LETTER

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

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Abstract

Current models of island biogeography treat endemic and non-endemic species as if they were functionally equivalent, focussing primarily on species richness. Thus, the functional composition of island biotas in relation to island biogeographical variables remains largely unknown. Using plant trait data (plant height, leaf area and flower length) for 895 native species in the Canary Islands, we related functional trait distinctiveness and climate rarity for endemic and non-endemic species and island ages. Endemics showed a link to climatically rare conditions that is consistent with island geological change through time. However, functional trait distinctiveness did not differ between endemics and non-endemics and remained constant with island age. Thus, there is no obvious link between trait distinctiveness and occupancy of rare climates, at least for the traits measured

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here, suggesting that treating endemic and non-endemic species as functionally equivalent in island biogeography is not fundamentally wrong.

INTRODUCTION

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

In a set of species, some traits are more distinct than others. Functional trait distinctiveness (herein functional distinctiveness) is a relatively recent index that measures how distinct species traits are relative to a given set of species (e.g. a community, an island biota and a regional species pool, Violle et al., 2017). Assessing patterns of trait distinctiveness of endemic and non-endemic native species on oceanic islands may shed light on the biogeographical, ecological and evolutionary processes that influence the composition of island biotas.

Due to strong dispersal and environmental filters, oceanic island biotas are often a non-random subset of the continental source pool with certain phylogenetic groups, and potentially functional traits, being under- or over-represented (Carlquist, 1974; König et al., 2021). Evolutionary processes therefore occur from an already biased set of species. Many adaptive radiations involve endemic species (Carlquist, 1974; Schluter, 2000; Stuessy et al., 2006), where trait divergence is high but genetic differentiation is low. Thus, a number of distinct characteristics, often referred to as island syndromes (Burns, 2019), are typical for island species—a well-known example being the evolution of secondary woodiness in plants (Lens et al., 2013; Zizka et al., 2022). Given

the unique circumstances under which oceanic island biotas are shaped and the distinctive qualities of island endemic species, we might expect to see distinct combinations of functional traits (Hanz et al., 2022; Keppel et al., 2018; Ottaviani et al., 2020; Veron et al., 2021). On the other hand, speciation on islands may not always be driven by strong adaptation. Species can evolve through non-adaptive processes, such as drift, which may not necessarily reflect adaptive change (Stuessy et al., 2006). Therefore, we might expect the traits of endemics to change very little following in situ evolution. Comparing trait composition of endemic and non-endemic species could provide insight into the processes influencing trait evolution on oceanic islands.

Oceanic islands vary in their climatic heterogeneity, often as a function of age. Elevational range and topography change over the geological lifespan of an island due to volcanic activity and erosional processes, influencing the climate by creating strong climatic gradients (Whittaker et al., 2008). Climate heterogeneity plays a key role in determining species' composition and evolutionary outcomes on islands (Carvajal-Endara et al., 2017; Irl et al., 2015; Taylor et al., 2019). Thus, the links between species traits and climate likely influence species distinctiveness (Raphael & Molina, 2013). Species radiating into empty niches may become specialised to geographically scarce habitats (Gaston, 1994). Recent evidence from the Canary Islands shows that evolutionarily successful lineages (including many endemics) are abundant in marginal habitats (Fernández-Palacios et al., 2021) and many island endemics are associated with rare environments at high elevations (Steinbauer, Field, Grytnes, et al., 2016). If species traits have adapted to these once-empty niches, then trait distinctiveness should be linked to climate rarity. On the other hand, if species utilise generalist strategies to occupy a broad array of environmental conditions, the relationship between trait distinctiveness and climatic rarity may be weak. We also cannot discount the role of stochastic processes: allopatric divergence and genetic drift could create scenarios where species traits are not explicitly linked to their environment via adaptive processes. Thus, an unanswered question is: by occupying rare climates, do endemic species evolve distinct traits?

Ecological and evolutionary outcomes on oceanic islands are influenced by island area, isolation and heterogeneity (MacArthur & Wilson, 1967; Schluter, 2000; Simpson, 1953). These island features themselves change through time (see Figure 1a). The General
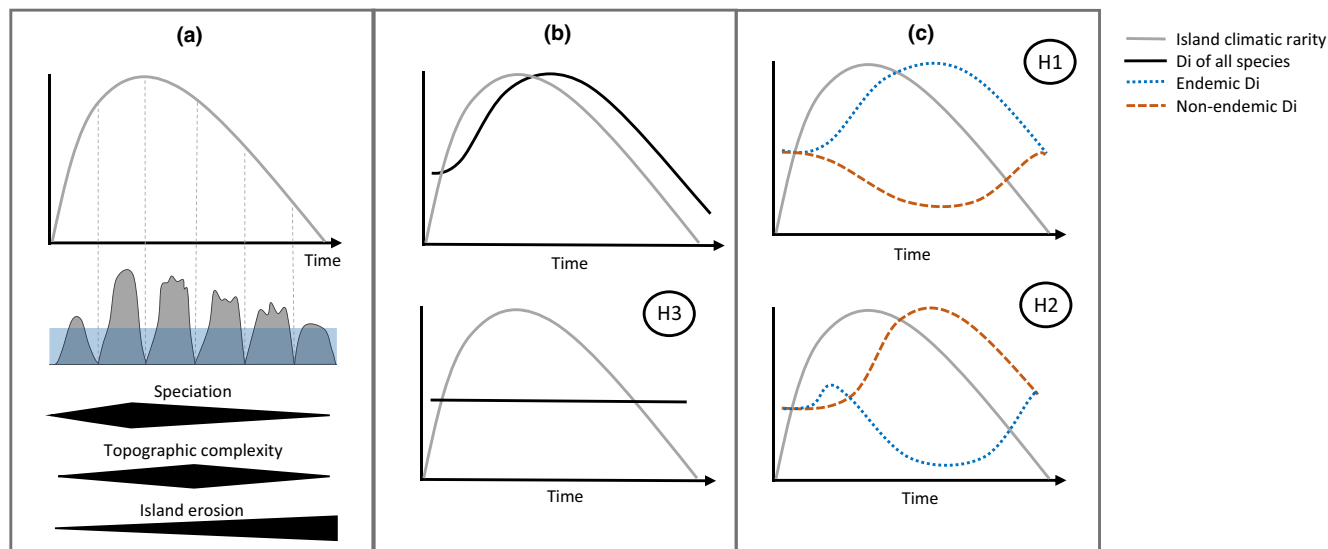
FIGURE 1 Different scenarios of how functional trait distinctiveness (D_i) changes with respect to climatic through island ontogeny: a workflow of our hypotheses. Panel (a) shows how we expect climatic rarity to change as islands age. The shaded humps represent cross-sections of islands at different stages in their geological evolution, the black bars represent the variation in speciation, topographic complexity and island erosion through time (Borregaard et al., 2017; Whittaker et al., 2008, 2017). This island ontogeny is what is considered on the x-axis of all plots. Panel (b) shows two alternative scenarios for D_i: the top graph shows D_i tracking climatic rarity, the bottom graph shows no change in D_i with island ontogeny. In the instance that D_i does track climatic rarity, panel (c) shows how this may play differently for endemic and non-endemic species. (H1) The endemic specialisation hypothesis, (H2) The endemic expansion hypothesis and (H3) The endemic release hypothesis. Note that D_i is relative.

Dynamic Model (GDM; Whittaker et al., 2008) proposes how changes in these parameters influence immigration, speciation and extinction over the course of an island's geological development (from emergence to subsidence). Furthermore, the GDM postulates that species diversity is related to topographic heterogeneity, predicting a unimodal relationship through time. Here, we use the GDM's framework to make predictions for the functional rarity dynamics of endemic species on oceanic islands, specifically the relationships between functional distinctiveness, climate rarity and endemism. We test three competing hypotheses: (1) the endemic specialisation hypothesis, (2) the endemic expansion hypothesis and (3) the endemic release hypothesis (Figure 1), which we outline below. For each hypothesis, we predict how the functional distinctiveness and climatic rarity of endemics and non-endemics change through island ontogeny.

The endemic specialisation hypothesis states that species colonising islands become established in the coastal, lowland climate zones, followed by niche differentiation and speciation associated with inland expansion, with the resulting endemic species characterised by increased specialisation as they speciate into climatically rare, montane areas (Ricklefs & Bermingham, 1999; Ricklefs & Cox, 1972, 1978). This may lead to the evolution of many distinct species that support new functions (Borregaard et al., 2017). As islands age, high-elevation environments are created by volcanic activity and then lost to erosion and submergence, leading to the extinction of endemic species. Thus, we expect trait distinctiveness of endemics

to follow a hump-shaped relationship (Figure 1, H1). For non-endemic native species, we expect the opposite relationship for functional distinctiveness, in part because rarity is relative, but also because the distinctiveness of endemics may enhance the colonising success of immigrating species by reducing competition (Darwin, 1859; Park et al., 2020; Strauss et al., 2006). Many non-endemics are subject to continued gene flow, increasing the genetic variation and potentially phenotypic variation of the non-endemic pool. Thus, we expect non-endemics to be less distinct and less specialised as they are widespread, occupying both rare and common climates. Functional distinctiveness of endemics and non-endemics collapse as islands reach old age.

The endemic expansion hypothesis begins similarly to the previous hypothesis: endemic species initially speciate through inland expansion into rarer climates (hence the small hump in Figure 1, H2). However, this is followed by expansion across climate zones—based on the idea that populations of established endemics can undergo multiple expansions (Ricklefs & Bermingham, 1999), and that they are not doomed to continued range restriction and specialisation. Therefore, this hypothesis predicts that endemics occupy rare climates in the youngest islands, but quickly spread to occupy both rare and common climates. Under this scenario, immigrating non-endemic species become less competitive and so the colonising space for incoming non-endemics becomes progressively smaller. Thus, in contrast to the previous hypothesis, non-endemics are more functionally distinct than endemics. These hypotheses show strong similarities to the

taxon cycle (Wilson, 1961). Currently, there is little evidence linking plants to this concept.

Both the endemic specialisation and the endemic expansion hypotheses predict that trait distinctiveness tracks climatic rarity, in that species with distinct traits occur in rare climates, while species with common traits occur in common climates. This contrasts with the endemic release hypothesis, which predicts no relationship between climatic rarity and functional distinctiveness (Figure 1, H3). This suggests that endemic species evolve with little trait change as they spread inland and to higher elevations (Steinbauer, Field, Grytnes, et al., 2016). Lower species richness on islands compared to the mainland (Kreft et al., 2008; Whittaker & Fernández-Palacios, 2007) could result in weak interspecific competition (Schluter, 1988), reducing the selective pressure to occupy and adapt to rare climates and resulting in little trait change (or a very long lag behind the shift into rare climates).

We tested these hypotheses for endemic and non-endemic native (NEN) plants on the Canary Islands. Because part of our aim was to compare between different islands, we consider functional distinctiveness and climatic rarity at both the island level and archipelago level. Therefore, we divided the endemic species into single-island endemics (SIEs—species whose entire geographical distribution is restricted to a single island in the archipelago) and multi-island endemics (MIEs—species whose entire geographical distribution is restricted to two or more islands in the archipelago). NENs were those species found on both the mainland and on the archipelago. For each group, we used plant functional trait data and climatic variables to estimate functional distinctiveness and climatic rarity, respectively, and tested whether differences between the endemic groups differ within and between islands of different ages, as predicted by our hypotheses.

METHODS

Study area

The Canary Islands (Spain), an active volcanic archipelago (the Tajogaite eruption occurred in La Palma 2021), comprise of seven major islands (Figure 2). The climate is subtropical Mediterranean-type, varying quite drastically within islands, particularly in the higher elevation islands due to the north-eastern trade winds generating a precipitation gradient from the north-east to the south-west slopes (del Arco Aguilar et al., 2010). In contrast, the lower elevation eastern islands of Fuerteventura and Lanzarote are relatively uniform in climate. The strong climatic gradients and high environmental heterogeneity (Barajas-Barbosa et al., 2020), particularly on the younger islands, have generated considerable ecosystem diversity, which manifests as habitat zones in elevational belts from the coast to the mountaintops (del Arco Aguilar et al., 2010; Fernández-Palacios et al., 1995). Approximately, one third of the current Canarian seed plant flora are endemic to the archipelago, one third native non-endemic and one third introduced (Arechavaleta et al., 2009). Several of the plant lineages are thought to have undergone adaptive radiations, including *Aeonium*,
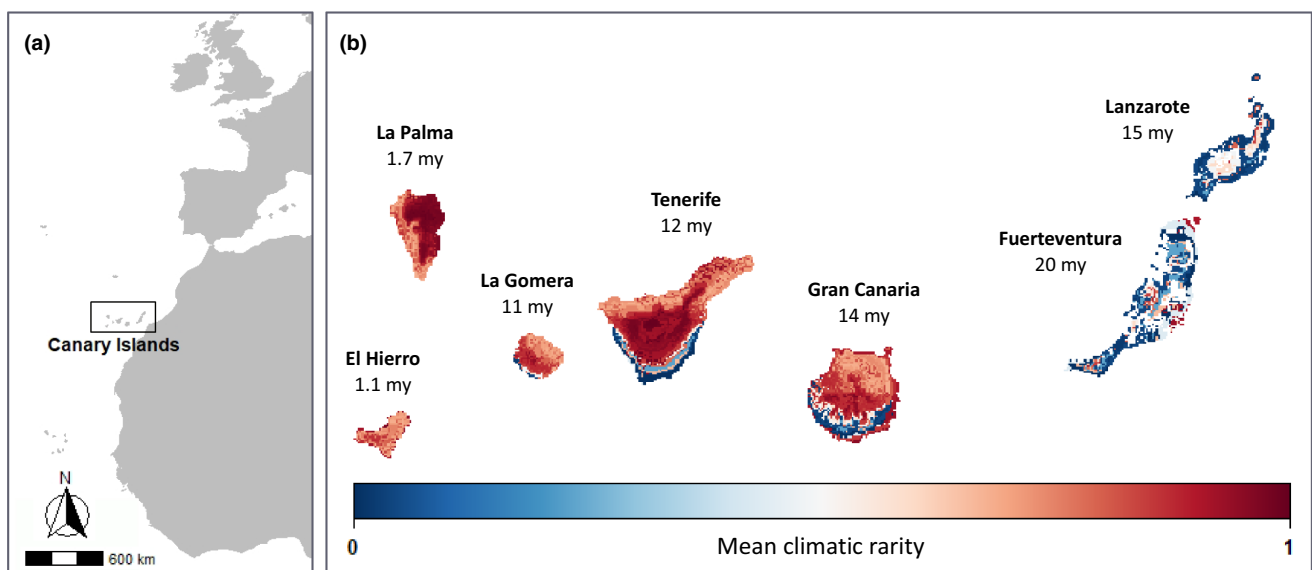

FIGURE 2 (a) Map of the location of the Canary Islands. (b) Map of the Canary Islands. Colour gradient indicates the climatic rarity index for 500 × 500 m grid cells (before it is aggregated by species). Climatic rarity is scaled between 0 and 1 with values closer to 1 indicating a rare climate. This is calculated at the archipelago level, thus the values for each grid cell indicate the rarity of that cell relative to all other cells in the archipelago. Islands are labelled with their approximate ages (van den Bogaard, 2013). my, million years. Areas of white space appear where grid cells have missing data.

Argyranthemum, *Cistus, Echium, Micromeria, Sonchus* and *Tolpis* (Schenk, 2021).

Trait data

We used three plant traits: maximum plant height, maximum leaf area and maximum flower length. Plant height, a common measure of plant size, influences a plant's ability to compete for light and is important for seed dispersal (Muller-Landau et al., 2008; Westoby et al., 2002). Measuring leaf size, leaf area is important for carbon acquisition, transpiration, CO_2 uptake and light interception (Press, 1999). Flower length (proxy for flower size) is important for pollination, energy balance and transpiration (Harrap & Rands, 2022; von Arx et al., 2012). All three traits show relationships with environmental variables, including temperature and precipitation (Dong et al., 2020; Moles et al., 2009; Paušič et al., 2019). We used maximum trait values as they reflect the species fitness response to environmental gradients and generally have better data coverage.

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

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

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

The current plant checklist for the Canary Islands places species into six categories: definitely native (including endemics), probably native, possibly native, probably introduced, introduced non-invasive and introduced invasive (Arechavaleta et al., 2009). We only include species that are in the first three of these categories (i.e. excluding introduced species). We used principal components analysis to visualise where endemics and non-endemics sit in Canary Island trait space.

Plant trait data are scarce for the Canary Islands, with many species missing from online and literature sources (Beierkuhnlein et al., 2021; Cutts et al., 2021), which limits us to the aforementioned traits. However, trait choice can strongly influence results (Mouillot et al., 2021; Zhu et al., 2017) because the position of a species in trait space relative to other species may change depending on the traits chosen. To understand the impact of our choice of traits, we also examined an expanded set of traits for Tenerife species (sufficient data on additional traits were not available for other islands). In addition to the three traits mentioned above, we have field measurements for the following traits for Tenerife species: specific leaf area (SLA), stem specific density (SSD) and leaf dry matter content (LDMC). See supporting information S1 for trait measurement protocols.

Species occurrence data

To estimate the mean climatic conditions within each species' range, we used species occurrence data from Atlantis 3.1 (www.biodiversidadcanarias.es/biota), a governmental, open-access database with occurrence data of Canary Islands species. The data are presence-only, at a resolution of 500×500 m and reflect sampling effort (Hortal et al., 2007), but are particularly good for endemic species, for which there has been long-term sampling. Steinbauer, Field, Fernández-Palacios, et al. (2016) provide an informative review of the data quality in their supporting information. We updated the species presence data and taxonomy using the most recent checklist for Canary Island plants—FloCan (Beierkuhnlein et al., 2021), which revealed duplicates of two species: *Arenaria serpyllifolia* was measured twice under different names and *Serapias mascaensis* was included as both a species and a subspecies. In both instances, we removed the smaller of the two as we use maximum trait values.

Rarity indices

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

Functional distinctiveness

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

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

where N is the number of species, d_{ij} is the distance in trait space between species i and j (Grenié et al., 2017; Violle et al., 2017). All three traits were log-transformed and scaled. Five species had zero values for leaf area because they do not possess leaves (e.g. *Euphorbia canariensis*), creating an issue when transforming the data. We did not want to remove these species as they represent rare trait values, so

we replaced the zeros with an arbitrary value that is less than the minimum value for all the other species. As the minimum value for leaf area was $2.36\,mm^2$, we replaced the zeros with a value of $0.5\,mm^2$. D_i was scaled between 0 and 1 using the following formula: $(x–\min(x)) \div (\max(x) – \min(x))$.

Climatic rarity

We computed climatic rarity following Irl et al. (2015). Mean annual precipitation and mean annual temperature were interpolated, at a resolution of $500 \times 500\,m$ to match the occurrence data, using data obtained from meteorological stations on the Canary Islands, provided by Agencia Estatal de Meteorología (see Irl et al., 2015). Precipitation was log-transformed because ecologically meaningful variation among smaller values is underemphasised when using the raw data, which are strongly right-skewed. Climatic rarity was calculated as follows. First, temperature and precipitation variables were divided into equal sized bins. We trialled using 10, 20 and 30 bins. We report the results using 20 bins as this produced slightly higher R^2 values (see supporting information S2). Next, each grid cell was assigned a temperature and precipitation bin and the total number of cells in each bin calculated. Because rarer climates (bins) have fewer cells, the climate rarity index was calculated by subtracting each total from the maximum value and adding one, so that high values represent rare climates. The index was then scaled between 0 and 1 for ease of comparison with D_i. To obtain a climatic rarity value for each species, we took the median and third quartile of climatic rarity values of all the grid cells where the focal species was present. Thus, this index was centred on the species, not the geographical location. The median is less likely than the mean to be influenced by uncertainty or errors in distribution or environmental data. The index was calculated for the entire archipelago (archipelago-level climatic rarity) and separately for each island (island-level climatic rarity). Comparisons between endemism groups use archipelago-level climatic rarity, whereas comparisons between islands use island-level climatic rarity.

Statistical analysis

To compare D_i and climatic rarity between endemism groups and between islands, we conducted phylogenetically corrected ANOVAs using the 'caper' and 'phytools' packages in R (Orme et al., 2018; R Core Team, 2021; Revell, 2012). The phyANOVA() function is simulation-based and conducts post hoc comparisons of means between groups. We set the number of simulations to 10,000 and used Bonferroni correction for pairwise comparisons. Phylogenetic information for the Canary Island species was obtained by pruning a mega seed

plant phylogeny (Smith & Brown, 2018). The resulting tree contained polytomies at the species level with 25% of the nodes unresolved. Unresolved trees can underestimate phylogenetic diversity (Swenson, 2009), so we randomly resolved the phylogeny prior to analysis. Many of the species in our data occurred on multiple islands, which created multiple observations for the same species. This led to computational difficulties when preparing the data for the phylogenetic ANOVA, as the comparative.data() function in the caper package cannot handle duplicate species. To troubleshoot this, we added the duplicates to the phylogeny as sister species, with branch lengths of 0.001 (Grenié et al., 2017).

RESULTS

Overall, we collected trait, climate and phylogenetic data for 895 native species (271 SIE, 205 MIE, 419 NEN; Table 1). Fuerteventura and Lanzarote have very few SIEs, so their sample sizes are small. Missing trait data could bias our results as species occurring in rare climates may be less likely to have trait data. However, we found no significant differences in climatic rarity values between the sets of species with and without trait data (t test: SIE_{57}, $p = 0.61$; MIE_{42}, $p = 0.11$; NEN_{360}, $p = 0.14$).

Correlations between traits were significant but weak: plant height–leaf area $r = 0.35$, $p < 0.001$; plant height–flower length $r = 0.10$, $p < 0.001$; leaf area–flower length $r = 0.26$, $p < 0.001$. Principal components analysis revealed that the species groups strongly overlap in Canary Island trait space, with the endemic species nested within the non-endemic natives, which occupied the core and the periphery (Figure 3).

D_i and climatic rarity did not correlate overall ($r = -0.02$, $p = 0.52$), nor did they correlate within each endemism group (SIE $r = 0.04$, $p = 0.54$; MIE $r = -0.02$, $p = 0.78$; NEN $r = 0.00$, $p = 0.99$) or within each island (El

TABLE 1 Number of species with complete data, which includes all three traits (max plant height, max leaf area and max flower length), climatic rarity and phylogenetic data.

	SIE	MIE	NEN
El Hierro	12	98	245
La Palma	34	137	281
La Gomera	30	127	273
Tenerife	104	177	386
Gran Canaria	71	125	350
Fuerteventura	8	56	268
Lanzarote	12	46	240
Total	271	205	419

Note: Note that (except for SIEs) many of the species occur on multiple islands, so that adding the island figures surpasses the archipelagic total.

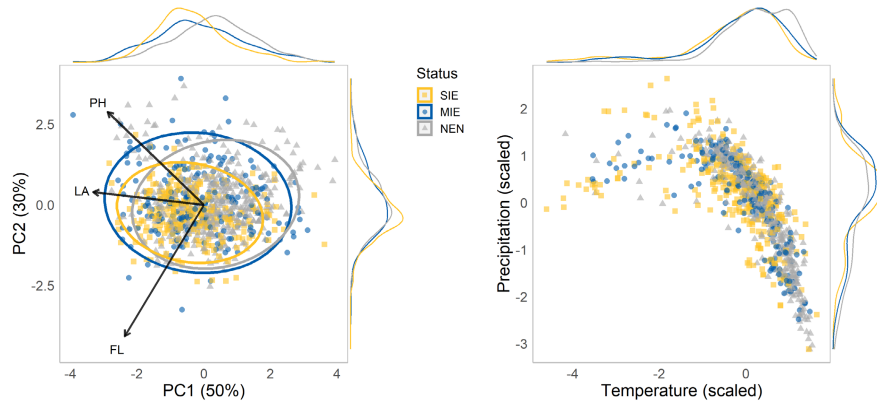Abbreviations: MIE, multi-island endemic; NEN, non-endemic native; SIE, single-island endemic.

FIGURE 3 Left: Functional trait space represented using principal component analysis for the Canary Islands based on three traits: maximum plant height (PH), maximum leaf area (LA) and maximum flower length (FL). Ellipses show 95% confidence. Right: Position of species in climate space (mean annual temperature and precipitation). Precipitation is log-transformed. At the top and right of each graph, marginal density distribution plots are shown for each endemism group. SIE, single-island endemic ($n = 271$), MIE, multi-island endemic ($n = 205$), NEN, non-endemic native ($n = 419$).
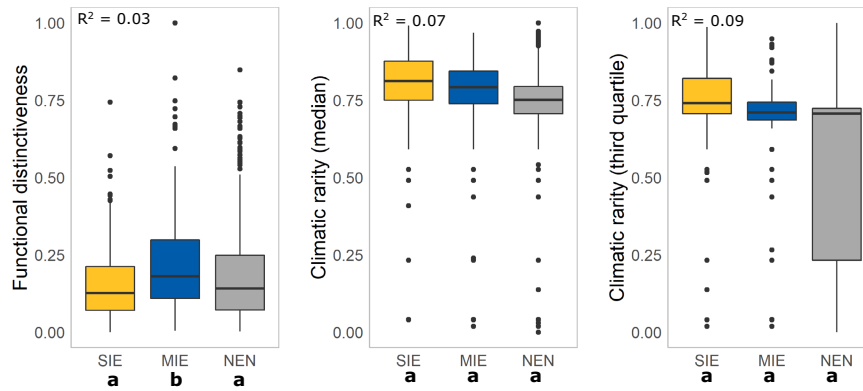

FIGURE 4 Functional distinctiveness and archipelago-level climatic rarity for each endemism group across the entire Canary archipelago. Differing letters indicate pairwise significant differences between groups ($p < 0.05$). SIE, single-island endemic, MIE, multi-island endemic, NEN, non-endemic native.

Hierro $r = 0.05$, $p = 0.37$; La Palma $r = 0.06$, $p = 0.18$; La Gomera $r = 0.04$, $p = 0.35$; Tenerife $r = 0.04$, $p = 0.37$; Gran Canaria $r = 0.04$, $p = 0.33$; Lanzarote $r = -0.02$, $p = 0.88$; Fuerteventura $r = 0.01$, $p = 0.82$).

Functional distinctiveness

A phylogenetic ANOVA revealed no significant difference in D_i between the endemism groups ($F = 14.17$, $p = 0.24$, $R^2 = 0.03$; Figure 4). However, pairwise comparisons showed a significant difference between SIEs and MIEs, with MIEs being more distinct ($p = 0.005$). For between-islands comparisons of D_i, a phylogenetic ANOVA indicated no significant difference for SIEs ($F = 1.85$, $p = 0.11$, $R^2 = 0.04$) or MIEs ($F = 0.40$, $p = 0.54$, $R^2 = 0.003$), and a significant effect for NENs ($F = 4.40$, $p = 0.005$, $R^2 = 0.01$). Pairwise comparisons revealed some differences for NENs, with D_i lower in Lanzarote and Fuerteventura, but no pairwise differences were

found between islands for SIEs or MIEs. In all cases, the proportion of variance in functional distinctiveness explained by endemism class or island was small.

Climatic rarity

There was a noticeable difference between the five high-elevation islands in the west, which possess more rare climates, and the two older islands (Fuerteventura and Lanzarote) in the east, which contain very few areas of rare climate (Figure 2b, S3). Within islands, rare climates tend to be found at areas of high elevation or high topographic complexity (Figure 2b). Climate space is shown in Figure 3, where endemic species appear to occupy a wider range of climates, including cold and dry climates, than non-endemics.

Occupancy of rare climates increased with increasing endemism, but weakly (for the median: $F = 31.02$, $p = 0.05$, $R^2 = 0.07$ for third quartile: $F = 42.61$, $p = 0.02$, $R^2 = 0.09$).

Pairwise comparisons showed no significant differences between pairs of endemism groups (for median: SIE–MIE: $p = 0.35$; SIE–NEN: $p = 0.16$; MIE–NEN: $p = 0.33$; for the third quartile: SIE–MIE: $p = 0.17$; SIE–NEN: $p = 0.06$; MIE–NEN: $p = 0.18$; Figure 4). Comparing between islands revealed a strong pattern for SIEs (median: $F = 77.09$, $p < 0.001$, $R^2 = 0.62$; third quartile: $F = 158.42$, $p > 0.001$, $R^2 = 0.62$), which are found in rare climates in the young and middle-aged islands, El Hierro, La Palma and La Gomera (for which there were no pairwise differences), but are found in progressively less rare climates as the islands increase in age (Figure 5). MIEs show a similar, but much less pronounced, pattern across islands (median: $F = 47.21$, $p < 0.001$, $R^2 = 0.27$; third quartile: $F = 52.01$, $p > 0.001$, $R^2 = 0.28$), and the pattern for NENs is similar but weak (median: $F = 41.75$, $p < 0.001$, $R^2 = 0.07$; third quartile: $F = 21.38$, $p > 0.001$, $R^2 = 0.06$). See supporting information S4, S5 and S6 for ANOVA tables, pairwise P values and boxplots.

Assessing the impact of trait choice using Tenerife data

To investigate the impact of our choice of traits, we calculated D_i (within Tenerife) using an expanded set of traits for Tenerife species. The two measures of D_i (3-trait and 6-trait) showed a strong positive correlation ($r = 0.79$, $p < 0.001$) and in both cases, functional distinctiveness showed similar patterns in relation to endemicity. Again, principal components analysis revealed a nested pattern, but this pattern was much clearer when using the expanded set of traits. These results are shown in supporting information S7.

DISCUSSION

The General Dynamic Model of oceanic island biogeography (GDM) posits that the geological evolution of an island influences the evolution of species, thus linking species diversity to island age (Whittaker et al., 2008). In this study in the Canary Islands, we investigated how this translates to species traits, specifically examining functional distinctiveness of endemic and non-endemic species, and how they relate to the rarity of the climate where species occur. All species showed a decline in the occupancy of rare climates with increasing island age, but no concordant pattern is seen for functional distinctiveness, which remains constant through time and does not differ between endemism groups. The lack of relationship between functional distinctiveness and climatic rarity rejects the endemic specialisation and endemic expansion hypotheses. Both hypotheses predict functional distinctiveness to relate to climatic rarity, and functional distinctiveness to differ markedly between endemic and non-endemic species. Therefore, our results most closely align with the endemic release hypothesis, which predicts no relationship between climatic rarity and functional distinctiveness and no trend of functional distinctiveness with island age.

One of the main premises of the GDM is that topographic heterogeneity will be maximised on middle-aged islands (Whittaker et al., 2008), but more recent work shows environmental heterogeneity and species richness to peak early during island ontogeny (Barajas-Barbosa et al., 2020; Steinbauer et al., 2013). Here, we found that endemics, particularly single-island endemics, are already occupying rare climates in the younger islands, with the decline beginning at middle age (La Gomera-Tenerife), suggesting
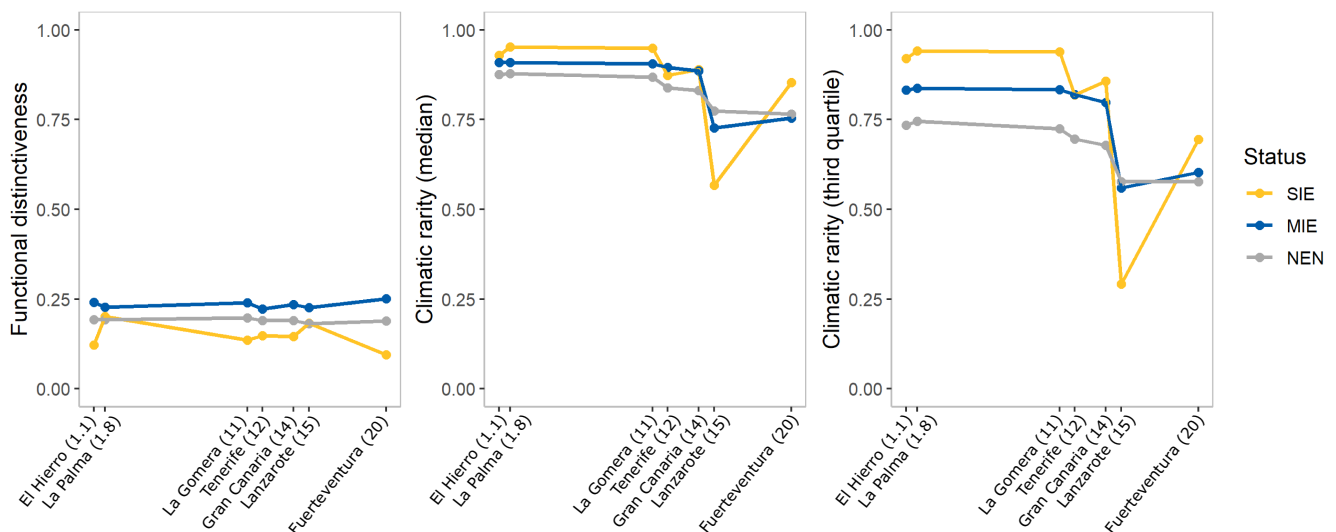

FIGURE 5 Line graphs representing functional distinctiveness and island-level climatic rarity (of the species) with increasing island age. Island ages are obtained from van den Bogaard (2013) and shown in brackets (million years old). Points correspond to mean values for each island. SIE, single-island endemic, MIE, multi-island endemic, NEN, non-endemic native. See S6 in Supporting Information for box and whisker plots showing variation in the data.

an early peak in the diversity of available niche space, co-inciding with changes in elevation (Borregaard et al., 2017). The decline in occupation of rare climates by endemics on older islands may be primarily driven by fewer opportunities to occupy rare climates, as topographic heterogeneity decreases due to erosion and subsidence. However, even when we considered climatic rarity on a per-island basis, we found no evidence of a late shift into relatively rare climates on older islands, suggesting that the invasion of rare climates predominantly happens early in island ontogeny as new niche space becomes available. Non-endemics occupied rare climates similarly through time, thus, endemic species appear to be more closely linked to the rarity of the climate than non-endemics.

Evolution on islands is typified by high rates of trait diversification following ecological opportunity (Carlquist, 1974; Givnish et al., 2009; Jorgensen & Olesen, 2001; Losos & Ricklefs, 2009) and speciation is thought to be maximised in middle-aged islands when topography is highly dissected (Whittaker et al., 2008). However, we do not see differences in functional distinctiveness between islands of different ages (perhaps indicating that species occurring on multiple islands tend to occupy the same climates). Furthermore, we found that endemics are no more distinct in their traits than non-endemic natives, despite occupying rare climates. We would expect species with distinct traits to occupy the peripheries of trait space but our results show considerable overlap of the species groups. This may reflect specialisation and niche packing (Hanz et al., 2022), particularly considering that endemics occupy a wide range of climate space overall (Figure 3). Therefore, it is possible that endemics are experiencing selection without it driving them into novel areas of trait space. In fact, diversifying lineages may decrease trait distinctiveness by producing more similar species. Alternatively, it could be that there is a lag between climate shifts and trait divergence, particularly for species that have colonised more recently. Additionally, as much of the speciation islands is allopatric, we cannot assume that it is adaptive. The amount of non-adaptive speciation occurring will influence the effect of evolutionary drift, which could weaken the difference in traits between endemics and non-endemics.

Multi-island endemic species are more distinct in their traits than single-island endemics (Figure 4), while single-island endemics are more clustered in trait space (Figure 3). Thus, single-island endemics show higher trait similarity (and this is not an artefact of species richness), yet are more widely spread in climate space, suggesting they exploit a variety of environments, which is not reflected in their traits. It could be that there is a lag between climate shifts and trait divergence, particularly for species that have colonised more recently. Or it may simply reflect that multi-island endemics are more successful at exploiting unique resources.

We have focused on how climatic rarity changes during island ontogeny, but island biogeographical gradients other than age may also influence climatic rarity on islands, including area, isolation and position relative to broader climatic gradients. The level of isolation can influence where species colonise from: less isolated islands are mainly colonised from the continent, whereas more isolated islands are more likely to be colonised from nearby islands. Traits from more isolated islands are therefore limited to those already existing in the archipelago. Island area and isolation not only affect species trait composition directly but also through interactions with island age. This is particularly true in the Canary Islands where the youngest islands are also the smallest, the most isolated (furthest from the continent) and possess the rarest climates. Nevertheless, we see no significant difference in functional distinctiveness between islands. Our result could be specific to the Canary Island system, therefore extending this research to other archipelagos is key to understanding island trait dynamics (Kraemer et al., 2022).

Trait choice can greatly influence the outcome of hypothesis tests (Mouillot et al., 2021; Zhu et al., 2017). Plant trait data are scarce for island endemics (Cutts et al., 2021), which limited our choice of traits. The traits we used—plant height, leaf area and flower length—have been linked to temperature and precipitation conditions (Byars et al., 2007; Givnish et al., 2014; Guerin et al., 2012; Paušič et al., 2019; Tao et al., 2016). Even so, we used data for a broader suite of traits, available only for Tenerife, to determine whether expanding our trait set would fundamentally alter patterns of functional distinctiveness. It did not—functional distinctiveness followed the same pattern with respect to endemism. Still, even the Tenerife example may be a victim of trait choice. Identifying the most relevant functional traits to assess evolutionary differences within islands still requires more research and more detailed trait data (especially on intraspecific variation of multi-island species between islands) to allow stronger tests of the ideas we present here.

Future research in functional island biogeography should examine different aspects of functional trait space in relation to endemism, not only using additional trait data (when available) but also by focusing on different facets of functional diversity. For example, this study only considers aboveground traits, which do not reflect the full extent of trait differences across species, particularly when linking those differences to climate (Laughlin et al., 2021). We are still far from an all encompassing set of traits that capture functions related to dispersal, growth, reproduction and survival, allied with an understanding of how these traits link to the abiotic environment.

CONCLUDING REMARKS

Island endemics have fuelled the curiosity of generations of biologists because of their spectacular radiations and unique characteristics. However, trait evolution on

islands remains a rather elusive subject. Some species demonstrate ecological shifts (e.g. Kim et al., 1996), but whether these shifts are followed by trait divergence is less well understood and rigorous tests are lacking. We found that rare climate occupancy by island endemics is dynamic with increasing island age, yet we found no signal in the distinctiveness of their traits. While the hypotheses we laid out here do not capture all the possible influences and stochastic processes that shape functional trait composition, our work represents a step towards integrating functional traits into island theory, and towards understanding the functional signatures of island species.

AUTHOR CONTRIBUTIONS

VC, RF, ACA, FS and MJS developed the initial idea and hypotheses. MPBB collected Tenerife field data. VC and DH digitised herbarium specimens. VC, RF, ACA, FS analysed the data. All authors provided feedback throughout the process, commented on and edited the final article.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.