Global Ecology and Biogeography · A Journal of Macroecology · WILEY

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

Dagmar M. Hanz[1] | Vanessa Cutts[2] | Martha Paola Barajas-Barbosa[3,4,5] | Adam C. Algar[6] | Carl Beierkuhnlein[7,8,9] | José-María Fernández-Palacios[10] | Richard Field[2] | Holger Kreft[3] | Manuel J. Steinbauer[8,11,12] | Patrick Weigelt[3] | Severin D. H. Irl[1,8]

[1]Biogeography and Biodiversity Lab, Institute of Physical Geography, Goethe-University Frankfurt, Frankfurt am Main, Germany

[2]School of Geography, University of Nottingham, Nottingham, UK

[3]Biodiversity, Macroecology and Conservation Biogeography Group, Faculty of Forest Sciences and Forest Ecology, University of Göttingen, Göttingen, Germany

[4]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

[5]Department of Computer Science, Martin Luther University Halle-Wittenberg, Halle, Germany

[6]Department of Biology, Lakehead University, Thunder Bay, Ontario, Canada

[7]Department of Biogeography, University of Bayreuth, Bayreuth, Germany

[8]BayCEER, Bayreuth Centre of Ecology and Environmental Research, University of Bayreuth, Bayreuth, Germany

[9]GIB Geographical Institute Bayreuth, Bayreuth, Germany

[10]Island Ecology and Biogeography Group, Instituto Universitario de Enfermedades Tropicales y Salud Pública de Canarias, Universidad de La Laguna, Tenerife, Spain

[11]Department of Sport Science, University of Bayreuth, Bayreuth, Germany

[12]Department of Biological Sciences, University of Bergen, Bergen, Norway

Correspondence
Dagmar M. Hanz, Biogeography and Biodiversity Lab, Institute of Physical Geography, Goethe-University Frankfurt, Altenhöferallee 1, 60438 Frankfurt am Main, Germany.
Email: hanz@geo.uni-frankfurt.de

Funding information
Deutsche Forschungsgemeinschaft, Grant/Award Number: RTG 1644 and FOR 2716

Handling Editor: Jonathan Davies

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.

1 | INTRODUCTION

Functional traits determine the responses of species 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). Functional traits not only help us to understand how environmental processes have influenced the ecological strategies of species, but also can inform about how evolutionary conditions have led to adaptation and specialization of species, especially in oceanic archipelagos (Whittaker et al., 2014). However, studies on the functional diversity of oceanic island floras that apply island biogeographical 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 how functional diversity patterns compare between islands (Ottaviani et al., 2020; Patiño et al., 2017; 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, 2018; Blonder et al., 2014). On the one hand, expansion of the functional trait volume of an assemblage with increasing species richness might 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 specialization or greater overlap of ecological niches (Klopfer & MacArthur, 1961; Pigot et al., 2016). Thus, measuring functional

diversity might help us to gain a better understanding of 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 (Kier et al., 2009; Kreft et al., 2008; Taylor et al., 2019). Oceanic islands harbour species that have colonized from the mainland, overcoming strong dispersal filters, and eventually evolved or even diversified into endemic species (Stuessy et al., 2006). This evolution in isolation might 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 (Fernández-Palacios, Kreft, et al., 2021; Macinnis-Ng et al., 2021; Veron et al., 2019). Given the high, possibly unique, trait diversity on oceanic islands and its inherent vulnerability, it is important to understand how endemic species, non-endemic native species and alien species are distributed in space and the nature of their adaptations to island environments.

Oceanic islands, and in particular islands of volcanic origin, are often distinguished by highly heterogeneous environments with distinct orographic precipitation regimes over short geographical distances (Kier et al., 2009; Weigelt et al., 2013). Water availability is a well-known driver of functional diversity and species richness (Poorter et al., 2010; Wright et al., 2007). In arid conditions,

HANZ ET AL.

Global Ecology
and **Biogeography**

A Journal of
Macroecology

WILEY | 1315

functional diversity tends to be low, because 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 et al., 2019). Thus, dry environments should select species with water-efficient traits, such as smaller statures, leaves and flowers (Kuppler & Kotowska, 2021; Moles et al., 2009; Wright et al., 2017). However, other mechanisms, such as the limiting similarity of coexisting species (MacArthur & Levins, 1967), can shape the distribution of trait values. In contrast, the distribution of alien species on oceanic islands is determined mainly by their pathway of introduction (Pauchard et al., 2009). Alien species decline from low elevations, where they have been introduced predominantly, to high elevations owing 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 in arid conditions, because species with narrow climatic niches tend to be filtered out selectively along a humidity gradient (Alexander et al., 2011; Irl et al., 2021).
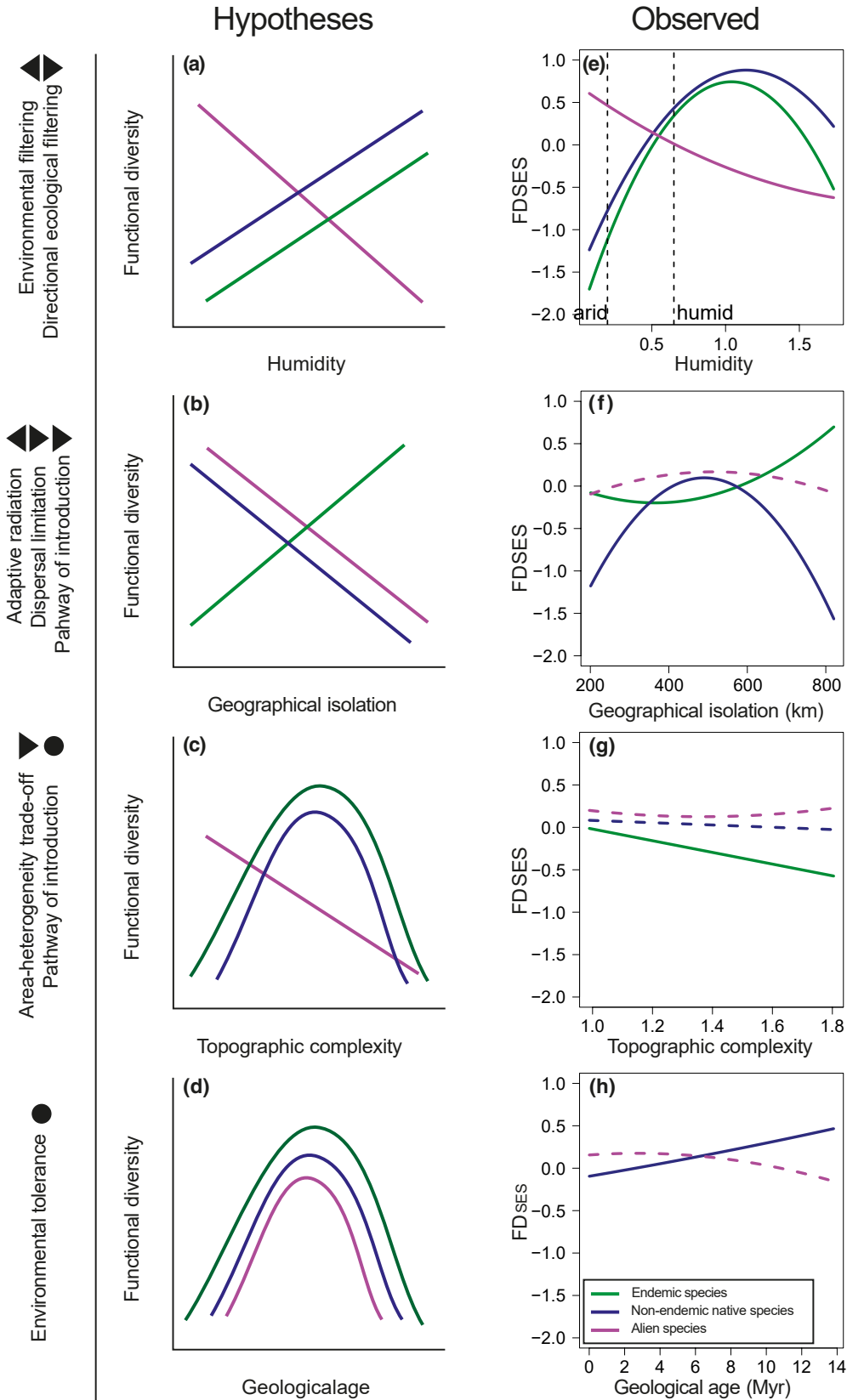
Island biogeographical models predict that diversity of species assemblages on oceanic islands varies in relationship to isolation, area and island age as a result of immigration, speciation and extinction (MacArthur & Wilson, 1967; Schrader et al., 2021; Whittaker et al., 2008). The models suggest that isolated areas are less diverse in species owing to reduced dispersal probability with greater distance to the mainland, influencing the chance of colonization (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, because tall and small-seeded species can disperse their diaspores further owing to their lower settling velocity (Greene & Johnson, 1993; Thomson et al., 2011; Venable & Brown, 1988). Hence, it can be expected that plant height and diaspore size of colonizers (i.e., non-endemic native species) are more similar in isolated habitats, because primarily species with similar trait combinations might reach those habitats. Functional diversity of endemic species should increase with isolation relative to species richness, because speciation rates should be higher where colonizing assemblages are disharmonic (König et al., 2020). 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 (Steinbauer et al., 2012; Whittaker & Fernández-Palacios, 2007). Hence, adaptive speciation might 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 also profit from unoccupied niches, 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).

Likewise, 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 homogenization through hybridization; Herrera & Bazaga, 2008), possibly leading to an increase of functional diversity. Moreover, it has been shown that topography predicts habitat diversity (Barajas-Barbosa et al., 2020; Keppel et al., 2016), 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 because the effective area of individual habitats is reduced, especially for species with narrow niches (Allouche et al., 2012). Given that flat environments have low habitat diversity and topographically complex environments have limited effective area per habitat, functional diversity of native assemblages might have a unimodal relationship with topographic complexity. Alien species are more likely to be subject to directional ecological filtering, because human introduction to easily accessible areas might so far have impeded colonization of topographically complex areas on oceanic islands (Alexander et al., 2011; Steinbauer et al., 2017).

We also 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 can act as an ecological filter on functional properties of plants (Laliberté et al., 2013; Lambers et al., 2008). Hence, we expect species assemblages in early and late successional stages to be functionally less diverse relative to species richness owing to lower geological heterogeneity and nutrient depletion on very young and old sites.

In this study, we analyse how the functional diversity of endemic, non-endemic native and alien assemblages changes across ecological gradients, using a 500 m × 500 m gridded distribution dataset for the flora of the Canary Islands (Figure 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 1a). For alien assemblages, we expect the pattern to be the opposite, owing to the introduction of alien species to arid coastal environments and the subsequent directional ecological filtering (Figure 1a). Second, we analyse whether the mechanisms invoked by classical island biogeographical theory predict variation in functional diversity relative to species richness. Based on theory, we expect a positive relationship between functional diversity and geographical

Hypotheses

Observed

(a) Functional diversity vs Humidity

(e) FDSES vs Humidity (arid / humid)

(b) Functional diversity vs Geographical isolation

(f) FDSES vs Geographical isolation (km)

(c) Functional diversity vs Topographic complexity

(g) FDSES vs Topographic complexity

(d) Functional diversity vs Geological age

(h) FD$_{SES}$ vs Geological age (Myr)

Legend: Endemic species; Non-endemic native species; Alien species

Row labels (left margin):
- Environmental filtering / Directional ecological filtering
- Adaptive radiation / Dispersal limitation / Pathway of introduction
- Area-heterogeneity trade-off / Pathway of introduction
- Environmental tolerance

isolation for endemic assemblages and a negative relationship for non-endemic native and alien assemblages (Figure 1b). We also expect a hump-shaped relationship with topographic complexity for endemic and non-endemic native assemblages and a negative relationship for alien assemblages (Figure 1c). Finally, we expect a hump-shaped relationship between functional diversity and geological age for endemic, non-endemic native and alien assemblages (Figure 1d).

FIGURE 1 (a–d) Hypothesized and (e–h) observed relationships of standardized effect sizes of functional diversity (FD$_{SES}$) for endemic (green), non-endemic native (blue) and alien (violet) plant species assemblages, based on 500 m × 500 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 and Figure 4). The mechanisms on which we based our hypotheses are indicated on the left-hand side of the figure. Triangles indicate either a hypothesized increase or decrease of FD$_{SES}$ along the respective environmental gradient. Circles indicate a hypothesized unimodal relationship of FD$_{SES}$ along the respective environmental gradient
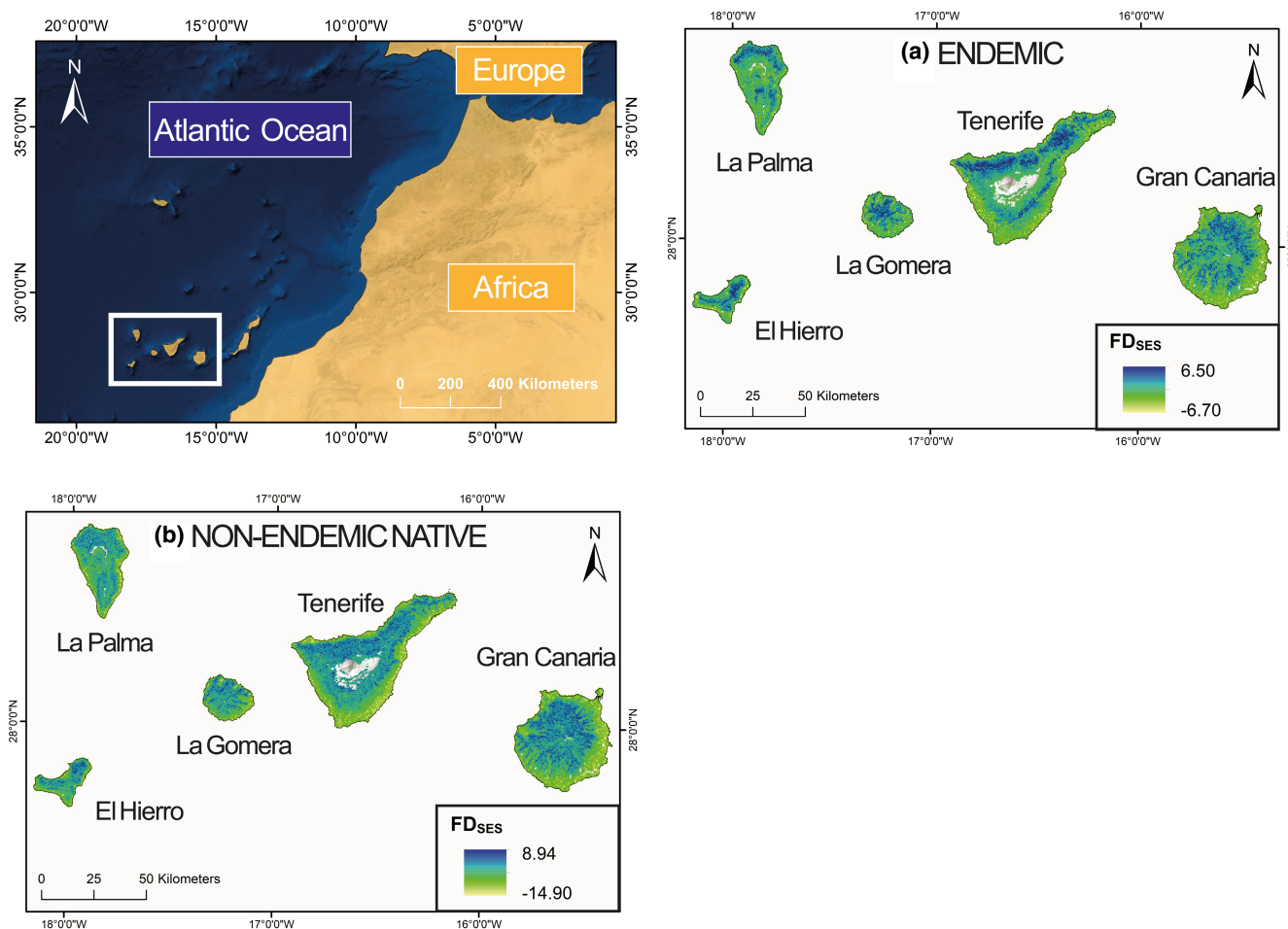
FIGURE 2 Map of the spatial distribution of modelled standardized effect size of functional diversity (FD$_{SES}$) values per 500 m × 500 m across the five studied Canary Islands for (a) endemic and (b) non-endemic native assemblages. Source of general map: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN and the GIS User Community

2 | METHODS

2.1 | Study area

We tested our hypotheses using the Flora of the Canary Islands (excluding Fuerteventura and Lanzarote owing to underrepresented species occurrence data from very limited sampling; Figure 2). The Canary Islands are an active volcanic archipelago characterized 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 1). The high-elevation alpine ecosystems of La Palma and Tenerife are the most environmentally isolated, because 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 1). Owing to high volcanic activity, each island is composed of older eroded terrain units and younger parts, leading to great variation

TABLE 1 Climatic and biogeographical 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 the mean annual precipitation in relationship 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 three- and two-dimensional surface area. We derived the 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 species analysed per island and the respective percentage of endemic, non-endemic native and alien plant species.

in topographic complexity, especially on emerging islands, such as La Palma and Tenerife (Table 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 1).

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 15th 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, because large villages and agricultural settings are located mainly near the coast, and human population density becomes low above 1,000 m a.s.l. (Arévalo et al., 2005). Currently, the Canary Island flora encompasses *c.* 2,000 species, of which roughly a third of the species are endemic, non-endemic native and alien species, respectively (Acebes Ginovés et al., 2009).

2.2 | Species occurrences and species distribution models

We collected occurrence data from Atlantis 3.3, an open-access database for all seed plant species, in a raster of 500 m × 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., 2016). Therefore, we also interpolated species occurrences using species distribution models (SDMs; Calabrese et al., 2014), which were parameterized following Irl et al. (2020) (see Supporting Information Appendix S1). 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.

2.3 | 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 digitized plant specimens and extracted from descriptions of the species (a list of the data sources is given in Appendix 1; for further information, see Supporting Information Appendix S2). We collected data on maximum trait values from floras, because the expected maximum at maturity reflects responses of the fitness of species 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 because it affects the ability of a plant 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, because leaves need to be supplied with water without risking a xylem embolism (hydraulic limitation hypothesis; Moles et al., 2009; Ryan et al., 2006). Furthermore, plant height is more positively associated than seed mass with the seed dispersal distance of species (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 (Cutts et al., 2021; Shi et al., 2019). Leaf size has important consequences for the energy and water balance of plants

(Parkhurst & Loucks, 1972). Smaller leaves are more water efficient, because they cool down more quickly and maintain lower leaf temperatures (Leigh et al., 2016). Larger leaves with a less efficient energy exchange capacity are more beneficial in humid habitats because they have higher photosynthetic capacities while being able to provide enough water for sufficient transpirational cooling (Parkhurst & Loucks, 1972). For stem-photosynthesizing 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, because flower petals can transpire significant amounts of water (Roddy, 2019; Roddy et al., 2016). 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 (Muñoz et al., 2017; Rossetto & Kooyman, 2005; Wheelwright, 1993) and can inform about the dispersal probability and seedling survival of the plant (Greene & Johnson, 1993; Moles & Westoby, 2004; Thompson et al., 1993; Venable & Brown, 1988). In long-term isolated habitats, plants tend to have larger seeds to increase their establishment and persistence, but also to decrease their dispersal ability (Kavanagh & Burns, 2014; 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 standardized 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 $r < .33$ in all cases).

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 because it classifies the type of climate in relationship 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 (Zarch et al., 2015). Humidity index ranged approximately from 0.07 (arid) to 2.05 (humid) across the five islands (Table 1; see Supporting Information Appendix S3, Figure S3.1a).

We also 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 had a mean annual temperature within 1°C, following Steinbauer et al. (2016). Geographical isolation of the island grid cells ranged from 196.5 to 885 km to the closest continental grid cell with similar environmental conditions (Table 1; see Supporting Information Appendix S3, Figure S3.1b).

We calculated topographic complexity per grid cell because 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 1; see Supporting Information Appendix S3, Figure S3.1c).

Furthermore, we calculated geological age per grid cell because it represents a proxy for plant nutrient availability (Laliberté et al., 2013; Lambers et al., 2008), 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, whereas phosphorus is derived from rock weathering and declines as soils age (ecosystem regression; Laliberté et al., 2013; Lambers et al., 2008; 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). The mean geological age per grid cell ranged from 6 kyr to 13.8 Myr (Table 1; see Supporting Information Appendix S3, Figure S3.1d).

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 standardization, we calculated correlation coefficients (Pearson's r) between the environmental variables, in addition to elevation (see Supporting Information Appendix S3, Table S3.1). Humidity was highly correlated with geographical isolation (Pearson's $r = .80$, $p < .001$) and elevation (Pearson's $r = .72$, $p < .001$).

2.5 | Functional diversity of oceanic island floras

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 to establish whether 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 recognizes 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 (2× 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% of the estimated probability density was 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 were not sensitive to species richness, we compared the functional diversity values of every floristic group with null-model expectations (for relationships between functional diversity and species richness, see Supporting Information Appendix S4). Therefore, we calculated values from 10 sets of randomized assemblages created with the "quasiswapcount" algorithm ("vegan" package; Oksanen et al., 2017), 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 the species richness of grid cells. We computed the standardized effect size of functional diversity (FD_{SES}) as follows: $FD_{SES} = (FD - \text{mean randomized } FD)/SD$ of randomized FD. Values of FD_{SES} lower than zero indicate functional clustering (FD lower than expected for a given species richness), whereas values of FD_{SES} higher than zero suggest functional overdispersion (FD higher than expected for a given species richness), and values of FD_{SES} approximately equal to zero indicate a random functional structure.

2.6 | Phylogenetic signal at the genus and assemblage levels

Given that the floristic groups could be structured phylogenetically (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 super-tree of seed plants (Smith & Brown, 2018). Given that 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 Supporting

Information Appendix S5, Figure S5.4). 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 with the signal under a Brownian motion model of trait evolution on a phylogeny (Blomberg et al., 2003). Values of *K* closer to zero correspond to a random or convergent pattern of evolution, whereas values of *K* greater than one 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.

2.7 | Statistical analyses

We ran generalized 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 of all explanatory variables, because traits do not necessarily change in a linear manner along environmental gradients. We ran an initial full model including all four environmental variables but excluding elevation owing to collinearity with humidity and geographical isolation. We ran additional models that excluded either humidity or geographical isolation owing to collinearity. Subsequently, we chose a model selection procedure, based on minimizing the Akaike information criterion (AIC; Burnham & Anderson, 2002). We performed AIC model selection using the function *dredge* in the R package MuMIn (Barton, 2022) to obtain the overall best model. Given that 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 because they accounted best for the spatial structure in the analysed dataset (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 and for the GLM and SAR residuals are provided in the Supporting Information (Appendix S6, Figure S6.5). All analyses were performed using R v.3.6.2 (R Core Team, 2020).

3 | RESULTS

Some alien species had trait values outside the range of traits of endemic and non-endemic native species and expanded the trait space of the Canary Islands within all trait dimensions. Around 27% of the functional trait space of alien species was shared by endemic species, and c. 28% of the functional trait space of aliens was 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 3).

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; Figures 1e and 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; Figures 1f and 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; Figures 1g and 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 increased linearly, whereas occurrence-based FD_{SES} of alien assemblages decreased non-significantly (Table 2; Figures 1h and 4). Hence, the functional diversity of endemic assemblages was highest on the more humid and isolated north-eastern slopes in less topographically complex habitats. Likewise, 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 4).

In the models excluding humidity, geographical isolation had a stronger explanatory power for functional diversity of endemic, non-endemic native and alien assemblages (see Supporting Information Appendix S6, Table S6.2; Figure S6.6). However, overall model fit according to AIC and explained variance was better for the models that included all environmental variables in comparison 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).

The FD_{SES} patterns of the modelled data were broadly consistent with the occurrence-based FD_{SES} models (see Supporting Information Appendix S6, Table S6.3; Figures S6.7 and S6.8). 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 used only for graphical illustration of endemic and non-endemic assemblages (see Figure 2) and not discussed further in this study.

Spatial autoregressive models were selected over GLMs because they improved model fit consistently. According to the R^2, accounting for spatial structure increased the explained variation between 41% (for alien assemblages) and 26% (for endemic assemblages; Table 2; see Supporting Information Appendix S6, Table S6.3 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: $K = 2.57$, $p < .001$; alien: $K = 1.90$, $p < .001$; see Supporting Information Appendix S6, Table S6.4). 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: $K = 0.58$, $p < .05$; non-endemic native: $K = 0.26$, $p < .05$) and fruit length (endemic: $K = 0.81$, $p < .05$; non-endemic native: $K = 0.25$, $p < .05$; alien: $K = 0.43$, $p < .001$). Blomberg's K did not show any statistical significance in flower length across the floristic groups.

Occurrence-based FD_{SES} had a slightly positive correlation with the phylogenetic diversity of endemic and non-endemic native assemblages (endemics: Pearson's $r = .23$, $p < .001$; non-endemic natives: Pearson's $r = .25$, $p < .001$; see Supporting Information Appendix S6, Figure S6.9a,b). For alien assemblages, occurrence-based FD_{SES} had a slightly negative correlation with phylogenetic diversity (Pearson's $r = −.05$, $p = .003$; see Supporting Information Appendix S6, Figure S6.9c).

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 km^2 grid cell scale, the functional diversity of endemic assemblages is highest in humid and isolated conditions, and functional diversity of non-endemic native assemblages is highest in 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.
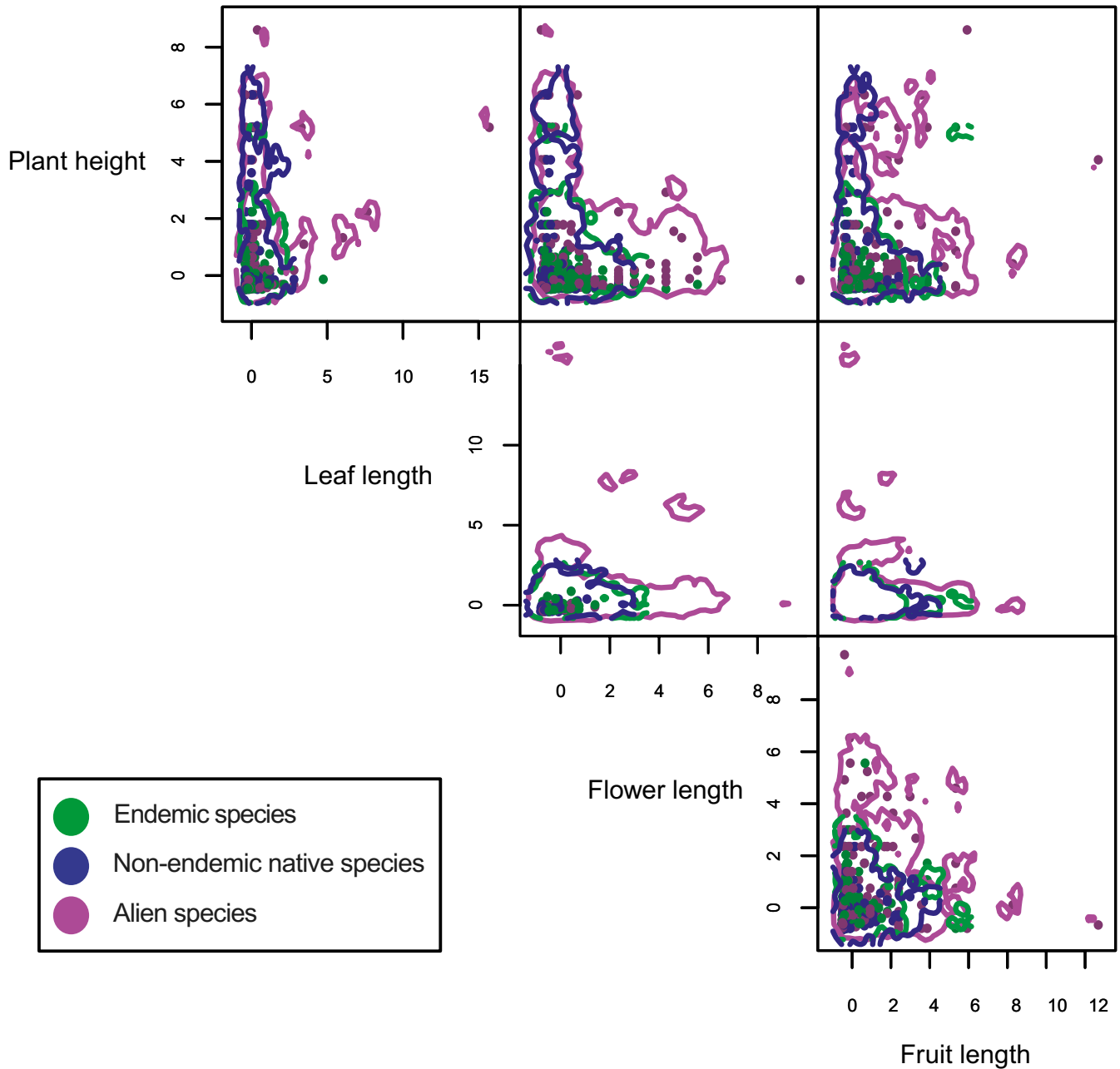
FIGURE 3 Estimated four-dimensional hypervolumes for endemic (green; $n = 347$), non-endemic native (blue; $n = 306$) and alien (violet; $n = 240$) seed plant species on the Canary Islands. The coloured points represent the different plant species, and the coloured lines reflect the areas filled by random 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%

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 arise either through very fine morphological specializations or through overlap in resource use (Klopfer & MacArthur, 1961; Pigot et al., 2016).

However, there are also species that 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. Furthermore, 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) and to use similar resources to native species (Klopfer & MacArthur, 1961). However, given that the observed

TABLE 2 Explained variation of generalized linear models (GLMs) and spatial autoregressive (SAR) models analysing the combined effect of humidity, geographical isolation, topographic complexity and geological age on the standardized effect size of functional diversity for endemic, non-endemic native and alien seed plant assemblages based on 500 m × 500 m grid cells across the Canary Islands

|	GLM			SAR model		
Species	**% dev.**	**AIC**	**Moran's *I***	**% dev.**	**AIC**	**Moran's *I***
Endemic	27.3	9,772.8	.56	53.2	8,427.2	−.08
Non-endemic native	20.1	10,868	.68	60.6	8,706.3	−.10
Alien	7.6	10,394	.62	48.8	8,591	−.09

Note: The standardized effect size of functional diversity (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 ($n = 3,065$). The percentage of total deviance explained (% dev.), Akaike information criterion (AIC) and Moran's *I* are given. Model coefficients of SAR models are given in Figure 4.

patterns represent *c.* 43% of the Canary Island flora, they might be dependent on the species considered.

4.2 | Functional diversity of endemic and non-endemic native plant assemblages

Our results indicate that humidity and geographical isolation might be important factors driving functional diversity patterns in native assemblages on the Canary Islands. However, owing to their high collinearity with each other and with elevation, we cannot disentangle their effects on functional diversity clearly. 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). 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), whereas 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 (Peppe et al., 2011; Poorter et al., 2010; 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, 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 can select against dispersal ability by increasing fruit and seed size to reduce dispersal into the sea (Kavanagh & Burns, 2014; Rossetto & Kooyman, 2005). Larger seeds have increased nutrient reserves and thus a highly competitive vigour during establishment (Moles & Westoby, 2004; Thompson et al., 1993). 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 might foster adaptive speciation in endemic summit scrub and rock communities of the Canary Islands (Fernández-Palacios, Otto, 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 (Leishmann 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, because our metric of isolation considers the distance to climatically suitable mainland and ignores other factors, such as wind and ocean currents, in addition to climatically similar areas on other islands, as possible modifiers to these distances (Muñoz et al., 2004; Price, 2004). Moreover, studies on edaphic islands have shown that target effect (i.e., indicating the increased probability of a larger island to be colonized than a smaller island given the same isolation) might play a key role in determining plant diversity patterns (Conti et al., 2022; Mendez-Castro et al., 2021). Ignoring these additional isolation metrics might lead to an under- or overestimation of geographical 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).
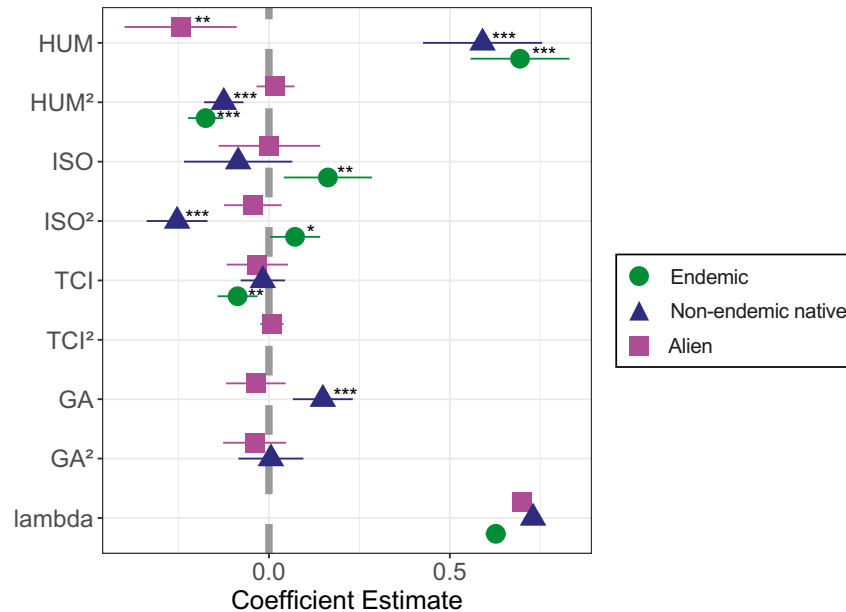
FIGURE 4 Multipredictor spatial autoregressive models of humidity (HUM), geographical isolation (ISO), topographic complexity index (TCI) and geological age (GA) on the occurrence-based standardized effect size of functional diversity (FD_{SES}) of endemic ($n = 347$ species), non-endemic native ($n = 306$ species) and alien ($n = 240$ species) plant assemblages 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 × 500 m grid cells. Shown are the respective best models according to a model comparison approach. Standardized estimates are provided for each predictor. Error bars represent confidence intervals of the coefficient estimates. Asterisks denote statistical significance (***$p < .001$; **$p < .01$; *$p < .05$)

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 might diverge to new endemic allopatric species, augmenting the number of species but not the functional diversity (Badgley et al., 2017). However, we must be careful with the interpretation of these results. Species that occur in very steep sites are rarely reported; 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 the 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 (Laliberté et al., 2013; Lambers et al., 2008; Mueller-Dombois & Boehmer, 2013). However, the explained variation of the models is low, and the results should be interpreted with caution. Furthermore, our measurement of geological age was approximate and might not be precise enough to reflect mechanisms of soil development on plant functional diversity.

4.3 | Functional diversity of alien plant assemblages

Alien assemblages show a decrease of functional diversity with increasing humidity, geographical isolation and geological age, in addition to 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 attributable 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., 2018; 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.

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 attributable to their recent island-specific introductions. Furthermore, 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 analyse the relationship between functional diversity and highly humid environments only 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 reflect, at least in part, trait conservatism (Blomberg et al., 2003). However, application of 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 to be feasible using a pruned tree with polytomies, as is the case for the tree used in the present study. We conclude that although our results might be influenced, in part, 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.

4.5 | Conclusion

Our study indicates that endemic species do not differ substantially, in a functional sense, 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, the 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 dissimilar, in a functional sense, 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 the functional diversity of both endemic and non-endemic native assemblages and 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 provide a better link between trait functions and hypotheses concerning water-use efficiency. In particular, functional diversity patterns in different types growth forms should be analysed in future studies, because growth form can have important implications for community assembly across climatic and biogeographical gradients (Irl et al., 2020; Schrader et al., 2020). Moreover, further analyses with entire floras 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.

AUTHOR CONTRIBUTIONS

D.M.H., S.D.H.I. and C.B. conceived the ideas. D.M.H., M.P.B.-B., S.D.H.I. and M.J.S. collected the data. D.M.H., V.C. and M.J.S. analysed the data. D.M.H. led the writing, and all authors contributed to the interpretation of the results and the writing process.

DATA AVAILABILITY STATEMENT

All morphological trait data are deposited on DRYAD (https://doi.org/10.5061/dryad.wdbrv15r1). The data provided include the full list of species names, trait data and the respective references.

ORCID

Dagmar M. Hanz https://orcid.org/0000-0002-8821-9044
Vanessa Cutts https://orcid.org/0000-0002-4986-2934
Martha Paola Barajas-Barbosa https://orcid.org/0000-0002-9040-0766

Adam C. Algar https://orcid.org/0000-0001-8095-0097

Carl Beierkuhnlein https://orcid.org/0000-0002-6456-4628

José-María Fernández-Palacios https://orcid.org/0000-0001-9741-6878

Richard Field https://orcid.org/0000-0003-2613-2688

Severin D. H. Irl https://orcid.org/0000-0002-1734-8607

REFERENCES

Acebes Ginovés, J. R., León Arencibia, M. C., Rodríguez Navarro, M. L., del Arco Aguilar, M. J., García Gallo, A., Pérez de Paz, P. L., Delgado, O. R., & Wildpret de la Torre, W. (2009). *Spermatophyta. Lista de especies silvestres de Canarias. Hongos, plantas y animales terrestres* (pp. 122–172). Gobierno de Canarias.

Alexander, J. M., Kueffer, C., Daehler, C. C., Edwards, P. J., Pauchard, A., Seipel, T., Arévalo, J., Cavieres, L., Dietz, H., Jakobs, G., McDougall, K., Naylor, B., Otto, R., Parks, C. G., Rew, L., & Walsh, N. (2011). Assembly of nonnative floras along elevational gradients explained by directional ecological filtering. *Proceedings of the National Academy of Sciences*, 108, 656–661. https://doi.org/10.1073/pnas.1013136108

Allouche, O., Kalyuzhny, M., Moreno-Rueda, G., Pizarro, M., & Kadmon, R. (2012). Area–heterogeneity tradeoff and the diversity of ecological communities. *Proceedings of the National Academy of Sciences*, 109, 17495–17500. https://doi.org/10.1073/pnas.1208652109

Amatulli, G., Domisch, S., Tuanmu, M. N., Parmentier, B., Ranipeta, A., Malczyk, J., & Jetz, W. (2018). Data Descriptor: A suite of global, cross-scale topographic variables for environmental and biodiversity modeling. *Scientific Data*, 5, 180040. https://doi.org/10.1038/sdata.2018.40

Arévalo, J. R., Delgado, J. D., Otto, R., Naranjo, A., Salas, M., & Fernández-Palacios, J. M. (2005). Distribution of alien vs. native plant species in roadside communities along an altitudinal gradient in Tenerife and Gran Canaria (Canary Islands). *Perspectives in Plant Ecology, Evolution and Systematics*, 7, 185–202. https://doi.org/10.1016/j.ppees.2005.09.003

Badgley, C., Smiley, T. M., Terry, R., Davis, E. B., DeSantis, L. R. G., Fox, D. L., Hopkins, S. S. B., Jezkova, T., Matocq, M. D., Matzke, N., McGuire, J. L., Mulch, A., Riddle, B. R., Roth, V. L., Samuels, J. X., Strömberg, C. A. E., & Yanites, B. J. (2017). Biodiversity and topographic complexity: Modern and geohistorical perspectives. *Trends in Ecology and Evolution*, 32, 211–226. https://doi.org/10.1016/j.tree.2016.12.010

Barajas-Barbosa, M. P., Weigelt, P., Borregaard, M. K., Keppel, G., & Kreft, H. (2020). Environmental heterogeneity dynamics drive plant diversity on oceanic islands. *Journal of Biogeography*, 47, 2248–2260. https://doi.org/10.1111/jbi.13925

Barton, K. (2022). MuMIn: Multi-Model Inference. R package version 1.46.0. https://cran-project.org/package=MuMIn

Bellido Mulas, F., Pineda Velasco, A., Sainz, Gómez, de Aja, J. A., & Barrera, J. L. (2020). Mapa Geológico Digital continuo E. 1:25,000, Zona Canarias. *GEODE. Mapa Geológico Digital continuo de Espana.*

Bermúdez, A. M., Fernández-Palacios, J. M., González-Mancebo, J. M., Patiño, J., Arévalo, J. R., Otto, R., & Delgado, J. D. (2007). Floristic and structural recovery of a laurel forest community after clear-cutting: A 60 years chronosequence on La Palma (Canary Islands). *Annals of Forest Science*, 64, 109–119. https://doi.org/10.1051/forest:2006094

Bernard-Verdier, M., Navas, M. L., Vellend, M., Violle, C., Fayolle, A., & Garnier, E. (2012). Community assembly along a soil depth gradient: Contrasting patterns of plant trait convergence and divergence in a Mediterranean rangeland. *Journal of Ecology*, 100, 1422–1433. https://doi.org/10.1111/1365-2745.12003

Bivand, R. S., Pebesma, E., & Gomez-Rubio, V. (2013). *Applied spatial data analysis with R*, 2nd ed. Springer.

Blomberg, S. P., Garland, T., & Ives, A. R. (2003). Testing for phylogenetic signal in comparative data: Behavioral traits are more labile. *Evolution*, 57, 717–745. https://doi.org/10.1111/j.0014-3820.2003.tb00285.x

Blonder, B. (2018). Hypervolume concepts in niche- and trait-based ecology. *Ecography*, 41, 1441–1455. https://doi.org/10.1111/ecog.03187

Blonder, B., Lamanna, C., Violle, C., & Enquist, B. J. (2014). The n-dimensional hypervolume. *Global Ecology and Biogeography*, 23, 595–609.

Brown, J. H., & Kodric-Brown, A. (1977). Turnover rates in insular biogeography: Effect of immigration on extinction. *Ecology*, 58, 445–449. https://doi.org/10.2307/1935620

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach*, 2nd ed. Springer.

Calabrese, J. M., Certain, G., Kraan, C., & Dormann, C. F. (2014). Stacking species distribution models and adjusting bias by linking them to macroecological models. *Global Ecology and Biogeography*, 23, 99–112. https://doi.org/10.1111/geb.12102

Callaway, R. M., Brooker, R. W., Choler, P., Kikvidze, Z., Lortie, C. J., Michalet, R., Paolini, L., Pugnaire, F. I., Newingham, B., Aschehoug, E. T., Armas, C., Kikodze, D., & Cook, B. J. (2002). Positive interactions among alpine plants increase with stress. *Nature*, 417, 844–848. https://doi.org/10.1038/nature00812

Carine, M. A., Santos Guerra, A., Guma, I. R., & Reyes-Betancort, J. (2010). Endemism and evolution of the Macaronesian flora. In D. M. Williams & S. Knapp (Eds.), *Beyond cladistics: The branching of a paradigm* (pp. 101–124). University of California Press.

Carvajal, D. E., Loayza, A. P., Rios, R. S., Delpiano, C. A., & Squeo, F. A. (2019). A hyper-arid environment shapes an inverse pattern of the fast–slow plant economics spectrum for above-, but not below-ground resource acquisition strategies. *Journal of Ecology*, 107, 1079–1092. https://doi.org/10.1111/1365-2745.13092

Conti, L., Méndez-Castro, F. E., Chytrý, M., Götzenberger, L., Hájek, M., Horsák, M., Jiménez-Alfaro, B., Klimešová, J., Zelený, D., & Ottaviani, G. (2022). Insularity promotes plant persistence strategies in edaphic island systems. *Global Ecology and Biogeography*, 31, 753–764. https://doi.org/10.1111/geb.13465

Cornwell, W. K., & Ackerly, D. D. (2009). Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monographs*, 79, 109–126. https://doi.org/10.1890/07-1134.1

Cutts, V., Hanz, D. M., Barajas-Barbosa, M. P., Algar, A. C., Steinbauer, M. J., Irl, S. D. H., Kreft, H., Weigelt, P., Fernandez 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, e12996. https://doi.org/10.1111/jvs.12996

de Nascimento, L., Nogué, S., Naranjo-Cigala, A., Criado, C., McGlone, M., Fernández-Palacios, E., & Fernández-Palacios, J. M. (2020). Human impact and ecological changes during prehistoric settlement on the Canary Islands. *Quaternary Science Reviews*, 239, 106332. https://doi.org/10.1016/j.quascirev.2020.106332

del Arco Aguilar, M. J., González-González, R., Garzón-Machado, V., & Pizarro-Hernández, B. (2010). Actual and potential natural vegetation on the Canary Islands and its conservation status. *Biodiversity and Conservation*, 19, 3089–3140. https://doi.org/10.1007/s10531-010-9881-2

Devkota, R., Field, R., Hoffmann, S., Walentowitz, A., Medina, F., Vetaas, O., Chiarucci, A., Weiser, F., Jentsch, A., & Beierkuhnlein, C. (2020). Assessing the potential replacement of laurel forest by a novel ecosystem in the steep terrain of an Oceanic Island. *Remote Sensing*, 12, 4013. https://doi.org/10.3390/rs12244013

Díaz, S., & Cabido, M. (2001). Vive la différence: Plant functional diversity matters to ecosystem processes. *Trends in Ecology and Evolution*, 16, 646–655. https://doi.org/10.1016/S0169-5347(01)02283-2

Dormann, C. F., M. McPherson, J., B. Araújo, M., Bivand, R., Bolliger, J., Carl, G., G. Davies, R., Hirzel, A., Jetz, W., Daniel Kissling, W., Kühn, I., Ohlemüller, R., R. Peres-Neto, P., Reineking, B., Schröder, B., M. Schurr, F., & Wilson, R. (2007). Methods to account for spatial autocorrelation in the analysis of species distributional data: A review. *Ecography*, 30, 609–628. https://doi.org/10.1111/j.2007.0906-7590.05171.x

Falster, D. S., & Westoby, M. (2003). Plant height and evolutionary games. *Trends in Ecology and Evolution*, 18, 337–343. https://doi.org/10.1016/S0169-5347(03)00061-2

Felsenstein, J. (1985). Phylogenies and the comparative method. *The American Naturalist*, 125, 1–15. https://doi.org/10.1086/284325

Fernández-Palacios, J. M., De Nascimento, L., Otto, R., Delgado, J. D., García-Del-Rey, E., Arévalo, J. R., & Whittaker, R. J. (2011). A reconstruction of Palaeo-Macaronesia, with particular reference to the long-term biogeography of the Atlantic island laurel forests. *Journal of Biogeography*, 38, 226–246. https://doi.org/10.1111/j.1365-2699.2010.02427.x

Fernández-Palacios, J. M., Kreft, H., Irl, S. D. H., Norder, S., Ah-Peng, C., Borges, P. A. V., Burns, K. C., de Nascimento, L., Meyer, J.-Y., Montes, E., & Drake, D. R. (2021). Scientists' warning—The outstanding biodiversity of islands is in peril. *Global Ecology and Conservation*, 31, e01847. https://doi.org/10.1016/j.gecco.2021.e01847

Fernández-Palacios, J. M., Otto, R., Borregaard, M. K., Kreft, H., Price, J. P., Steinbauer, M. J., Weigelt, P., & Whittaker, R. J. (2021). Evolutionary winners are ecological losers among oceanic island plants. *Journal of Biogeography*, 48, 2186–2198. https://doi.org/10.1111/jbi.14143

Funk, J. L., Cleland, E. E., Suding, K. N., & Zavaleta, E. S. (2018). Restoration through reassembly: Plant traits and invasion resistance. *Trends in Ecology and Evolution*, 23, 695–703. https://doi.org/10.1016/j.tree.2008.07.013

Galland, T., Adeux, G., Dvořáková, H., E-Vojtkó, A., Orbán, I., Lussu, M., Puy, J., Blažek, P., Lanta, V., Lepš, J., Bello, F., Pérez Carmona, C., Valencia, E., & Götzenberger, L. (2019). Colonization resistance and establishment success along gradients of functional and phylogenetic diversity in experimental plant communities. *Journal of Ecology*, 107, 2090–2104. https://doi.org/10.1111/1365-2745.13246

García-Verdugo, C., Monroy, P., Pugnaire, F. I., Jura-Morawiec, J., Moreira, X., & Flexas, J. (2020). Leaf functional traits and insular colonization: Subtropical islands as a melting pot of trait diversity in a widespread plant lineage. *Journal of Biogeography*, 47, 2362–2376. https://doi.org/10.1111/jbi.13956

Garzón-Machado, V., Otto, R., & del Arco Aguilar, M. J. (2014). Bioclimatic and vegetation mapping of a topographically complex oceanic island applying different interpolation techniques. *International Journal of Biometeorology*, 58, 887–899.

Gates, D. M. (1965). Energy, plants, and ecology. *Ecology*, 46, 1–13. https://doi.org/10.2307/1935252

Gaudet, C. L., & Keddy, P. A. (1988). A comparative approach to predicting competitive ability from plant traits. *Nature*, 334, 242–243. https://doi.org/10.1038/334242a0

Greene, D. F., & Johnson, E. A. (1993). Seed mass and dispersal capacity in wind-dispersed diaspores. *Oikos*, 67, 69–74. https://doi.org/10.2307/3545096

Herrera, C. M., & Bazaga, P. (2008). Adding a third dimension to the edge of a species' range: Altitude and genetic structuring in mountainous landscapes. *Heredity*, 100, 275–285. https://doi.org/10.1038/sj.hdy.6801072

Hortal, J., Triantis, K. A., Meiri, S., Thébault, E., & Sfenthourakis, S. (2009). Island species richness increases with habitat diversity. *The American Naturalist*, 174, E205–E217. https://doi.org/10.1086/645085

Irl, S. D. H., Harter, D. E. V., Steinbauer, M. J., Gallego Puyol, D., Fernández-Palacios, J. M., Jentsch, A., & Beierkuhnlein, C. (2015). Climate vs. topography—spatial patterns of plant species diversity and endemism on a high-elevation island. *Journal of Ecology*, 103, 1621–1633. https://doi.org/10.1111/1365-2745.12463

Irl, S. D. H., Obermeier, A., Beierkuhnlein, C., & Steinbauer, M. J. (2020). Climate controls plant life form patterns on a high-elevation oceanic island. *Journal of Biogeography*, 47, 2261–2273. https://doi.org/10.1111/jbi.13929

Irl, S. D. H., Schweiger, A. H., Steinbauer, M. J., Ah-Peng, C., Arévalo, J. R., Beierkuhnlein, C., Chiarucci, A., Daehler, C. C., Fernández-Palacios, J. M., Flores, O., Kueffer, C., Maděra, P., Otto, R., Schweiger, J. I., Strasberg, D., Jentsch, A., & Lavergne, S. (2021). Human impact, climate and dispersal strategies determine plant invasion on islands. *Journal of Biogeography*, 48, 1889–1903. https://doi.org/10.1111/jbi.14119

Jenness, J. S. (2004). Calculating landscape surface area from digital elevation models. *Wildlife Society Bulletin*, 32, 829–839.

Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Tautenhahn, S., Werner, G. D. A., Aakala, T., Abedi, M., Acosta, A. T. R., Adamidis, G. C., Adamson, K., Aiba, M., Albert, C. H., Alcántara, J. M., Alcázar C, C., Aleixo, I., Ali, H., … Wirth, C. (2020). TRY plant trait database – enhanced coverage and open access. *Global Change Biology*, 26, 119–188. https://doi.org/10.1111/gcb.14904

Kavanagh, P. H., & Burns, K. C. (2014). The repeated evolution of large seeds on islands. *Proceedings of the Royal Society B: Biological Sciences*, 281, 20140675. https://doi.org/10.1098/rspb.2014.0675

Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., Blomberg, S. P., & Webb, C. O. (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, 26, 1463–1464. https://doi.org/10.1093/bioinformatics/btq166

Keppel, G., Gillespie, T. W., Ormerod, P., & Fricker, G. A. (2016). Habitat diversity predicts orchid diversity in the tropical south-west Pacific. *Journal of Biogeography*, 43, 2332–2342. https://doi.org/10.1111/jbi.12805

Kier, G., Kreft, H., Lee, T. M., Jetz, W., Ibisch, P. L., Nowicki, C., Mutke, J., & Barthlott, W. (2009). A global assessment of endemism and species richness across island and mainland regions. *Proceedings of the National Academy of Sciences*, 106, 9322–9327. https://doi.org/10.1073/pnas.0810306106

Klopfer, P. H., & MacArthur, R. H. (1961). On the causes of tropical species diversity: Niche overlap. *The American Naturalist*, 95, 223–226. https://doi.org/10.1086/282179

König, C., Weigelt, P., Taylor, A., Stein, A., Dawson, W., Essl, F., Pergl, J., Pyšek, P., van Kleunen, M., Winter, M., Chatelain, C., Wieringa, J. J., Krestov, P., & Kreft, H. (2020). Source pools and disharmony of the world's island floras. *Ecography*, 44, 44–55. https://doi.org/10.1111/ecog.05174.

Kreft, H., Jetz, W., Mutke, J., Kier, G., & Barthlott, W. (2008). Global diversity of island floras from a macroecological perspective. *Ecology Letters*, 11, 116–127.

Kuppler, J., & Kotowska, M. M. (2021). A meta-analysis of responses in floral traits and flower–visitor interactions to water deficit. *Global Change Biology*, https://doi.org/10.1111/gcb.15621.

Laliberté, E., Grace, J. B., Huston, M. A., Lambers, H., Teste, F. P., Turner, B. L., & Wardle, D. A. (2013). How does pedogenesis drive plant diversity? *Trends in Ecology & Evolution*, 28, 331–340. https://doi.org/10.1016/j.tree.2013.02.008

Lamanna, C., Blonder, B., Violle, C., Kraft, N. J. B., Sandel, B., Šímová, I., Donoghue, J. C., Svenning, J.-C., McGill, B. J., Boyle, B., Buzzard, V., Dolins, S., Jørgensen, P. M., Marcuse-Kubitza, A., Morueta-Holme, N., Peet, R. K., Piel, W. H., Regetz, J., Schildhauer, M., … Enquist, B. J. (2014). Functional trait space and the latitudinal diversity gradient. *Proceedings of the National Academy of Sciences*, 111, 13745–13750. https://doi.org/10.1073/pnas.1317722111

Lambers, H., Brundrett, M. C., Raven, J. A., & Hopper, S. D. (2011). Plant mineral nutrition in ancient landscapes: High plant species diversity on infertile soils is linked to functional diversity for nutritional strategies. *Plant and Soil*, 348, 7–27. https://doi.org/10.1007/s11104-011-0977-6

Lambers, H., Raven, J. A., Shaver, G. R., & Smith, S. E. (2008). Plant nutrient-acquisition strategies change with soil age. *Trends in*

Ecology and Evolution, 23, 95–103. https://doi.org/10.1016/j.tree.2007.10.008

Leishman, M. R., Westoby, M., & Jurado, E. (1995). Correlates of seed size variation: A comparison among five temperate floras. *Journal of Ecology*, 83, 517–529. https://doi.org/10.2307/2261604

Leigh, A., Sevanto, S., Close, J. D., & Nicotra, A. B. (2016). The influence of leaf size and shape on leaf thermal dynamics: does theory hold up under natural conditions? *Plant, Cell & Environment*, 40, 237–248. https://doi.org/10.1111/pce.12857.

Losos, J. B., & Ricklefs, R. E. (2009). Adaptation and diversification on islands. *Nature*, 457, 830–836. https://doi.org/10.1038/nature07893

MacArthur, R. H. (1965). Patterns of species diversity. *Biological Reviews*, 40, 510–533. https://doi.org/10.1111/j.1469-185X.1965.tb00815.x

MacArthur, R., & Levins, R. (1967). The limiting similarity, convergence, and divergence of coexisting species. *The American Naturalist*, 101, 377–385. https://doi.org/10.1086/282505

MacArthur, R. H., & Wilson, E. O. (1967). *The theory of island biogeography*. Princeton University Press.

Macinnis-Ng, C., Mcintosh, A. R., Monks, J. M., Waipara, N., White, R. S. A., Boudjelas, S., Clark, C. D., Clearwater, M. J., Curran, T. J., Dickinson, K. J. M., Nelson, N., Perry, G. L. W., Richardson, S. J., Stanley, M. C., & Peltzer, D. A. (2021). Climate-change impacts exacerbate conservation threats in island systems: New Zealand as a case study. *Frontiers in Ecology and the Environment*, 19, 216–224. https://doi.org/10.1002/fee.2285

Marques, D. A., Meier, J. I., & Seehausen, O. (2019). A combinatorial view on speciation and adaptive radiation. *Trends in Ecology & Evolution*, 34, 531–544. https://doi.org/10.1016/j.tree.2019.02.008

Mendez-Castro, F. E., Conti, L., Chytrý, M., Jiménez-Alfaro, B., Hájek, M., Horsák, M., Zelený, D., Malavasi, M., & Ottaviani, G. (2021). What defines insularity for plants in edaphic islands? *Ecography*, 44, 1249–1258. https://doi.org/10.1111/ecog.05650

Moles, A. T., & Leishman, M. R. (2008). The seedling as part of a plant's life history strategy. In M. A. Leck, V. T. Parker, & R. L. Simpson (Eds.), *Seedling ecology and evolution* (pp. 217–238). Cambridge University Press.

Moles, A. T., Warton, D. I., Warman, L., Swenson, N. G., Laffan, S. W., Zanne, A. E., Pitman, A., Hemmings, F. A., & Leishman, M. R. (2009). Global patterns in plant height. *Journal of Ecology*, 97, 923–932. https://doi.org/10.1111/j.1365-2745.2009.01526.x

Moles, A. T., & Westoby, M. (2004). Seedling survival and seed size: A synthesis of the literature. *Journal of Ecology*, 92, 372–383. https://doi.org/10.1111/j.0022-0477.2004.00884.x

Mueller-Dombois, D., & Boehmer, H. J. (2013). Origin of the Hawaiian rainforest and its transition states in long-term primary succession. *Biogeosciences*, 10, 5171–5182. https://doi.org/10.5194/bg-10-5171-2013

Muñoz, J., Felicisimo, A. M., Cabezas, F., Burgaz, A. R., & Martinez, I. (2004). Wind as a long-distance dispersal vehicle in the southern hemisphere. *Science*, 304, 1144–1147. https://doi.org/10.1126/science.1095210

Muñoz, M. C., Schaefer, H. M., Böhning-Gaese, K., & Schleuning, M. (2017). Importance of animal and plant traits for fruit removal and seedling recruitment in a tropical forest. *Oikos*, 126, 823–832. https://doi.org/10.1111/oik.03547

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoeces, E., & Wagner, H. (2017). *Vegan: Community ecology package*. R package version 2.4-4.

Ottaviani, G., Keppel, G., Götzenberger, L., Harrison, S., Opedal, Ø. H., Conti, L., Liancourt, P., Klimešová, J., Silveira, F. A. O., Jiménez-Alfaro, B., Negoita, L., Doležal, J., Hájek, M., Ibanez, T., Méndez-Castro, F. E., & Chytrý, M. (2020). Linking plant functional ecology to island biogeography. *Trends in Plant Science*, 25, 329–339. https://doi.org/10.1016/j.tplants.2019.12.022

Otto, R., Whittaker, R. J., von Gaisberg, M., Stierstorfer, C., Naranjo-Cigala, A., Steinbauer, M. J., Borregaard, M. K., Arévalo, J. R., Garzón-Machado, V., del Arco, M., & Fernández-Palacios, J. M. (2016). Transferring and implementing the general dynamic model of oceanic island biogeography at the scale of island fragments: The roles of geological age and topography in plant diversification in the Canaries. *Journal of Biogeography*, 43, 911–922. https://doi.org/10.1111/jbi.12684

Paradis, E., & Schliep, K. (2019). Ape 5.0: An environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, 35, 526–528. https://doi.org/10.1093/bioinformatics/bty633

Parkhurst, D. F., & Loucks, O. L. (1972). Optimal leaf size in relation to environment. *Journal of Ecology*, 60, 505–537. https://doi.org/10.2307/2258359

Patiño, J., Whittaker, R. J., Borges, P. A. V., Fernández-Palacios, J. M., Ah-Peng, C., Araújo, M. B., Ávila, S. P., Cardoso, P., Cornuault, J., de Boer, E. J., de Nascimento, L., Gil, A., González-Castro, A., Gruner, D. S., Heleno, R., Hortal, J., Illera, J. C., Kaiser-Bunbury, C. N., Matthews, T. J., … Emerson, B. C. (2017). A roadmap for island biology: 50 fundamental questions after 50 years of The Theory of Island Biogeography. *Journal of Biogeography*, 44, 963–983.

Pauchard, A., Kueffer, C., Dietz, H., Daehler, C. C., Alexander, J., Edwards, P. J., Arévalo, J. R., Cavieres, L. A., Guisan, A., Haider, S., Jakobs, G., McDougall, K., Millar, C. I., Naylor, B. J., Parks, C. G., Rew, L. J., & Seipel, T. (2009). Ain't no mountain high enough: Plant invasions reaching new elevations. *Frontiers in Ecology and the Environment*, 7, 479–486. https://doi.org/10.1890/080072

Paušič, I., Lipovšek, M., Jakely, D., Pavlec, N., Ivajnšič, D., & Kaligarič, M. (2019). Local climate and latitude affect flower form of *Ophrys fuciflora* (Orchidaceae): Evidence for clinal variation. *Botany Letters*, 166, 499–512.

Peppe, D. J., Royer, D. L., Cariglino, B., Oliver, S. Y., Newman, S., Leight, E., Enikolopov, G., Fernandez-Burgos, M., Herrera, F., Adams, J. M., Correa, E., Currano, E. D., Erickson, J. M., Hinojosa, L. F., Hoganson, J. W., Iglesias, A., Jaramillo, C. A., Johnson, K. R., Jordan, G. J., … Wright, I. J. (2011). Sensitivity of leaf size and shape to climate: Global patterns and paleoclimatic applications. *New Phytologist*, 190, 724–739. https://doi.org/10.1111/j.1469-8137.2010.03615.x

Pigot, A. L., Trisos, C. H., & Tobias, J. A. (2016). Functional traits reveal the expansion and packing of ecological niche space underlying an elevational diversity gradient in passerine birds. *Proceedings of the Royal Society B: Biological Sciences*, 283, 1–9. https://doi.org/10.1098/rspb.2015.2013

Pillar, V. D., & Duarte, L. d. S. (2010). A framework for metacommunity analysis of phylogenetic structure. *Ecology Letters*, 13, 587–596. https://doi.org/10.1111/j.1461-0248.2010.01456.x

Poorter, H., Niinemets, Ü., Walter, A., Fiorani, F., & Schurr, U. (2010). A method to construct dose-response curves for a wide range of environmental factors and plant traits by means of a meta-analysis of phenotypic data. *Journal of Experimental Botany*, 61, 2043–2055. https://doi.org/10.1093/jxb/erp358

Price, J. P. (2004). Floristic biogeography of the Hawaiian Islands: Influences of area, environment and paleogeography. *Journal of Biogeography*, 31, 487–500. https://doi.org/10.1046/j.0305-0270.2003.00990.x

R Core Team (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, AT.

Ricklefs, R. E., & Starck, M. J. (1996). Applications of phylogenetically independent contrasts: A mixed progress report. *Oikos*, 77, 167–172. https://doi.org/10.2307/3545598

Roddy, A. B. (2019). Energy balance implications of floral traits involved in pollinator attraction and water balance. *International Journal of Plant Sciences*, 180, 944–953. https://doi.org/10.1086/705586

Roddy, A. B., Brodersen, C. R., & Dawson, T. E. (2016). Hydraulic conductance and the maintenance of water balance in flowers. *Plant, Cell & Environment*, 39, 2123–2132. https://doi.org/10.1111/pce.12761

Roddy, A. B., Jiang, G. F., Cao, K., Simonin, K. A., & Brodersen, C. R. (2019). Hydraulic traits are more diverse in flowers than in leaves. *New Phytologist*, *223*, 193–203. https://doi.org/10.1111/nph.15749

Rohle, F. J. (2006). A comment on phylogenetic correction. *Evolution*, *60*, 1509–1515. https://doi.org/10.1111/j.0014-3820.2006.tb01229.x

Rossetto, M., & Kooyman, R. M. (2005). The tension between dispersal and persistence regulates the current distribution of rare palaeo-endemic rain forest flora: A case study. *Journal of Ecology*, *93*, 906–917. https://doi.org/10.1111/j.1365-2745.2005.01046.x

Rundell, R. J., & Price, T. D. (2009). Adaptive radiation, nonadaptive radiation, ecological speciation and nonecological speciation. *Trends in Ecology and Evolution*, *24*, 394–399. https://doi.org/10.1016/j.tree.2009.02.007

Ryan, M. G., Phillips, N., & Bond, B. J. (2006). The hydraulic limitation hypothesis revisited. *Plant, Cell and Environment*, *29*, 367–381. https://doi.org/10.1111/j.1365-3040.2005.01478.x

Schrader, J., König, C., Triantis, K. A., Trigas, P., Kreft, H., & Weigelt, P. (2020). Species–area relationships on small islands differ among plant growth forms. *Global Ecology and Biogeography*, *29*, 814–829. https://doi.org/10.1111/geb.13056

Schrader, J., Wright, I. J., Kreft, H., & Westoby, M. (2021). A roadmap to plant functional island biogeography. *Biological Reviews*, *96*, 2851–2870. https://doi.org/10.1111/brv.12782

Shi, P., Liu, M., Yu, X., Gielis, J., & Ratkowsky, D. A. (2019). Proportional relationship between leaf area and the product of leaf length and width of four types of special leaf shapes. *Forests*, *10*, 178. https://doi.org/10.3390/f10020178

Smith, S. A., & Brown, J. W. (2018). Constructing a broadly inclusive seed plant phylogeny. *American Journal of Botany*, *105*, 302–314. https://doi.org/10.1002/ajb2.1019

Spasojevic, M. J., Grace, J. B., Harrison, S., & Damschen, E. I. (2014). Functional diversity supports the physiological tolerance hypothesis for plant species richness along climatic gradients. *Journal of Ecology*, *102*, 447–455. https://doi.org/10.1111/1365-2745.12204

Spasojevic, M. J., & Suding, K. N. (2012). Inferring community assembly mechanisms from functional diversity patterns: The importance of multiple assembly processes. *Journal of Ecology*, *100*, 652–661. https://doi.org/10.1111/j.1365-2745.2011.01945.x

Steinbauer, M. J., Field, R., Grytnes, J.-A., Trigas, P., Ah-Peng, C., Attorre, F., Birks, H. J. B., Borges, P. A. V., Cardoso, P., Chou, C.-H., De Sanctis, M., de Sequeira, M. M., Duarte, M. C., Elias, R. B., Fernández-Palacios, J. M., Gabriel, R., Gereau, R. E., Gillespie, R. G., Greimler, J., … Beierkuhnlein, C. (2016). Topography-driven isolation, speciation and a global increase of endemism with elevation. *Global Ecology and Biogeography*, *25*, 1097–1107. https://doi.org/10.1111/geb.12469

Steinbauer, M. J., Irl, S. D. H., González-Mancebo, J. M., Breiner, F. T., Hernández-Hernández, R., Hopfenmüller, S., Kidane, Y., Jentsch, A., & Beierkuhnlein, C. (2017). Plant invasion and speciation along elevational gradients on the oceanic island La Palma, Canary Islands. *Ecology and Evolution*, *7*, 771–779. https://doi.org/10.1002/ece3.2640

Steinbauer, M. J., Otto, R., Naranjo-Cigala, A., Beierkuhnlein, C., & Fernández-Palacios, J. M. (2012). Increase of island endemism with altitude–speciation processes on oceanic islands. *Ecography*, *35*, 23–32. https://doi.org/10.1111/j.1600-0587.2011.07064.x

Stuessy, T. F., Jakubowsky, G., Gomez, R. S., Pfosser, M., Schluter, P. M., Fer, T., Sun, B.-Y., & Kato, H. (2006). Anagenetic evolution in island plants. *Journal of Biogeography*, *33*, 1259–1265. https://doi.org/10.1111/j.1365-2699.2006.01504.x

Taylor, A., Weigelt, P., König, C., Zotz, G., & Kreft, H. (2019). Island disharmony revisited using orchids as a model group. *New Phytologist*, *223*, 597–606. https://doi.org/10.1111/nph.15776

Thompson, J. D. (2001). How do visitation patterns vary among pollinators in relation to floral display and floral design in a generalist pollination system? *Oecologia*, *126*, 386–394. https://doi.org/10.1007/s004420000531

Thompson, K., Band, S. R., & Hodgson, J. G. (1993). Seed size and shape predict persistence in soil. *Functional Ecology*, *7*, 236–241. https://doi.org/10.2307/2389893

Thomson, F. J., Moles, A. T., Auld, T. D., & Kingsford, R. T. (2011). Seed dispersal distance is more strongly correlated with plant height than with seed mass. *Journal of Ecology*, *99*, 1299–1307. https://doi.org/10.1111/j.1365-2745.2011.01867.x

Thornthwaite, C. W. (1948). An approach toward a rational classification of climate. *Geographical Review*, *38*, 55–94. https://doi.org/10.2307/210739

UNEP. (1992). *World atlas of desertification*. Edward Arnold.

Venable, D. L., & Brown, J. S. (1988). The selective interactions of dispersal, dormancy, and seed size as adaptations for reducing risk in variable environments. *The American Naturalist*, *131*, 360–384. https://doi.org/10.1086/284795

Veron, S., Mouchet, M., Govaerts, R., Haevermans, T., & Pellens, R. (2019). Vulnerability to climate change of islands worldwide and its impact on the tree of life. *Scientific Reports*, *9*, 1–14. https://doi.org/10.1038/s41598-019-51107-x

Violle, C., Navas, M. L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional! *Oikos*, *116*, 882–892. https://doi.org/10.1111/j.0030-1299.2007.15559.x

Weigelt, P., Jetz, W., & Kreft, H. (2013). Bioclimatic and physical characterization of the world's islands. *Proceedings of the National Academy of Sciences*, *110*, 15307–15312. https://doi.org/10.1073/pnas.1306309110

Weigelt, P., & Kreft, H. (2013). Quantifying island isolation—insights from global patterns of insular plant species richness. *Ecography*, *36*, 417–429. https://doi.org/10.1111/j.1600-0587.2012.07669.x

Westoby, M. (1998). A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil*, *199*, 213–227.

Wheelwright, N. T. (1993). Fruit size in a tropical tree species: Variation, preference by birds, and heritability. *Vegetatio*, *107*, 163–174. https://doi.org/10.1007/BF00052219

Whittaker, R. J., & Fernández-Palacios, J. M. (2007). *Island biogeography: Ecology, evolution, and conservation*, 2nd ed. Oxford University Press.

Whittaker, R. J., Rigal, F., Borges, P. A. V., Cardoso, P., Terzopoulou, S., Casanoves, F., Pla, L., Guilhaumon, F., Ladle, R. J., & Triantis, K. A. (2014). Functional biogeography of oceanic islands and the scaling of functional diversity in the Azores. *Proceedings of the National Academy of Sciences*, *111*, 13709–13714. https://doi.org/10.1073/pnas.1218036111

Whittaker, R. J., Triantis, K. A., & Ladle, R. J. (2008). A general dynamic theory of oceanic island biogeography. *Journal of Biogeography*, *35*, 977–994.

Wright, I. J., Ackerly, D. D., Bongers, F., Harms, K. E., Ibarra-Manriquez, G., Martinez-Ramos, M., Mazer, S. J., Muller-Landau, H. C., Paz, H., Pitman, N. C. A., Poorter, L., Silman, M. R., Vriesendorp, C. F., Webb, C. O., Westoby, M., & Wright, S. J. (2007). Relationships among ecologically important dimensions of plant trait variation in seven neotropical forests. *Annals of Botany*, *99*, 1003–1015. https://doi.org/10.1093/aob/mcl066

Wright, I. J., Dong, N., Maire, V., Prentice, I. C., Westoby, M., Díaz, S., Gallagher, R. V., Jacobs, B. F., Kooyman, R., Law, E. A., Leishman, M. R., Niinemets, Ü., Reich, P. B., Sack, L., Villar, R., Wang, H., & Wilf, P. (2017). Global climatic drivers of leaf size. *Science*, *357*, 917–921. https://doi.org/10.1126/science.aal4760

Zarch, M. A. A., Sivakumar, B., & Sharma, A. (2015). Assessment of global aridity change. *Journal of Hydrology*, *520*, 300–313. https://doi.org/10.1016/j.jhydrol.2014.11.033

BIOSKETCH

Dagmar M. Hanz is a PhD student working on functional island biogeography and ecology. She is investigating functional diversity patterns, with particular focus on endemic and non-endemic native plant species in isolated island systems.

Vanessa Cutts is a PhD student interested in patterns of endemism on oceanic islands. Her research investigates the trait–environment relationships of plant species with differing degrees of endemism.

Martha Paola Barajas-Barbosa is a PhD candidate. Her research focuses on the complexity of oceanic island environments and the functional diversity of islands across scales.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Hanz, D. M., Cutts V., Barajas-Barbosa M. P., Algar A. C., Beierkuhnlein C., Fernández-Palacios J.-M., Field R., Kreft H., Steinbauer M. J., 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, 1313–1331. https://doi.org/10.1111/geb.13507

APPENDIX 1

DATA SOURCES

Alamo, E. C., Baudet, A. B., & Gómez, M. V. M. (2007). Estudio morfológico de frutos, semillas y plántulas especiales amenazadas de las Islas Canarias. Revista de la Academia Canaria de Ciencias, *19*, 35–42.

del Arco Aguilar, & Acebes Ginovés. (1981). *Teline salsoloides* M. del Arco & J. R. Acebes, sp. nov. (Fabaceae-Genistaeae), una nueva especie para la isla de Tenerife (I. Canarias). *Vieraea*, 11, 251–266.

del Arco Aguilar, M. (2000). Notes on the taxonomy and nomenclature of *Teline pallida* (Poir.) G. Kunkel. *Taxon*, 49, 17–25.

Baudet, Á. B. (2002). On some poorly known taxa of Aichryson sect. Aichryson and A. bituminosum sp. nova (Crassulaceae). *Willdenowia*, 32, 221–230.

Baudet, Á. B., Rodríguez, A. A., & Beaumont, Á. R. (2013). *Monanthes subrosulata*, a new species of M. sect. Sedoidea (Crassulaceae). from La Palma, Canary Islands, Spain. *Willdenowia*, 43, 25–31.

Boyce, P. C. (1994). The genera *Dracunculus* and *Helicodiceros* (Araceae: Aroideae). *Thaiszia*, 4, 175–182.

Bramwell, D. (1972). A revision of the genus *Echium* in Macaronesia. *Lagascalia*, 2, 37–115.

Bramwell, D. (1975). Some morphological aspects of the adaptive radiation of Canary Islands *Echium* species. *Anales del Instituto Botánico. A. J. Cavanilles*, 32, 241–254.

Bramwell, D. (1995a). A new *Lotus* species from Gran Canaria. *Botánica Macaronésica*, 22, 113–116.

Bramwell, D. (1995b). A new *Silene* Species from Gran Canaria. *Botánica Macaronésica*, 22, 121–122.

Chaisongkram, W., & Chantaranothai, P. (2006). A revision of the genus *Aristida* L. (Poaceae) in Thailand. *Tropical Natural History*, 6, 125–134.

de Paz, P. L. P. (1973). "*Micromeria glomerata*", una nueva especie del Gén. "*Micromeria*" Benth. en la isla de Tenerife. *Vieraea*, 3, 77–81.

de Paz, P. L. P. (1977). *Revisión del género Micromeria Bentham (Lamiaceae-Stachyoideae) en la región macaronésica*. Doctoral dissertation, Universidad de La Laguna.

de Paz, P. L. P., & Hernríquez, F. E. R. (1981). Sobre" *Sideritis dendrochahorra*" bolle en Tenerife (Islas Canarias). *Vieraea*, 11, 283–302.

Eggli, U. (2002). *Sukkulenten-Lexikon Band 2: Zweikeimblättrige Pflanzen (Dicotyledonen)*. Eugen Ulmer, Stuttgart.

Gaisberg, M. V., & Wagenitz, G. (2002). *Carduus baeocephalus* subsp. *microstigma* Gaisberg & Wagenitz, a new subspecies from the Canary Islands (Cardueae, Carduinae)-a facultative autogamous descendant of *Carduus baeocephalus* Webb subsp. *baeocephalus*. *Candollea*, 57, 271–282.

Galván, M. F., & Guerra, A. S. (1988). Sobre la taxonomía y corología de *Sideritis marmorea* Bolle. *Botánica Macaronésica*, 16, 53–60.

Gonzáles, J. G., Morales Mateos, J. B., Gonzáles, M. L. J., & Mesa Coello, R. (2013). *Vicia voggenreiteriana* (Fabaceae) a new species from the island of La Gomera (Canary Islands). *Vieraea*, 41, 189–201.

Halliday, P. (1986). The genus *Kleinia* (Compositae) in North Africa and the Canary Islands. *Kew bulletin*, 41, 279–285.

Hansen, A. (1972). A new *Rubus* species from the Canary Islands. *Botaniska Notiser*, 125, 379–382.

Hohenester, A., & Welß, W. (1993). *Exkursionsflora für die Kanarischen Inseln*, Ulmer, E.

Humphries, C. J. (1976). A Revision of the Macaronesian Genus *Argyranthemum* Webb Ex Schultz Bip. (Compositae-Anthemideae). *Bulletin of the British Museum (Natural History). Botany*, 5, 147–240.

Kilian, N. (1988). Die Lactuceae (Compositae) der Kapverdischen Inseln (W-Afrika). *Willdenowia*, 18, 113–216.

Kyncl, T., Suda, J., Wild, J., Wildová, R., & Herben, T. (2006). Population dynamics and clonal growth of *Spartocytisus supranubius* (Fabaceae), a dominant shrub in the alpine zone of Tenerife, Canary Islands. *Plant Ecology*, 186, 97–108.

La Serna, I. (1980). *Bystropogon wildpretii*, una nueva especie del género Bystropogon LHer. en la isla de La Palma (Islas Canarias). *Vieraea*, 10, 83–94.

La Serna, I., & Wildpret, W. (1980). Contribución al estudio taxonómico y ecológico de Bystropogon odoratissimus. *Bolle. Anal. Inst. Bot. Cavanilles*, 35, 129–144.

Liu, H. Y. (1986). *A monograph of the genus Aeonium (Crassulaceae-sempervivoideae)*. Doctoral dissertation, The Ohio State University.

HANZ ET AL.

Global Ecology
and Biogeography

A Journal of
Macroecology

WILEY | **1331**

Marrero, Á., Almeida, R. S., & González-Martín, M. (1998). A new species of the wild dragon tree, *Dracaena* (Dracaenaceae) from Gran Canaria and its taxonomic and biogeographic implications. *Botanical Journal of the Linnean Society, 128*, 291–314.

Marrero, Á., & Navarro, B. (2003). *Sideritis amagroi* sp. nov. (Lamiaceae) una nueva especie para Gran Canaria (Islas Canarias). *Botánica Macaronésica, 24*, 57–66.

Marrero, Á. (2008). *Sideritis guayedrae* sp. nov. (Lamiaceae), una nueva especie para Gran Canaria (Islas Canarias). *Botánica Macaronésica, 27*, 3–16.

Marrero, Á. (2013). Revisión cariológico-taxonómica del complejo *Sideritis brevicaulis* (Lamiaceae) del Macizo de Teno en Tenerife, islas Canarias. *Vieraea, 41*, 293–318.

Mendoza-Heuer, I. (1987). Makaronesische Endemiten: zur Blütenbiologie von *Plocama pendula* Ait. (Rubiaceae). *Bauhinia, 8*, 235–241.

Montelongo, V., Bramwell, D., & Fernández-Palacios, O. (2003). *Parolinia glabriuscula* (Brassicaceae), a new species from Gran Canaria (Canary Islands, Spain). *Botánica Macaronésica (España), 24*, 67–72.

Muer, T., Sauerbier, H., & Calixto, F. C. (2016). *Die Farn- und Blütenpflanzen der Kanarischen Inseln*, Margraf, Weikersheim.

Negrín-Sosa, M. L., & de Paz, P. L. P. (1988). Consideraciones acerca del género *Sideritris* L. (Lamiaceae) en Tenerife (Islas Canarias). *Lagascalia, 15*, 295–318.

Nogales, M., Valido, A., Medina, F. M., & Delgado, J. D. (1999). Frugivory and factors influencing visitation by birds at 'Balo' (*Plocama pendula* Ait., Rubiaceae) plants in the Canary Islands. *Ecoscience, 6*, 531–538.

Pedrola-Monfort, J., & Caujapé-Castells, J. (1998). The *Androcymbium* species of the Canary Islands. *Curtis's Botanical Magazine, 15*, 67–77.

Prina, A. O., & Martinez-Laborde, J. B. (2008). A taxonomic revision of *Crambe* section Dendrocrambe (Brassicaceae). *Botanical Journal of the Linnean Society, 156*, 291–304.

Rodríguez, M., Fariña, B., & Moreno, J. (2010). *Arrhenatherum calderae* A. Hansen (Poaceae) y *Petrorhagia nanteuilii* (Burnat) PW Ball & Heywood (Caryophyllaceae) en el cono del volcán Teide, Parque Nacional del Teide (Tenerife, Islas Canarias). *Academia Canaria Ciencias, 21*, 45–48.

Sandral, G., Remizowa, M. V., & Sokoloff, D. D. (2006). A taxonomic survey of Lotus section Pedrosia (Leguminosae, Loteae). *Wulfenia, 13*, 97–192.

Santos-Guerra, A. (2014). Contribución al conocimiento del género *Helianthemum* Miller (Cistaceae) en las islas Canarias: *Helianthemum cirae* A. Santos sp. nov. y *H. linii* A. Santos sp. nov., especies nuevas para la isla de la Palma. *Vieraea, 42*, 295–308.

Scholz, H., & Böcker, R. (1996). Ergänzungen und Anmerkungen zur Grasflora (Poaceae) der Kanaren. *Willdenowia, 25*, 571–582.

Scholz, H., Stierstorfer, C. H., & Gaisberg, M. v. (2000). *Lolium edwardii* sp. *nova* (Gramineae) and its relationship with *Schedonorus* sect. *Plantynia* Dumort. *Feddes Repertorium, 111*, 561–565.

Schönfelder, P., & Schönfelder, I. (2018a). *Die Kosmos-Kanarenflora: mehr als 640 charakteristische Kanarenpflanzen im Porträt, extra 62 Tropische Nutzhölzer*, Kosmos, Stuttgart.

Schönfelder, P., & Schönfelder, I. (2018b). *Die Kosmos-Mittelmeerflora: über 1600 Arten und 1600 Fotos* (2nd edn). Franckh Kosmos Verlag.

Sprague, T. A., & Hutchinson, J. (1914). Echiums from the Atlantic Islands: I. *Bulletin of Miscellaneous Information (Royal Botanic Gardens, Kew), 1914*, 116–122.

Stearn, W. T. (1972). *Kunkeliella*, a new genus of Santalaceae in the Canary Islands. *Cuaderno Botanica Canariensis, 16*, 11–26.

Upson, T. M., & Andrews, S. (2003). A new species of *Lavandula* L. (Lamiaceae) from Gran Canaria, Canary Islands. *Kew bulletin, 58*, 903–907.

Valcárcel, J. F. R., Alamo, E. C., Baudet, A. B., & Marrero, M. (2001). Estudio morfológico de frutos, semillas y plántulas de algunos endemismos vegetales del piso bioclimático supracanario seco. *Vieraea, 29*, 1–15.

Verloove, F. (2010). *Sporobolus copei* sp. nov. (Poaceae: Chloridoideae) from Tenerife (Canary Islands, Spain). *Nordic Journal of Botany, 28*, 465–468.

Vitales, D., García-Fernández, A., Pellicer, J., Vallès, J., Santos-Guerra, A., Cowan, R. S., Fay, M. F., Hidalgo, O., & Garnatje, T. (2014). Key processes for *Cheirolophus* (Asteraceae) diversification on oceanic islands inferred from AFLP data. *PloS one, 9*, e113207.

Weigelt, P., König, C., & Kreft, H. (2020). GIFT – A global inventory of floras and traits for macroecology and biogeography. *Journal of Biogeography, 47*, 16–43. https://doi.org/10.1111/jbi.13623

Wildpret de la Torre, W. (1973). *Micromeria rivas-martinezii* nuevo endemismo del Gén. *Micromeria* Benth en las Islas Canarias. *Vieraea, 3*, 71–76.

Wood, J. R., Williams, B. R., Mitchell, T. C., Carine, M. A., Harris, D. J., & Scotland, R. W. (2015). A foundation monograph of *Convolvulus* L. (Convolvulaceae). *PhytoKeys, 51*, 1–282.