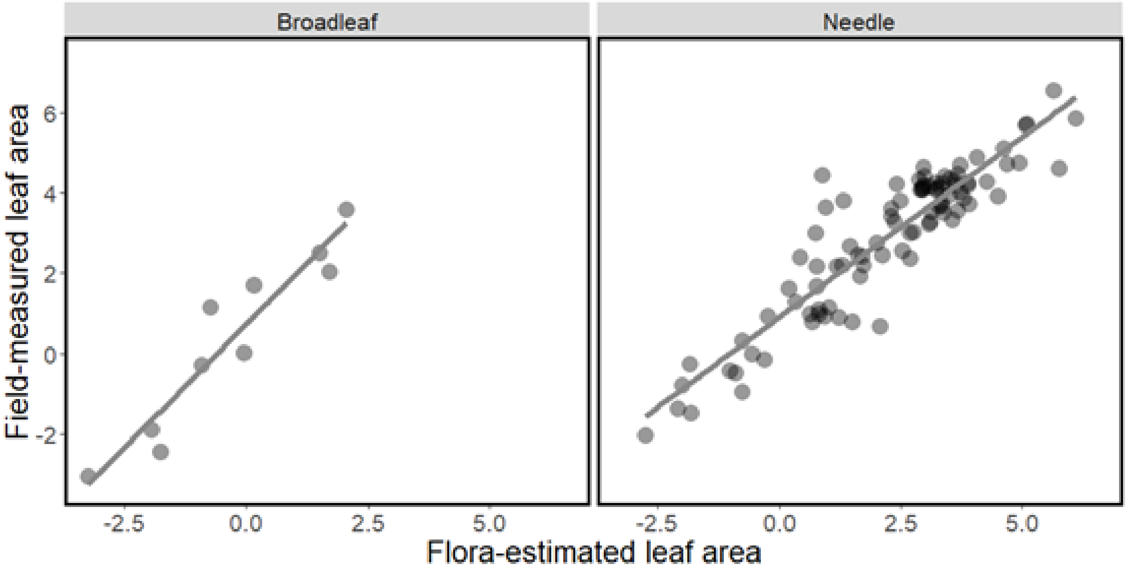


Figure S5.2 Scatter plots showing field-measured leaf area on the Y-axis and Flora-estimated leaf area on the X-axis for broad leaves and needle-like leaves. Solid lines indicate a significant relationship.

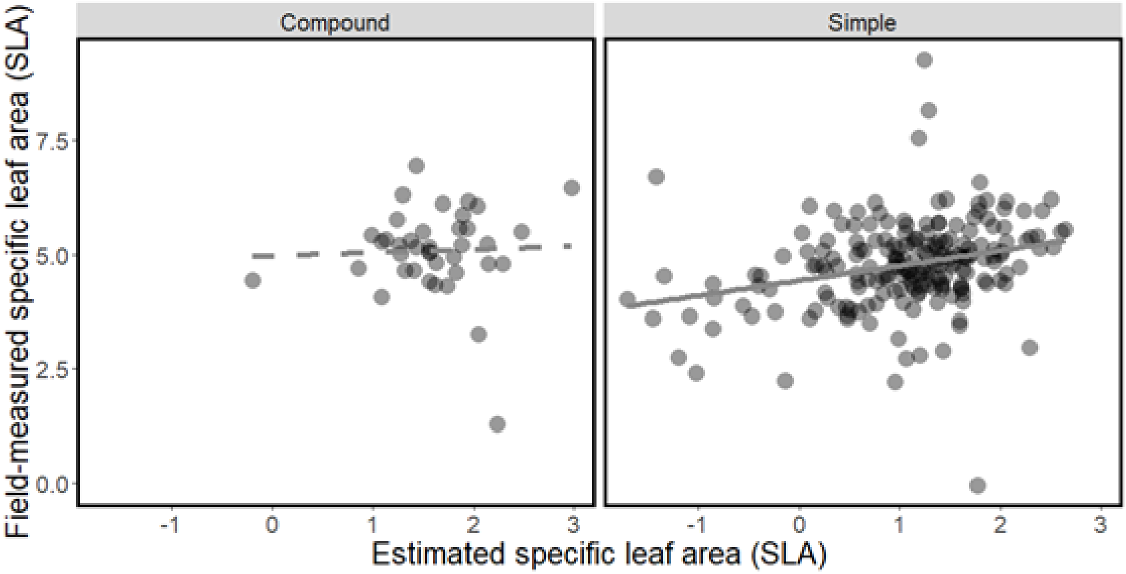


Figure S5.3 Scatter plots showing field-measured SLA on the Y-axis and SLA estimated using 1/Lth from field data on the X-axis for compound leaves and simple leaves. Solid lines indicate a significant relationship.

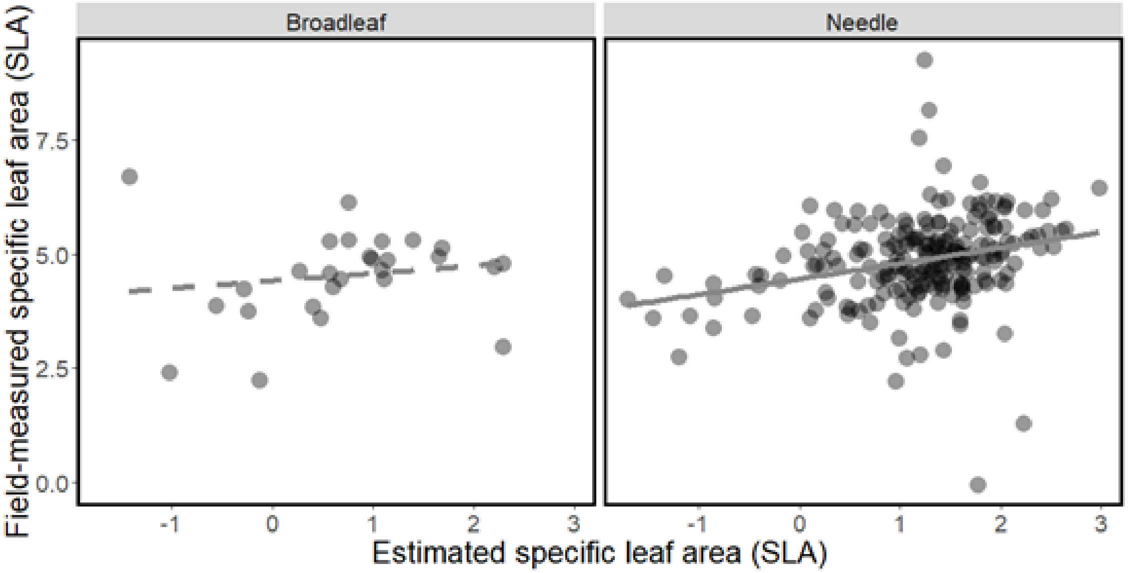


Figure S5.4 Scatter plots showing field-measured SLA on the Y-axis and SLA estimated using 1/Lth from field data on the X-axis for broad leaves and needle-like leaves. Solid lines indicate a significant relationship.

Chapter 6

Effects of climate change on the distribution of plant species and plant traits on the Canary Islands

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Diversity and Distributions (in preparation)

Abstract

Aim: Oceanic islands possess unique floras with high proportions of endemic species relative to their small land areas. Island floras are expected to be severely affected by changing climatic conditions as species on islands have limited distribution ranges, small population sizes and face the constraints of insularity to track their climatic niche. We aim to assess how ongoing climate change affects the range sizes of oceanic island plants to identify species of particular conservation concern.

Location: Canary Islands, Spain

Methods: We combined species occurrence data from single-island endemic, archipelago endemic, and non-endemic native plant species of the Canary Islands, representing ~71% (n = 503 species) of the certainly native Canary Island flora, with data on current and future climatic conditions. We used Bayesian Additive Regression Trees to assess the effect of climate change on species distributions. To further assess how climate change interacts with plant functional traits, we collected data on woodiness and succulence.

Results: Single-island endemic species were projected to lose a greater proportion of their climatically suitable area ($\tilde{x} = -0.36$) than archipelago endemic ($\tilde{x} = -0.28$) or non-endemic native species ($\tilde{x} = -0.26$), especially on Lanzarote and Fuerteventura, which are expected to experience a reduction in annual precipitation in the future. Moreover, we found that herbaceous single-island endemics were projected to gain less and lose more climatically suitable areas than insular woody ones. In contrast, we found that succulent single-island endemics and non-endemic natives gain more and lose less climatically suitable areas.

Main conclusions: We emphasise the conservation importance of all native species, but especially single-island endemic species not characterised by traits associated with water use efficiency. Our results are particularly critical for other oceanic island floras not constituted by a vast diversity of insular woody species as on the Canary Islands.

Left photo: *Sideritis gomerae*, a rare single-island endemic on La Gomera (Canary Islands), growing in the Barranco del Cabrito (own photo).

6.1 Introduction

Oceanic islands are nature’s laboratories, often having unique floras and faunas because of their ontogeny, remoteness and evolutionary potential (Whittaker & Fernández-Palacios, 2007). However, the biodiversity of oceanic islands is considered to be disproportionately threatened by causes directly or indirectly related to human activities (Fernández-Palacios et al., 2021a; Tershy et al., 2015), particularly climate change (Fernández-Palacios et al., 2021a). To date, climate change research on land has mainly been focused on continents, even though changing temperature and precipitation patterns on oceanic islands will have particular relevance for island biota (Harter *et al.*, 2015). Given the disproportionately large contribution of islands to global biodiversity (Fernández-Palacios et al., 2021a; Kier et al., 2009), the implications of climate change for oceanic island biodiversity are globally important.

The United Nations Intergovernmental Panel on Climate Change (IPCC) states that global surface temperatures will rise leading to severe alterations in precipitation patterns within the 21st century (IPCC, 2021). These climatic changes could have severe impacts on oceanic island floras (Harter *et al.*, 2015). For one thing, most island biota can only retreat to potential refuge habitats within their island or neighbouring islands, if within reach (Gillespie *et al.*, 2008). Also, oceanic islands are restricted in area, limiting the range size of endemic species. Limited range is often associated with low population sizes, leading to higher vulnerability of species to environmental and demographic stochasticity (Lande, 1993). Many island-endemic species are already under pressure from habitat loss, intensification of land use, and the introduction of invasive alien species. Consequently, many island species are listed as at imminent risk of extinction on the IUCN Red List of Threatened Species (www.iucnredlist.org; Romeiras et al., 2016). Furthermore, according to 21st-century climate change scenarios, ongoing climate change will exacerbate island plants’ high threat levels (Gillespie *et al.*, 2008; Fortini *et al.*, 2013). However, climatic alterations and their consequences on the diversity and floristic composition (e.g. species richness, endemism, traits) of an entire archipelago have not been assessed yet.

Under changing climatic conditions, species populations need to track their climatic niche (Chen *et al.*, 2011; Lenoir & Svenning, 2015) or adapt to the novel climatic conditions to survive (Bradshaw & Holzapfel, 2006; Hoffmann & Sgrò, 2011). The tracking of climatic niches requires that climatically suitable habitat is still available within species’ dispersal range (Zurell *et al.*, 2016; Zanatta *et al.*, 2020). However, many island species are bound to their islands and have narrow climatic niches (Fernández-Palacios et al., 2021b), which could increase their risk of extinction under changing environmental conditions (Thuiller *et al.*, 2005; Fortini *et al.*, 2013). For example, species assemblages in high-elevation areas on oceanic islands are disproportionately rich in endemic species (Steinbauer *et al.*, 2016b), and alpine plants on islands have been found to be particularly vulnerable to changing precipitation patterns (Sperling *et al.*, 2004; Marrero-Gómez *et al.*, 2007) and increasing temperatures (Giambelluca *et al.*, 2008). Moreover, species occurring in arid areas may be particularly threatened because drought is expected to increase in frequency and intensity due to climate change in many regions, including islands in the subtropical zone (Harter *et al.*, 2015; IPCC, 2021). In addition, islands hold a higher proportion of keystone species than mainland regions, and their shift in space or possible extinction might dramatically affect entire ecosystems (Olano *et al.*, 2017). Hence, understanding climate change-induced effects on the potential distribution of island plants is vital to understanding the conservation need of endemic and native floras.

Insular woodiness is one of the key syndromes of island endemic plants (Carlquist, 1974; Lens *et al.*, 2013a; Burns, 2019) and describes the evolutionary transition from herbaceous species to woody species on islands. There are several hypotheses on the origin of insular woodiness, but one particularly well-supported hypothesis invokes that insular woodiness may be induced by drought stress, which demands better protection of root-to-shoot water transport against hydraulic dysfunction (Lens *et al.*, 2013b; Dória *et al.*, 2018; Hooft van Huysduynen *et al.*, 2021; Zizka *et al.*, 2022). Hence, insular woody species may be better protected from increasing drought under future climatic conditions, likely giving them a more prominent role than herbaceous and primary woody species in island floras. However, due to dispersal limitations, long generation times, and the longevity of many woody plant species, a time lag in the response of woody plants to climate change can be expected (Kissling *et al.*, 2010). Therefore, it is unclear whether insular woody species have an advantage or disadvantage under future climatic conditions.

Succulent plants are drought-tolerant as they store water to sustain their metabolism when hygric stress occurs (Griffiths & Males, 2017). Additionally, succulence goes along with a CAM (crassulacean acid metabolism) photosynthetic pathway in some clades, leading to higher water use efficiency due to a shift of CO_2 fixation from day to night (Griffiths & Males, 2017). Hence, succulent species could have an advantage over non-succulent species if hot and dry climatic conditions increase due to anthropogenic climate change. However, previous studies are ambiguous on the resilience of succulent species to climate change; they have shown a high susceptibility of succulents to drought intensity (Midgley and Thuiller 2007, Young et al. 2016) as well as no effect (Thuiller et al. 2006, Schmiedel et al. 2012) or a lesser impact than on non-succulent species (Hoffman et al. 2009). Nonetheless, as arid environments are predicted to expand due to ongoing climate change (Seneviratne *et al.*, 2012; Zscheischler *et al.*, 2018), succulent species may be able to track their climatic niche, while non-succulent species could lose climatically suitable habitat. Nonetheless, the role of succulence in the resilience of oceanic island floras to changing climatic conditions has yet to be assessed.

In this study, we aim to assess how much potential climatically suitable area will be lost or gained for native seed plant species (single-island endemics, archipelago endemics, and non-endemic natives) of the Canary Islands, and their associated plant functional traits, under different climate change scenarios. We test the following thre hypotheses: 1) We expect single-island endemics to be most susceptible to changing climatic conditions as they may have narrower climatic niches and smaller range sizes than other species and a limited possibility of range shifts. 2) We predict that high and low elevations are expected to have a greater loss of potential climatically suitable area than mid-elevations due to their arid conditions in all floristic groups. This loss of potential climatically suitable area might be due to difficulties for species to elevationally track their climatic requirements. 3) We postulate that herbaceous, primary woody and non-succulent species will face higher climate change-related reductions in potential climatically suitable areas than insular woody and succulent species. This is because we expect increases in temperature and decresases in precipitation across the Canary Islands – conditions that are less favourable for these plant functional traits.

6.2 Methods

6.2.1 Study area

The Canary Islands are an oceanic archipelago situated 96 km off the Northwest African coast (Figure 6.1a). The archipelago spans an age gradient from the easternmost island of Fuerteventura (21 Ma) to the westernmost island of El Hierro (1.1 Ma; Carracedo et al., 2002; Florencio et al., 2021). The old, eastern islands of Lanzarote and Fuerteventura are eroded and relatively flat (highest peak = 807 m a.s.l.), whereas the western isles are steeper and more rugged, reaching a maximum elevation on Tenerife (3718 m a.s.l., Mt. Teide). The Canary Islands are characterised by a Subtropical-Mediterranean climate regime (del Arco Aguilar et al., 2010). The average temperature decreases gradually from the inframediterranean zone (18-22°C), through the thermo- and mesomediterranean zone (11-18°C) up to the supra- and oromediterranean zone (3.5-11°C; del Arco Aguilar et al., 2010). The NE trade winds influence the western and central islands, and rain shadow effects cause water availability to differ between the windward and leeward slopes. Annual rainfall is 50-500 mm in the lower parts, 300-800 mm in the mid-level areas (with maxima up to 1,400 mm in the cloud zone), and 500-600 mm in the upper parts (Patiño *et al.*, in preparation). The leeward slopes are generally drier, with a more continuous climatic gradient from coast to summit.

The archipelago represents an appropriate study system to analyse climate change-induced shifts in suitable areas of endemic and non-endemic native plant species as it offers diverse environmental conditions and a large proportion of endemic species throughout different zonal ecosystems (del Arco Aguilar & Rodríguez-Delgado, 2018). It can roughly be divided into the following zonal belts (from coast to summit): succulent scrub, thermophilous forest and woodland, evergreen laurel forest (only on the windward side), pine woodland, summit broom scrub and Teide violet community (del Arco Aguilar & Rodríguez-Delgado, 2018). Water stress and adaptation to arid conditions are important determinants of species distribution in the low- and high-elevation ecosystems of the archipelago (del Arco Aguilar et al. 2010), whereas mid-elevation ecosystems strongly depend on the trade-wind layer and constant humid conditions with low-temperature variation (García-Santos et al. 2004). The native flora of the Canary Islands has a dominant Mediterranean influence, but the laurel forest is considered rich in Tertiary relictual palaeoendemics (del Arco Aguilar & Rodríguez-Delgado, 2018; but see Kondraskov et al., 2015). Currently, the Canary Island vascular flora encompasses about 2,400 species, of which roughly 60% is considered native and c. 42% endemic (Beierkuhnlein *et al.*, 2021).

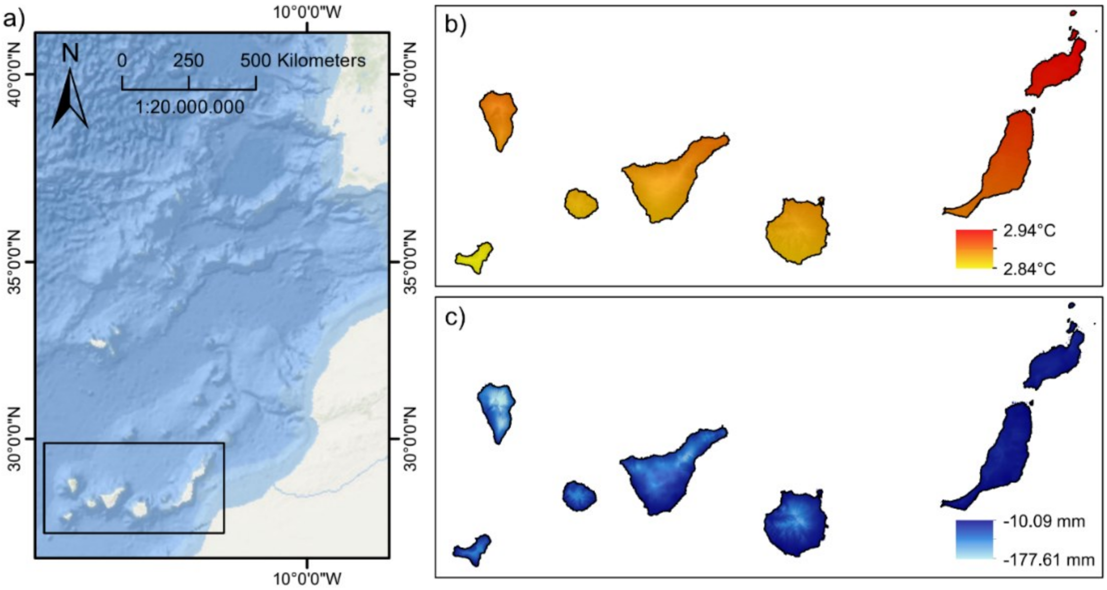

Figure 6.1 a) Location of the Canary Islands (Spain) location; **b)** 2071-2100 mean annual near-surface air temperature, and **c)** mean annual precipitation anomalies from the 1979-2013 reference period. Data shown are for an ensemble of five GCMs (including GFDL-ESM4, IPSL-CM6A-LR, MPI-ESM1-2-LR, MRI-ESM2-0, UKESM1-0-LL). Basemap source: Esri, Garmin, GEBCO, NOAA, NGDC, and other contributors.

6.2.2 Plant occurrence data

We collected occurrence data from the Banco de Datos de Biodiversidad de Canarias, an open-access database, for single-island endemic (SIE), archipelago endemic (AE) and certainly non-endemic native (NEN) seed plant species (excluding subspecies) in a raster of 500 m x 500 m grid cells covering the Canary Islands (https://www.biodiversidadcanarias.es/biota/) [*accessed 14/03/2022*]. The database includes all species listed in the checklist of the Banco de Datos de Biodiversidad de Canarias across 31,628 grid cell assemblages and species occurrences range from 1 to 4,466 cells. The Banco de Datos de Biodiversidad de Canarias provides presence-only information, which is spatially biased towards sampling effort (Hortal *et al.*, 2007). However, the sampling bias of SIEs, AEs and NENs is less compared to overall species richness patterns as studies incorporated into the database focused on extensive sampling of endemic and non-endemic native species (https://www.biodiversidadcanarias.es/biota/documentos). We considered a species as pseudo-absent if it was not recorded at a site, although we recognise that there is a debate whether these truly represent non-detections or not.

We excluded from the analysis 153 species with fewer than ten occurrences (97 SIEs, 25 AEs and 31 NENs) in the database. However, we acknowledge that range-restricted species are often particularly threatened under climate change (Ohlemüller *et al.*, 2008) and that our models are to some extent biased against SIEs and non-succulent herbs within AEs and NENs (Appendix S6.1; Table S6.1.2). Furthermore, we restricted frequent species to 500 occurrences to avoid sampling bias (seven AEs and six NENs). We excluded the frequently cultivated *Phoenix canariensis* from the dataset as its occurrence is overrepresented in the database (n = 4,446 occurrences), and the current species' distribution does not reflect its climatic niche. A list of the number of occurrences for all species is given in the Supporting Information (Appendix S6.2, Table S6.2.1).

6.2.3 Plant trait data

We collected data on insular woodiness and succulence, plant traits necessary for a species' response to changing climatic conditions. As insular woodiness can be challenging to distinguish from primary woodiness and herbaceousness, we mostly referred to literature sources from extensive studies on the woodiness of Canary Island plants (Lens *et al.*, 2013a; Hooft van Huysduynen *et al.*, 2021; Zizka *et al.*, 2022). We defined plants as succulent if they display thickened or fleshy leaves or stems. The thickness or fleshiness of plant organs indicates the ability of those organs to store water in their tissue (including moderately succulent species such as *Rumex lunaria*). We retrieved information on woodiness and succulence from Muer et al. (2016) and taxonomic monographs which have been shown to be a reliable source for trait data (Cutts *et al.*, 2021).

6.2.4 Climate data

We implemented species distribution models focusing on 19 climatic variables with potentially direct or indirect impact on species occurrences (Xu & Hutchinson, 2013). Bioclimatic variables were generated based on a bias corrected downscaling from 30-arc-second to 100 m resolution of climatological normals (1979-2013) of mean, maximum, and minimum daily near surface air-temperatures and precipitation from CHELSA v1.2 (Karger *et al.*, 2017) using data from meteorological stations (Patiño *et al.*, in preparation). The bias-correction was applied on the 30 arc second resolution and the subsequent downscaling was achieved by applying an atmospheric lapse rate correction following the approach described in Karger *et al.*, (2017). Future high resolution (2071-2100) climate data were generated by a Delta change anomaly interpolation. This computed and downscaled the anomalies between present and future monthly climatic maps at 30-arc second resolution, resulting from a downscaling of Global Circulation Models (GCMs) from the 6th phase of the Climate Model Intercomparison Project (CMIP6) using the CHELSA CMIP6 module (https://gitlabext.wsl.ch/karger/chelsa_cmip6; Karger et al., 2021). The anomalies were then downscaled using a B-spline interpolation to 30 arc seconds and applied to present maps at 100 m (Patiño *et al.*, in preparation).

We used three Shared Socioeconomic Pathways (SSPs) to represent a range of future socioeconomic conditions: from sustainable development and equality (SSP1 or 'sustainability') and a world of resurgent nationalism (SSP3 or 'regional rivalry') to rapid and unconstrained growth in economics and energy use (SSP5 or 'fossil-fuelled development'; Gidden et al., 2019). Five Global Circulation Models (GCMs; including GFDL-ESM4, IPSL-CM6A-LR, MPI-ESM1-2-LR, MRI-ESM2-0, UKESM1-0-LL) from the Impact Model Intercomparison Project (ISIMIP) were considered for this study (Lange, 2019; Lange & Büchner, 2021). All the climatic maps were then aggregated for this study to a resolution of 500 m to match the occurrence data resolution in R, using the raster package (Hijmans, 2019). Hence, we analysed 15 projections of the potential distribution of Spermatophytes native to the Canary Islands for 2100. Differences between projected future (mean of five GCMs under SSP3) and current mean annual temperature and annual precipitation are mapped in Figure 6.1b, c (see also Appendix S6.1, Table S6.1.1, for mean differences per island).

6.2.5 Modelling

We used Bayesian additive regression trees (BARTs), implemented with the R package 'embarcadero' (Carlson, 2020), to model plant species' current and future distribution. BART is a classification tree method defined by a prior probability distribution and a likelihood for returning occurrence predictions that quantifies uncertainty around the projections (Carlson, 2020). BARTs have been proven to be statistically powerful, excellent in performance and robust to changes in parameter choices (Baquero *et al.*, 2021; Pinto-Ledezma & Cavender-Bares, 2021; Carlson *et al.*, 2022; Dansereau *et al.*, 2022). Before modelling species distribution, we randomly sampled pseudo-absences from the background for each species. We tested the same number of pseudo-absences as unique presences, avoiding spatial overlap with the presence data (Descombes *et al.*, 2022). To find the main subset of predictors, we ran an automated variable selection implemented in the R package 'embarcadero', following the recommendations of Chipman et al. (2012). The variables with the lowest average model root mean square error (RMSE) and, therefore, the highest accuracy, are selected (Carlson *et al.*, 2022). The BART algorithm is insensitive to multi-collinearity and can simultaneously model many predictors (Chipman *et al.*, 2012). We ran final models separately for each species with the reduced variable set using default BART model settings (200 trees, 1,000 posterior draws with a burn-in of 100 draws) and hyperparameters (power = 2.0, base = 0.95). For SIEs, we conducted each model under the assumption of full dispersal (i.e. dispersal across all islands of the archipelago is possible) and again assuming limited dispersal (i.e. dispersal is only possible within the islands with current occurrences). The results for limited dispersal models are given in the Supporting Information (Appendix S6.5).

As we had many species with few occurrences in our dataset, we fitted our models on ten random subsets of 70% of the data and validated them against the remaining 30% of data. To evaluate model performance, we pooled the suitability values of the hold-out data across replicates (Collart *et al.*, 2021) to compute the Area Under the receiver operating characteristic Curve (AUC) and the Boyce index, which is used for presence-only data (Hirzel *et al.*, 2006), using the R package 'ecospat' (Di Cola *et al.*, 2017; Broennimann *et al.*, 2022). The final variable sets, AUC and Boyce index for each species are given in the Supporting Information (Appendix S6.2, Table S6.2.1).

We used baseline and projected distributions for a total of 554 species, including 228 SIEs, 209 AEs and 117 NENs. The five most frequent climatic variables with the highest importance were precipitation seasonality (bio 15), precipitation of wettest quarter (bio 16), precipitation of wettest month (bio 13), annual precipitation (bio 12), precipitation of driest quarter (bio 17). Species-specific probabilities of occurrences were averaged across GCMs and for each SSP scenario, resulting in three different climate change scenarios. Subsequently, we converted the projected probabilities of occurrence for the current and future distribution to a binary outcome according to the threshold that maximised the True Skill Statistic (maxTSS) for each species (Allouche *et al.*, 2006; Liu *et al.*, 2013). Species for which models performed poorly (AUC < 0.7, Boyce < 0.4 or maxTSS < 0.4) were not included in the analyses (i.e. 26 SIEs, 15 AEs, 11 NENs). After the exclusion of species for which models performed poorly, the quality of models ranged from an AUC of 1.00 to 0.72 (mean 0.94 ± 0.05) and Boyce index of 0.4 to 1.00 (mean 0.82 ± 0.17), indicating overall good model performance (Hirzel et al., 2006; Lantz, 2019; Appendix S6.1, Table S6.1.1). Our analysis's ODMAP protocol (Zurell *et al.*, 2020) are available in the Supplementary Information (Appendix S6.3).

6.2.6 Statistical analyses

We quantified the gain and loss in climatic suitable area between the current and future period by summing the binarized numbers of gained presences and lost presences for each species, respectively. Subsequently, we divided the gains and losses by the total number of occupied grid cells to obtain the proportional gains and losses per species. We performed Kruskal-Wallis tests to test whether the relative difference in area of potential climatic niche is significantly different between floristic groups. We further performed Kruskal-Wallis and Mann-Whitney U-test to analyse whether the change in potential climatically suitable area differs between herbaceous, primary woody and insular woody species and between non-succulent and succulent species within each floristic group. If necessary, post-hoc testing was performed using a Dunnett's test with Bonferroni adjustment for multiple comparisons. We repeated the analysis for each of the three SSP scenarios. All analyses were performed in R 4.1.1 (R Core Team, 2021).

6.3 Results

6.3.1 Change in potential climatically suitable area between and within floristic groups

Overall, we found a significantly smaller gain and greater loss in potential climatically suitable area for SIEs than for AEs under climate change scenario SSP1 (Dunnett's test - gain: SIE – AE, P = .020; Dunnett's test - loss: SIE – AE, P = .031; Figure 6.2). NENs gained significantly more potential climatically suitable area than SIEs under SSP1 and SSP5 (Dunnett's test – SSP1: SIE – NEN, P < .001; Dunnett's test – SSP5: SIE – NEN, P = .021). SIEs had the overall highest loss in climatically suitable area (SSP1: mean ± standard deviation =-0.25 ± 0.2, median = -0.22; SSP3: -0.38 ± 0.3, -0.36; SSP5: -0.40 ± 0.3, -0.38). Moreover, loss in potential climatically suitable area increased with the intensity of climate change scenarios in SIEs (Kruskal-Wallis test: χ^2 = 9.93, *P* = .015) and AEs (Kruskal-Wallis test: χ^2 = 17.68, *P* < .001). A total loss in potential climatically suitable area was predicted for 25 species including ten SIEs (*Aeonium lancerottense, Argyranthemum maderense, Carduus bourgeaui, Cheirolophus satarataensis, Convolvulus lopezsocasii, Dactylis metlesicsii, Echium lancerottense, Erigeron calderae, Helichrysum monogynum, Senecio bollei*), eleven AEs (*Aeonium balsamiferum, Aichryson tortuosum, Androcymbium psammophilum, Asteriscus intermedius, Bupleurum handiense, Crepis canariensis, Limonium bourgeaui, Limonium puberulum, Polycarpaea divaricate, Reichardia famarae, Sideritis pumila*) and four NENs (*Caralluma burchardii, Carex paniculata*, *Lolium saxatile*, *Sonchus pinnatifidus*) under at least one of the climate scenarios. (e.g. see Figure 6.3a for the Lanzarote and Fuerteventura endemic *Ferula lancerotensis*). One of the highest gains was predicted for the Tenerife endemic *Sideritis cretica* (+ 400% or +104 grid cells under climate scenario SSP5; Figure 6.3b). Results considering island-bound climatic niches of SIEs show qualitatively similar results to results considering the archipelago-wide climatic niche (Appendix S6.5,

Figure S6.5.1). There was a significantly greater gain in potential climatically suitable area in AEs and NENs than dispersal-limited SIEs under SSP1, SSP3 and SSP5 (Dunnett's test SIE – AE, *P* < .001; SIE – NEN, P < .001).

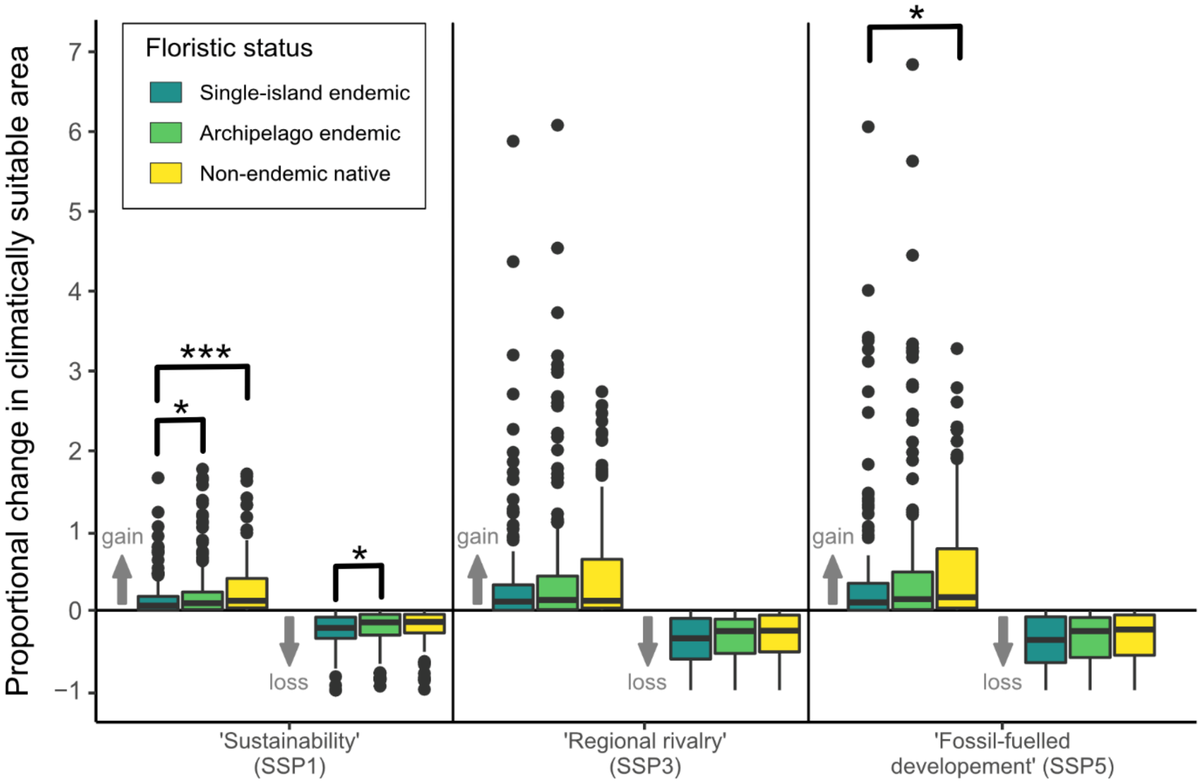

Figure 6.2 Proportional gain and loss in climatically suitable area by 2100 in single-island endemic (n = 202); archipelago endemic (n = 194) and non-endemic native plant species (n = 106) on the Canary Islands using three different climate change scenarios (SSP1, SSP3 and SSP5). SSP1 describes a world with strong economic growth via sustainability, SSP3 describes a future with high inequality between countries and SSP5 describes a world with strong economic growth via fossil fuel pathways. Single-island endemics have a significantly lower gain and higher loss of potential climatically suitable area than archipelago endemics under SSP1. Moreover, single-island endemics have a significantly lower gain of climatically suitable area than non-endemic natives under climate change scenarios SSP1 and SSP5. Asterisks denote statistical significance (**P* <= .05, **P <= .01, ***P <= 0.001).

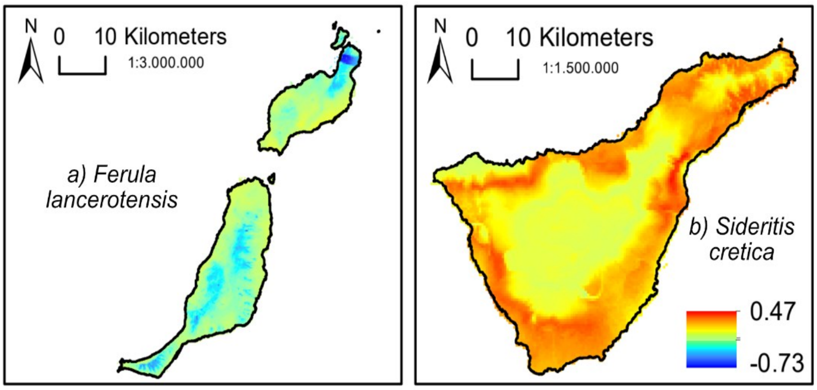

Figure 6.3 Example maps showing the differences in potential climatically suitable area between projected future climate (2071-2100; mean of five GCMs under SSP3) and current climate (2081-2010) for two example species: **a)** *Ferula lancerotensis* (Lanzarote and Fuerteventura endemic) and **b)** *Sideritis cretica* (Tenerife endemic). Blue tones represent loss, and red tones represent gain in potential climatically suitable area.

6.3.2 Inter-island comparison of change in climatically suitable area

The median proportional gain and loss in potential climatically suitable area was different for each island of the Canary Islands archipelago (Figure 6.4). Under each climate change scenario, SIEs gained least and lost most of their potential climatically suitable area on Fuerteventura (SSP1: median gain = 0 / median loss= -0.62; SSP3: 0 / -0.75; SSP5: 0.005 / -0.62) and Lanzarote (SSP1: 0 / -0.49; SSP3: 0 / -0.79; SSP5: 0 / -0.89). Moreover, on Fuerteventura and Lanzarote AEs had the highest median losses in climatically suitable area, whereas NENs had the highest median gains on Lanzarote. On Lanzarote in particular, there was greater loss in species richness in SIEs and AEs in the *Risco de Famara* but a gain in NEN species richness in flatter areas (Appendix S6.4, Figure S6.4.3). The mean proportional loss increased with increasing severity of the climate change scenarios across all islands and floristic groups. Results for dispersal-limited SIEs are given in the Supporting Information (Appendix S6.5, Figure S6.5.2).

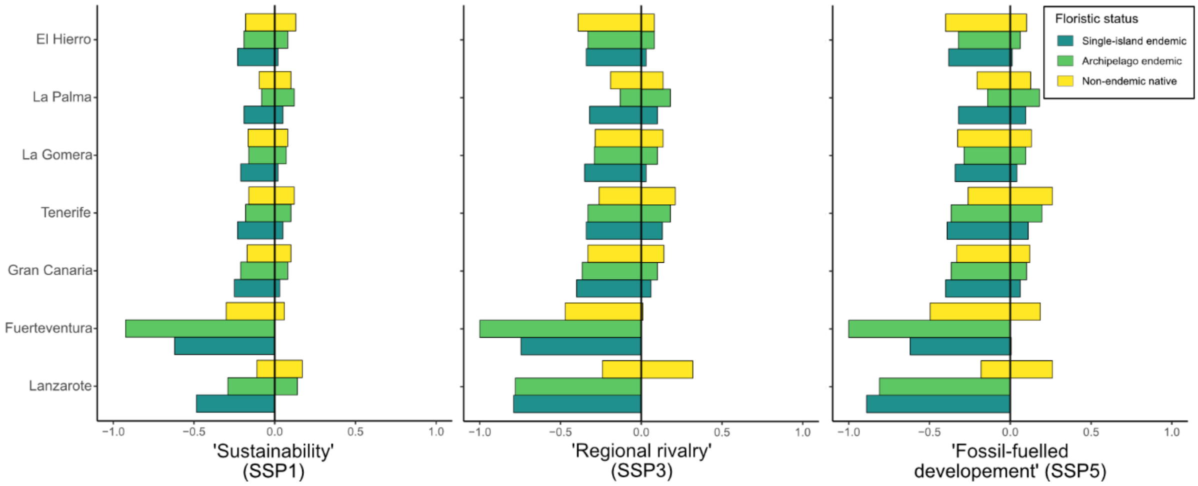

Figure 6.4 Median proportional gain and loss in potential climatically suitable area for each floristic group on all seven islands of the Canary Islands by 2100. The change was calculated under three different climate change scenarios (SSP1, SSP3, SSP5).

6.3.3 Effect of woodiness and succulence on change in potential climatically suitable area

We compared 128 herbaceous species (SIE = 31; AE = 60; NEN = 37) to 205 primary woody species (SIE = 64; AE = 72; NEN = 69) and 169 insular woody species (SIE = 107; AE = 62). There was a significantly lower gain in potential climatically suitable area in herbaceous than in primary and insular woody SIEs under SSP3 (Kruskal-Wallis test: $\chi^2 = 14.97$, $P < .001$; Figure 6.5b). We further found a significantly higher loss in potential climatically suitable area in herbaceous than insular woody SIEs under SSP3 (Dunnett's test: herbaceous – insular woody, P = .009; Figure 6.5b). Moreover, we compared 382 non-succulent species (SIE = 158; AE = 145; NEN = 79) to 120 succulent species (SIE = 44; AE = 49; NEN = 27). Non-succulent species show a significantly lower gain and higher loss in potential climatically suitable area than succulent species in SIEs and NENs under SSP3 (Mann–Whitney U test: gain – SIE, $P = .008$; loss – SIE, P = .008; gain – NEN, $P < .001$; loss – NEN, P = .009; Figure 6.5c). Results for climate change scenarios SSP1 and SSP5 and dispersal-limited SIEs show qualitatively similar results and can be found in the Supporting Information (Figure S6.4.1, S6.4.2 and S6.5.3).

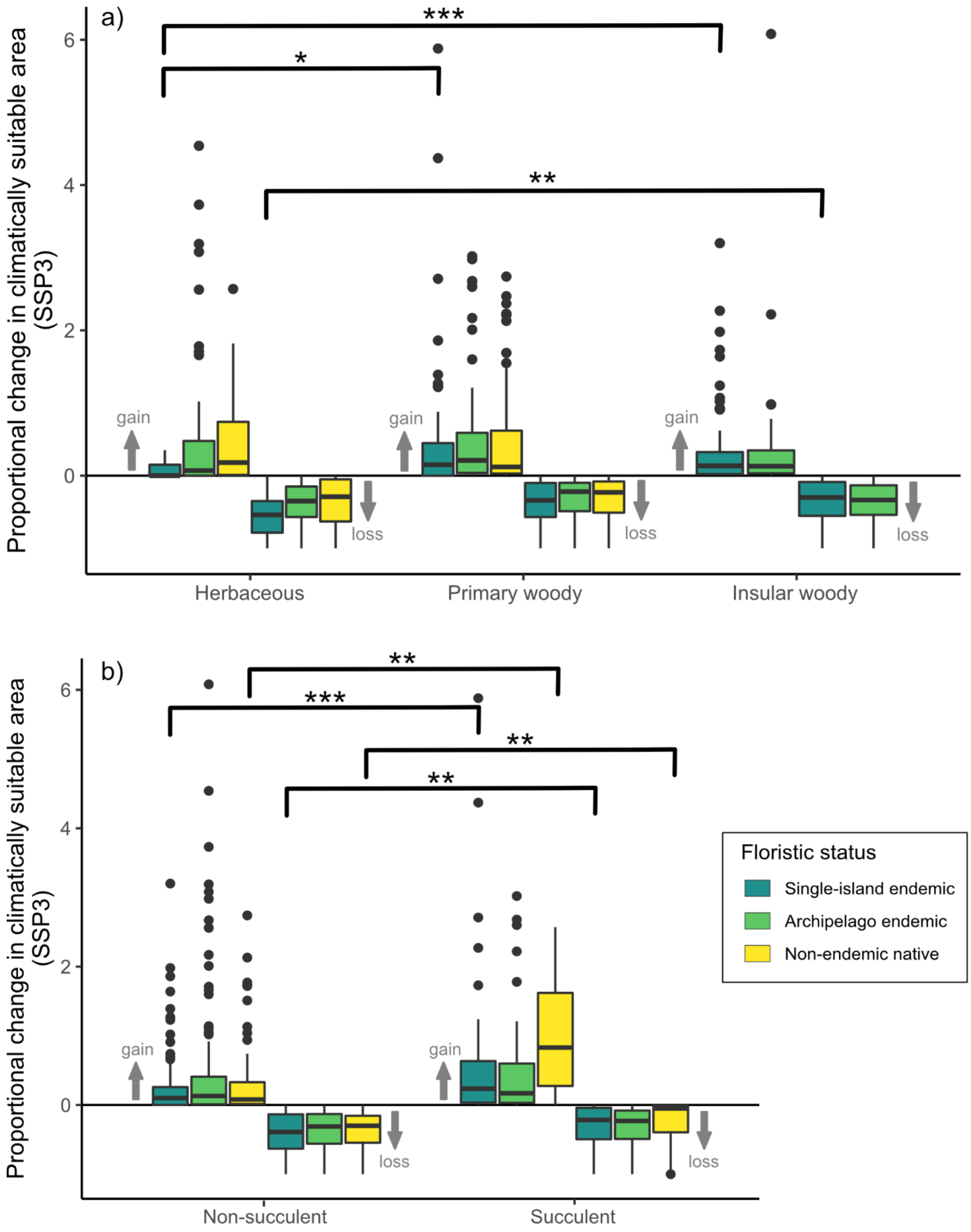

Figure 6.5 Proportional gain and loss in potential climatically suitable area (SSP3) for single-island endemic (n = 202), archipelago endemic (n = 194) and non-endemic native species (n = 106) on the Canary Islands when accounting for different traits. **a)** Herbaceous species have a significantly lower gain and higher loss of climatically suitable area than insular woody species in single-island endemics. **b)** Non-succulent species have a significantly lower gain and higher loss of climatically suitable area than succulent species in single-island endemics and non-endemic natives. Asterisks denote statistical significance (*$P <= .05$, **$P <= .01$, ***$P <= .001$).

6.4 Discussion

In this study, we investigated the effect of climate change on the potential climatically suitable area of plant species native to the Canary Islands, an archipelago renowned for its exceptional plant endemism (Fernández-Palacios & Whittaker, 2008). As hypothesised, we found that single-island endemic species that currently occur in predominantly arid regions will have the highest loss in potential climatically suitable areas. Functional traits can determine whether a plant will be vulnerable to climate change or not (Butt & Gallagher, 2018; Dudley *et al.*, 2019; Andrew *et al.*, 2022). Indeed, we found that species characterised by woodiness or succulence are affected differently by climate change. Nevertheless, climate change is a substantial threat to most plant species native to the Canary Islands and species vulnerable to environmental and demographic stochasticity, or species characterised by specific traits, are exceedingly threatened.

We find that single-island endemic species are more vulnerable than non-endemic native species under a mild climate change scenario on the Canary Islands, possibly due to the species' inherent small ranges and population sizes (Lande, 1993). This loss indicates that species on islands have limited opportunities to escape unfavourable climatic conditions and may be unable to track their climatic niches (Harter *et al.*, 2015). Climate is predicted to become warmer and drier on the Canary Islands by 2100 under all three analysed climatic scenarios. Precipitation, in particular, seems to play an essential role for Canary Island native species as the five most critical climatic variables across all species were related to precipitation, not temperature. In general, the increase in temperature and the decrease in precipitation is more severe under scenarios SSP3 and SSP5 than under SSP1. This indicates that a socioeconomic pathway favouring sustainability and equality might be able to prevent many species from oceanic island floras from losing their climatic niche.

The inter-island comparison indicates that endemic species on older and less elevated islands, i.e. Lanzarote and Fuerteventura, will experience an above-average loss of climatically suitable area. This disproportionate loss might result from the already existing water scarcity and predominantly arid climatic conditions on these two islands (del Arco Aguilar *et al.*, 2010), in which many species already experience physiological limitations due to drought stress. Species occurring on the topographically more complex *Risco de Famara* (Lanzarote) or the *Macizo de Jandía* (Fuerteventura) are predicted to be especially vulnerable. For example, the archipelago endemic *Ferula lancerotensis* occurs on these two hills and is predicted to lose almost its entire suitable climatic niche on the Canary Islands by 2100. *Ferula lancerotensis* depends on the moist conditions and lower insolation on the windward slopes of the Famara and Jandía hills (Scholz & Reyes-Betancort, 2013). However, temperature is predicted to increase while precipitation is predicted to decrease in these areas, likely making climatic conditions unsuitable for most native species in the future.

Not only are species from the inframediterranean zone disproportionately affected by climate change; species which occur in the supra- and oromediterranean zone (> 2.000 m) may also be particularly vulnerable to changing climatic conditions, e.g. *Viola cheiranthifolia* (Tenerife endemic) and *Echium gentianoides* (La Palma endemic). In contrast, species which currently occur across mid elevation, e.g.

the lower *Teno* massif (peak at 1.345 m), may be able to increase their range size. For example, the potential climatically suitable area for *Sideritis cretica* is projected to increase disproportionately in the future. These results indicate that upward range shifts might provide compensation for lost habitats where possible, but an upward shift into the highest elevational areas (e.g. Teide or Roque de los Muchachos) might not be possible. Disproportionate temperature increases at high elevations (Sperling *et al.*, 2004; Expósito *et al.*, 2015; Krushelnycky *et al.*, 2016), water stress and area reduction with elevation can restrict upslope migration, making high elevational species highly vulnerable to climate change (Dullinger *et al.*, 2012; Costion *et al.*, 2015; Rumpf *et al.*, 2018; Steinbauer *et al.*, 2018). Even though floristic groups across all islands might lose climatically suitable area on average, we identify the Famara and Jandía hills, the summit broom scrub of Tenerife and La Palma, and the Teide violet community (Tenerife) as the most vulnerable regions to climate change in the 21st century.

We found that insular woody species may gain more and lose less climatically suitable area than herbaceous species in single-island endemics. This finding can be linked to the theory that palaeodrought was a major driver for insular woodiness in Canary Island lineages (Lens *et al.*, 2013a; Hooft van Huysduynen *et al.*, 2021; Zizka *et al.*, 2022). As there is evidence that *in-situ* wood development coincided with palaeoclimatic aridification (Hooft van Huysduynen *et al.*, 2021), insular woody endemic species could be better adapted to drought than perennial herbaceous endemic species. Indeed, insular woody species are less sensitive to drought-induced gas embolisms than related herbaceous species (Lens *et al.*, 2013b; Dória *et al.*, 2018). Hence, insular woody endemics could have an advantage given the predicted decrease in precipitation and expansion of dry habitats on the Canary Islands. Insular woody genera include *Aeonium, Argyranthemum, Cheirolophus, Crambe, Echium, Limonium, Lotus, Micromeria, Sideritis* and *Sonchus* (Lens *et al.*, 2013a). However, the evolution of insular woodiness may also be driven by lower past climate change velocity in precipitation on oceanic islands (Carlquist, 1974; Zizka *et al.*, 2022) favouring an increase of plant longevity (Smith & Donoghue, 2008; Givnish, 2010). Hence, an adaptation to stable climates and long generation times could be posing a possible conflict with rapid climate change-induced range shifts in insular and primary woody species.

Our results suggest that succulent species may be more likely to gain climatically suitable area than non-succulent species in single-island endemics and non-endemic natives by 2100. Succulent plants may have an advantage over non-succulent plants under more arid conditions due to their ability to store water and their water-efficient metabolism (Vendramini *et al.*, 2002; Griffiths & Males, 2017). For example, *Euphorbia canariensis*, a keystone species in the succulent scrub, is predicted to increase its suitable climatic area by 78% under climate change scenario SSP3. Hence, succulence seems to be an effective trait in the face of climate change, especially in native plants with pre-adaptations to arid conditions (e.g. the 'dragon tree' *Dracaena draco* subsp. *draco.*, but see a predicted decrease in climatic area for *Dracaena draco* subsp. *caboverdeana* on Cabo Verde; Varela et al., 2022).

Even though our models provide robust predictions for the change in potential climatically suitable area of species native to the Canary Islands, we must address the fact that our models did not include biotic factors, such as species interactions or dispersal. In particular, interspecific competition with succulent invasive species, such as *Opuntia* and *Agave*, might be favoured and accelerated by climate change (Arévalo *et al.*, 2017). Besides habitat destruction, grazing by introduced herbivores poses a massive additional threat to many native species on the Canary Islands. A poignant example is the Jandía peninsula, Fuerteventura, where feral cattle are found in high numbers most of the year (Scholz & Reyes-Betancort, 2013). Moreover, in high-elevation areas, climate change-induced high rabbit densities are already threatening the persistence of native plant species (Cubas *et al.*, 2018) as well as in most other ecosystems of the archipelago (Cubas *et al.*, 2019). Hence, additional threats, such as invasive species, habitat loss and resource overexploitation (Fernández-Palacios *et al.*, 2021), strongly influence whether species will be able to shift their range to a climatically suitable area in the future. Additionally, we acknowledge that we analysed the native species' realised niches and not their fundamental niches. Hence, our results may underestimate the climatic niche of native species. Consequentially our predictions must be tested in experimental settings to fully understand the impact of climate change on thermal niches of plant species native to the Canary Islands.

6.5 Conclusion

While it has been recognised that climate change is a growing threat to the outstanding biodiversity of oceanic islands (Harter *et al.*, 2015), the impact of climate change on trait characteristics of island floras is less clear. We find that endemic species in aridity-dominated environments are particularly threatened by future decreasing precipitation. However, insular woody and succulent species may have an advantage under a climate that will be warmer and drier than today on the Canary Islands. Indeed, the Canary Islands are a hotspot of insular woody species and succulent plants (Irl *et al.*, 2020; Barajas-Barbosa *et al.*, 2022; Zizka *et al.*, 2022), which suggests that a large proportion of the Canary Islands flora could be resilient to the predicted climatic changes. Nonetheless, with ongoing climate change, a net loss of species with unique functions seems inevitable, leading to a functional homogenisation and a possible deterioration of ecosystem stability (Olden *et al.*, 2004; Clavel *et al.*, 2011). Hence, we conclude that the conservation of the native Canary Island flora needs to go beyond the current efforts by considering the changes in climatically suitable area for native plant species under climate change.

Acknowledgements

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Data availability statement

If accepted, trait data will be deposited on FigShare.

Supporting Information

Appendix S6.1

Climate anomalies and rare species

Table S6.1.1 Climate anomalies for each island for the three climate change scenarios considered (SSP1, SSP3 and SSP5) until 2071-2100 (mean of five General Climate Models).

	Temperature [°C]						**Precipitation [mm]**					
	Annual			**Seasonality**			**Annual**			**Seasonality**		
	SSP1	SSP3	SSP5	SSP1	SSP3	SSP5	SSP1	SSP3	SSP5	SSP1	SSP3	SSP5
Lanzarote	1.3	2.9	3.4	0.6	10.3	10.9	-7.3	-21.3	-19.2	-1.6	-0.1	-0.3
Fuerteventura	1.3	2.9	3.4	1.8	11.5	12.1	-9.1	-19.7	-17.6	-2.3	-0.5	-0.8
Gran Canaria	1.3	2.9	3.3	0	8.4	7.6	-16.7	-37.3	-30.0	-2.7	-2.5	-2.4
Tenerife	1.3	2.9	3.3	-0.4	8.6	7.0	-17.2	-46.7	-38.9	-3.0	-2.2	-2.8
La Gomera	1.3	2.9	3.3	-0.3	8.5	7.0	-17.4	-43.9	-37.5	-2.1	1.1	0
La Palma	1.3	2.9	3.4	0	9.5	7.6	-25.1	-86.3	-73.0	-1.9	0.3	-1.0
El Hierro	1.3	2.9	3.3	-0.7	7.5	5.3	-17.4	-46.7	-40.1	-2.7	1.4	1.0

Table S6.1.2 Distribution of plant functional traits across species that were excluded from the analyses due to very few occurrences (<10 occurrences) in the database.

	Single-island endemic (%)	**Archipelago endemic (%)**	**Non-endemic native (%)**
Woodiness			
Herbaceous	21 (21.6)	16 (64)	20 (64.5)
Primary woody	40 (41.2)	5 (20)	11 (35.5)
Insular woody	36 (37.1)	4 (16)	-
Succulence			
Non-succulent	79 (81.4)	19 (76)	27 (87.1)
Succulent	18 (18.6)	6 (24)	4 (12.9)

Appendix S6.2

Model performance and bioclimatic variables

Table S6.2.1 Area Under the receiver operating characteristic Curve (AUC) and Boyce values from species distribution models (using Bayesian additive regression trees) for plant species native to the Canary Islands, Spain. The most parsimonious subset of bioclimatic variables was chosen according to an automatic variable selection according to Chipman et al. (2012). The taxonomy follows the Banco de Datos de Biodiversidad de Canarias (https://www.biodiversidadcanarias.es/biota/).

Species	**Nb. grid cells**	**AUC**	**Boyce**	**Bioclimatic variables**
Adenocarpus foliolosus	189	0.93	0.94	bio1, bio3, bio6, bio9, bio10, bio12, bio13, bio14, bio16, bio18
Adenocarpus ombriosus	17	0.99	1.00	bio9, bio13, bio15, bio16
Adenocarpus viscosus	127	0.98	0.92	bio1, bio8, bio10, bio13, bio14, bio15, bio16
Aeonium arboreum	346	0.86	0.97	bio3, bio4, bio6, bio8, bio9, bio11, bio12, bio13, bio15, bio16, bio17, bio19
Aeonium aureum	59	0.95	0.85	bio1, bio3, bio4, bio6, bio7, bio11, bio16, bio18
Aeonium balsamiferum	42	0.99	0.91	bio8, bio12, bio16, bio19
Aeonium canariense	438	0.93	0.97	bio2, bio3, bio4, bio6, bio8, bio12, bio13, bio15, bio16, bio17, bio19
Aeonium castello paivae	48	0.96	0.91	bio2, bio14, bio15
Aeonium ciliatum	41	0.96	0.85	bio2, bio3, bio15, bio17, bio18
Aeonium cuneatum	26	0.91	0.72	bio2, bio3, bio6, bio12, bio13, bio16, bio17
Aeonium davidbramwellii	159	0.99	0.85	bio3, bio4, bio12, bio18
Aeonium decorum	44	0.87	0.71	bio4, bio5, bio15, bio16, bio17, bio18
Aeonium diplocyclum	291	0.96	0.98	bio2, bio3, bio12, bio14, bio15, bio16, bio17, bio18, bio19
Aeonium gomerense	20	0.96	0.39	bio5, bio13, bio15, bio16
Aeonium goochiae	29	0.98	0.37	bio7, bio8, bio12
Aeonium haworthii	89	0.95	0.91	bio2, bio9, bio14, bio17
Aeonium hierrense	48	0.95	0.89	bio6, bio12, bio16, bio18
Aeonium lancerottense	41	0.98	0.20	bio3, bio5, bio6, bio9, bio12, bio16, bio18, bio19
Aeonium lindleyi	183	0.97	0.85	bio2, bio3, bio14, bio16, bio19
Aeonium nobile	76	0.96	0.94	bio3, bio12, bio13, bio15, bio18
Aeonium percarneum	68	0.91	0.96	bio1, bio2, bio4, bio5, bio6, bio8, bio12
Aeonium pseudurbicum	38	0.99	0.93	bio5, bio13, bio15, bio18
Aeonium saundersii	48	0.95	0.83	bio5, bio8, bio15, bio16, bio17, bio18
Aeonium sedifolium	30	0.96	0.87	bio2, bio5, bio10, bio14, bio16, bio17
Aeonium simsii	36	0.93	0.87	bio4, bio7, bio15
Aeonium spathulatum	169	0.95	0.95	bio4, bio6, bio8, bio12, bio13, bio16, bio17, bio18, bio19
Aeonium tabuliforme	103	0.95	0.91	bio9, bio12, bio14, bio17
Aeonium undulatum	28	0.96	0.67	bio2, bio5, bio6, bio7, bio8, bio14, bio15, bio17, bio19
Aeonium urbicum	143	0.91	0.94	bio2, bio5, bio9, bio12, bio13, bio16, bio17, bio19
Aeonium valverdense	32	0.95	0.71	bio5, bio10, bio12, bio14, bio16, bio17, bio19
Aichryson bituminosum	18	1.00	1.00	bio4, bio12, bio13, bio16, bio17, bio18
Aichryson bollei	96	0.99	0.7	bio6, bio13, bio14, bio16
Aichryson brevipetalum	10	1.00	1.00	bio12, bio13, bio15, bio16

Aichryson laxum	181	0.91	0.96	bio5, bio8, bio12, bio13, bio14, bio15, bio16, bio17, bio18
Aichryson pachycaulon	44	0.94	0.66	bio1, bio2, bio3, bio7, bio8, bio11, bio12, bio13, bio16
Aichryson palmense	77	0.99	0.76	bio2, bio6, bio12, bio13, bio16, bio19
Aichryson parlatorei	25	0.87	0.55	bio4, bio13, bio16, bio17
Aichryson porphyrogennetos	22	0.90	0.45	bio2, bio5, bio7, bio13, bio15, bio19
Aichryson punctatum	34	0.93	0.49	bio1, bio4, bio6, bio11, bio19
Aichryson roseum	11	0.93	0.40	bio2, bio4, bio7
Aichryson tortuosum	49	0.98	0.93	bio4, bio8, bio9, bio11, bio12, bio16, bio19
Aizoon canariense	174	0.85	0.96	bio4, bio6, bio7, bio10, bio11, bio14, bio15
Allagopappus canariensis	80	0.89	0.84	bio3, bio5, bio10, bio13, bio16, bio18
Allagopappus viscosissimus	10	0.97	0.23	bio4, bio7, bio18
Anagyris latifolia	187	0.94	0.96	bio4, bio5, bio6, bio8, bio10, bio13, bio14, bio15, bio16, bio17, bio18, bio19
Androcymbium hierrense	48	0.98	0.78	bio5, bio8, bio11, bio15, bio19
Androcymbium psammophilum	346	0.98	0.99	bio4, bio9, bio10, bio11, bio13, bio19
Andryala perezii	39	0.93	0.93	bio8, bio13, bio18
Andryala pinnatifida	357	0.95	0.96	bio2, bio3, bio4, bio12, bio13, bio14, bio15, bio16, bio17, bio18, bio19
Apollonias barbujana	135	0.90	0.91	bio1, bio4, bio8, bio9, bio11, bio12, bio13, bio14, bio15, bio16, bio17, bio19
Arbutus canariensis	45	0.94	0.91	bio2, bio5, bio6, bio15, bio17, bio19
Argyranthemum adauctum	102	0.92	0.97	bio3, bio4, bio6, bio7, bio9, bio11, bio13, bio14, bio18,
Argyranthemum broussonetii	30	0.95	0.80	bio2, bio3, bio7, bio13, bio14, bio15, bio16, bio17, bio19
Argyranthemum callichrysum	60	0.91	0.80	bio2, bio3, bio5, bio9, bio10, bio13, bio14, bio15, bio16, bio17, bio18
Argyranthemum escarrei	13	0.97	0.80	bio7, bio12, bio17
Argyranthemum filifolium	11	1.00	1.00	bio4, bio5, bio15, bio18
Argyranthemum foeniculaceum	42	0.97	0.61	bio2, bio4, bio5, bio7, bio14, bio15, bio17, bio18
Argyranthemum frutescens	367	0.85	0.99	bio1, bio2, bio3, bio4, bio8, bio9, bio10, bio12, bio13, bio15
Argyranthemum gracile	37	0.93	0.71	bio5, bio10, bio15, bio18
Argyranthemum haouarytheum	128	0.99	0.82	bio4, bio12, bio14, bio19
Argyranthemum hierrense	21	1.00	1.00	bio4, bio12, bio14, bio19
Argyranthemum lemsii	22	0.95	0.44	bio2, bio3, bio7, bio15, bio16, bio18
Argyranthemum lidii	60	0.99	0.68	bio4, bio12, bio14, bio15, bio16, bio17
Argyranthemum maderense	24	1.00	1.00	bio2, bio5, bio9, bio10, bio12, bio13, bio18
Argyranthemum sundingii	19	0.99	0.68	bio3, bio15, bio17
Argyranthemum tenerifae	29	0.97	0.20	bio1, bio2, bio6, bio7, bio8, bio9, bio10, bio11, bio18
Argyranthemum webbii	16	0.99	0.32	bio12, bio13, bio15, bio16
Argyranthemum winteri	12	1.00	1.00	bio2, bio15, bio18
Arisarum simorrhinum	21	0.72	0.31	bio1, bio6, bio13, bio15
Aristida adscensionis	100	0.88	0.92	bio4, bio8, bio9, bio10, bio11, bio12, bio13, bio14, bio15, bio16, bio17, bio18, bio19
Arrhenatherum calderae	97	1.00	0.88	bio1, bio4, bio5, bio6, bio8, bio9, bio10, bio11, bio12, bio13, bio14, bio16, bio17, bio18, bio19
Artemisia reptans	11	0.96	0.56	bio2, bio11, bio13, bio15, bio16

Artemisia thuscula	380	0.89	0.97	bio1, bio3, bio5, bio6, bio7, bio8, bio12, bio14, bio15, bio16, bio17, bio19
Arthrocnemum macrostachyum	77	0.97	0.70	bio1, bio4, bio5, bio6, bio11, bio19
Asparagus arborescens	47	0.66	0.28	Bio6, bio11, bio12, bio13
Asparagus fallax	72	0.97	0.63	bio3, bio10, bio14, bio19
Asparagus horridus	16	0.98	0.72	bio9, bio12, bio16, bio18
Asparagus nesiotes	161	0.98	0.98	bio4, bio6, bio7, bio15, bio16, bio18, bio19
Asparagus pastorianus	63	0.98	0.86	bio2, bio3, bio12, bio13, bio16, bio18
Asparagus plocamoides	68	0.88	0.89	bio5, bio12, bio15
Asparagus scoparius	49	0.91	0.83	bio4, bio5, bio12, bio17
Asparagus umbellatus	118	0.87	0.96	bio4, bio6, bio11, bio12, bio13, bio17, bio18, bio19
Asteriscus graveolens	15	0.98	0.25	bio3, bio4, bio12, bio17
Asteriscus intermedius	32	0.97	0.52	bio2, bio3, bio5, bio6, bio9, bio12, bio13, bio16, bio17, bio18
Asteriscus schultzii	39	0.84	0.42	bio4, bio13, bio18
Asteriscus sericeus	83	0.94	0.91	bio1, bio2, bio7, bio9, bio11, bio17
Astydamia latifolia	160	0.89	0.97	bio2, bio8, bio11, bio13, bio15, bio16
Athamanta cervariifolia	141	0.95	0.95	bio3, bio4, bio6, bio12, bio15, bio16, bio17, bio18
Athamanta montana	116	0.98	0.93	bio4, bio6, bio12, bio13, bio14, bio16, bio18
Atractylis arbuscula	21	1.00	0.61	bio3, bio13, bio15, bio16
Atractylis preauxiana	52	0.97	0.79	bio9, bio11, bio13, bio16
Babcockia platylepis	38	0.95	0.64	bio3, bio4, bio6, bio7
Bassia tomentosa	95	0.91	0.96	bio7, bio8, bio13, bio15, bio19
Bencomia caudata	94	0.91	0.87	bio7, bio8, bio12, bio13, bio14, bio17
Bencomia exstipulata	64	1.00	0.15	bio1, bio8, bio11, bio13, bio16, bio19
Bencomia sphaerocarpa	21	0.92	0.60	bio13, bio14, bio15, bio16
Bethencourtia hermosae	24	0.96	0.44	bio6, bio15, bio17
Bethencourtia palmensis	199	0.99	0.94	bio4, bio6, bio13, bio17
Bosea yervamora	78	0.86	0.96	bio3, bio6, bio7, bio8, bio13, bio17, bio18
Brachypodium arbuscula	85	0.94	0.85	bio4, bio6, bio8, bio12, bio13, bio15, bio16, bio17, bio19
Bromus rubens	49	0.86	0.76	bio4, bio12, bio13, bio17, bio18, bio19
Bryonia verrucosa	34	0.91	0.67	bio12, bio13, bio19
Bupleurum handiense	37	0.99	0.51	bio2, bio9, bio12, bio13, bio18
Bupleurum salicifolium	185	0.90	0.97	bio1, bio3, bio6, bio12, bio13, bio14, bio15, bio16
Bupleurum semicompositum	15	0.94	0.50	bio2, bio12, bio18
Bystropogon canariensis	115	0.92	0.88	bio1, bio10, bio11, bio14, bio17
Bystropogon odoratissimus	50	0.94	0.91	bio2, bio13, bio15, bio19
Bystropogon origanifolius	294	0.96	0.96	bio4, bio6, bio12, bio13, bio14, bio15, bio16, bio17
Bystropogon plumosus	14	0.99	0.49	bio2, bio6, bio18
Bystropogon wildpretii	12	1.00	1.00	bio4, bio12, bio13, bio15, bio17
Campanula dichotoma	17	0.95	0.88	bio3, bio6, bio19
Camptoloma canariense	40	0.93	0.95	bio4, bio6, bio12, bio16
Campylanthus salsoloides	104	0.77	0.92	bio5, bio6, bio7, bio8, bio9, bio10, bio12, bio13, bio14, bio15, bio16, bio17, bio19

Canaria tortuosa	16	0.90	0.61	bio5, bio9, bio19
Canarina canariensis	97	0.89	0.85	bio2, bio3, bio4, bio5, bio7, bio10, bio12, bio13, bio14, bio15, bio16, bio17
Caralluma burchardii	188	0.91	0.91	bio4, bio9, bio13, bio18, bio19
Carduus baeocephalus	20	0.96	0.46	bio5, bio16, bio18
Carduus bourgeaui	18	0.98	0.46	bio2, bio4, bio18
Carduus clavulatus	49	0.83	0.27	bio12, bio17, bio19
Carex canariensis	29	0.96	0.68	bio10, bio13, bio14, bio16
Carex paniculata	27	0.96	0.67	bio1, bio3, bio9, bio10, bio11, bio13
Carex perraudieriana	31	0.95	0.54	bio1, bio3, bio5, bio9, bio10, bio13, bio14, bio16, bio17
Carlina canariensis	37	0.95	0.48	bio4, bio6, bio7, bio12, bio16, bio17
Carlina falcata	225	0.99	0.86	bio3, bio4, bio12, bio13, bio15, bio16, bio17, bio18, bio19
Carlina salicifolia	370	0.84	0.97	bio1, bio2, bio3, bio5, bio7, bio8, bio10, bio13, bio15, bio16, bio17
Carlina xeranthemoides	37	0.98	0.36	bio6, bio11, bio15
Caroxylon tetrandrum	15	1.00	1.00	bio11, bio13, bio15
Caroxylon vermiculatum	99	0.84	0.83	bio4, bio9, bio12, bio15, bio16, bio17
Ceballosia fruticosa	123	0.85	0.94	bio2, bio3, bio4, bio5, bio6, bio8, bio16, bio18
Cedronella canariensis	159	0.97	0.68	bio1, bio2, bio3, bio5, bio6, bio8, bio9, bio10, bio11, bio12, bio13, bio14, bio15, bio16, bio17
Cerastium sventenii	129	0.99	0.85	bio1, bio9, bio11, bio12, bio13, bio14, bio16, bio17
Ceropegia dichotoma	190	0.92	0.96	bio2, bio4, bio5, bio7, bio8, bio12, bio13, bio14, bio16, bio17, bio18
Ceropegia fusca	84	0.92	0.94	bio8, bio9, bio12, bio15, bio19
Chamaecytisus proliferus	526	0.91	0.99	bio1, bio2, bio4, bio6, bio13, bio14, bio15, bio16, bio17, bio18, bio19
Cheirolophus arboreus	49	0.96	0.82	bio4, bio7, bio12, bio13, bio16, bio18
Cheirolophus arbutifolius	51	0.96	0.98	bio4, bio6, bio15, bio16, bio17
Cheirolophus burchardii	12	0.95	0.50	bio5, bio9, bio15, bio19
Cheirolophus canariensis	12	1.00	1.00	bio4, bio5, bio7
Cheirolophus duranii	12	0.97	0.46	bio12, bio14, bio15, bio16
Cheirolophus falcisectus	11	1.00	1.00	bio4, bio7, bio12
Cheirolophus ghomerythus	19	1.00	1.00	bio14, bio18, bio19
Cheirolophus santos-abreui	12	1.00	1.00	bio13, bio15, bio16
Cheirolophus satarataensis	32	0.98	0.86	bio1, bio5, bio6, bio7, bio14, bio18
Cheirolophus sventenii	37	0.99	0.92	bio2, bio4, bio5, bio6, bio7, bio8, bio10, bio11, bio12, bio13, bio15, bio16, bio18, bio19
Cheirolophus teydis	54	0.98	0.54	bio1, bio2, bio5, bio6, bio7, bio8, bio9, bio10, bio11, bio12, bio13, bio15, bio16, bio17, bio18, bio19
Cheirolophus webbianus	26	0.92	0.55	bio3, bio4, bio9, bio11, bio12, bio14, bio15, bio17, bio19
Chenopodiastrum coronopus	13	0.87	0.57	bio9, bio11, bio15
Chrysoprenanthes pendula	35	0.99	0.74	bio4, bio5, bio6, bio12, bio16
Cicer canariense	96	0.99	0.64	bio1, bio6, bio16, bio17, bio18
Cistus chinamadensis	31	0.94	0.21	bio11, bio16, bio17
Cistus horrens	21	1.00	1.00	bio2, bio4, bio5, bio7, bio12, bio15
Cistus ochreatus	14	1.00	1.00	bio4, bio5, bio7
Cistus osbeckiifolius	23	1.00	0.59	bio6, bio9, bio11, bio15
Cistus palmensis	15	1.00	1.00	bio12, bio13, bio16, bio19

Cistus symphytifolius	358	0.95	0.97	bio3, bio4, bio6, bio7, bio11, bio13, bio14, bio15, bio16, bio17, bio19
Convolvulus canariensis	69	0.95	0.90	bio5, bio11, bio14, bio19
Convolvulus caput medusae	109	0.97	0.94	bio3, bio6, bio9, bio15, bio16, bio19
Convolvulus floridus	182	0.86	0.94	bio1, bio6, bio8, bio9, bio13, bio14, bio15, bio16, bio17
Convolvulus fruticulosus	220	0.95	0.95	bio3, bio6, bio7, bio13, bio14, bio17, bio18
Convolvulus lopezsocasii	21	0.99	0.30	bio3, bio5, bio6, bio9, bio13, bio15, bio16, bio18
Convolvulus subauriculatus	28	0.91	0.81	bio7, bio9, bio12, bio15, bio16, bio17
Convolvulus volubilis	20	0.83	0.72	bio3, bio13, bio15, bio16, bio19
Crambe arborea	17	0.97	0.88	bio2, bio3, bio4, bio7, bio13, bio17
Crambe feuilleei	22	0.94	0.61	bio14, bio16, bio19
Crambe gomerae	26	0.91	0.86	bio3, bio5, bio13, bio15, bio16
Crambe laevigata	34	0.99	0.82	bio3, bio4, bio5, bio10, bio14, bio15, bio17
Crambe microcarpa	88	0.98	0.80	bio4, bio6, bio12, bio15, bio16, bio18
Crambe pritzelii	58	0.96	0.90	bio2, bio4, bio16, bio18, bio19
Crambe scaberrima	30	0.98	0.96	bio2, bio12, bio18
Crambe scoparia	87	0.99	0.87	bio2, bio6, bio8, bio15, bio17
Crambe strigosa	50	0.85	0.63	bio2, bio8, bio10, bio12, bio14, bio15, bio16, bio17, bio19
Crambe sventenii	15	0.99	0.86	bio2, bio15, bio18
Crambe tamadabensis	14	0.88	0.62	bio7, bio13, bio15
Crepis canariensis	103	0.98	0.94	bio1, bio3, bio4, bio6, bio8, bio9, bio10, bio11, bio12, bio13, bio15, bio16, bio17, bio19
Crithmum maritimum	16	0.97	0.84	bio8, bio13, bio17
Cynara cardunculus	21	0.93	0.57	bio1, bio8, bio11, bio13
Cyperus capitatus	33	0.98	0.49	bio2, bio5, bio12, bio18
Dactylis metlesicsii	21	1.00	1.00	bio1, bio2, bio3, bio6
Dactylis smithii	111	0.96	0.94	bio3, bio4, bio12, bio13, bio17, bio18
Daphne gnidium	50	0.96	0.84	bio1, bio2, bio3, bio6, bio7, bio14, bio15, bio17, bio19
Daucus elegans	45	0.97	0.69	bio1, bio9, bio10, bio11, bio12, bio13, bio14, bio15, bio16, bio17, bio18
Dendriopoterium menendezii	47	1.00	0.67	bio6, bio13, bio15, bio17
Dendriopoterium pulidoi	52	1.00	0.92	bio2, bio6, bio11, bio15
Descurainia artemisioides	45	0.99	0.82	bio6, bio7, bio13, bio15
Descurainia bourgeauana	37	1.00	1.00	bio1, bio8, bio11
Descurainia gilva	62	0.99	0.69	bio1, bio2, bio3, bio5, bio6, bio7, bio8, bio9, bio10, bio11, bio12, bio13, bio14, bio15, bio16, bio19
Descurainia lemsii	16	1.00	1.00	bio4, bio6, bio7
Descurainia millefolia	177	0.93	0.98	bio2, bio8, bio14, bio16, bio18
Descurainia preauxiana	37	0.99	0.80	bio4, bio6, bio12, bio16
Dicheranthus plocamoides	61	0.95	0.97	bio3, bio5, bio14, bio15, bio17
Digitalis canariensis	58	0.92	0.84	bio4, bio11, bio13, bio14, bio17
Digitalis chalcantha	16	0.94	1.00	bio7, bio14, bio17
Digitalis isabelliana	37	0.96	0.58	bio3, bio4, bio6, bio7, bio8
Dioscorea communis	82	0.90	0.86	bio4, bio6, bio7, bio8, bio9, bio11, bio12, bio13, bio15, bio16, bio17, bio18
Dorycnium broussonetii	35	0.87	0.67	bio3, bio10, bio11, bio12, bio14, bio15, bio18, bio19
Dorycnium eriophthalmum	26	0.87	0.39	bio6, bio8, bio11, bio13, bio14, bio15, bio16, bio19

Dracaena draco	241	0.92	0.98	bio1, bio3, bio8, bio14, bio16, bio17, bio18, bio19
Dracaena tamaranae	49	0.97	0.86	bio1, bio7, bio9, bio15
Dracunculus canariensis	40	0.86	0.26	bio6, bio12, bio15, bio18, bio19
Drimia maritima	66	0.83	0.92	bio3, bio12, bio14
Drusa glandulosa	29	0.83	0.84	bio3, bio15, bio17
Echium acanthocarpum	44	0.98	0.58	bio1, bio4, bio5, bio9, bio12, bio16
Echium aculeatum	92	0.90	0.92	bio3, bio5, bio8, bio11, bio12, bio14, bio15, bio16, bio17
Echium auberianum	123	0.99	0.69	bio6, bio9, bio16
Echium bethencourtii	21	1.00	1.00	bio9, bio11, bio13, bio16
Echium bonnetii	14	0.92	0.66	bio6, bio15, bio18
Echium brevirame	60	0.99	0.94	bio4, bio5, bio8, bio15, bio16, bio18, bio19
Echium callithyrsum	58	0.98	0.91	bio3, bio4, bio7, bio15, bio19
Echium decaisnei	388	0.90	0.98	bio1, bio2, bio3, bio4, bio5, bio6, bio7, bio8, bio9, bio10, bio13, bio16, bio17, bio18
Echium gentianoides	85	1.00	0.56	bio1, bio8, bio9, bio10, bio11, bio12, bio13, bio16, bio19
Echium giganteum	50	0.99	0.86	bio3, bio4, bio9, bio17
Echium hierrense	30	0.94	0.9	bio6, bio12, bio14, bio16, bio19
Echium lancerottense	29	0.93	0.56	bio2, bio3, bio6, bio12, bio13, bio16, bio18, bio19
Echium leucophaeum	49	0.98	0.55	bio2, bio3, bio15, bio19
Echium onosmifolium	255	0.95	0.96	bio6, bio7, bio10, bio12, bio13, bio15, bio17
Echium perezii	94	1.00	0.70	bio8, bio12, bio14, bio16, bio17
Echium pininana	31	1.00	1.00	bio12, bio16, bio19
Echium simplex	50	0.92	0.94	bio4, bio5, bio17, bio19
Echium strictum	74	0.89	0.87	bio6, bio11, bio12, bio17, bio19
Echium triste	166	0.98	0.96	bio2, bio3, bio8, bio15, bio16, bio18
Echium virescens	75	0.88	0.84	bio2, bio4, bio5, bio6, bio7, bio12, bio13, bio15, bio16, bio17, bio18
Echium webbii	138	1.00	0.80	bio4, bio12, bio14, bio16, bio18
Echium wildpretii	32	0.99	0.61	bio1, bio4, bio6, bio8, bio9, bio11, bio13, bio14, bio17, bio19
Ephedra fragilis	18	0.83	0.72	bio3, bio15, bio19
Ephedra major	24	1.00	0.59	bio1, bio4, bio6, bio8, bio9, bio10, bio11, bio13, bio15, bio16, bio19
Erica canariensis	774	0.92	0.98	bio2, bio7, bio10, bio13, bio15, bio16, bio17
Erica platycodon	75	0.95	0.79	bio1, bio2, bio3, bio5, bio12, bio13, bio14, bio15, bio16, bio17, bio19
Erigeron calderae	34	1.00	0.50	bio1, bio2, bio3, bio4, bio5, bio6, bio7, bio8, bio9, bio10, bio11
Erucastrum canariense	15	0.93	0.34	bio4, bio12, bio18
Erysimum scoparium	134	0.98	0.80	bio1, bio3, bio4, bio6, bio8, bio9, bio10, bio11, bio12, bio13, bio14, bio16, bio17, bio19
Erysimum virescens	7	0.88	0.78	bio1, bio6, bio8, bio9, bio13, bio15, bio16
Euphorbia aphylla	70	0.90	0.91	bio4, bio7, bio11, bio12, bio13, bio15, bio19
Euphorbia atropurpurea	117	0.97	0.98	bio2, bio5, bio10, bio14, bio15, bio18
Euphorbia balsamifera	537	0.86	0.99	bio3, bio6, bio8, bio9, bio11, bio12, bio15, bio18
Euphorbia berthelotii	70	0.95	0.95	bio3, bio5, bio15, bio16, bio18
Euphorbia bourgeana	114	0.95	0.94	bio2, bio5, bio14, bio15, bio16, bio17
Euphorbia bravoana	17	0.95	0.68	bio2, bio7, bio18
Euphorbia canariensis	628	0.90	0.99	bio1, bio2, bio6, bio15, bio16, bio18
Euphorbia handiensis	25	0.96	1.00	bio12, bio15, bio19
Euphorbia lamarckii	653	0.88	0.99	bio1, bio3, bio5, bio6, bio8, bio10, bio11, bio12, bio13, bio15, bio16, bio17, bio18, bio19
Euphorbia mellifera	64	0.97	0.93	bio1, bio11, bio14, bio16

Euphorbia regis-jubae	539	0.85	0.99	bio2, bio3, bio6, bio10, bio15, bio16
Ferula lancerotensis	33	0.99	0.17	bio9, bio13, bio18
Ferula latipinna	60	0.97	0.66	bio6, bio14, bio17, bio18
Ferula linkii	111	0.84	0.95	bio6, bio15, bio17, bio18, bio19
Festuca agustinii	173	0.98	0.86	bio1, bio4, bio12, bio14, bio16, bio17, bio18
Forsskaolea angustifolia	257	0.88	0.98	bio4, bio10, bio11, bio12, bio18, bio19
Frankenia capitata	101	0.89	0.93	bio1, bio4, bio10, bio11, bio14
Frankenia ericifolia	70	0.87	0.65	bio1, bio2, bio3, bio4, bio5, bio6, bio8, bio9, bio10, bio11, bio12, bio15
Genista benehoavensis	51	1.00	0.63	bio1, bio6, bio8, bio9, bio10, bio11, bio12, bio13, bio15, bio16, bio17, bio18, bio19
Geranium reuteri	95	0.92	0.71	bio2, bio6, bio7, bio13, bio14, bio15, bio16, bio17, bio18, bio19
Gesnouinia arborea	78	0.96	0.89	bio1, bio4, bio17, bio18
Globularia salicina	237	0.91	0.97	bio3, bio6, bio8, bio13, bio14, bio15, bio16, bio17, bio19
Globularia sarcophylla	15	1.00	1.00	bio4, bio7, bio18
Gonospermum canariense	78	0.97	0.93	bio2, bio6, bio12, bio13, bio16, bio18, bio19
Gonospermum fruticosum	104	0.91	0.65	bio1, bio3, bio8, bio12, bio13, bio17, bio19
Gonospermum gomerae	27	0.94	0.84	bio3, bio16, bio17
Gonospermum ptarmiciflorum	20	0.97	0.56	bio3, bio4, bio6, bio7
Gonospermum revolutum	11	0.83	0.29	bio2, bio7, bio14, bio15
Gymnocarpos decandrus	24	0.91	-0.26	bio5, bio9, bio10, bio15
Gymnosporia cassinoides	108	0.86	0.90	bio2, bio6, bio8, bio13, bio15, bio17, bio18
Gymnosporia cryptopetala	14	0.82	0.37	bio4, bio6, bio12, bio13, bio17, bio18
Habenaria tridactylites	65	0.87	0.80	bio5, bio10, bio12, bio15, bio17, bio18, bio19
Heberdenia excelsa	67	0.90	0.93	bio2, bio5, bio7, bio8, bio10, bio12, bio14, bio17, bio19
Hedera canariensis	115	0.95	0.95	bio1, bio8, bio16, bio17, bio18
Helianthemum broussonetii	14	0.84	0.62	bio15, bio18, bio19
Helianthemum canariense	107	0.88	0.95	bio3, bio4, bio5, bio6, bio7, bio11, bio12, bio19
Helianthemum juliae	11	1.00	1.00	bio1, bio2, bio6, bio7, bio11
Helianthemum teneriffae	10	1.00	1.00	bio2, bio4, bio6, bio7, bio18
Helianthemum tholiforme	16	1.00	1.00	bio4, bio7, bio12, bio18
Helichrysum gossypinum	56	0.99	0.34	bio5, bio9, bio15, bio18
Helichrysum monogynum	62	0.98	0.75	bio3, bio4, bio5, bio6, bio7, bio9, bio12, bio13, bio16, bio18, bio19
Heliotropium ramosissimum	117	0.90	0.90	bio3, bio7, bio12, bio16, bio17
Herniaria canariensis	35	0.95	0.84	bio9, bio11, bio15
Himantoglossum metlesicsianum	45	0.97	0.82	bio2, bio6, bio15, bio19
Hyparrhenia hirta	324	0.88	0.99	bio3, bio4, bio6, bio8, bio11, bio16, bio17, bio18, bio19
Hypericum canariense	244	0.89	0.90	bio6, bio9, bio11, bio16, bio17, bio19
Hypericum coadunatum	29	0.96	0.53	bio4, bio6, bio11
Hypericum glandulosum	51	0.88	0.70	Bio1, bio3, bio11, bio15
Hypericum grandifolium	503	0.95	0.97	bio1, bio2, bio7, bio12, bio14, bio15, bio16

Hypericum reflexum	191	0.88	0.95	bio3, bio4, bio5, bio6, bio7, bio10, bio13, bio16, bio17
Ilex canariensis	289	0.96	0.98	bio1, bio7, bio14, bio15, bio16
Ilex perado	40	0.99	0.45	bio1, bio11, bio16, bio18
Ixanthus viscosus	61	0.97	0.91	bio1, bio8, bio9, bio11, bio14, bio16, bio17
Jasminum odoratissimum	194	0.90	0.98	bio1, bio4, bio6, bio7, bio8, bio11, bio12, bio13, bio14, bio16, bio17, bio18, bio19
Juniperus cedrus	400	0.97	0.98	bio1, bio2, bio4, bio7, bio9, bio10, bio12, bio15, bio16
Juniperus turbinata	430	0.90	0.99	bio5, bio6, bio12, bio14, bio15, bio16
Justicia hyssopifolia	25	0.98	0.79	bio1, bio2, bio3, bio11, bio16, bio18
Kickxia sagittata	62	0.85	0.52	bio4, bio6, bio12, bio17, bio18
Kickxia scoparia	37	0.82	0.70	bio1, bio3, bio6, bio11, bio12, bio15, bio18
Kleinia neriifolia	1156	0.76	0.99	bio1, bio2, bio3, bio4, bio5, bio6, bio7, bio8, bio9, bio11, bio12, bio13, bio14, bio16
Lactuca palmensis	210	1.00	0.94	bio1, bio2, bio3, bio4, bio6, bio7, bio8, bio12, bio13, bio15, bio16, bio18, bio19
Lactucosonchus webbii	37	1.00	0.41	bio1, bio3, bio12, bio13, bio19
Launaea arborescens	1068	0.88	0.99	bio4, bio6, bio7, bio9, bio11, bio16
Laurus novocanariensis	447	0.95	0.91	bio1, bio2, bio3, bio7, bio8, bio9, bio10, bio11, bio12, bio13, bio14, bio15, bio16, bio17, bio18, bio19
Lavandula buchii	153	0.97	0.84	bio2, bio3, bio5, bio6, bio7, bio10, bio12, bio14, bio15, bio17
Lavandula canariensis	352	0.87	0.99	bio1, bio6, bio9, bio16, bio17, bio19
Lavandula minutolii	46	0.93	0.65	bio4, bio6, bio14
Lavandula pinnata	24	0.99	0.63	bio3, bio6, bio9, bio13, bio16, bio18
Lavatera acerifolia	56	0.89	0.74	bio10, bio12, bio15, bio16
Limonium arboreum	48	0.99	0.79	bio3, bio8, bio9, bio14, bio16, bio17
Limonium bourgeaui	19	0.99	0.84	bio4, bio9, bio13, bio18
Limonium brassicifolium	22	0.96	0.91	bio2, bio5, bio12, bio15
Limonium dendroides	21	0.99	0.94	bio3, bio5, bio15, bio16
Limonium imbricatum	52	0.99	0.94	bio6, bio9, bio10, bio11, bio12, bio15, bio17
Limonium macrophyllum	30	1.00	0.97	bio2, bio6, bio7, bio14, bio15, bio17, bio18
Limonium papillatum	175	0.99	0.72	bio3, bio5, bio6, bio8, bio15, bio19
Limonium pectinatum	123	0.94	0.96	bio1, bio3, bio4, bio8, bio9, bio10, bio11, bio15, bio18, bio19
Limonium preauxii	58	0.98	0.72	bio4, bio7, bio15, bio18
Limonium puberulum	32	1.00	1.00	bio2, bio4, bio12, bio13
Limonium redivivum	14	1.00	1.00	bio4, bio5, bio13, bio15, bio16
Limonium sventenii	18	1.00	1.00	bio7, bio12, bio17
Limonium tuberculatum	19	0.99	0.62	bio12, bio18, bio19
Lobularia canariensis	311	0.89	0.98	bio1, bio6, bio8, bio11, bio13, bio15, bio16, bio17, bio18, bio19
Lolium canariense	18	0.77	0.50	bio2, bio6, bio13, bio15, bio17
Lolium saxatile	16	1.00	1.00	bio5, bio9, bio13, bio18
Lotus arinagensis	27	1.00	1.00	bio2, bio9, bio13
Lotus callis-viridis	20	1.00	1.00	bio7, bio12, bio13
Lotus campylocladus	118	0.95	0.72	bio4, bio6, bio7, bio8, bio11, bio12, bio13, bio14, bio16, bio17, bio19
Lotus dumetorum	16	0.93	0.67	bio2, bio13, bio14, bio15
Lotus glaucus	14	0.81	0.87	bio3, bio6, bio9, bio14, bio15, bio18
Lotus holosericeus	11	1.00	1.00	bio4, bio7, bio15, bio18
Lotus lancerottensis	97	0.93	0.89	bio4, bio6, bio9, bio12, bio18, bio19
Lotus mascaensis	14	1.00	1.00	bio4, bio7, bio1
Lotus sessilifolius	83	0.94	0.94	bio5, bio6, bio8, bio10, bio11, bio12, bio13, bio15, bio16, bio17,

Lotus spartioides	30	0.98	0.73	bio4, bio6, bio7, bio8, bio13, bio15, bio18
Lotus tenellus	12	0.89	0.46	bio9, bio15, bio19
Luzula canariensis	24	0.93	0.30	bio1, bio3, bio8, bio11, bio14
Luzula elegans	16	1.00	1.00	bio13, bio15, bio16
Lycium intricatum	446	0.85	0.98	bio1, bio2, bio4, bio6, bio7, bio9, bio11, bio13, bio14, bio15, bio16
Marcetella moquiniana	36	0.95	0.68	bio8, bio9, bio10, bio11, bio12, bio13, bio16
Micromeria benthamii	23	0.95	0.17	bio4, bio6, bio7, bio13
Micromeria canariensis	14	0.85	0.13	bio4, bio7, bio16
Micromeria gomerensis	12	0.72	0.34	bio5, bio12, bio15, bio16, bio19
Micromeria helianthemifolia	33	0.96	0.66	bio4, bio5, bio6, bio7, bio12, bio15
Micromeria herpyllomorpha	311	0.99	0.92	bio2, bio3, bio4, bio5, bio12, bio13, bio15, bio16, bio17, bio18, bio19
Micromeria hierrensis	26	0.94	0.71	bio14, bio15, bio19
Micromeria hyssopifolia	177	0.87	0.99	bio5, bio6, bio7, bio8, bio11, bio15, bio16, bio17
Micromeria lachnophylla	10	0.98	0.44	bio1, bio2, bio6, bio7
Micromeria lanata	28	0.99	0.51	bio6, bio7, bio12
Micromeria lepida	66	0.88	0.63	bio3, bio5, bio7, bio14, bio15, bio16, bio17
Micromeria leucantha	42	1.00	0.98	bio2, bio6, bio11, bio15
Micromeria mahanensis	58	0.97	0.79	bio9, bio12, bio18, bio19
Micromeria pineolens	26	0.99	0.53	bio4, bio6, bio7, bio13, bio15
Micromeria teneriffae	14	0.86	0.30	bio7, bio13, bio18
Micromeria tenuis	10	0.88	0.10	bio4, bio7, bio12
Micromeria tragothymus	51	0.88	0.86	bio4, bio5, bio6, bio7, bio13, bio16
Micromeria varia	75	0.94	0.89	bio1, bio2, bio7, bio8, bio9, bio11, bio12, bio13, bio14, bio15, bio16, bio17
Monanthes anagensis	10	0.98	0.79	bio2, bio15, bio18
Monanthes brachycaulos	33	0.80	0.75	bio6, bio13, bio16, bio17
Monanthes laxiflora	73	0.85	0.83	bio2, bio5, bio8, bio14, bio15
Monanthes minima	10	0.79	-0.03	bio3, bio12, bio18
Monanthes muralis	36	0.95	0.91	bio3, bio12, bio15, bio18
Monanthes pallens	38	0.89	0.42	bio5, bio10, bio15, bio16, bio17
Monanthes polyphylla	113	0.95	0.95	bio2, bio4, bio8, bio12, bio13, bio14, bio15, bio16, bio17, bio19
Monanthes subrosulata	69	0.99	0.86	bio3, bio4, bio5, bio6, bio8, bio13, bio16, bio17, bio18, bio19
Morella faya	507	0.94	0.99	bio9, bio13, bio15, bio16, bio17, bio19
Morella rivas-martinezii	37	0.95	0.85	bio10, bio15, bio16
Navaea phoenicea	56	0.99	0.94	bio4, bio9, bio10, bio13, bio14, bio16, bio17
Neochamaelea pulverulenta	338	0.92	0.97	bio2, bio3, bio4, bio6, bio8, bio11, bio12, bio15, bio18, bio19
Nepeta teydea	48	0.98	0.61	bio1, bio6, bio8, bio9, bio10, bio11, bio12, bio13, bio16, bio18, bio19
Ocotea foetens	48	0.96	0.78	bio4, bio8, bio11, bio13, bio14, bio16, bio17
Olea cerasiformis	207	0.90	0.98	bio2, bio7, bio11, bio13, bio17, bio19
Oligomeris linifolia	65	0.97	0.82	bio2, bio4, bio7, bio12, bio14, bio17, bio18, bio19
Ononis angustissima	96	0.96	0.92	bio2, bio3, bio4, bio6, bio7, bio11, bio12, bio13, bio15, bio16, bio17, bio19
Ononis christii	13	1.00	1.00	bio7, bio15, bio18
Ononis hesperia	15	0.94	0.33	bio13, bio16, bio18
Onopordum carduelium	22	1.00	1.00	bio4, bio6, bio11, bio14

Orchis canariensis	36	0.95	0.44	bio1, bio6, bio11, bio12, bio15
Osyris lanceolata	33	0.91	0.69	bio4, bio8, bio12, bio14, bio19
Pancratium canariense	86	0.84	0.93	bio4, bio7, bio9, bio11, bio13
Parietaria filamentosa	13	0.90	0.23	bio5, bio7, bio9, bio15
Parolinia filifolia	28	0.99	0.64	bio2, bio6, bio7, bio12, bio13, bio16
Parolinia intermedia	11	0.83	0.52	bio2, bio3, bio10, bio15
Parolinia ornata	27	0.98	0.84	bio4, bio5, bio9, bio16
Parolinia platypetala	34	1.00	1.00	bio2, bio4, bio8, bio18
Paronychia canariensis	233	0.94	0.98	bio3, bio4, bio6, bio8, bio12, bio13, bio15, bio16, bio18, bio19
Patellifolia patellaris	137	0.85	0.95	bio1, bio2, bio3, bio4, bio6, bio8, bio9, bio11, bio12, bio13, bio15, bio16
Patellifolia procumbens	13	0.89	0.60	bio4, bio9, bio16, bio19
Patellifolia webbiana	18	0.81	0.51	bio3, bio9, bio13, bio15, bio16
Pericallis appendiculata	70	0.97	0.69	bio11, bio14, bio15
Pericallis cruenta	12	0.89	0.25	bio2, bio6, bio12, bio15, bio19
Pericallis echinata	29	0.92	0.94	bio2, bio5, bio7, bio8, bio14, bio16, bio17, bio18
Pericallis hansenii	50	0.99	0.86	bio2, bio14, bio16, bio17
Pericallis lanata	79	0.95	0.86	bio6, bio7, bio12, bio17
Pericallis multiflora	26	1.00	1.00	bio2, bio3, bio6, bio12, bio17
Pericallis murrayi	36	0.97	0.83	bio1, bio3, bio12, bio14, bio15, bio16, bio17
Pericallis papyracea	86	0.97	0.95	bio3, bio4, bio12, bio13, bio14, bio15, bio16, bio18, bio19
Pericallis steetzii	77	0.96	0.85	bio1, bio5, bio8, bio12, bio14, bio15, bio16, bio17
Pericallis tussilaginis	34	0.94	0.64	bio1, bio3, bio11, bio13, bio14, bio15, bio16, bio17, bio19
Pericallis webbii	58	0.86	0.89	bio2, bio4, bio8, bio15, bio17
Periploca laevigata	442	0.86	0.98	bio1, bio6, bio11, bio12, bio14, bio16, bio17
Persea indica	165	0.97	0.95	bio1, bio3, bio4, bio5, bio6, bio8, bio9, bio10, bio11, bio12, bio13, bio14, bio15, bio16, bio17, bio18, bio19
Phagnalon umbelliforme	34	0.95	0.93	bio3, bio4, bio5, bio8, bio10, bio15, bio16, bio19
Phyllis nobla	331	0.94	0.95	bio3, bio4, bio6, bio7, bio11, bio12, bio13, bio16, bio17, bio18
Phyllis viscosa	29	0.99	0.69	bio5, bio10, bio14, bio17
Picconia excelsa	151	0.94	0.86	bio1, bio8, bio9, bio10, bio14, bio15, bio17
Pimpinella anagodendron	21	0.93	0.58	bio3, bio15, bio17
Pimpinella cumbrae	19	1.00	1.00	bio1, bio8, bio9, bio10
Pimpinella dendrotragium	190	0.99	0.90	bio1, bio4, bio12, bio13, bio14, bio16, bio17, bio18, bio19
Pimpinella junionae	20	0.94	0.59	bio2, bio5, bio7, bio12, bio13, bio15, bio16
Pinus canariensis	1177	0.91	0.98	bio1, bio2, bio3, bio4, bio5, bio6, bio7, bio8, bio9, bio10, bio11, bio12, bio13, bio14, bio16, bio19
Pistacia atlantica	183	0.91	0.92	bio1, bio4, bio5, bio6, bio7, bio8, bio11, bio12, bio13, bio14, bio15, bio16, bio17, bio18, bio19
Pistacia lentiscus	22	0.83	0.44	bio8, bio13, bio18
Plantago arborescens	87	0.92	0.89	bio2, bio3, bio4, bio8, bio12, bio13, bio14, bio15, bio16, bio18, bio19
Plantago famarae	14	0.97	0.37	bio2, bio7, bio16, bio18
Plantago webbii	70	0.99	0.84	bio8, bio9, bio13, bio19
Pleiomeris canariensis	122	0.97	0.87	bio2, bio4, bio9, bio13, bio14, bio15, bio16, bio19
Pleudia aegyptiaca	23	0.87	0.84	bio7, bio15, bio18
Pleudia herbanica	21	0.99	0.44	bio2, bio15, bio18
Plocama pendula	748	0.93	0.98	bio2, bio3, bio7, bio11, bio13, bio18, bio19
Polycarpaea carnosa	58	0.97	0.85	bio5, bio8, bio10, bio14, bio15, bio17

Polycarpaea divaricata	234	0.91	0.92	bio3, bio4, bio6, bio9, bio13, bio16, bio19
Polycarpaea nivea	88	0.93	0.87	bio3, bio15, bio16
Polycarpaea robusta	57	1.00	1.00	bio4, bio12, bio18, bio19
Polycarpaea smithii	121	0.99	0.91	bio3, bio4, bio12, bio13, bio14, bio16, bio17, bio18
Polycarpaea tenuis	52	0.95	0.73	bio1, bio4, bio7, bio8, bio11, bio12, bio13, bio14, bio15, bio16, bio17, bio19
Polygonum balansae	10	0.96	0.56	bio2, bio5, bio7, bio9, bio10, bio12, bio15, bio16, bio18
Polygonum maritimum	21	0.91	0.82	bio11, bio15, bio16
Prunus lusitanica	55	0.99	0.89	bio1, bio2, bio3, bio11, bio12, bio14, bio15, bio17, bio18
Pterocephalus dumetorus	44	0.93	0.65	bio1, bio7, bio8, bio12, bio14, bio17, bio19
Pterocephalus lasiospermus	59	0.94	0.84	bio2, bio6, bio7, bio8, bio9, bio15
Pterocephalus porphyranthus	101	0.99	0.66	bio1, bio2, bio3, bio6, bio9, bio11, bio12, bio13, bio16, bio17, bio18, bio19
Pterocephalus virens	12	0.93	0.32	bio2, bio15, bio18
Pulicaria burchardii	15	1.00	1.00	bio2, bio15, bio18
Pulicaria canariensis	115	0.95	0.89	bio5, bio6, bio9, bio13, bio15, bio16, bio18, bio19
Ranunculus cortusifolius	144	0.86	0.92	bio1, bio2, bio3, bio4, bio6, bio8, bio9, bio15, bio16
Reichardia crystallina	15	0.97	0.86	bio3, bio5, bio12
Reichardia famarae	96	0.99	0.94	bio3, bio4, bio9, bio13
Reichardia ligulata	223	0.93	0.97	bio2, bio3, bio4, bio6, bio8, bio12, bio14, bio15, bio16, bio17, bio19
Reseda crystallina	42	0.96	0.91	bio4, bio9, bio12, bio18
Reseda scoparia	20	0.83	0.28	bio2, bio11, bio12
Retama rhodorhizoides	118	0.93	0.94	bio5, bio8, bio15, bio17, bio19
Rhamnus crenulata	201	0.91	0.93	bio1, bio4, bio10, bio11, bio13, bio14, bio19
Rhamnus glandulosa	66	0.96	0.81	bio1, bio3, bio11, bio14, bio17, bio19
Rhamnus integrifolia	23	0.90	0.76	bio7, bio15, bio18
Rhaponticum canariense	18	0.97	0.43	bio1, bio7, bio9, bio10
Romulea columnae	19	0.73	0.01	bio1, bio15, bio19
Rubia fruticosa	536	0.85	0.99	bio1, bio2, bio3, bio5, bio6, bio11, bio12, bio14, bio16, bio17
Rubia occidens	81	0.94	0.92	bio2, bio6, bio7, bio8, bio9, bio11, bio13, bio14, bio16
Rubus bollei	34	0.91	0.45	bio1, bio2, bio3, bio5, bio8, bio9, bio10, bio11, bio13, bio14, bio16, bio18
Rubus palmensis	17	0.97	0.38	bio3, bio11, bio12, bio16
Rumex bucephalophorus	29	0.83	0.77	bio1, bio6, bio8, bio9, bio10, bio12, bio13, bio14, bio15, bio16, bio17, bio19
Rumex lunaria	877	0.81	0.98	bio2, bio3, bio4, bio6, bio8, bio12, bio13, bio14, bio16, bio18, bio19
Rumex maderensis	149	0.94	0.96	bio2, bio3, bio6, bio9, bio10, bio12, bio13, bio15, bio16, bio17
Ruta microcarpa	21	0.96	0.88	bio3, bio12, bio15
Ruta oreojasme	89	0.99	0.91	bio3, bio4, bio7, bio13, bio15, bio16, bio18
Ruta pinnata	27	0.93	0.65	bio2, bio3, bio7, bio11, bio14, bio15, bio17, bio18
Rutheopsis herbanica	140	0.96	0.88	bio3, bio11, bio19
Salix canariensis	422	0.87	0.98	bio2, bio6, bio12, bio17, bio18
Salsola divaricata	105	0.92	0.95	bio4, bio6, bio8, bio9, bio10, bio11, bio13, bio15, bio17
Salvia broussonetii	29	1.00	0.54	bio3, bio14, bio17
Salvia canariensis	352	0.89	0.99	bio3, bio4, bio6, bio9, bio10, bio13, bio14
Sambucus nigra	109	0.93	0.78	bio6, bio7, bio8, bio9, bio10, bio12, bio14, bio17
Sarcocornia perennis	14	1.00	1.00	bio11, bio16, bio18
Schizogyne glaberrima	210	0.98	0.88	bio3, bio9, bio11, bio13, bio15

Schizogyne sericea	466	0.90	0.99	bio1, bio3, bio5, bio7, bio8, bio11, bio15, bio16, bio17, bio18
Scilla haemorrhoidalis	75	0.85	0.89	bio1, bio8, bio9, bio17
Scilla latifolia	40	0.89	0.76	bio4, bio6, bio15, bio16
Scrophularia arguta	50	0.87	0.90	bio4, bio5, bio15, bio18
Scrophularia calliantha	44	0.94	0.74	bio2, bio3, bio4, bio6, bio7, bio8, bio14
Scrophularia glabrata	53	0.95	0.55	bio1, bio3, bio6, bio12, bio13
Scrophularia smithii	37	0.94	0.54	bio1, bio14, bio16, bio17
Semele androgyna	79	0.94	0.95	bio4, bio6, bio8, bio9, bio13, bio17
Semele gayae	51	0.96	0.83	bio2, bio4, bio5, bio8, bio10, bio14, bio15, bio17, bio19
Senecio bollei	15	1.00	1.00	bio5, bio7, bio18
Sideritis barbellata	117	1.00	0.86	bio3, bio4, bio6, bio12, bio13, bio14, bio16, bio17, bio19
Sideritis brevicaulis	37	1.00	0.49	bio3, bio4, bio7, bio14, bio15, bio17
Sideritis canariensis	34	0.88	0.65	bio1, bio2, bio11, bio12, bio13, bio15, bio17, bio19
Sideritis cretica	26	0.96	0.69	bio2, bio4, bio9, bio11, bio14, bio19
Sideritis dasygnaphala	25	0.98	0.57	bio1, bio4, bio6, bio18
Sideritis dendrochahorra	56	0.99	0.67	bio2, bio3, bio15
Sideritis discolor	11	0.97	0.50	bio4, bio5, bio7, bio14
Sideritis ferrensis	17	0.97	0.91	bio12, bio13, bio14, bio15, bio16
Sideritis gomerae	20	0.98	0.49	bio5, bio13, bio15, bio16, bio19
Sideritis guayedrae	10	1.00	1.00	bio4, bio7, bio18
Sideritis infernalis	21	0.99	0.64	bio5, bio6, bio12, bio17
Sideritis kuegleriana	22	0.97	0.81	bio12, bio14, bio17
Sideritis lotsyi	32	0.97	0.56	bio7, bio9, bio16
Sideritis macrostachys	24	0.93	0.67	bio2, bio7, bio12, bio13, bio14, bio15, bio16, bio17, bio18
Sideritis nervosa	17	0.98	0.29	bio5, bio7, bio9, bio10, bio14, bio15, bio19
Sideritis nutans	18	0.96	0.23	bio2, bio4, bio6, bio7, bio8, bio12, bio15, bio19
Sideritis oroteneriffae	26	0.98	0.50	bio3, bio4, bio6
Sideritis pumila	33	1.00	0.70	bio4, bio9, bio16, bio18
Sideritis soluta	24	0.99	0.28	bio2, bio3, bio4, bio6, bio7, bio15
Sideritis spicata	41	0.97	0.82	bio2, bio16, bio18
Sideritis sventenii	46	0.96	0.91	bio4, bio6, bio12, bio13, bio16
Sideroxylon canariensis	156	0.91	0.98	bio3, bio4, bio6, bio8, bio12, bio13, bio15, bio17, bio19
Silene berthelotiana	16	0.95	-0.34	bio11, bio15, bio16
Silene bourgeaui	10	0.95	0.64	bio4, bio7, bio15, bio16, bio18
Silene nocteolens	48	1.00	0.42	bio9, bio11, bio18
Silene pogonocalyx	159	0.99	0.96	bio12, bio14, bio16
Smilax aspera	26	0.83	0.38	bio8, bio11, bio14
Smilax canariensis	36	0.95	0.83	bio1, bio3, bio11, bio13, bio14, bio15, bio16, bio17, bio18
Solanum lidii	23	0.95	1.00	bio4, bio15, bio16, bio18
Solanum vespertilio	67	0.98	0.69	bio2, bio6, bio13, bio14, bio15, bio16
Sonchus acaulis	202	0.88	0.97	bio3, bio6, bio9, bio10, bio15, bio16
Sonchus canariensis	41	0.90	0.72	bio2, bio5, bio15, bio16, bio19
Sonchus capillaris	29	0.93	0.83	bio2, bio5, bio17, bio18
Sonchus congestus	117	0.91	0.98	bio11, bio12, bio13, bio14, bio17, bio18
Sonchus fauces orci	20	0.99	0.76	bio5, bio7, bio13, bio15
Sonchus gandogeri	25	0.97	0.32	bio6, bio12, bio13, bio14, bio15, bio16, bio17, bio19

Sonchus gomerensis	41	0.91	0.90	bio2, bio5, bio9, bio13, bio15, bio16
Sonchus gummifer	12	0.98	0.31	bio2, bio7, bio18
Sonchus hierrensis	373	0.96	0.98	bio2, bio3, bio6, bio8, bio12, bio15, bio16, bio18, bio19
Sonchus leptocephalus	166	0.84	0.97	bio1, bio2, bio3, bio5, bio6, bio9, bio10, bio12, bio13, bio16, bio17
Sonchus microcarpus	17	0.99	0.44	bio2, bio5, bio7, bio14, bio15
Sonchus ortunoi	55	0.88	0.93	bio2, bio4, bio5, bio8, bio12, bio13, bio14, bio15, bio16, bio17, bio18
Sonchus palmensis	30	0.96	0.33	bio4, bio6, bio7, bio12, bio13, bio16, bio18, bio19
Sonchus pinnatifidus	167	0.97	0.97	bio1, bio3, bio4, bio5, bio6, bio9, bio10, bio13, bio16, bio17, bio18, bio19
Sonchus radicatus	57	0.88	0.65	bio3, bio14, bio15, bio19
Sonchus sventenii	33	0.91	0.38	bio4, bio5, bio15, bio16
Sonchus wildpretii	19	0.89	0.46	bio2, bio6, bio10, bio14, bio15, bio16, bio17
Spartocytisus filipes	101	0.95	0.91	bio6, bio8, bio13, bio15, bio16, bio17, bio19
Spartocytisus supranubius	86	0.97	0.66	bio1, bio2, bio3, bio4, bio5, bio6, bio7, bio8, bio9, bio10, bio11, bio12, bio13, bio14, bio15, bio16, bio17, bio18
Suaeda vera	54	0.89	0.83	bio2, bio5, bio7, bio8, bio11, bio12, bio13, bio16, bio19
Sventenia bupleuroides	26	1.00	0.44	bio4, bio5, bio6, bio7, bio13, bio15
Tamarix canariensis	95	0.72	0.85	bio2, bio8, bio11, bio15, bio18
Teline canariensis	105	0.95	0.50	bio3, bio4, bio13, bio14, bio16, bio17, bio18
Teline microphylla	155	0.94	0.95	bio4, bio6, bio14, bio15
Teline osyrioides	33	0.95	0.51	bio2, bio4, bio6, bio7, bio12, bio14, bio18
Teline pallida	40	0.90	0.46	bio4, bio12, bio14, bio19
Teline rosmarinifolia	93	0.95	0.97	bio2, bio4, bio6, bio12, bio15
Teline splendens	29	1.00	1.00	bio2, bio4, bio7, bio8, bio12, bio13, bio16, bio19
Teline stenopetala	251	0.98	0.96	bio4, bio5, bio10, bio12, bio13, bio14, bio15, bio16, bio17, bio18, bio19
Tetraena fontanesii	93	0.91	0.93	bio2, bio8, bio11, bio12, bio13, bio15, bio16, bio18
Tetraena gaetula	35	0.98	0.26	bio1, bio11, bio13, bio16
Teucrium heterophyllum	44	0.92	0.83	bio1, bio3, bio4, bio5, bio7, bio10, bio12, bio13, bio16, bio19
Thesium retamoides	19	1.00	1.00	bio2, bio6, bio7, bio13
Todaroa aurea	88	0.92	0.93	bio3, bio4, bio5, bio12, bio15, bio16, bio17
Tolpis calderae	12	0.99	0.32	bio1, bio9, bio11
Tolpis crassiuscula	15	0.99	0.40	bio2, bio5, bio7, bio9, bio15
Tolpis glabrescens	10	1.00	1.00	bio2, bio7, bio15, bio18
Tolpis laciniata	45	0.90	0.70	bio3, bio8, bio12, bio15
Tolpis lagopoda	23	0.92	0.61	bio6, bio7, bio11, bio13, bio15
Tolpis proustii	41	0.92	0.80	bio3, bio5, bio15, bio16
Tolpis webbii	31	0.99	0.40	bio1, bio2, bio3, bio6, bio8, bio9, bio11
Traganum moquinii	156	0.96	0.96	bio2, bio6, bio19
Tricholaena teneriffae	257	0.96	0.99	bio3, bio5, bio6, bio9, bio11, bio13, bio15, bio18
Trigonella stellata	11	0.96	0.44	bio1, bio15, bio18
Urtica morifolia	143	0.97	0.85	bio1, bio2, bio3, bio5, bio6, bio7, bio8, bio10, bio11, bio12, bio13, bio14, bio15, bio16
Viburnum rugosum	308	0.94	0.93	bio2, bio10, bio12, bio14, bio16, bio17, bio19
Vicia aphylla	43	0.83	0.77	bio3, bio10, bio12, bio13, bio16, bio19
Vicia filicaulis	28	0.98	0.75	bio6, bio7, bio12
Vieria laevigata	69	0.99	0.64	bio5, bio10, bio14, bio15, bio17
Viola cheiranthifolia	56	1.00	0.55	bio1, bio6, bio9, bio18
Viola odorata	12	0.91	0.33	bio8, bio13, bio16,
Viola palmensis	46	1.00	0.55	bio8, bio16, bio19

Visnea mocanera	97	0.84	0.95	bio1, bio2, bio3, bio5, bio9, bio10, bio13, bio15, bio17
Volutaria bollei	38	0.95	0.78	bio3, bio4, bio13, bio15, bio16
Volutaria canariensis	35	0.88	0.83	bio1, bio3, bio8, bio10, bio11, bio15, bio19
Wahlenbergia lobelioides	390	0.93	0.98	bio3, bio4, bio7, bio10, bio12, bio14, bio15, bio16, bio17, bio18, bio19
Withania aristata	67	0.93	0.91	bio2, bio9, bio13, bio15, bio16, bio19

Appendix S6.3

ODMAP protocol

section	**subsection**	**element**	**Value**
Overview	Authorship	Study title	Effects of climate change on the distribution of plant species and plant traits on the Canary Islands
		Author names	Dagmar M. Hanz, Vanessa Cutts, Martha Paola Barajas-Barbosa, Adam Algar, Carl Beierkuhnlein, Flavien Collart, José María Fernández-Palacios, Richard Field, Dirk N. Karger, David R. Kienle, Holger Kreft, Jairo Patiño, Franziska Schrodt, Manuel J. Steinbauer, Patrick Weigelt & Severin D.H. Irl
		Contact	hanz@geo.uni-frankfurt.de
	Model objective	Model objective	Forecast and transfer
		Target output	Mean proportional change in climatically suitable area
	Focal Taxon	Focal Taxon	Native plant species of the Canary Islands
	Location	Location	Canary Islands, Spain
	Scale of Analysis	Spatial extent	27.637400, 29.415900, -18.161100, -13.335200 (xmin, xmax, ymin, ymax)
		Spatial resolution	0.5 km x 0.5 km
		Temporal extent	Current climate (mean of 1981-2010) and future climate (mean of 2071-2100)
		Boundary	natural
	Biodiversity data	Observation type	field survey
		Response data type	presence-only
	Predictors	Predictor types	climatic
	Hypotheses	Hypotheses	1) We hypothesise that there is an overall reduction in potential climatic suitable area for all floristic groups due to the narrow realised ecological niche of many oceanic island plants (Fernández-Palacios et al., 2021). However, we expect single-island endemics to be most susceptible to changing climatic conditions as they may have a narrower climatic niche than other species and a limited possibility of vital range shifts. 2) We hypothesise that islands which comprise high-elevation habitats or only are slightly elevated (and therefore dominated by arid conditions) will have an above-average loss of potential climatic suitable area for all floristic groups due to difficulties for species to elevationally track their climatic requirements. 3) We hypothesise that trees, climbers and forbs, as well as non-woody and non-succulent species, will face above-average climate change-related reduction in potential climatically suitable areas as we expect an increase in heat and drought across the Canary Islands' conditions that are less favourable for these plant functional types and traits.
	Assumptions	Model assumptions	We assumed that the geographic range, which we exclusively projected with climatic predictors, represents the climatic niche of each species (Hutchinson 1957)
	Algorithms	Modelling techniques	BART
		Model averaging	No model averaging was used

	Software	Software	Analyses were run in the R statistical programming language (R Core Team 2021), SDMs were implemented in the *emarcadero* R-package (Carlson 2020).
		Data availability	Species occurrence data are available under www.biodiversidadcanarias.es/biota/
Data	Biodiversity data	Taxon names	Spermatophyta
		Taxonomic reference system	The taxonomy follows the official checklist of the Canary Islands' flora Arechavaleta et al. (2010).
		Ecological level	species
		Data sources	We collected occurrence data from the Banco de Datos de Biodiversidad de Canarias, an open-access database (www.biodiversidadcanarias.es/biota) [accessed 14/03/2022].
Data	Biodiversity data	Sampling design	The occurrence database consists of 28,536 500 m x 500 m grid cells across the Canary Islands and is based on actual and expert-based assessments of species occurrences.
		Sample size	The final dataset contained presence-only data for 491 species
		Clipping	Canary Islands, Spain
		Cleaning	We only used confidence level 'seguro' and precision level '1' for species occurrences
		Background data	We randomly sampled pseudo-absences from the background for each species
		Errors and biases	Spatial bias towards sampling effort
	Data partitioning	Training data	We fitted our models on ten random subsets of 70% of the data.
		Validation data	We validated our models against the remaining 30% of the data.
	Predictor variables	Predictor variables	We included 19 climatic variables widely used in species distribution modelling and with potentially direct or indirect impact on species occurrences (annual mean temperature, mean diurnal range, isothermality, temperature seasonality, Max temperature of warmest month, min temperature of coldest month, temperature annual range, mean temperature of wettest quarter, mean temperature of driest quarter, mean temperature of warmest quarter, mean temperature of coldest quarter, annual precipitation, precipitation of wettest month precipitation of driest month, precipitation seasonality, precipitation of wettest quarter, precipitation of driest quarter, precipitation of warmest quarter, precipitation of coldest quarter).
		Data sources	All climate variables are available from the CHELSA v1.2 raster of current (mean of 1979-2013) and future (mean of 2071-2100) climate at a resolution of 30 arc-sec (1-km grid cell scale).
		Spatial extent	27.637400, 29.415900, -18.161100, -13.335200 (xmin, xmax, ymin, ymax)
		Spatial resolution	0.5 km x 0.5 km
		Coordinate reference system	WGS 1984 UTM Zone 28N
		Temporal extent	Current climate (mean of 198-2010) and future climate (mean of 2071-2100)
Model	Multicollinearity	Multicollinearity	The BART algorithm is insensitive to multi-collinearity and can simultaneously model a large number of predictors.
	Model settings	Model settings (fitting)	BART: trees (200), posterior draws (1000), burn-in draws (100), power (2.0), base (0.95)
	Model estimates	Coefficients	Posterior distribution of estimated classification probabilities
		Parameter uncertainty	95% credible interval from the 2.5% and 97.5% quantiles of the posterior probability
		Variable importance	To find the main subset of predictors, we ran an automated variable selection implemented in *embarcadero*, following the recommendations of Chipman et al. (2012). The variables with the lowest average model root mean square error (RMSE) and, therefore, highest accuracy is selected (Carlson et al. 2022).

	Threshold selection	Threshold selection	We converted the projected probabilities of occurrence for the current and future distribution to a binary outcome according to the threshold that maximised the True Skill Statistic (TSS) for each species' present occurrences (Allouche et al. 2006).
Assessment	Performance statistics	Performance on training data	AUC, Boyce index
	Plausibility check	Response shapes	Plausibility of individual species responses was not evaluated

Appendix S6.4

SSP 1, SSP5 results and species richness maps

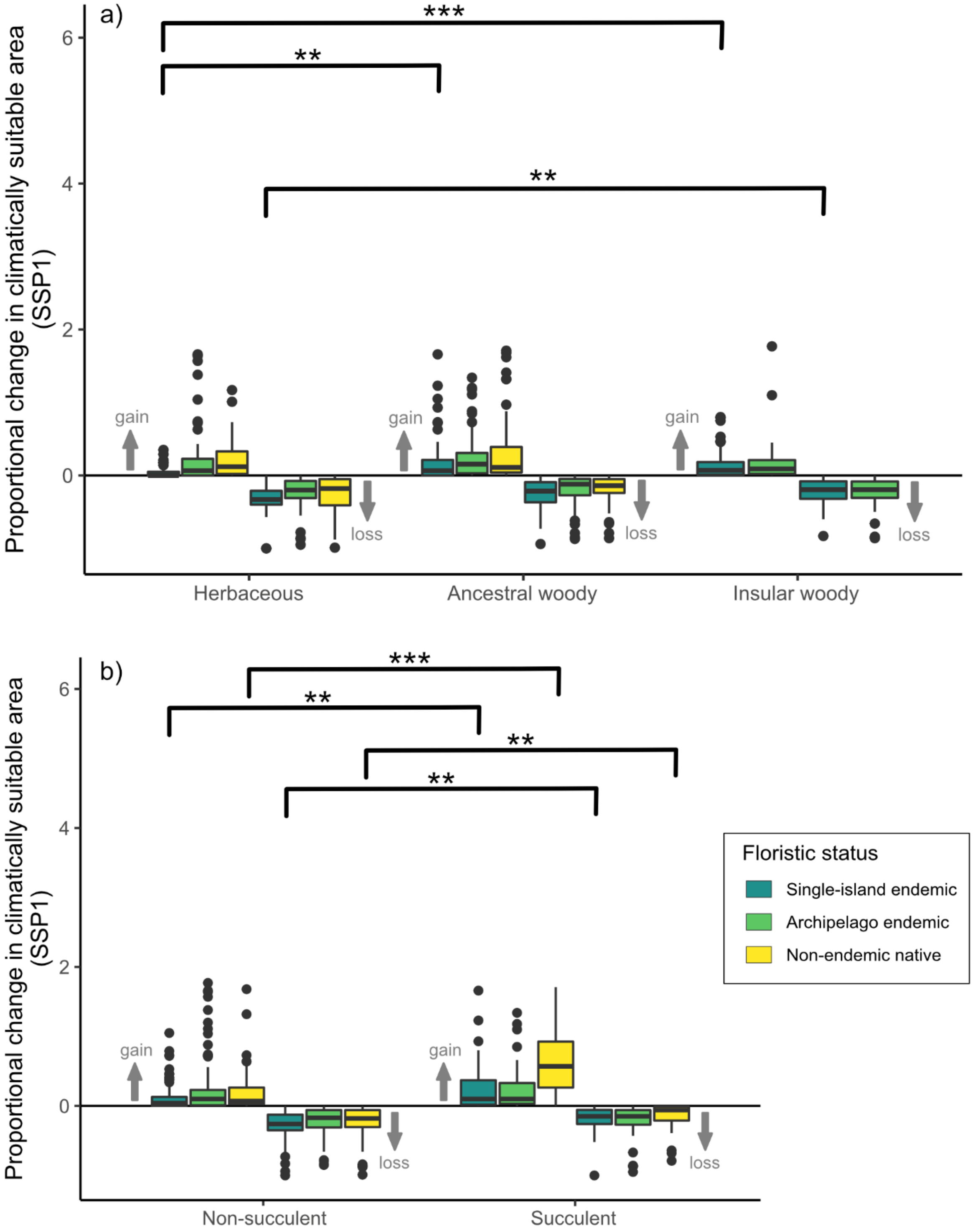

Figure 6.4.1 Proportional change in potential climatically suitable area (**SSP1**) for single-island endemic (n = 203), archipelago endemic (n = 194) and non-endemic native species (n = 106) on the Canary Islands when accounting for different traits. **a)** Herbaceous species have a significantly lower gain and higher loss of climatically suitable area than insular woody species in single-island endemics. **b)** Non-succulent species have a significantly lower gain and higher loss of climatically suitable area than succulent species in single-island endemics and non-endemic natives. Asterisks denote statistical significance (**P* <= .05, ***P* <= .01, ****P* <= .001).

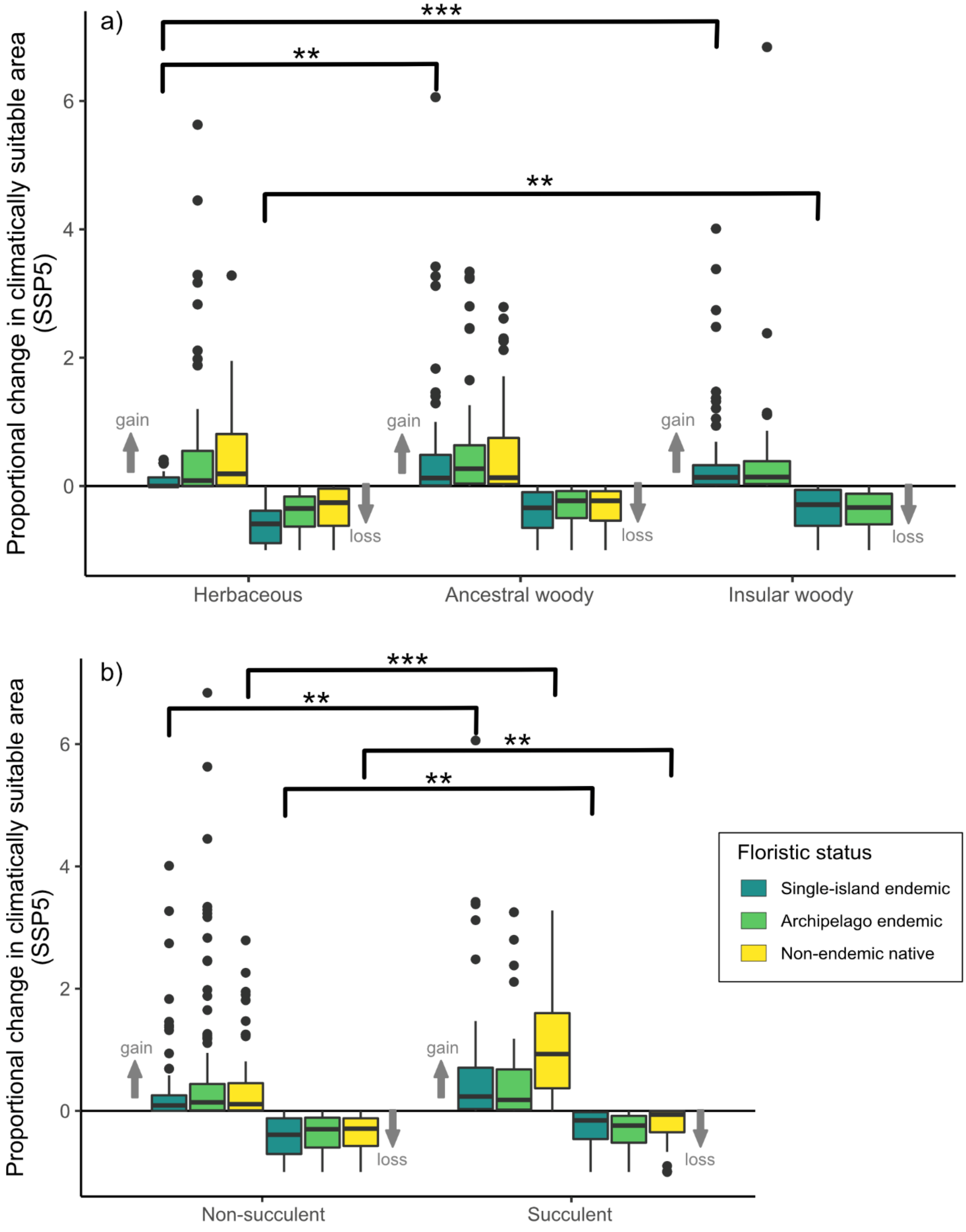

Figure 6.4.2 Proportional change in potential climatically suitable area (**SSP5**) for single-island endemic (n = 203), archipelago endemic (n = 194) and non-endemic native species (n = 106) on the Canary Islands when accounting for different traits. **a)** Herbaceous species have a significantly lower gain and higher loss of climatically suitable area than insular woody species in single-island endemics. **b)** Non-succulent species have a significantly lower gain and higher loss of climatically suitable area than succulent species in single-island endemics and non-endemic natives. Asterisks denote statistical significance (*$P <= .05$, **$P <= .01$, ***$P <= .001$).

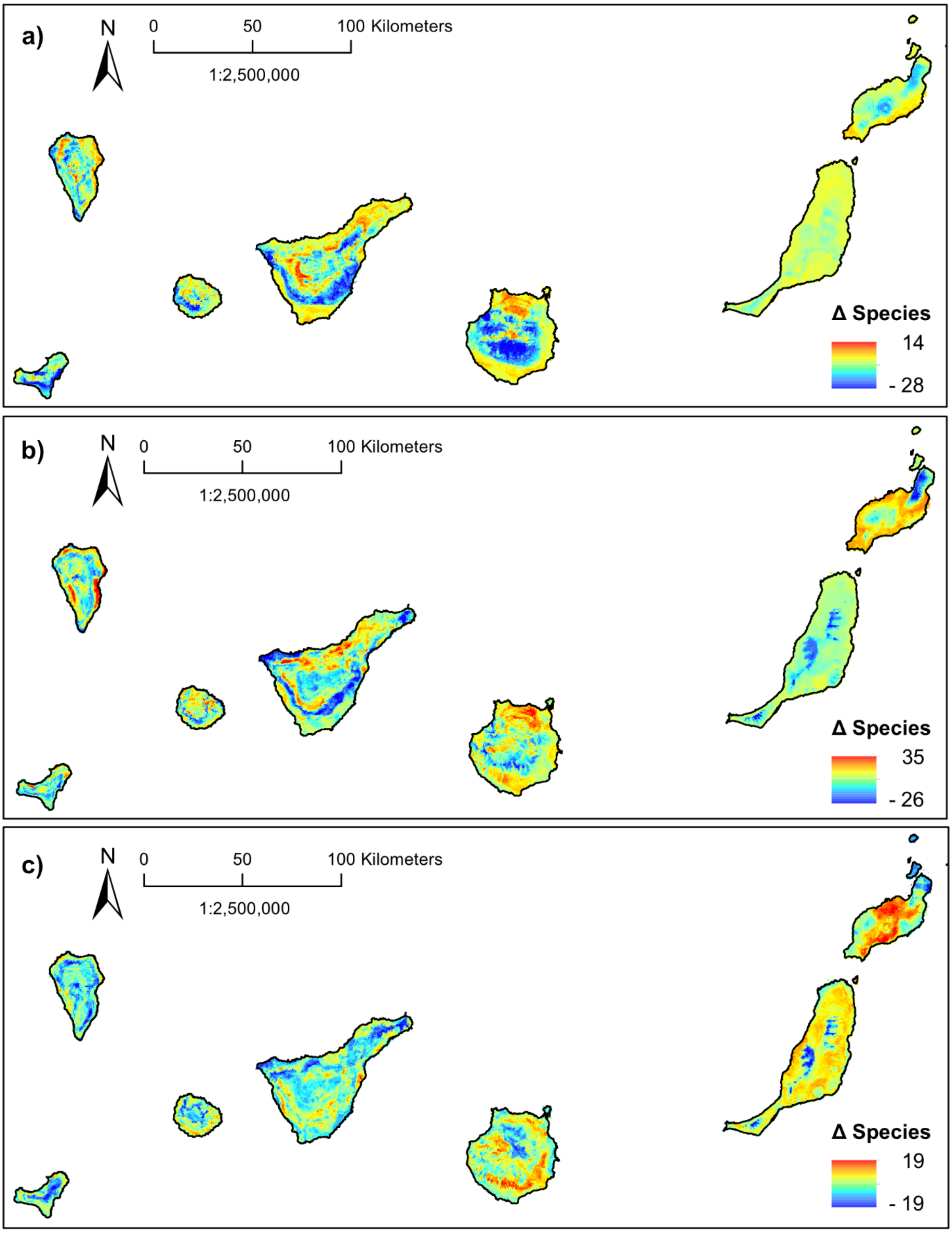

Figure S6.4.3 Maps are displaying differences in species richness between projected future climate (2071-2100; mean of five GCMs under SSP3) and current climate (1973-2013) for **a)** Single-island endemics, **b)** archipelago endemics and **c)** non-endemic natives. Blue tones represent loss, and red tones represent gain in species richness.

Appendix S6.5

Results from models with dispersal limitation for single-island endemics

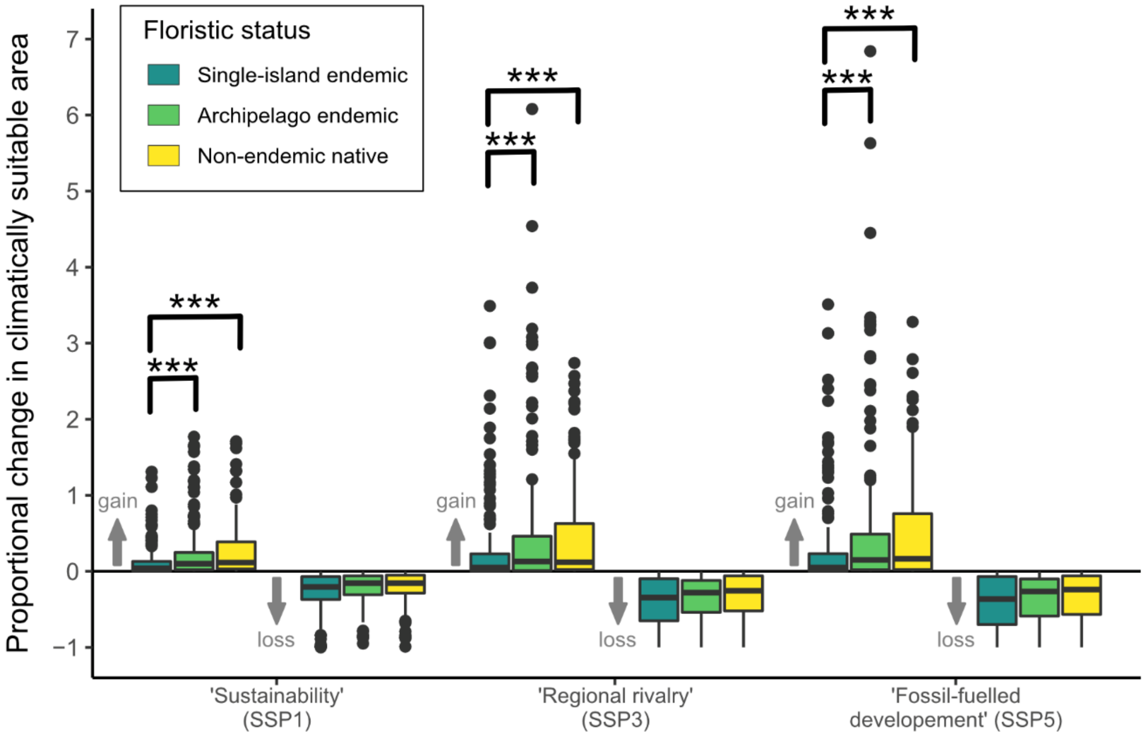

Figure S6.5.1 Proportional change in climatically suitable area by 2100 in **dispersal-limited** single-island endemic (n = 202); archipelago endemic (n = 194) and non-endemic native plant species (n = 106) on the Canary Islands using three different climate change scenarios (SSP1, SSP3 and SSP5). SSP1 describes a world with strong economic growth via sustainability, SSP3 describes a future with high inequality between countries and SSP5 describes a world with strong economic growth via fossil fuel pathways. Single-island endemics have a significantly lower gain of potential climatically suitable area than archipelago endemics and non-endemic natives under climate change scenarios SSP1, SSP3 and SSP5. Asterisks denote statistical significance (*P <= .05, **P <= .01, ***P <= 0.001).

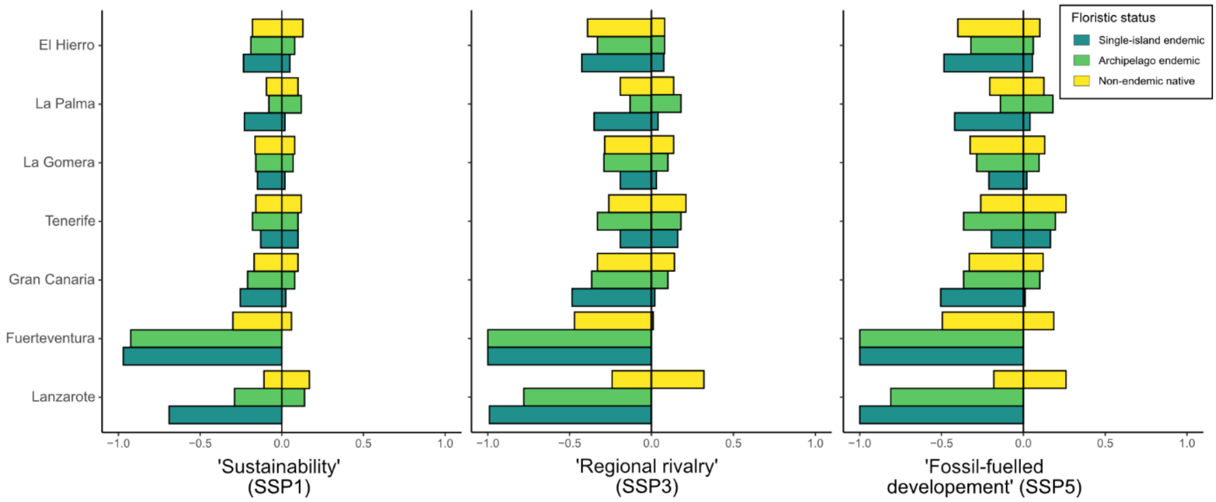

Figure S6.5.2 Mean proportional change in potential climatically suitable area for **dispersal-limited** single-island endemic, archipelago endemic and non-endemic native species on all seven islands of the Canary Islands archipelago until 2100. The change was calculated under three different climate change scenarios (SSP1, SSP3, SSP5). Outliers are not displayed for reasons of clarity and comprehensibility.

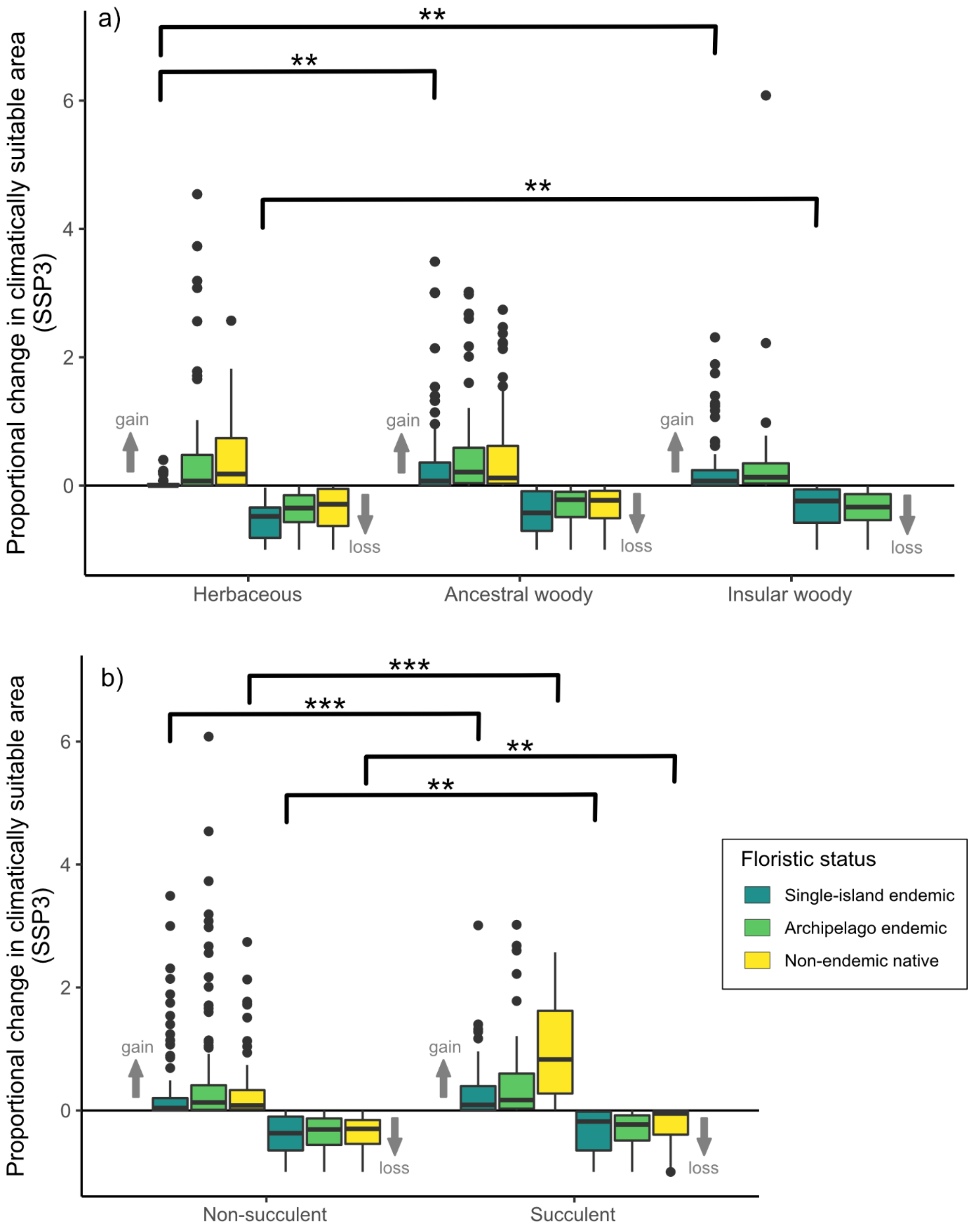

Figure S6.5.3 Proportional change in potential climatically suitable area (SSP3) for **dispersal-limited** single-island endemic (n = 202), archipelago endemic (n = 194) and non-endemic native species (n = 106) on the Canary Islands when accounting for different traits. **a)** Herbaceous species have a significantly lower gain and higher loss of climatically suitable area than insular woody species in single-island endemics. **b)** Non-succulent species have a significantly lower gain and higher loss of climatically suitable area than succulent species in single-island endemics and non-endemic natives. Asterisks denote statistical significance ($*P <= .05$, $**P <= .01$, $***P <= .001$).

Chapter 7

Synthesis

Left photo: The Macaronesian endemic *Semele androgyna* growing in Los Tilos, one of the most important laurel forests on La Palma, Canary Islands (own photo). *S. androgyna* does not develop leaves but leaf-shaped phylloclades to photosynthesize.

7.1 Synthesis

Trait-based research in insular systems has received a surge in attention over the last few years (e.g. Whittaker *et al.*, 2014; Negoita *et al.*, 2016; Burns, 2019; Taylor *et al.*, 2019). However, a comprehensive and large-scale study which attempts to unravel general patterns and processes that drive the functional diversity of oceanic island floras is still missing, even though island biota contribute disproportionately to global biodiversity and provide critical ecosystem functions (Wardle *et al.*, 1997; Kier *et al.*, 2009). However, understanding the drivers of plant diversity on oceanic islands is urgent as oceanic island floras are inherently vulnerable and are directly or indirectly threatened by human activities (Fernández-Palacios *et al.*, 2021). This dissertation aims to unravel the patterns and drivers of functional trait diversity in oceanic island floras by combining island biogeography theories and ecological mechanisms with trait-based approaches, using the Canary Islands as a model system. Firstly, I have analysed how environmental factors, biogeography and evolution drive the functional diversity of oceanic island floras (**Chapters 2 and 3**). I show that plant traits on the Canary Islands are mainly driven by water availability and, to a lesser extent, by island biogeographical variables. In particular, my results suggest that aridity causes functional convergence in endemic and non-endemic native species, whereas it causes functional divergence in alien species on oceanic islands. Secondly, the results from **Chapter 3** suggest that functional distinctiveness in island plants is independent of the occupancy of rare climates, thus implying non-adaptive radiation. Thirdly, I present evidence that aridity drives intraspecific variation in endemic and non-endemic plants to increase individual species' fitness under environmental stress on La Palma (**Chapter 4**). The work presented in **Chapters 2, 3 and 4** further suggests that plants native to oceanic islands experience similar ecological constraints to non-native plants due to their overall similarity in inter- and intraspecific trait composition. Fourthly, this dissertation reveals for the first time that scientific floras can be used as reliable sources for trait data of oceanic island floras (**Chapter 5**). In **Chapter 6**, I corroborate that water availability is one of the major drivers of the Canary Islands' flora and could become even more critical in shaping the islands' flora with ongoing climate change. Most importantly, I show that the functional composition of the Canary Islands' flora is projected to become homogenised as species with drought-tolerant traits are more likely to be resilient under future drought and heat stress. Forthcoming, I synthesise the contribution of my dissertation to understanding plant diversity patterns on oceanic islands (Figure 7.1).

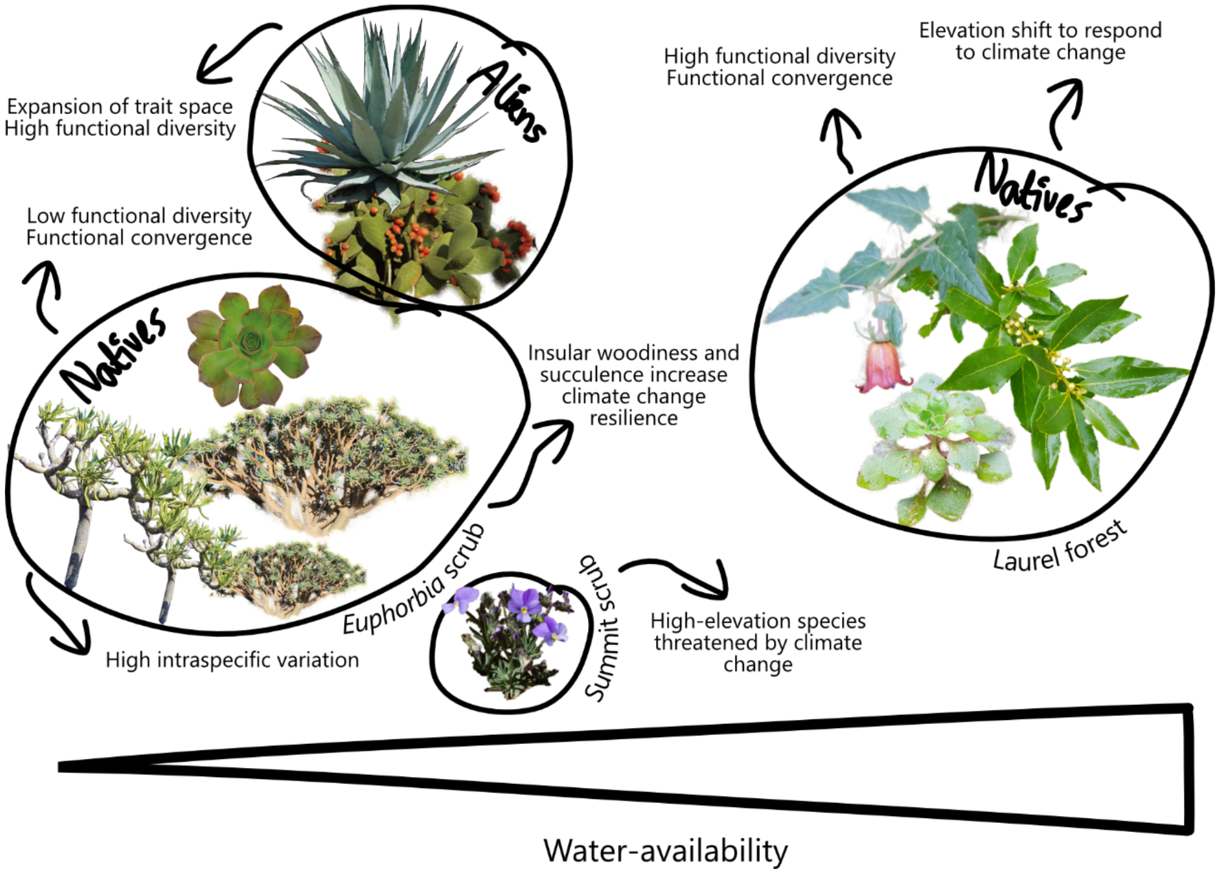

Figure 7.1 Schematic representation of my thesis's most critical results. In this dissertation, I show for the first time that endemic plant species do not extend the trait space of oceanic islands but rather display convergent traits to non-endemic native plants (Chapters 2 and 3). Water availability is a major factor influencing the functional diversity of species assemblages on the Canary Islands, leading to low functional diversity in water-limited systems, such as the succulent and summit scrub, and high functional diversity in humid systems, such as the laurel forest (Chapter 2). In contrast, I show that alien species on oceanic islands show a high functional diversity under arid conditions and could, therefore, pose an inordinate threat to native species assemblages in the succulent scrub (Chapter 2). Moreover, I found that as an adaptation to drought stress, oceanic island plants display high intraspecific variation under arid conditions (Chapter 4). Interestingly, island biogeographical variables play a less critical role in influencing the functional diversity of oceanic island floras (Chapters 2 and 3). I show this by investigating functional traits retrieved from scientific floras, which we have shown to be reliable sources of trait data (Chapter 5; not pictured here). The results of my thesis also suggest that functional adaptations to drought (insular woodiness and succulence) may increase the resilience of the succulent scrub to climate change (Chapter 6). However, species that cannot shift their range in elevation are predicted to be highly threatened by climate change, independent of the species' functional characteristics. Overall, my dissertation shows that trait-based approaches in island biogeography can help to improve our understanding of the mechanisms that drive insular biodiversity.

7.2 Functional composition of native island floras

Classic island biogeography theories, i.e. the *Equilibrium Theory of Island Biogeography* (MacArthur & Wilson, 1967) and the *General Dynamic Model of Oceanic Island Biogeography* (Whittaker *et al.*, 2008), are based on the assumption that plant species are functionally equivalent. However, functional traits play an important role in determining whether a species can arrive and establish itself on an island and how it responds to the island environment (Whittaker *et al.*, 2017; Ottaviani *et al.*, 2020). Moreover, it is not well understood which evolutionary processes cause endemic species to functionally diverge from their mainland progenitors (Patiño *et al.*, 2017; Schrader *et al.*, 2021).

Hence, it is crucial to analyse how functional characteristics and ecological strategies differ between endemic and non-endemic native species on oceanic islands.

I have found that endemic and non-endemic native species on the Canary Islands show a high functional overlap suggesting niche packing and trait convergence (**Chapters 2 and 3**). These results contrast with the previous understandings of island speciation which have assumed that radiated species significantly increase the functional diversity of islands (Patiño *et al.*, 2017). So far, it has been assumed that speciation increases trait diversification due to the occupation of novel ecological niches on islands via adaptive radiation (Carlquist, 1974; Givnish *et al.*, 2009; Losos & Ricklefs, 2009). In fact, island endemic genera are often used as examples of spectacular adaptive radiation (Schluter, 2000; Schenk, 2021). However, our results suggest that *in situ* speciation is non-adaptive on the Canary Islands as endemic species only marginally increase functional diversity. A recent study on Tenerife concurs with our results by showing that cladogenetic plant species are tightly packed in trait space (Barajas-Barbosa *et al.*, 2022). A relaxed competition on oceanic islands may allow genetic drift to become dominant over adaptive processes (Stuessy *et al.*, 2006). In addition, the environmental conditions in the Canary Islands could yield an explanation for the packing of islands' native species in trait space. A Mediterranean climate with drought seasons characterises the lowlands of the Canary Islands (del Arco Aguilar *et al.*, 2010), hence, the low water availability in the Canary Islands may have driven the evolution of relevant plant functional traits. Insular woodiness is known to be a dominant trait characteristic in water-limited systems as woody species are more resilient to drought-induced embolism (Lens *et al.*, 2016; Dória *et al.*, 2018; Hooft van Huysduynen *et al.*, 2021; Zizka *et al.*, 2022). Therefore, the results presented in **Chapters 2 and 3** suggest that the environmental conditions in the Canary Islands favour speciation, colonisation and the establishment of insular woody plant functional types (see also **Chapter 6**), such as shrubs and dwarf shrubs, leading to a functional convergence of traits in native island species.

7.3 Climatic and biogeographical filters acting on functional traits of island floras

Environmental filtering via climate is one of the major processes that drives trait diversity of mainland biota (Cornwell & Ackerly, 2009; Spasojevic & Suding, 2012; Laliberté *et al.*, 2014). However, it is unclear whether environmental filtering is similarly essential in shaping plant functional diversity on oceanic islands. Notably, it is not well understood how biogeographical filters influence the spatial distribution of plant form and function and how these filters compare to the importance of climatic filters. It is necessary to quantify the functional composition of island floras under diverse environmental conditions in order to improve our understanding of how plant species functionally respond to the island environment.

I have revealed that water availability is the primary driver of both plant functional diversity and trait variability across the Canary Islands (**Chapters 2, 4 and 6**). Moreover, I found that low water availability, indeed, drives a strong convergence of traits in island floras (**Chapter 2**). Arid environments were found to have a lower plant functional diversity than expected by chance, indicating that environmental filters select species with relevant adaptations to droughts (Cornwell &

Ackerly, 2009), for example, species with a low stature and small leaves and flowers. Similarly, I have determined that humid environments had a higher plant functional diversity than expected, possibly due to an ecological opportunity for niche differentiation (Rundell & Price, 2009). Hence, on the Canary Islands, the laurel forest, with its mild climate and continual humidity, has a high functional diversity. In contrast, the dry succulent and summit scrubs are characterised low functional diversity. The importance of climate for functional diversity was found to be consistent across spatial scales since we found water availability to drive the functional trait composition of plants at the archipelago and island levels (**Chapters 2 and 4**). My findings align with seminal studies which show that environmental filtering is a major constraint to plant functional diversity at the macroscale (de Bello *et al.*, 2013; Spasojevic *et al.*, 2014; Bruelheide *et al.*, 2018). Hence, my results suggest that the functional diversity of the Canary Islands is driven by environmental filtering via water availability, a constraint that acts similarly on mainland floras.

Interestingly, the results presented in **Chapters 2 and 3** suggest that island biogeographical variables (geographical isolation, topographic complexity and geological age) play a subordinate role in functional diversification. Nevertheless, I have shown that functional diversity of endemic species increases with geographical isolation, whereas functional diversity of non-endemic native species shows a hump-shaped relationship with geographical isolation. My results indicate that isolation likely the limits gene flow and fosters functional diversification in endemic species (Losos & Ricklefs, 2009; Marques *et al.*, 2019). In fact, it has been shown that endemic summit scrub and rock assemblages, the most isolated assemblages on the Canary Islands, are particularly rich in highly diversified lineages (Fernández-Palacios *et al.*, 2021). Furthermore, I show that the functional diversity of non-endemic species is driven by isolation, possibly due to the dispersal limitation of these species. It is plausible that more isolated habitats on islands are likely to be colonised by lineages with long-distance dispersal favouring species with specific functional trait compositions, e.g. herbaceous species are assumed to be better long-distance dispersers than trees (Carlquist, 2009). However, species assemblages with disharmonic dispersal traits seem to dominate in habitats of intermediate isolation. On the Canary Islands, the laurel forest is in a location of intermediate isolation; non-endemic native plants of diverse functional types, such as trees, herbs and climbers, are found to inhabit this vegetation type. However, the effect of isolation on plant functional diversity cannot be distinguished from the effect of trade wind-induced humidity and needs to be tested further on other islands. Furthermore, from the results presented in **Chapter 2**, I show that topographic complexity decreases the functional diversity of endemic species on the Canary Islands. These results support the area-heterogeneity trade-off hypothesis which states that the effective area for species in topographically complex areas gets reduced and, thus, increases the possibility of the extinction of narrow-niche species (Allouche *et al.*, 2012). These results concur with other studies that have found area to be one of the most critical factors driving diversity patterns on islands due to a reduction of extinction rates in species (Triantis *et al.*, 2012; Whittaker *et al.*, 2014; Barajas-Barbosa *et al.*, 2020).

The *General Dynamic Model* predicts that species richness can be linked to island age due to the hump-shaped relationship of environmental heterogeneity with island age (Whittaker *et al.*, 2008). Indeed, the results of **Chapter 3** indicate that the existence of rare climates decrease with increasing island age. However, this dissertation shows that geological age neither drives functional diversity in endemic plant species (**Chapter 2**) nor functional distinctiveness in native plant species (**Chapter 3**). Hence, in contrast to the assumption that species' functional diversity is highly dynamic during an island's ontogeny (Borregaard *et al.*, 2016), I have found that the functional composition of island plants remains constant throughout time. Notably, these results suggest that functional diversification is already high at an early stage of an island's ontogeny and remains high for an extended time. The early gain of climatic rarity and functional diversity is corroborated by other studies that have found an early plateau in environmental heterogeneity and plant taxonomic diversity across oceanic islands (Steinbauer *et al.*, 2013; Barajas-Barbosa *et al.*, 2020). Thus, ecological opportunity and available niche space at an early stage of an island's ontogeny are virtual drivers for the functional diversity of oceanic island floras.

From the results presented in **Chapter 4**, I have revealed that trait variation in endemic and non-endemic species assemblages is mainly characterised by species turnover, despite endemic and non-endemic native species' distinct evolutionary histories. Interestingly, intraspecific variation becomes more critical in response to the environment when water availability is limited. Phenotypic intraspecific variation has previously been identified as a valuable strategy for plants to respond to changed environmental conditions (Hoffmann & Merilä, 1999; Badyaev, 2005; Ghalambor *et al.*, 2007). This finding indicates that both endemic and non-endemic species may be able to maintain their fitness under stressful environmental conditions. Thus, the results of **Chapter 4** help to further understand the effect of global change on oceanic island species. The results could be particularly relevant in the future as the arid conditions of the Canary Islands are expected to increase with climate change (see **Chapter 6**).

7.4 Ecological niche and environmental drivers of alien plant functional diversity on oceanic islands

Alien and invasive alien species present major threats to biodiversity and yield disproportional negative effects on island biota (Pyšek *et al.*, 2020; Fernández-Palacios *et al.*, 2021). Up to the present day, it has been analysed how native island floras are taxonomically affected by alien species (Vitousek, 1988; Mauchamp, 1997; Kueffer *et al.*, 2010; Blackburn *et al.*, 2016). However, how entire native floras are functionally affected by alien species has not, thus far, been assessed, even though it has been shown that the spread of alien species leads to a functional homogenisation with yet unknown consequences for ecosystem functions (Olden *et al.*, 2004; Castro-Díez *et al.*, 2016; Tordoni *et al.*, 2019).

In this dissertation, I explored how species native to oceanic islands functionally compare to alien species that did not have to overcome dispersal filters or undergo *in situ* speciation (**Chapter 2**). Firstly, I found that alien species on the Canary Islands overlap with and extend the native trait space.

I further found that the functional diversity of alien plant assemblages is highest in low-elevation habitats that are characterised by aridity on the Canary Islands. This high functional diversity in alien species assemblages is in contrast to the patterns found in native island species assemblages which are characterised by low functional diversity in arid environments. These contrasting results may have important implications for the Canary Islands' native flora as species assemblages with low trait diversity are more susceptible to invasion due to gaps in niche space which can be exploited (Dukes, 2001). Moreover, due to the overlap in trait space, alien species are expected to use similar resources to native species, thus, this could increase the possibility of alien species outcompeting native species (Funk *et al.*, 2008). The functional characteristics of alien species may have even more problematic implications for future biodiversity as the climate on the Canary Islands is projected to become more arid (see **Chapter 6**), and alien species are expected to spread with increasing aridity (Walther *et al.*, 2009). However, whether the spread of alien species leads to a functional homogenisation on the Canary Islands remains debatable as alien species extend the archipelago's trait space (**Chapter 2**). Nevertheless, the consequences of the spread of alien species on ecosystem functions and resilience are still unclear and should be further investigated on oceanic islands.

7.5 Quality and availability of trait data for trait-based research on oceanic islands

Functional traits are ecologically relevant as they influence how species respond to their abiotic and biotic environment (Díaz & Cabido, 2001; McGill *et al.*, 2006). However, even though trait data are becoming increasingly available, high-quality trait data for oceanic island floras are still scarce. Most studies have assessed trait-environment relationships on mainland systems by using the data from global trait databases (Kattge *et al.*, 2020), however, these databases have incomplete species coverage for oceanic islands.

This dissertation shows for the first time that scientific floras can be useful and reliable sources for some quantitative trait data of oceanic island floras **(Chapter 5)**. We used this knowledge to collect the first comprehensive data set of essential functional traits from scientific floras and species monographs in order to analyse functional trait patterns and drivers of an entire island flora **(Chapters 2, 3 and 6)**. Using alternative sources for trait data is important in order to avoid destructive trait data collection in the field and has become increasingly important during the global COVID-19 pandemic that has prevented many scientists from travelling and undertaking fieldwork. Hence, our research is the first step into sustainable and holistic functional island biogeography research. Nonetheless, I acknowledge that the results of **Chapter 5** also point to a need to conduct more fieldwork in order to fill the gaps and reduce bias in trait datasets. However, we can conclude that scientific floras remain irreplaceable resources in the research on functional island biogeography.

7.6 Climate change may alter the functional composition of oceanic island floras

Climate change is one of the major anthropogenic threats to biodiversity on oceanic islands (Fernández-Palacios *et al.*, 2021). Increasing temperatures and changes in precipitation patterns are expected to change the distribution and composition of species assemblages on islands (Harter *et al.*, 2015). However, it is, as yet, unclear which consequences climate change may have on the functional composition of oceanic island floras. This lack of knowledge is particularly critical as the low population and range sizes, together with the unique functional adaptations and island syndromes of plants may increase the vulnerability of island floras to climate change.

From the results presented in **Chapter 6**, I have found that precipitation is the major driver of plant distribution in the Canary Islands, which concurs with the results from **Chapters 2** and **4**. Furthermore, I found that functional adaptations to aridity, i.e. insular woodiness and succulence, are vital for the survival of island biota under changing climatic conditions. Interestingly, 80% of the insular lineages on the Canary Islands are woody, possibly due to an aridification event that started 7 Myr ago (Hooft van Huysduynen *et al.*, 2021). This high proportion of insular woody species may lead to a more robust climate change resilience of the Canary Islands flora than on other oceanic islands not defined by such a high proportion of insular woody species. Insular woody species have an advantage over their herbaceous continental ancestors in arid environments due to high wood density and avoidance of turgor loss that may lead to drought-induced embolisms (Lens *et al.*, 2016; Dória *et al.*, 2018). Our results align with those of the earliest notions in island biogeographic research, stating that woody species are better competitors on islands than herbaceous species (Darwin, 1859). Moreover, I found that succulent plants are more likely to increase their potential climatically suitable area on the Canary Islands by 2100 than non-succulent plants. Succulence is a trait of increasing importance because succulent plants generally have a higher water-use efficiency and are, therefore, better adapted to arid environments (Griffiths & Males, 2017). Even though the Canary Island flora is rich in insular woody and succulent species, climate change may greatly alter species assemblages throughout the Canary Islands. An overall functional homogenisation can be expected due to the irreversible loss of unique functional groups and niches that herbaceous and non-succulent native species possess. Hence, the stability and functions of ecosystems may change profoundly in the face of climate change (Olden *et al.*, 2004; Clavel *et al.*, 2011) in the Canary Islands. A possible functional homogenisation of the native flora is particularly relevant when considering alien species' relatively higher functional diversity under arid conditions (**Chapter 2**). My results indicate that functional diverse alien species assemblages would be expected to be more likely to outcompete native species in the future, a further indirect impact of climate change on island floras.

7.7 Emerging research questions in functional island biogeography

This dissertation offers the first step towards a trait-based understanding of the assembly of oceanic island floras. I have addressed several of the fundamental questions in island biology (Patiño *et al.*, 2017) and functional island biogeography (Ottaviani *et al.*, 2020; Schrader *et al.*, 2021) and have also formulated novel research questions that have, so far, not been raised despite their importance for a holistic understanding of patterns and drivers in island biodiversity. Nonetheless, many research questions on functional island biogeography and ecology remain unanswered, whilst several further open research questions have arisen as a consequence of my research. Thus, I would like to present the most prominent questions for future functional island biogeography and ecology research.

The choice of traits strongly influences the outcome of trait-based studies and is, therefore, of great importance (Zhu *et al.*, 2017; Mouillot *et al.*, 2021). As the sources for trait data are limited for island endemics, the choice of available traits in this dissertation was limited. More functional traits should be considered for future investigations, especially traits linked to island syndromes such as dispersal. Dispersal traits are relevant for island floras as insularity strongly affects the composition of dispersal traits (Gillespie *et al.*, 2012) and speciation rates on islands (Kisel & Barraclough, 2010). Moreover, below-ground traits, such as specific root length or mycorrhizal association, are of particular importance for resource-acquisition in plants and should therefore not be neglected in future research (Laliberté, 2017; Carmona *et al.*, 2021). Even though using traits from scientific floras and taxonomic monographs is a first step in the unravelling of research questions in functional island biogeography, we still lack empirical functional trait measurements for other ecologically meaningful functional traits (e.g. specific leaf area, stem specific density and seed mass). Hence, other plant functional traits should be systematically collected on oceanic islands to test whether our results are robust.

The functional composition of species can be strongly influenced by the evolutionary history of species (Weiher *et al.*, 1998). However, whether functional diversity can be used as a proxy for phylogenetic diversity is debatable (Winter *et al.*, 2013), particularly when considering that the morphological specialisation of species does not result in trait diversification, as I have shown for species native to the Canary Islands. A phylogenetic approach is especially relevant considering the relatedness of phylogenetic diversity to ecosystem functioning and services (Faith *et al.*, 2010). Hence, research on phylogenetic diversity in island biogeography should complement the trait-based research in order to better understand and conserve insular biodiversity. In particular, the evolutionary history of endemic species' ancestors should be further investigated to test which functional traits endemic species have developed. Such analyses should also provide good insights into the processes shaping the functional diversity of island floras.

In this dissertation, I have focussed on functional traits in order to analyse the influence of the abiotic environment on island floras. However, functional traits can also help to quantify biotic interactions (Schleuning *et al.*, 2015). For example, trait matching between plants and pollinators is essential for the structure and complexity of interaction networks (Maglianesi *et al.*, 2015; Dalsgaard *et al.*, 2021). It has been shown that a functional disruption of trophic interactions can impair ecosystem functioning (Schleuning *et al.*, 2015; Heinen *et al.*, 2020). Species interactions are particularly vulnerable in species-poor systems, such as those found on oceanic islands, as interaction diversity is low and vulnerable to disruptions (Traveset *et al.*, 2016). Hence, in order to conserve vital biotic interactions, it is necessary to understand how species interact using trait-based approaches.

Most of all, it is important to understand the influence of growing anthropogenic pressures on island floras. Recent anthropogenic environmental changes are likely to promote the rapid extinction of many endemic taxa, especially those with small population sizes (Caujapé-Castells *et al.*, 2010). Besides habitat loss and the intensification of land use, herbivores introduced to islands present the greatest threat to native island plants (Fernández-Palacios *et al.*, 2021). Therefore, which functional traits render native species more resistant to animal grazing should be investigated and how trait matching may influence these antagonistic interactions (Le Provost *et al.*, 2017). Furthermore, alien invasive plants threaten island floras (Kueffer *et al.*, 2010; Fernández-Palacios *et al.*, 2021). Even though invasive alien plants cause biodiversity losses on islands, it is still disputed as to which combination of functional traits makes an alien plant become invasive on oceanic islands. Hence, to conduct a robust risk assessment on invasive species, functional traits of species should be analysed in combination with anthropogenic disturbance regimes (Kueffer *et al.*, 2010).

I have analysed environmental and island biogeographical drivers of functional diversity across an entire archipelago. Nonetheless, the trait-based approach I developed in this dissertation is more widely applicable. Hence, the questions and hypotheses raised in this dissertation should also be applied to islands and archipelagos in other geographic regions. For example, a global analysis across oceanic islands could be conducted to study whether general climatic and biogeographic drivers of plant functional diversity can be identified. Studying global environmental drivers of functional trait diversity could further reveal essential insights into the impact of climate change on oceanic island floras (e.g. see Stewart *et al.*, 2022 for a study of global impacts of climate change on avian functional diversity).

7.8 Conclusion

In this dissertation, I have captured how biogeography and ecology influence the functional trait composition of island floras. Specifically, I have shown that functional diversity of native species assemblages does not necessarily increase with speciation. Moreover, I have shown that environmental filtering via water availability is the primary driver of interspecific trait convergence in plants native to the Canary Islands. High trait convergence in arid environments could pose a risk to native plants, considering that functionally diverse alien species assemblages are expected to spread under climate change-induced aridification on the Canary Islands. However, as an adaptation to arid environments, native species can develop high intraspecific variation in order to increase their fitness. Moreover, functional adaptations to aridity, such as insular woodiness and succulence, are overrepresented in the Canary Islands and could increase the resilience of the Canary Islands flora to climate change. Nonetheless, island endemic species have limited distributions and low population sizes, and the effect of insularity hinders their climate niche tracking. Overall, my dissertation has contributed to the knowledge of the integration of functional traits and island biogeography, and towards understanding the functional signatures of island plant species. This dissertation allows us to have a better understanding of how biodiversity responds to environmental change and how we can improve the conservation of unique, yet vulnerable, island floras. Due to the disproportionately large contribution of island floras to global biodiversity, the implications of this dissertation are highly relevant.

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Left photo: View of the Tabaibal-Cardonal vegetation zone with focus on a dragon tree (*Dracaena draco*) near El Palmar on La Palma, Canary Islands (own photo).

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Photo next page: Laurel forest in the Garajonay National Park on La Gomera (Canary Islands; own photo). The laurel forest on La Gomera is the most pristine laurel forest on the Canary Islands.

Summary

Oceanic islands only comprise a small amount of the Earth's land area but harbour a disproportionate amount of global biodiversity. This vast diversity is not only reflected in the taxonomic uniqueness of island biota but also in the remarkable evolution of functional traits. Functional traits, i.e. measurable characteristics that strongly influence the fitness of species, determine how a species responds to its environment and can help to gain more insights into the biogeographical, ecological and evolutionary processes that have shaped island biodiversity. However, research in island biogeography has primarily focused on species richness, and knowledge of functional trait patterns on oceanic islands is scarce. Hence, in this dissertation, I have explored how trait-based approaches can increase our understanding of how biodiversity on oceanic islands assembles and how it is driven by the environment. The Canary Islands (Spain) are a particularly suitable model system to investigate patterns and drivers of biodiversity. The archipelago is characterised by a high variation in environmental heterogeneity and inhabits a unique and well-described native flora. Therefore, I have investigated five principal research questions using the flora (Spermatophytes) of the Canary Islands as a study object. First, I have analysed how climate and biogeography shape the assembly of the Canary Islands flora using a novel trait-based approach. Second, the question of whether rare climates link to functional trait distinctiveness in the native Canary Islands flora was addressed. Third, I have examined how intraspecific trait variation is represented in the native flora of oceanic islands focusing on the succulent scrub of La Palma (Canary Islands). Fourth, this dissertation investigated whether scientific floras can be reliable sources for trait data of plants native to oceanic islands. Finally, I have explored how climate change may impact the native Canary Islands flora by analysing possible climate change-induced shifts in plant species distribution and plant traits.

The results of my dissertation expand the understanding of the importance of biogeography and the environment in determining the functional composition of island floras. I have assessed that traits of endemic plant species did not expand the functional trait space of the Canary Islands but were packed with the ones of non-endemic species. This result hints at a trait convergence in endemic species, possibly driven by non-adaptive speciation processes. Moreover, I have evidenced that humidity is a critical driver of functional diversity in native plant assemblages and particularly leads to a high trait convergence in arid environments via environmental filtering. In contrast, alien species have expanded the Canary Islands flora's functional trait space. I further have shown that in contrast to native species assemblages, alien species assemblages are characterised by an increasing functional diversity with increasing aridity. This contrasting pattern of functional diversity could pose a potential risk to the native flora of the Canary Islands as a low functional diversity is expected to reduce the resilience of species assemblages to the establishment of more functionally diverse alien plant species. However, in this dissertation, I also have revealed that endemic plant species on the Canary Islands show a high intraspecific variation in arid environments, possibly as an adaptation to environmental stress. Intraspecific variation could help endemic plant species have a competitive advantage over alien species and be more resilient to environmental changes. Furthermore, in this dissertation, I have shown that scientific floras and taxonomic monographs could be used to gain information on quantitative functional traits of plants native to oceanic islands. This finding is particularly relevant for advances in trait-based research, as coverage of trait data for oceanic island floras is extremely poor in global trait databases. Hence, for some of the studies included in this dissertation, trait data were retrieved from scientific floras and taxonomic monographs and used to answer novel scientific research questions. Thus, I have used trait data from the literature to analyse the effect of climate change on the range size of plants native to the Canary Islands. Identifying plant species of particular conservation concern is critical on oceanic islands as many island species have limited distributions and small population sizes, and their niche tracking is impeded by insularity. I have revealed that single-island endemic plants gain less and lose more climatically suitable areas than archipelago endemic and non-endemic native plants due to a climate change-induced decrease in precipitation until 2100. Moreover, I have assessed that insular woody and succulent plant species are more likely to gain more and lose less climatically suitable areas than herbaceous, non-insular woody and non-succulent species with ongoing climate change. Hence, this study strongly emphasises the conservation importance of single-island endemic species, which are not characterised by traits associated with water use efficiency. The results of this dissertation could also be critical to other oceanic island floras, particularly if they are predicted to experience a substantial decrease in precipitation in the future.

In my dissertation, I have shown that trait-based approaches are promising tools for studying patterns and drivers of island biodiversity. For this, I encourage future functional island biogeography and functional ecology research to expand to other geographic areas in order to assess the generality of the results and conclusions laid out in this dissertation. Moreover, I encourage the use and further development of the methodological approaches I have developed here to analyse drivers and patterns of oceanic island biodiversity. All in all, a trait-based perspective could reliably help to unravel how global change may impact island biodiversity. This knowledge could help to facilitate the conservation of the Earth’s unique yet vulnerable island flora.

Zusammenfassung

Ozeanische Inseln machen nur einen kleinen Teil der Landfläche der Erde aus, beherbergen aber einen unverhältnismäßig großen Teil der weltweiten Artenvielfalt. Diese enorme Vielfalt spiegelt sich nicht nur in der taxonomischen Einzigartigkeit der Inselbiota wider, sondern auch in der bemerkenswerten evolutionären Entwicklung funktionaler Merkmale. Funktionale Merkmale, d. h. messbare Eigenschaften, die die Fitness von Arten stark beeinflussen, bestimmen, wie eine Art auf ihre Umwelt reagiert. Sie können dazu beitragen mehr Erkenntnisse über die biogeographischen, ökologischen und evolutionären Prozesse zu gewinnen, die die biologische Vielfalt auf Inseln geprägt haben. Die Forschung im Bereich der Inselbiogeographie hat sich bisher jedoch in erster Linie auf den Artenreichtum konzentriert, und den Erkenntnisgewinn über funktionale Merkmalsmuster auf ozeanischen Inseln vernachlässigt. In dieser Dissertation habe ich daher untersucht, wie die Analyse funktionaler Merkmale unser Verständnis dafür verbessern kann, wie sich die biologische Vielfalt auf ozeanischen Inseln zusammengesetzt hat und von ihrer Umwelt beeinflusst wird. Die Kanarischen Inseln (Spanien) sind ein besonders geeignetes Modellsystem, um die Muster und Triebkräfte der biologischen Vielfalt zu untersuchen. Der Archipel zeichnet sich durch eine große Umweltheterogenität aus und beherbergt eine einzigartige und gut beschriebene einheimische Flora. Daher habe ich zur Analyse meiner Forschungsfragen die Flora (Spermatophyten) der Kanarischen Inseln als Studienobjekt herangezogen. Zuerst habe ich analysiert, wie Klima und biogeographische Faktoren die Zusammensetzung der kanarischen Flora beeinflussen, indem ich die funktionale Diversität der Artengemeinschaften entlang von Umweltgradienten untersucht habe. Zweitens hat sich diese Dissertation mit der Frage beschäftigt, ob seltene Klimazonen die funktionalen Merkmale der einheimischen Flora der Kanarischen Inseln beeinflussen. Drittens habe ich untersucht, wie sich die intraspezifische Merkmalsvariation in einer ozeanischen Inselflora darstellt. Um dieser Forschungsfrage nachzugehen, habe ich mich auf den Sukkulentenbusch von La Palma (Kanarische Inseln) konzentriert. Viertens habe ich in dieser Dissertation untersucht, ob wissenschaftliche Floren zuverlässige Quellen für Merkmalsdaten auf ozeanischen Inseln sein können. Zuletzt habe ich erforscht, wie sich der Klimawandel auf die einheimische Flora der Kanarischen Inseln auswirken könnte. Dafür habe ich Eigenschaften analysierte, die essenziell für Pflanzen auf ozeanischen Inseln sind, um auf Umweltveränderungen zu reagieren.

Um ökologische und biogeographische Prozesse zu identifizieren, die die funktionale Vielfalt von Pflanzenarten unterschiedlicher evolutionärer Herkunft auf den Kanarischen Inseln bestimmen, habe ich essenzielle funktionale Merkmale der Kanarenflora entlang eines Umweltgradienten und über geologische Zeitalter hinweg untersucht. Dazu habe ich Daten zu vier funktionalen Merkmalen (Pflanzenhöhe, Blattlänge, Blütenlänge und Fruchtlänge), die mit Ressourcenerwerb, Konkurrenzfähigkeit, Fortpflanzung und Ausbreitungsfähigkeit assoziiert sind, von 893 endemischen, nicht-endemisch einheimischen und gebietsfremden Pflanzenarten gesammelt. Die Daten zu diesen vier Eigenschaften stammen aus wissenschaftlichen Floren und taxonomischen Monographien, und decken ca. 43 % der kanarischen Flora ab. Anschließend habe ich diese Eigenschaften mit

Artverbreitungsdaten über ein Raster von 500 m x 500 m verknüpft, um die funktionale Vielfalt für endemische, nicht-endemisch einheimische und gebietsfremde Arten zu berechnen. Die Berechnung habe ich unter Verwendung mehrdimensionaler funktionaler Hypervolumina durchgeführt. Die daraus resultierenden Muster habe ich anschließend in Beziehung zu klimatischen (Feuchtigkeit) und biogeographischen Gradienten (geographische Isolation, topographische Komplexität und geologisches Alter) gesetzt. Die Ergebnisse haben gezeigt, dass sich der Merkmalsraum der endemischen und nicht-endemischen einheimischen Arten erheblich überlappt hat. Gebietsfremde Arten hingegen haben neue Merkmalskombinationen hinzugefügt, die den gesamten funktionalen Raum der Kanarischen Inseln vergrößert haben. Darüber hinaus habe ich herausgefunden, dass die funktionale Vielfalt der endemischen Pflanzen in geographisch isolierten und feuchten Rasterzellen am höchsten war. Die funktionale Vielfalt der nicht-endemisch einheimischen Pflanzengruppen war in weniger geographisch isolierten, aber ebenfalls feuchteren Rasterzellen am höchsten. Im Gegensatz dazu war die funktionale Vielfalt gebietsfremder Artengemeinschaften in trockenen Rasterzellen am höchsten. Die topographische Komplexität und das geologische Alter hatten nur einen untergeordneten Einfluss auf die funktionale Vielfalt der drei floristischen Gruppen. Zusammenfassend lässt sich sagen, dass endemische und nicht-endemische einheimische Inselarten ähnliche funktionale Merkmale besitzen, während gebietsfremde Arten dazu neigen, den funktionalen Raum in Ökosystemen, in die sie eingeführt worden sind, zu vergrößern. Die räumliche Verteilung der funktionalen Vielfalt floristischer Gruppen ist über die Umweltgradienten hinweg sehr unterschiedlich, was darauf hindeutet, dass Artengemeinschaften unterschiedlicher evolutionärer Herkunft in verschiedenen Lebensräumen funktional gedeihen.

Die derzeitigen Modelle der Inselbiogeographie behandeln die Arten so, als ob sie funktional gleichwertig wären und fokussieren sich in erster Linie auf den Artenreichtum. Daher ist die funktionale Zusammensetzung von Inselbiota im Verhältnis zu inselbiogeographischen Variablen noch weitgehend unbekannt. Unter Verwendung von Daten zu Pflanzeneigenschaften (Pflanzenhöhe, Blattfläche, Blütenlänge) haben wir für 895 endemische und nicht-endemische Arten auf den Kanarischen Inseln die funktionale Distinktivität dieser Eigenschaften quantifiziert. Daraufhin haben wir die funktionale Distinktivität mit der durchschnittlichen klimatischen Seltenheit des Verbreitungsgebiets jeder Art in Verbindung gebracht. Dies haben wir für jede Insel des Archipels gemacht, wobei wir die Ausprägung der funktionalen Merkmale und die klimatische Seltenheit mit dem Alter der Inseln in Beziehung gesetzt haben. Endemiten zeigten eine Beziehung zu klimatisch seltenen Lebensräumen, die mit den geologischen Veränderungen der Inseln im Laufe der Zeit übereinstimmen. Die Ausprägung der funktionalen Merkmale unterschied sich jedoch nicht zwischen Endemiten und Nicht-Endemiten und blieb mit dem Alter der Insel konstant. Es gibt demnach keinen Zusammenhang zwischen der Ausprägung von funktionalen Merkmalen und der Besiedlung seltener Klimazonen. Die Hypothesen, die wir hier aufstellen, sind vereinfacht und erfassen nicht alle möglichen Einflüsse und stochastischen Prozesse, die die Zusammensetzung funktionaler Merkmale bestimmen. Dennoch sehen wir dies als einen praktischen Schritt zur Integration funktionaler Merkmale in die Inseltheorie und zum Verständnis der funktionalen Merkmale von Inselarten.

Sowohl der Artenwechsel als auch die intraspezifische Merkmalvariation können die Dynamik von Pflanzengemeinschaften entlang von Umweltgradienten beeinflussen. In meiner Dissertation habe ich untersucht, wie sich die Muster von Pflanzengemeinschaften in Bezug auf den Artenwechsel und die intraspezifische Variation zwischen endemischen und nicht-endemische Arten unterscheiden. Dazu habe ich die Hypothese aufgestellt, dass endemische Arten eine geringere intraspezifische Variation aufweisen als nicht-endemische Arten. Endemische Arten neigen dazu hohe Raten an *in situ* Speziation aufzuweisen. Dagegen ist bei nicht-endemischen Arten davon auszugehen ist, dass diese einen größeren Genpool haben und somit eine höhere phänotypische Plastizität. Um diese Hypothese zu überprüfen, habe ich 44 Probenahmestellen auf La Palma (Kanarische Inseln) entlang eines Gradienten für Niederschlag, Wärmebelastung, Bodenstickstoff, Phosphor und pH-Wert eingerichtet. Entlang dieses Gradienten habe ich die Abundanz der Arten geschätzt und drei Eigenschaften (Pflanzenhöhe, Blattfläche und Blattdicke) an mehrjährigen endemischen und nicht-endemischen Pflanzenarten gemessen. Insgesamt habe ich die Eigenschaften für 1.223 Pflanzenindividuen von 43 Arten erfasst. Anschließend habe ich die gemeinschaftsgewichteten Mittelwerte der Eigenschaften berechnet, um den relativen Beitrag des Artenwechsels, der intraspezifischen Variation und deren Kovariation entlang des untersuchten Gradienten zu messen. Der Beitrag der intraspezifischen Variation zur Gesamtvariation war ähnlich in endemischen und nicht-endemischen Artengemeinschaften. Bei der Pflanzenhöhe erklärte die intraspezifische Variation ungefähr so viel Variation wie der Artenwechsel. Bei der Blattfläche und der Blattdicke erklärte die intraspezifische Variation fast keine Variation. Die Auswirkungen des Artenwechsels waren hauptsächlich für die Merkmalsreaktionen entlang des Umweltgradienten ausschlaggebend. Allerdings war die intraspezifische Variation wichtig für die Reaktionen der Blattfläche auf Niederschläge. Trotz ihrer unterschiedlichen Evolutionsgeschichte zeigen endemische und nicht-endemische Pflanzengemeinschaften ähnliche Muster in Bezug auf den Artenwechsel und die intraspezifische Variation. Unsere Ergebnisse deuten darauf hin, dass der Artenwechsel die Hauptkomponente der Merkmalsvariation im zugrunde liegenden Studiensystem ist. Allerdings kann die intraspezifische Variation die Fitness der einzelnen Arten als Reaktion auf Niederschläge erhöhen. Insgesamt stellt unsere Studie die Theorie in Frage, dass die intraspezifische Merkmalsvariation für die Etablierung nicht-endemischer Arten wichtiger ist als für endemische Arten.

Merkmalsbasierte Herangehensweisen gewinnen in der Ökologie und Biogeographie zunehmend an Bedeutung. Fortschritte werden jedoch häufig durch die fehlende Verfügbarkeit von qualitativ hochwertigen quantitativen Merkmalsdaten, die im Feld erhoben wurden, verhindert. Zu den alternativen Quellen für Merkmalsdaten gehören wissenschaftliche Floren und taxonomische Monographien. Deswegen haben wir die Zuverlässigkeit und Nützlichkeit von Merkmalsdaten aus wissenschaftlichen Floren im Vergleich zu Merkmalsdaten, die im Feld gemessen wurden, und denen in TRY, der umfassendsten Datenbank für Pflanzeneigenschaften, getestet. Wir haben die Blattfläche und die spezifische Blattfläche von 451 Gefäßpflanzenarten, die auf Teneriffa und La Palma (Kanarische Inseln, Spanien) einheimisch sind, im Feld gemessen. Anschließend haben wir diese Daten mit entsprechenden Merkmalsdaten aus dem neusten und umfassendsten Führer der kanarischen Flora, sowie Daten aus TRY, verglichen. Wir haben die vor Ort gemessenen Eigenschaften mit ihren aus der Literatur geschätzten Äquivalenten regressiert und die Regressionsmodelle der einen Insel verwendet, um die Merkmalswerte der anderen Insel vorherzusagen. Für die Blattfläche haben die linearen Modelle eine gute Übereinstimmung zwischen den Werten aus der wissenschaftlichen Flora und den im Feld gemessenen Werten gezeigt ($R^2 = 0,86$). Diese Modelle waren räumlich über die Inseln hinweg übertragbar. Im Gegensatz dazu konnte für die spezifische Blattfläche nur eine schwache Beziehung zwischen den im Feld gemessenen Werten und den besten Schätzungen aus der wissenschaftlichen Flora festgestellt werden ($R^2 = 0,11$). In der TRY-Datenbank waren für unser Untersuchungsgebiet nicht genügend Daten verfügbar, um Merkmalskorrelationen mit anderen Datenquellen zu berechnen. Wir schließen daraus, dass wissenschaftliche Floren als nützliche Datenquellen für manche quantitative Pflanzeneigenschaften dienen können. Die TRY-Datenbank enthält viele Eigenschaften, ist aber in Bezug auf die Artenabdeckung für unser Untersuchungsgebiet und für ozeanische Inseln im Allgemeinen unvollständig.

Ozeanische Inseln besitzen eine einzigartige Flora mit einem hohen Anteil an endemischen Arten im Verhältnis zu ihren kleinen Landflächen. Es ist davon auszugehen, dass diese einzigartige Flora durch die sich ändernden klimatischen Bedingungen stark beeinträchtigt wird. Arten auf Inseln haben nämlich nur ein begrenztes Verbreitungsgebiet und kleine Populationsgrößen. Darüber hinaus müssen sich Inselarten den Begrenzungen der Insel stellen und können ihre klimatische Nische nur eingeschränkt verfolgen. Deswegen habe ich in dieser Dissertation untersucht, wie sich der Klimawandel auf die Verbreitungsgebiete von Pflanzen auf ozeanischen Inseln auswirkt, um besonders schützenswerte Arten zu identifizieren. Ich habe Daten über das Vorkommen von endemischen und nicht-endemischen Pflanzenarten der Kanarischen Inseln, die ~71 % ($n = 503$ Arten) der einheimischen Flora repräsentieren, mit Daten über aktuelle und zukünftige klimatische Bedingungen kombiniert. Anschließend habe ich Bayes'sche additive Regressionsbäume verwendet, um die Auswirkungen des Klimawandels auf die Ausbreitung der Arten zu bewerten. Um die Wechselwirkungen zwischen dem Klimawandel und den funktionalen Merkmalen der Pflanzen zu untersuchen, habe ich Daten zur holzigen Beschaffenheit und Sukkulenz gesammelt. Die Modelle haben prognostiziert, dass endemische Arten, die nur auf einer Insel vorkommen, einen größeren Anteil ihrer klimatisch geeigneten Fläche verlieren werden ($\tilde{x} = -0,36$) als endemische Arten, die auf mehreren Inseln vorkommen ($\tilde{x} = -0,28$), oder nicht-endemische einheimische Arten ($\tilde{x} = -0,26$). Dieser Trend betrifft insbesondere Lanzarote und Fuerteventura, für die in Zukunft ein hoher Rückgang der jährlichen Niederschläge erwartet wird. Darüber hinaus habe ich festgestellt, dass krautige Arten, die nur auf einer Insel endemisch sind, weniger an klimatisch geeigneten Gebieten gewinnen und mehr verlieren werden als holzige Inselarten. Im Gegensatz dazu habe ich festgestellt, dass sukkulente inselendemische Arten und nicht-endemische einheimische Arten mehr an klimatisch geeigneten Flächen gewinnen und weniger verlieren. Mit dieser Studie betone ich die Bedeutung der Erhaltung aller einheimischen Arten, insbesondere aber der endemischen Arten, die nur auf einer Insel vorkommen, und sich nicht durch Eigenschaften auszeichnen, die mit einer effizienten Wassernutzung verbunden sind. Die Ergebnisse sind besonders kritisch für andere ozeanische Inselfloren, die eine nicht so große Vielfalt von verholzenden Inselarten wie auf den Kanarischen Inseln besitzen.

Diese Dissertation ist der erste Schritt zu einem merkmalsbasierten Verständnis von ozeanischen Inselfloren. Ich habe mehrere grundlegende Fragen der Inselbiologie und der funktionalen Inselbiogeographie aufgegriffen und darüber hinaus neue Forschungsfragen formuliert, die trotz ihrer Bedeutung für ein ganzheitliches Verständnis von Mustern und Triebkräften der Inselbiodiversität bisher nicht gestellt wurden. Durch meine Dissertation haben sich jedoch auch neue wichtige Fragen für die künftige Forschung im Bereich der funktionalen Inselbiogeographie und -ökologie herausgestellt. Zum einen sollten künftige Untersuchungen mehr funktionale Merkmale in Betracht ziehen, um zu prüfen, ob die Ergebnisse dieser Dissertation robust sind. Insbesondere Eigenschaften, die für die Ausbreitung von Arten und den Ressourcenerwerb essenziell sind, sollten nicht vernachlässigt werden. Zum anderen sollte weiter untersucht werden, inwiefern die Evolutionsgeschichte von einheimischen Inselarten deren funktionale Zusammensetzung beeinflusst. Außerdem sollte zukünftig analysiert werden, inwiefern funktionale Merkmale dabei helfen können, wichtige biotische Interaktionen zu quantifizieren und zu erhalten. Vor allem ist es jedoch wichtig den Einfluss des zunehmenden anthropogenen Drucks auf die Flora von ozeanischen Inseln zu verstehen, da anthropogene Umweltveränderungen wahrscheinlich das rasche Aussterben vieler endemischer Taxa begünstigen werden. Zuletzt sollten zukünftige Studien die in dieser Dissertation aufgeworfenen Fragen und Hypothesen auf Inseln und Archipele in anderen geographischen Regionen übertragen. Durch einen solchen makroökologischen Ansatz würde sich untersuchen lassen, ob allgemeine klimatische und biogeographische Faktoren bestehen, die die funktionale Vielfalt von Pflanzen beeinflussen.

Die Ergebnisse dieser Dissertation zeigen, dass merkmalsbasierte Ansätze vielversprechende Instrumente für die Untersuchung von Mustern und Triebkräften der biologischen Vielfalt von Inseln sind. Aus diesem Grund ermutige ich künftige Forschungsarbeiten zur funktionalen Inselbiogeographie und funktionalen Ökologie auf andere geografische Gebiete auszudehnen, um die Allgemeingültigkeit der in dieser Dissertation dargelegten Ergebnisse und Schlussfolgerungen zu bewerten. Darüber hinaus ermutige ich die Verwendung und Weiterentwicklung der hier entwickelten methodischen Ansätze zur Analyse der Triebkräfte der biologischen Vielfalt von Inseln. Alles in allem könnte eine merkmalsbasierte Perspektive dazu beitragen, die Auswirkungen des globalen Wandels auf die biologische Vielfalt von Inseln zuverlässig zu entschlüsseln. Dieses Wissen könnte dazu beitragen, die Erhaltung der einzigartigen, aber gefährdeten, Inselflora dieser Erde zu erleichtern.

Appendices

Left photo: View of the *Risco de Famara* on Lanzarote (Canary Islands; own photo). Due to the topographic complexity and moist conditions the Famara massif is a biodiversity hotspot on Lanzarote

Declaration of own contribution

Manuscript 1: Hanz, D.M., Cutts, V., Barajas-Barbosa, M.P., Algar, A.C., Beierkuhnlein, C., Fernández-Palacios, J.M., Field, R., Kreft, H., Steinbauer, M., Weigelt, P. & Irl, S.D.H. (2022) Climatic and biogeographical drivers of functional diversity in the flora of the Canary Islands. *Global Ecology and Biogeography*, 31(7), 1313-1331. DOI: https://doi.org/10.1111/geb.13507

Personal contribution: I analysed the data, generated the results, prepared the text of the manuscript, and coordinated and integrated the author's contributions. I conceived the ideas with Carl Beierkuhnlein and Severin Irl. I collected the data together with Marth Paola Barajas-Barbosa and Severin Irl.

Manuscript 2: Cutts, V., Hanz, D.M., Barajas-Barbosa, M.P., Schrodt, F., Steinbauer, M., Beierkuhnlein, C., Denelle, P., Fernández-Palacios, J.M., Gaüzère, P., Grenié, M., Irl, S.D.H., Kraft, N., Kreft, H., Maitner, B., Munoz, F., Thuiller, W., Violle, C., Weigelt. P., Field, R. & Algar, A. (in review) Links to rare climates do not translate into distinct traits for island endemics. *Ecology Letters*

Personal contribution: I contributed to the conceptualization of the article as well as the data collection. I further discussed the results and commented on the manuscript.

Manuscript 3: Hanz, D.M., Beloiu, M., Wipfler, R., Beierkuhnlein, C., Field, R., Jentsch, A., Vetaas, O.R., Irl, S.D.H. (2022) High species turnover and low intraspecific trait variation in endemic and non-endemic plant species assemblages on an oceanic island. *Journal of Vegetation Science*, 33(1), e13120. DOI: https://doi.org/10.1111/jvs.13120

Personal contribution: I analysed the data, generated the results, prepared the text of the manuscript, and coordinated and integrated the author's contributions. Together with Mirela Beloiu, Raja Wipfler, Carl Beierkuhnlein and Severin Irl I conceptualized the manuscript. Together with Mirela Beloiu and Raja Wipfler I gathered the data for the manuscript.

Manuscript 4: Cutts, V., Hanz, D.M., Barajas-Barbosa, M.P., Algar, A.C., Steinbauer, M., Irl, S.D.H., Kreft, H., Weigelt, P., Fernández-Palacios, J.M., Field, R. (2021) Scientific floras can be reliable sources for some trait data in a system with poor coverage in global trait databases. *Journal of Vegetation Science*, 32(3), e12996. DOI: https://doi.org/10.1111/jvs.12996

Personal contribution: I contributed to the conceptualization of the article as well as the data collection. I further discussed the results and commented on the manuscript.

Manuscript 5: Hanz, D.M., Cutts, V., Barajas-Barbosa, M.P., Algar, A.C., Beierkuhnlein, C., Fernández-Palacios, J.M., Field, R., Kreft, H., Steinbauer, M., Weigelt, P., Irl, S.D.H. (in preparation) Effects of climate change on range size and functional traits of the Canary Islands' flora. ***Diversity and Distributions***

Personal contribution: I gathered and analysed the data, generated the results, prepared the text of the manuscript, and coordinated and integrated the author's contributions. Manuel Steinbauer, Dirk N. Karger, Severin Irl and I conceived the ideas.

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