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Assembly of functional diversity in an oceanic island flora

Martha Paola Barajas Barbosa[1,2,3 ✉], Dylan Craven[4,5], Patrick Weigelt[1,6,7], Pierre Denelle[1], Rüdiger Otto[8], Sandra Díaz[9], Jonathan Price[10], José María Fernández-Palacios[11] & Holger Kreft[1,6,7]

Oceanic island floras are well known for their morphological peculiarities and exhibit striking examples of trait evolution[1–3]. These morphological shifts are commonly attributed to insularity and are thought to be shaped by the biogeographical processes and evolutionary histories of oceanic islands[2,4]. However, the mechanisms through which biogeography and evolution have shaped the distribution and diversity of plant functional traits remain unclear[5]. Here we describe the functional trait space of the native flora of an oceanic island (Tenerife, Canary Islands, Spain) using extensive field and laboratory measurements, and relate it to global trade-offs in ecological strategies. We find that the island trait space exhibits a remarkable functional richness but that most plants are concentrated around a functional hotspot dominated by shrubs with a conservative life-history strategy. By dividing the island flora into species groups associated with distinct biogeographical distributions and diversification histories, our results also suggest that colonization via long-distance dispersal and the interplay between inter-island dispersal and archipelago-level speciation processes drive functional divergence and trait space expansion. Contrary to our expectations, speciation via cladogenesis has led to functional convergence, and therefore only contributes marginally to functional diversity by densely packing trait space around shrubs. By combining biogeography, ecology and evolution, our approach opens new avenues for trait-based insights into how dispersal, speciation and persistence shape the assembly of entire native island floras.

Oceanic islands have attracted great interest in biogeography[6,7] and serve as natural laboratories to study the assembly of floras and faunas[8,9]. Empirical tests of fundamental concepts in ecology and evolution using islands as model systems[2,10] assume that the results can be generalized to non-island contexts. Yet, a long-standing paradigm in island biogeography centres on the notion that insularity, as well as environmental factors linked to the ontogeny of oceanic islands, lead to evolutionarily unique[11,12] and functionally distinct[13,14] biota. These assumptions raise the question of how distinct—or similar— oceanic island biota are compared with other ecosystems around the world.

In contrast to neutral theories, such as the equilibrium theory of island biogeography[10], in which all species have the same chance to arrive on and colonize an island, a trait-based perspective leverages differences in ecological strategies among species determined by functional traits to disentangle the processes that have shaped island biota[4,5]. In functional ecology and functional island biogeography[5,15,16],

differences among species are quantified using morphological and physiological characteristics that impact how plants respond to environmental factors, affect other trophic levels and influence ecosystem properties[17,18]. Trait syndromes and trait coordination among individual traits reflect fundamental ecological strategies that structure plant life from individuals to species assemblages. This includes the conservative–acquisitive continuum captured by the leaf economics spectrum[19,20] and the size continuum (the stature of whole plants and seed mass, size and volume), which, together, define essential functional dimensions of seed plants (for example, the global spectrum of plant form and function, sensu[21]). Functional traits are also used to estimate functional diversity[21], which quantifies the diversity and distribution of ecological strategies in an assemblage[22] and can help to identify the factors that shape an assemblage, such as environmental conditions[23,24] or dispersal filters[12]. Biogeographical, ecological and evolutionary forces may either expand or constrain trait space, thereby driving functional divergence or convergence[25,26].

[1]Biodiversity, Macroecology & Biogeography, University of Göttingen, Göttingen, Germany. [2]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany. [3]Institute of Computer Science, Martin Luther University Halle-Wittenberg, Halle (Saale), Germany. [4]Centro de Modelación y Monitoreo de Ecosistemas, Universidad Mayor, Santiago, Chile. [5]Data Observatory Foundation, Santiago, Chile. [6]Campus-Institute Data Science, University of Göttingen, Göttingen, Germany. [7]Centre of Biodiversity and Sustainable Land Use (CBL), University of Göttingen, Göttingen, Germany. [8]Island Ecology and Biogeography Research Group, Department of Botany, Ecology and Plant Physiology, Universidad de La Laguna, Canary Islands, Spain. [9]Instituto Multidisciplinario de Biología Vegetal (IMBIV), Consejo Nacional de Investigaciones Científicas y Técnicas y Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, Córdoba, Argentina. [10]Department of Geography and Environmental Science, University of Hawai'i at Hilo, Hilo, HI, USA. [11]Island Ecology and Biogeography Research Group, Instituto Universitario de Enfermedades Tropicales y Salud Pública de Canarias (IUETSPC), Universidad de La Laguna, Tenerife, Canary Islands, Spain. ✉e-mail: paolabarajas@gmail.com

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However, shortfalls in trait and distribution data[27,28] usually restrict the geographical extent, spatial grain and taxonomic coverage of such studies, leading to an incomplete and potentially biased understanding of the factors that underpin trait space, across multiple spatial scales.

Crossing large expanses of ocean and adapting to island environments represents a considerable challenge for plants, probably filtering species with trait values that enhance dispersal, establishment and persistence[12,15] (but see ref. 29). Long-distance dispersal is expected to constrain island trait spaces compared with trait spaces of the source pools, leading to functional convergence, in which species share similar trait combinations. By contrast, evolutionary events, such as speciation via lineage splitting (cladogenesis[30]) or via gradual evolution of species (anagenesis[31]) are expected to expand trait space[32] by generating novel trait combinations that fill previously untapped trait space. In addition, the heterogeneous environments of oceanic islands[33] create ecological opportunities (that is, empty niche space)[11] for plants that could promote divergence of new trait combinations. Adaptive island radiations, such as the Hawaiian lobeliads, involve dramatic morphological shifts[34], yet the relative importance of biogeographical and evolutionary processes in shaping trait diversity and ecological strategies on oceanic islands remains elusive.

Here we studied the native seed plant flora of Tenerife (Canary Islands, Spain), an iconic oceanic island located in the Macaronesian meta-archipelago and an ideal natural laboratory[35] to test how biogeography and evolution can affect island functional diversity. Tenerife exhibits environmental gradients from arid coastal succulent scrub vegetation to humid laurel forests and high-elevation vegetation[36], and contains spectacular examples of insular radiations[32]. The native seed plant flora of Tenerife is well studied and includes 436 native seed plants[37]. Of these species, we have measured up to eight functional plant traits that cover a total of 80% of the species–trait combinations of all native seed plants (Extended Data Fig. 1a). We first explored matches and mismatches in trait syndromes between the native flora of Tenerife (that is, 348 species, with 95% coverage of species–trait combinations; Extended Data Fig. 1b) and the global spectrum in plant form and function[21] (Fig. 1). We then evaluated how biogeographical and evolutionary processes may have shaped the functional diversity of the flora of Tenerife by assessing the contribution of five species groups, which are associated with different dispersal and speciation mechanisms, to the overall island trait space (Fig. 2b–f): (1) non-endemic native species, which represent species that colonized the Canaries via long-distance dispersal without undergoing subsequent speciation[38], (2) Macaronesian endemic species, which are primarily associated with 'relictualization', a process that results from the survival of formerly widespread species on islands following the extinction of mainland populations, as well as speciation[39], (3) Canary Islands endemic species, which mainly represent speciation and inter-island dispersal across the archipelago, and (4) Tenerife endemic species, which represent in situ speciation and dispersal only within the island. As a fifth group, we also considered (5) cladogenetic species, an endemic group that is composed of immigrant lineages that diversified within the Macaronesian meta-archipelago.

An oceanic island flora fits within the global functional spectrum

Comparing the variation of traits in the native flora of Tenerife with the global spectrum of plant form and function[21] (Fig. 1 and Extended Data Fig. 2a,b), we found a considerable overlap between the island trait space and the global trait space (Sørensen similarity coefficient of 0.74, based on hypervolume overlap for both trait spaces; Extended Data Fig. 2c; see also the large overlap in distribution along principal component analysis axis 2 in Fig. 1). This suggests a remarkable diversity of different trait combinations and ecological strategies present
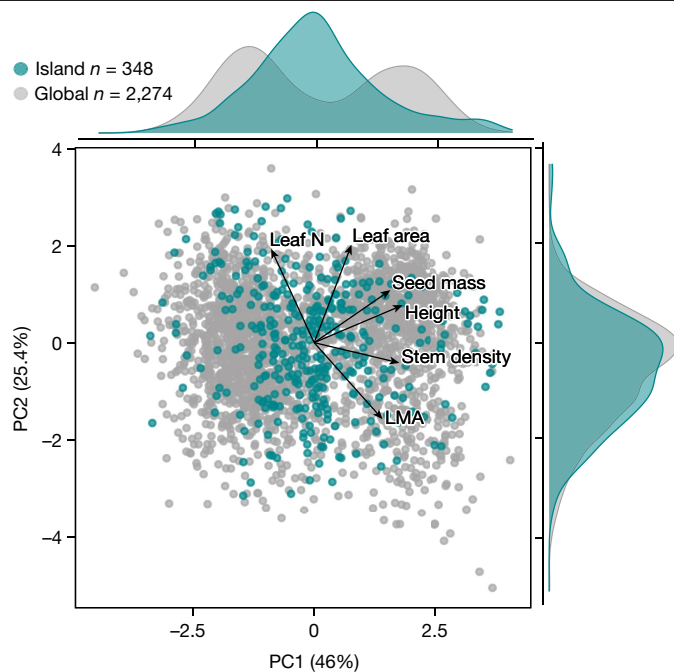

Fig. 1 | Trait space of the native flora of Tenerife fits within the global trait space and is subject to similar constraints to the global trait space but is biased towards medium-statured species with intermediate trait values (shrubby functional hotspot). The trait space of the native seed plant species of Tenerife (348 species; turquoise dots) in relation to the global spectrum of plant form and function (2,274 species; grey dots[21]). Projections of the first two dimensions of variation from a principal component (PC) analysis (trait data are log transformed) of six plant functional traits: leaf area (mm²), LMA (g m⁻²), leaf nitrogen content (leaf N; mg g⁻¹), maximum plant height (height; m), stem specific density (stem density; mg mm⁻³) and seed mass (mg). The density distributions of the first and second dimensions of island and global trait spaces are displayed on the upper and right sides of the trait spaces. The overlap between island and global trait spaces is 74%, as measured by the Sørensen index. For details on the PC analysis and overlap statistics, see Extended Data Fig. 2.

on the island and that plants on Tenerife largely experience similar constraints to plants on continents. However, the density distribution of the trait space in Tenerife deviates from the global one along the first trait space dimension (Fig. 1). The majority of island species are located between the two global functional hotspots, that is, small-statured, light-seeded herbaceous plants and tall, heavy-seeded trees[21]. The position of the species of Tenerife in relation to the global trait space indicates the dominance of shrubs and the underrepresentation of both small herbs and tall trees in the island flora (Figs. 1 and 2a). Most of the plants in Tenerife have a small-to-intermediate stature (average plant height of 2 m), moderate stem density (average stem specific density of 0.46 mg mm⁻³), light seeds (average seed mass of 19 mg) and leaves with intermediate size, leaf mass per area (LMA) and nitrogen content (average of leaf area of 3.5 mm², LMA of 94 g m⁻² and leaf nitrogen content of 19 mg g⁻¹, respectively) (Fig. 2a and Extended Data Fig. 3a,b).

The Mediterranean climate of Tenerife (Extended Data Fig. 4a) is marked by seasonal summer droughts and high aridity at low and high elevations and therefore tends to favour shrubs[40,41]. Aridification across the Canary Islands started 7 million years ago[41], which coincides with the emergence of a large proportion of shrubby plants (80% of insular lineages on the Canary Islands are woody[41,42], with Tenerife contributing to approximately half of Canarian woody species[3]). The higher stem-specific density of shrubs than herbaceous species decreases the risk of hydraulic failure[42,43]. In addition, sclerophylly and more
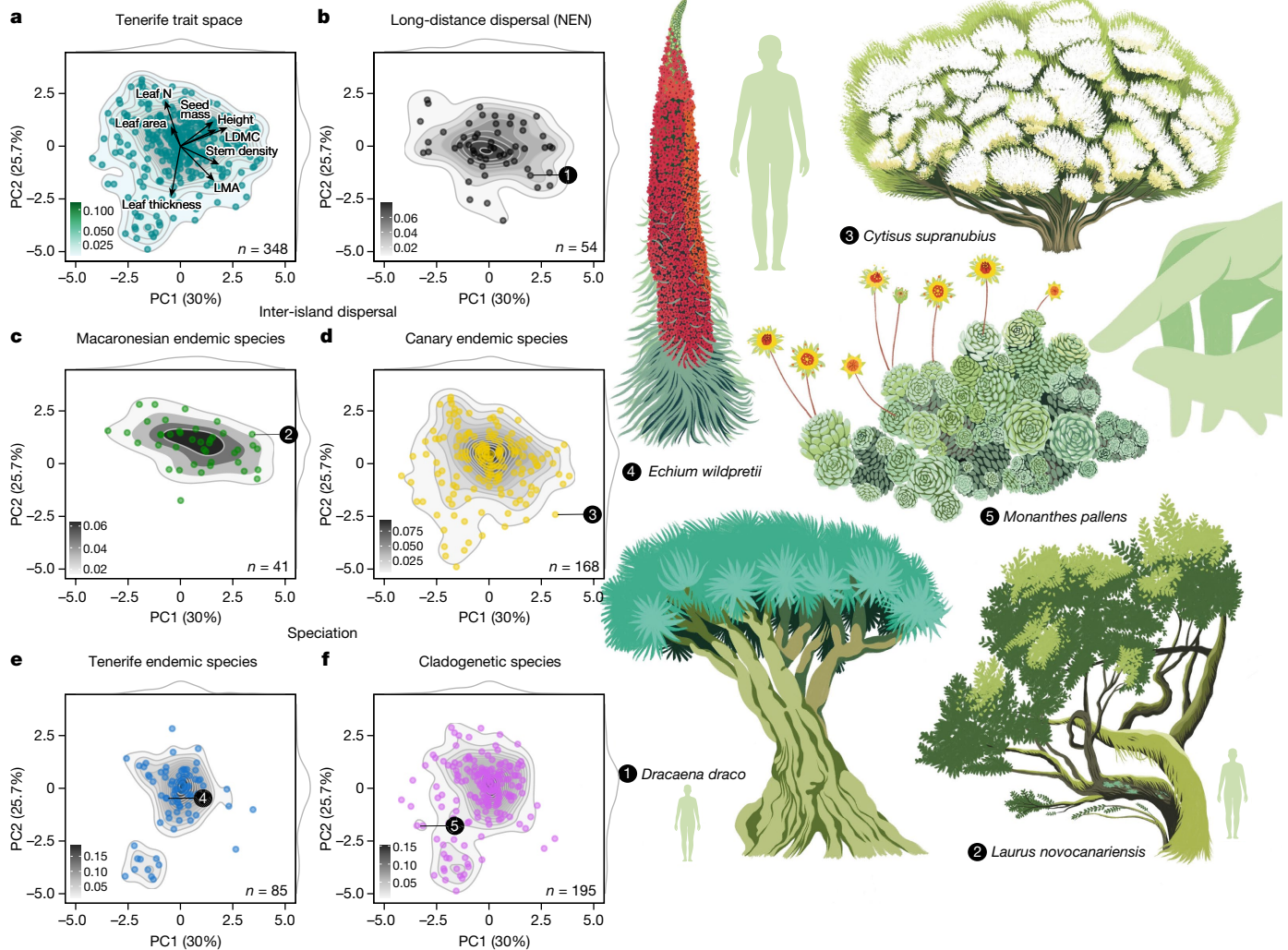
Fig. 2 | Imprint of biogeography and evolution on the trait space of Tenerife native flora. a–f, Tenerife native flora trait space (**a**) and dissection into five distinct species groups (**b–f**), illustrating the imprint of biogeography and evolution on the functional diversity of an oceanic island flora (n = 348 species). Traits included are leaf dry matter content (LDMC; mg g⁻¹), LMA, leaf N, leaf thickness (mm), stem specific density, seed mass and maximum plant height. Projections are of the first two dimensions of variation from the PC analysis (trait data are log transformed and scaled) of eight plant functional traits.

Contours are built using 2D kernel density estimation. Gradient legends (bottom-left side) correspond to the proportion of data contained in a contour break (see details on the PC analysis; Extended Data Fig. 3). In part **b**, iconic plant species from the native flora of Tenerife, each belonging to the species groups and illustrating different aspects of the island trait space are shown (right). NEN, non-endemic native species. Botanical and human hand illustrations, credit: Paulina Mocna.

conservative resource use strategies of shrubs, represented by high leaf dry matter content and LMA, lead to greater persistence in arid environments. Succulence, another key adaptation to aridity, is also well represented in the Canary Islands[44] (see leaf thickness; Fig. 2a) and is strongly coordinated with traits associated with persistence, that is, LMA and stem density (Fig. 2a).

The dominance of shrubby species on Tenerife is also consistent with the idea that small herbaceous colonizers gradually evolve into taller plants with increased stem density to avoid competition with other species[3,45]. Yet, recent research suggests that the evolution of many Tenerife shrub species and the subsequent increase in shrubbiness has mostly occurred in steep canyons and high-elevation ecosystems[46], where conditions are unfavourable for trees and competition with taller plants is low. The underrepresentation of tall plants in the trait space for Tenerife reflects the comparatively low number of tree species, which are restricted to thermophilous woodland ecosystems, laurel forest and pine forests, compared with shrubs. Overall, the functional

dominance of shrubs observed here is evidence of shrubbiness as a general syndrome for Tenerife. This syndrome drives the main divergence of the island trait space from the global trait space, and reflects the limited range in climatic conditions of the island, whereas the global trait space represents the capacity to persist and adapt to a wider range of conditions (Extended Data Fig. 4a).

Biogeography and evolution have jointly shaped island plant trait space

We analysed the relationship of eight plant functional traits (Fig. 2a and Extended Data Fig. 3) for the five species groups (Fig. 2b–f) and found that trait spaces of almost all groups are highly aggregated in the centre of the island trait space. The trait space of non-endemic native species (Fig. 2b) encompasses a large range of trait combinations, which are distributed across the island trait space, that is, from light-seeded, short plants to tall plants with heavy seeds (ranging from 0.01 to 230 mg seed
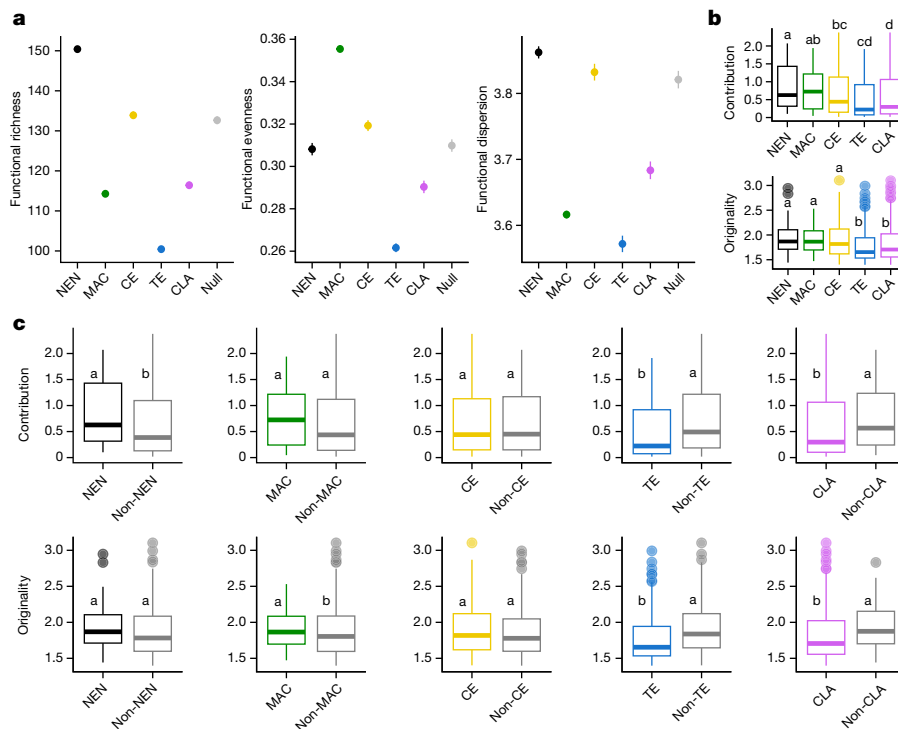
Fig. 3 | Contribution of biogeographical and evolutionary processes to the functional diversity of the native flora of Tenerife. Species groups are shown in different colours, that is, black for NEN, green for Macaronesian endemic species (MAC), yellow for Canary endemic species (CE), blue for Tenerife endemic species (TE) and purple for cladogenetic species (CLA). **a**, Functional richness (left), functional evenness (middle) and functional dispersion (right) were calculated using n-dimensional hypervolumes while controlling for the number of species for the five species groups ($n = 30$ species randomly sampled with replacement 999 times; see Methods). Null model results (that is, null) for functional convergence or divergence were created by randomly selecting species from the island species pool (see Methods). Dots and error bars correspond to the mean values and 95% confidence intervals, respectively, based on null models. **b**, Functional contribution and originality across the five different groups. Letters refer to differences across species groups (Kruskal–Wallis test; identical letters indicate no significant differences $P > 0.05$). **c**, Functional contribution and originality of each species group in comparison to all other island species. The different letters indicate that a species group has significantly higher or lower functional contribution or functional originality than other species on the island (Kruskal–Wallis test, $P < 0.05$). Functional diversity metrics are based on hypervolumes estimated from the three first PCs using eight plant functional traits (see PC analysis in Fig. 2a). In **b**,**c**, data per group (that is, NEN ($n = 54$), MAC ($n = 41$), CE ($n = 168$), TE ($n = 85$) and CLA ($n = 195$)) are represented as boxplots, in which the middle line is the median, the lower and upper hinges correspond to the 25th and 75th percentiles, and the upper and lower whiskers extend from the hinge to the largest and lowest value, respectively, no further than 1.5 times the interquartile range from the hinge.

mass and 0.1 to 20 m plant height), as well as plants covering large parts of the leaf economics spectrum (ranging from 20 to 544 g m^{-2} LMA and 5 to 45 mg g^{-1} leaf nitrogen content). Canary endemic species (Fig. 2d) also have a large range of trait combinations, but the trait space is highly dominated by shrubs and extends towards species with high leaf thickness, a trait associated with drought tolerance. The trait space of Canary endemic species also extends along the LMA and leaf nitrogen content continuum, and includes both conservative and acquisitive ecological strategies. The trait space of Tenerife endemic species (Fig. 2e) is mainly dominated by shrubs and succulent species. By contrast, the trait space of Macaronesian endemic species (Fig. 2c) has a distribution associated with the prevalence of both shrubs and trees. Trait combinations of tree species within the Macaronesian endemic species, for example, *Laurus novocanariensis* with its large stature and seed mass (25 m and 600 mg, respectively), have not emerged from in situ speciation but rather from the relictualization of laurel forests, an ecosystem that is largely extinct on the mainland[39]. Finally, cladogenetic species (Fig. 2f) also occur in the centre of the island trait space, with most species having intermediate stature, light seeds and thick leaves with low leaf dry matter content (typical for succulent leaves). Trait spaces of cladogenetic species and Tenerife endemic species are similar, as most Tenerife endemic species emerged via clado-genesis (76 out of 85 Tenerife endemic species (89.4%) belong to a radiated lineage).

Biogeography and evolution leave imprints on island functional diversity

To capture different aspects of trait distributions among all five species groups, we investigated three different components of functional diversity: functional richness, functional evenness and functional dispersion[26] (Fig. 3a). Furthermore, we assessed the contribution, that is, whether a group increases island trait space, and the uniqueness of each group within the island trait space by calculating functional contribution and originality[26] (Fig. 3b,c).

We found that functional richness (Fig. 3a), that is, the total amount of trait space[23], and functional dispersion (Fig. 3a), that is, the functional divergence or convergence of species within a trait space, exhibit a similar pattern among species groups and are highest for non-endemic native species and Canary Islands endemic species. The significant functional contribution of non-endemic native species (Fig. 3c) indicates that the group possesses unique trait combinations and expands the trait space of Tenerife. By contrast, we found that Tenerife endemic species have the lowest functional richness and dispersion among all groups (Fig. 3a). This contrasting pattern emerges because several non-endemic native species and Canary endemic species occupy the margins of the island trait space (that is, small herbs, tall shrubs and trees), whereas Tenerife endemic species are mainly found in the centre of the island trait space (that is, shrubs and small

succulents) (Figs. 2 and 3a). Non-endemic natives such as the up to 20-m-tall dragon tree, *Dracaena draco*, and Canary endemic species such as *Cytisus supranubius* (Fig. 2; plant illustration 3), a 4-m-tall shrub with very dense stems (stem specific density of 0.7 mg mm^{-3}), at the margins of the trait space for Tenerife, are examples of species with unique trait combinations that expand the island trait space. Overall, the notable high functional richness and dispersion of non-endemic native species (Fig. 3a) suggest that colonization via long-distance dispersal leads to greater functional divergence—and not functional convergence as expected—due to environmental filtering of the flora of Tenerife. The relatively high functional diversity of Canary Islands endemic species is consistent with the idea that insular species evolve new morphological characteristics to take advantage of unoccupied niche space, thereby avoiding interspecific competition[47]. The high habitat diversity of the Canary Islands[48], together with inter-island dispersal, provide ecological opportunities for species and can promote speciation. Conversely, Tenerife endemic species are functionally quite similar; these species occupy similar island habitats, have a low degree of niche differentiation and have probably emerged via allopatric speciation[46]. These results are supported by our phylogenetic analysis (hot node analysis[49]), which indicates that Tenerife endemic species are, in comparison with the other groups, highly concentrated within particular clades (Extended Data Fig. 5). This suggests that the unique trait combinations of Tenerife endemic species, which underpin persistence and drought tolerance, are phylogenetically conserved.

Functional evenness, that is, the regularity of species across the trait space, is significantly high for Macaronesian endemic species and Canary endemic species (Fig. 3a). The evenness values for Macaronesian endemic species indicate that the trait space of this group is evenly distributed among trees, shrubs and herbs (Fig. 3c). Furthermore, the high functional contribution of non-endemic native species (Fig. 3b,c) illustrates that colonization events could contribute disproportionately to island trait space by adding unique trait combinations to the island.

Unexpectedly, we found that cladogenetic species did not expand the trait space of Tenerife (compare intermediate functional richness and dispersion values in Fig. 3a and significantly lower functional contribution and originality in Fig. 3b,c). We attribute this result to a greater frequency of non-adaptive speciation events relative to adaptive speciation events[50]. Unlike adaptive radiations, in which species commonly evolve trait values to cope with changing environmental conditions[34], non-adaptive radiations[50] may not result in shifts in trait values because environmental conditions may be similar between isolated island populations and the mainland populations that they diverge from via genetic drift. This leads to newly evolved species that are functionally similar to the ancestral species. Furthermore, the uneven trait space of cladogenetic species (compare low functional evenness values; Fig. 3a) is consistent with the idea that environmental filtering results in convergence around similar trait combinations[51]. The aridification of the Canary Islands created new habitats, yet the harsh environmental conditions of these habitats apparently limit the number of viable trait combinations[48,52,53]. We note, however, that further analyses, such as ancestral-state reconstructions, are needed to test whether endemic species may have shifted trait values in response to increasing aridity of the Canary Islands.

How radiated lineages contribute to the island functional trait space

To gain insights into how speciation due to radiations may have shaped the trait space of Tenerife, we quantified the functional contribution and originality of 63 immigrant lineages present on Tenerife to the island trait space (Extended Data Fig. 6a,b). This group comprises 195 species (that is, cladogenetic species) that have radiated on Tenerife, Canary Islands and Macaronesia. We found that the *Aeonium* alliance,

the most diverse radiated lineage, and the *Polycarpaea* lineage contribute significantly to the expansion of the Tenerife trait space. Both the *Aeonium* alliance and *Polycarpaea* expand the trait space towards small plants with thick leaves (Extended Data Fig. 6c), suggesting that species in these lineages have evolved trait combinations, such as succulent leaves and remarkable size changes that allow them to exploit available niche space across various different habitats. This result further suggests that lineages such as the *Aeonium* alliance and *Polycarpaea* may have an adaptive origin. By contrast, the vast majority of radiated lineages do not increase the island trait space (Extended Data Fig. 6a,b). The minimal contributions of the other, less diverse radiated lineages to island trait space might indicate that these radiations are, to a large degree, non-adaptive. Yet, it could also indicate that newly evolved species appear to be similar to those of co-occurring species, but they may have evolved other traits not measured here, for example, resprouting capacity, clonality or floral traits that enable them to exploit empty niche space[16].

We conclude that evolution via different speciation pathways (anagenesis and cladogenesis) at the archipelago level, together with biogeographical processes such as colonization via long-distance dispersal, and inter-island dispersal at the (meta-)archipelago level, have jointly shaped the trait space of the native flora of Tenerife. Contrary to our hypothesis, cladogenesis tends to lead to functional convergence—not divergence—and therefore only contributes marginally to functional diversity. The predominance of shrubbiness and leaf succulence across the island flora additionally reflects a strong imprint of environmental filtering acting on the trait space of Tenerife. Overall, our results shed light on how functional diversity of an oceanic island flora emerges from the interaction among biogeographical, ecological and evolutionary processes. Our approach offers a first step towards better understanding, from a trait-based perspective, the assembly of an entire native island flora.

Online content

Any methods, additional references, Nature Portfolio reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41586-023-06305-z.

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Methods

Tenerife as a model system

Tenerife is the largest (2,058 km^2) and tallest (3,715 m above sea level) of the Canary Islands, an archipelago that belongs to the Macaronesian meta-archipelago, a floristic region off the coast of northern Africa and western Europe in the Atlantic Ocean[35]. The island is of volcanic origin and its oldest substrate is about 8 million years old[54]. Owing to its complex topography, dynamic geological history[54] and interaction with the northeastern trade wind system, Tenerife has a very high environmental heterogeneity and a wide range of different ecozones and habitats[55], with a predominantly semi-arid environment. We mapped the climate of Tenerife onto the main bioclimates of the world[56] (Extended Data Fig. 4a), using interpolated global mean values for temperature and precipitation obtained from ref. 46 and the plotbiomes function in the R package plotbiomes[57].

Floristic and biogeographical data of Tenerife

The native seed plant flora of Tenerife is composed of 436 native species listed in the latest version of the vascular plant species checklist of the Canary Islands[37]. As the native status of several Canary Islands species remains unresolved[38], we included only species categorized as native (that is, '*nativa segura*' status from the Canary Islands plant checklist). We then classified species into five different groups according to species endemism status from the checklist[37] as follows: non-endemic native, Macaronesian endemic species, Canary Islands endemic species and endemics to Tenerife. The cladogenetic species group analysed here is composed of 63 lineages, which have mainly radiated across the Canary Islands and some on Tenerife and Macaronesia (according to ref. 38); this group contains Macaronesian (14 species), Canary (104 species) and Tenerife (76 species) endemic species, and one native non-endemic species (*Dracaena draco*). Phylogenies are available for the vast majority (57 of 63) of the lineages that we studied here (see phylogenies references; Data availability). We placed species in the remaining six lineages (*Fumaria*, *Lolium*, *Pimpinella*, *Pterocephalus, Schizogyne* and *Scilla)*, in which morphological similarities among island taxa indicate a likely close phylogenetic relationship.

Tenerife trait sampling and measurement

We obtained plant trait data from fieldwork campaigns in 2017 and 2018 in Tenerife. We measured eight plant functional traits for 436 Tenerife native seed plant species, covering 80% of all species–trait combinations (Extended Data Fig. 1a). Specifically, we collected and measured leaf and stem traits[19,20] for approximately 80% and 76%, respectively, of all Tenerife native seed plants (350 and 330 species): leaf area (mm^2) as the one-side surface area of the individual lamina, leaf dry matter content (mg g^{-1}) as the leaf dry mass per unit of water-saturated fresh mass, LMA (g m^{-2}) as the leaf dry mass per unit of lamina surface area, leaf nitrogen content (leaf N; mg g^{-1}) as the nitrogen content per unit of lamina dry mass, leaf thickness (mm), and stem specific density (stem density; mg mm^{-3}) as the dry mass per unit of fresh stem volume. We sampled plants across the entire island at more than 500 locations (Extended Data Fig. 4b), covering the full range of elevational and climatic gradients of Tenerife from sea level to 2,700 m above sea level. We sampled rare species (when possible) at only one site for conservation reasons and a few rare species (*n* = 20) in botanical gardens[58] (Jardín de Aclimatación de La Orotava and Campus Universidad de La Laguna on Tenerife, and Jardín Botánico Canario Viera y Clavijo in Gran Canaria). We confirmed species identity with botanical experts, R. Otto and R. Barone, and identification books[59]. We collected three replicates (individuals per species) for 60% of sampled species, one to two replicates for 16% of sampled species and four to five replicates for 6% of sampled species. Our analysis was based on the mean value of a trait across replicates for each species.

Trait values for leaves, stems and seeds were measured following standardized protocols[60]. We collected healthy, fully expanded sun-exposed leaves from individual plants. Depending on the leaf size, we collected between 10 (for more than 1 cm^2 leaves) to 100 (for less than 1 cm^2 leaves) leaves per individual. To measure stem traits and ensure that plants were not damaged, we collected samples from the first adjacent branch of the main plant stem, when plants were shrubs. For small herbs and vines, we collected the plant organ acting as a stem. To sample the stem density of trees, we used an increment borer to extract a wood core from the bark inward (10-mm diameter core taken at approximately 1.2 m above ground). We stored the fresh plant material in coolers to prevent dehydration and measured fresh leaf mass using an analytical balance (0.01-mg precision from PCB 2500-2 Kern & Sohn) within 24 h after collection. Leaf thickness and leaf area (leaves smaller than 1 cm^2 were scanned at 600 dpi and leaves larger than 1 cm^2 at 300 dpi) were also measured within 24 h after collection. Leaf thickness was measured using a digital calliper. Leaf area was calculated using WinFOLIA software (version 2016b Pro, Regent Instruments Canada). To measure the volume of fresh stems, we first measured their length and diameter with a digital calliper. As stems are not perfect cylinders, we measured the diameter in three different stem sections and used the mean value per stem. We computed fresh stem volume using the following formula for cylinders: $V = \Pi r^2 h$, where Π is the constant Pi, r is radius, and h is height. We oven-dried leaves and stems at 80 °C for 48 h, or until a stable weight was reached, and then measured leaf and stem dry mass using the same analytical balance. Nitrogen content of the dry leaves was determined by a C/N elemental analyser (Vario EL III, Elementar).

We measured seed mass (mg) for 74% (322 species) of all native seed plants of Tenerife as the dried mass of an individual seed in the field (9 species) and at the seed bank from the Jardín Botánico Canario 'Viera y Clavijo' in Gran Canaria (313 species). We counted between 5 and 200 seeds per species and weighed them using an analytical balance (0.001-mg precision). We obtained individual seed mass by dividing the total mass of the seeds by the number of seeds. For very small seeds (less than 0.1 mm), we calculated seed mass using a test tube containing a volume of seeds for which the seed count was known. We obtained maximum plant height (height; m), which is the upper boundary of the main photosynthetic tissue at maturity in metres, for 97% (421 species) of all native species of Tenerife from the literature[59].

Measured and missing trait values

We analysed 348 species (Figs. 1 and 2 and Extended Data Fig. 2), that is, 80% of the native seed plant flora of Tenerife, for which we were able to collect a minimum of five traits per species in the field or extracted from the literature. For those 348 species, less than 5% of trait values were missing in the species–trait table (Extended Data Fig. 1b), which we subsequently filled following the phylogenetic imputation procedure suggested by ref. 61. In total, we imputed trait values including the complete Tenerife flora consisting of 436 species, that is, for 20% of leaf traits, 27% of stem density, 26% of seed mass and 3% of maximum plant height values. To this end, we built a phylogenetic tree including Tenerife native species using a dated mega-tree for vascular plants as the backbone (GBOTB.extended.tre[62]). To account for uncertainty associated with the placement of species that were absent from the mega-tree, we built 100 phylogenetic trees that resolve missing species by randomly placing them within genera or family ('scenario 2') using the phylo.maker function in the R package V.PhyloMaker[62]. We used a random forest algorithm using the missForest function in the MissForest R package[63] to predict missing trait values. Using out-of-bag error, we measured the prediction error of the random forest algorithm that included phylogenetic relationships among species against naive predictions, which do not include any phylogenetic relationship. We found that phylogenetically informed imputation performed better than the naive imputation for nearly all traits (Extended Data Table 1).

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Before analysis, we inspected the distribution of the missing data of the 348 species used for analysis and within each of the five species groups (Extended Data Fig. 1c). We also compared the density distribution of each trait for empirical and imputed data (Extended Data Fig. 1d). Finally, as closely related species tend to have similar trait values, we estimated the phylogenetic signal for each trait with Pagel's λ using the phylosig function in the R package phytools[64]. We estimated Pagel's λ for each trait across all 100 phylogenetic trees and calculated the average (Extended Data Table 2). We additionally tested for a phylogenetic signal in the missing trait values, for which we calculated the D statistic using the function phylo.d in the R package caper[65] (Extended Data Table 2). The D statistic tests whether missing trait values are phylogenetically independent ($D = 1$) or whether they follow a distribution expected under a Brownian motion model of evolution ($D = 0$). We estimated the D statistic for each trait across all phylogenetic trees and calculated the average.

Global trait data

We used the global trait data from ref. 21, which includes complete empirical measurements for six plant traits (leaf area, LMA, leaf N, seed mass, stem density and height) for 2,214 species. We updated the global trait data using openly available data from TRY[66], which we requested for all species available for the six traits on 17 May 2022; we selected trait information at the individual level with an error risk below 5, that is, z score < 5. After removing duplicate species that were identified after name taxonomic standardization[67], we added an additional 60 species with complete information for the six traits from TRY to the global trait data. Thus, we compared 2,274 species characterizing the global trait space with 348 Tenerife species.

Functional trait space visualization

We performed a principal component analysis (PCA) on the log-transformed and z-transformed (centred and rescaled to unit variance) mean trait values to map trait spaces. For the comparison of Tenerife versus global trait space of plant form and function, we used six plant functional traits (Fig. 1). For the detailed analysis of Tenerife and the five species groups associated with different dispersal and speciation mechanisms (Fig. 2 and Extended Data Fig. 3), we used eight plant functional traits (Fig. 2). We used the stat_density_2d function in the R package ggplot2 to plot the functional trait spaces[68].

Trait space overlap and functional diversity estimation

We used the n-dimensional functional hypervolume approach by ref. 69, which more accurately accounts for gaps in the trait space than traditional approaches[70] and, in doing so, avoids overestimation of functional diversity. We used the Gaussian method to build hypervolumes, as it is the least sensitive method to variation in bandwidth and fits the data loosely, which is suitable for functional diversity estimation[69]. To estimate the overlap between the global and the island trait spaces, we first built hypervolumes for each dataset using the first three principal components from the PCA analysis using the global and island data combined using six traits (compare Fig. 1). We used a fixed kernel bandwidth for both island and global hypervolumes computed using estimate_bandwidth (using cross-validation as the kernel estimator method) function in the R package Hypervolume[70]. Second, we calculated the overlap using the hypervolume_overlap_statistics function in the R package Hypervolume[71], which estimates the Sørensen similarity coefficient (that is, the volume of the intersection of the island trait space and the global trait spaces, divided by the volume of the union of island and global trait spaces) between the island and global trait spaces (compare Fig. 1). To ensure an accurate estimation of the overlap, we built a null model that first controls for the difference in species number between the global and island datasets, by selecting a minimum common number of species ($n = 300$) from each dataset. Second, the null model also controls for a potential underrepresentation of shrubs in the

global trait space, by sampling from the global data according to estimated global proportions of plant growth forms: 54% herbs, 24% shrubs and 21% trees[71]. The null model then computes both island and global hypervolumes using random sampling with replacement repeated 999 times. Last, we computed mean values and 95% confidence intervals based on all samples to estimate the overlap (Extended Data Fig. 2d). The plant growth form proportions are based on curated information from floras, checklists and trait collections for 188,212 plant species in GIFT (version 2.1)[72], which is approximately 50% of all known extant plants. We updated the global data[21] by assigning to each species a plant growth form, which we obtained for 2,175 species from GIFT[72], for 84 species from ref. 73 and for 15 species from the Internet (for detailed information, see the Data availability section). We compared the latter null model to a second null model, which only controls for the difference in species number by selecting a minimum common number of species ($n = 300$) from both the global and the Tenerife datasets (Extended Data Fig. 2d). Finally, to test whether Tenerife species fall within the global trait space, we projected the Tenerife trait space following ref. 74 and obtained contour lines indicating 0.5, 0.95 and 0.99 quantiles, using kernel density estimation (Extended Data Fig. 2c).

For each of the five species groups (non-endemic native species, Macaronesian endemic species, Canary endemic species, Tenerife endemic species and cladogenetic species), we estimated three components of functional diversity (Fig. 3) based on the hypervolume approach: functional richness, evenness and dispersion using the functions kernel.alpha, kernel.evenness and kernel.dispersion, respectively, in the R package BAT[26]. We used a fixed kernel bandwidth for all groups using cross-validation as the kernel estimator method. Functional richness is the total volume of a trait space. Functional dispersion quantifies how spread or dense a given trait space is, by calculating the average difference between the trait space centroid and random points (that is, randomly placed species) within the boundaries of the hypervolume[26]. Functional evenness quantifies how regular a given trait space is, by calculating the overlap between the observed hypervolume and a theoretical, perfectly even hypervolume[26]. The hypervolumes for each group were calculated using the three principal components from the PCA ran with the island data using the eight traits (Fig. 2). Because functional diversity metrics are commonly affected by the number of species[75], we used null models to obtain an unbiased comparison of the functional diversity metrics across the five groups. To this end, we selected a minimum common number of species ($n = 30$) across the five groups, which we randomly sampled 999 times with replacement, and calculated the three functional diversity metrics each time. We additionally tested whether the functional diversity metrics per group were higher (that is, species functionally diverge) or lower (that is, species functionally converge) than expected by chance. To this end, we estimated the three metrics for a null group composed of 30 species randomly selected 999 times from the island species pool. Thus, if a group has lower or higher value than the null group, it indicates functional convergence or divergence, respectively. We computed mean values and 95% confidence intervals from all samples to compare functional diversity metrics across groups (Fig. 3a).

To estimate the functional contribution (whether a group increases island trait space) and originality (a group with high originality value has unique trait combinations relative to the island trait space) of the five groups to the island trait space, we calculated functional contribution[26] as the net contribution of each single species to the total island hypervolume, and functional originality[26], as the average dissimilarity difference between a given species and a sample of random points (10% of the total random points) within the boundaries of the island hypervolume[26]. First, we assessed the differences of functional contribution and functional originality across species groups (Fig. 3b). Second, we assessed the functional contribution and originality of each species group to the island trait space by plotting the functional contribution and functional originality values of a given group against

all other species that do not belong to the group (Fig. 3c). We used Kruskal–Wallis tests ($P < 0.05$) to assess differences among the first and second principal components of the trait spaces of each group (Extended Data Fig. 3c), and to test the statistical significance of the functional contribution and originality of each species group (Fig. 3b,c), as well as those of 63 radiated lineages (Extended Data Fig. 6), to the island trait space. For the test, we used the kruskal function in the R package agricolae[76].

Phylogenetic 'hot node' analysis

To discern whether traits of any of the five species groups associated with different dispersal and speciation mechanisms have low or high functional differentiation, we performed a hot node analysis following ref. 49, which identifies clades (that is, nodes) with more species in a group than expected by chance (Extended Data Fig. 5). For each group i, the number of species assigned to i that descended from each node j of the phylogeny k was counted. We compared this value to a null distribution of values by randomly assigning trait values across the tips of the phylogeny k 1,000 times, and then calculated standardized effect sizes (SESs) for each node j of k. We considered nodes to be 'hot' if their SESs was greater than 1.96, for nodes that had at least 10 species and if their SESs exceeded 1.96 in at least 50 of the 100 sample trees[49]. We performed this analysis for all five species groups.

Finally, to test for the robustness of our analyses (that is, Figs. 2 and 3) to trait imputation, we performed a sensitivity analysis using only those species ($n = 237$) with complete empirical data for all eight traits (Extended Data Fig. 7). This sensitivity analysis revealed that the patterns for the 348 species (that is, 5% imputed traits) and the 237 species with complete empirical information were qualitatively similar. We performed all statistical analysis and data visualization using R software version 4.1.0 (ref. 77).

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

The trait data and floristic information of the species are available in a Figshare repository (https://doi.org/10.6084/m9.figshare.22355065.v1). Source data are provided with this paper.

Code availability

The analysis and data visualization performed in R software are available in a Figshare repository (https://doi.org/10.6084/m9.figshare.22355065.v1).

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Author contributions H.K. conceived the initial idea. M.P.B.B., D.C., P.W. and H.K. further developed the concepts and designed the research. M.P.B.B. collected and measured plant traits and performed the statistical analysis. D.C. and P.D. contributed to the statistical analysis. R.O. and J.M.F.-P. supported the fieldwork logistics and execution, that is, plant trait data collection and species identification. J.P. curated lineage information. S.D. supported trait data curation and writing the discussion. All authors contributed to the interpretation of the results and the writing of the paper.

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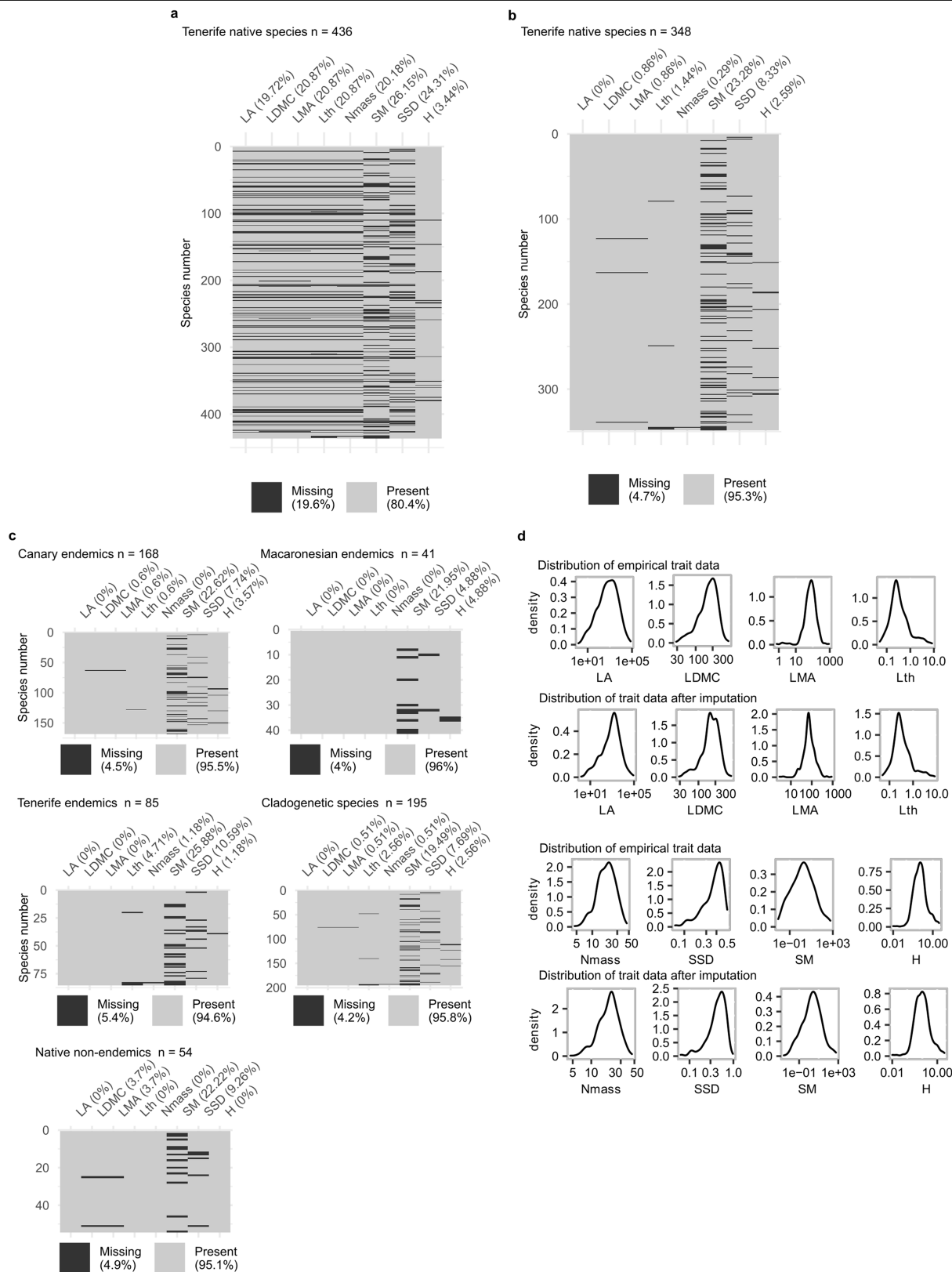
Extended Data Fig. 1 | Trait data overview and assessment. a. Present empirical data and missing data distribution across 100% (n = 436) of Tenerife native seed plant species. **b.** Present empirical data and missing data distribution across 80% (n = 348, i.e., species with minimum of five trait values) of Tenerife native seed plant species, and **c.** across five species groups included in the main analysis. The missing trait data represented in black, were filled using phylogenetically informed imputation (see Methods). Percentages reported for each trait refer to the proportion of missing data. **d.** Density distribution of the empirical trait values only, and including imputed trait values for each trait. Percentages correspond to the proportion of species with imputed trait values.
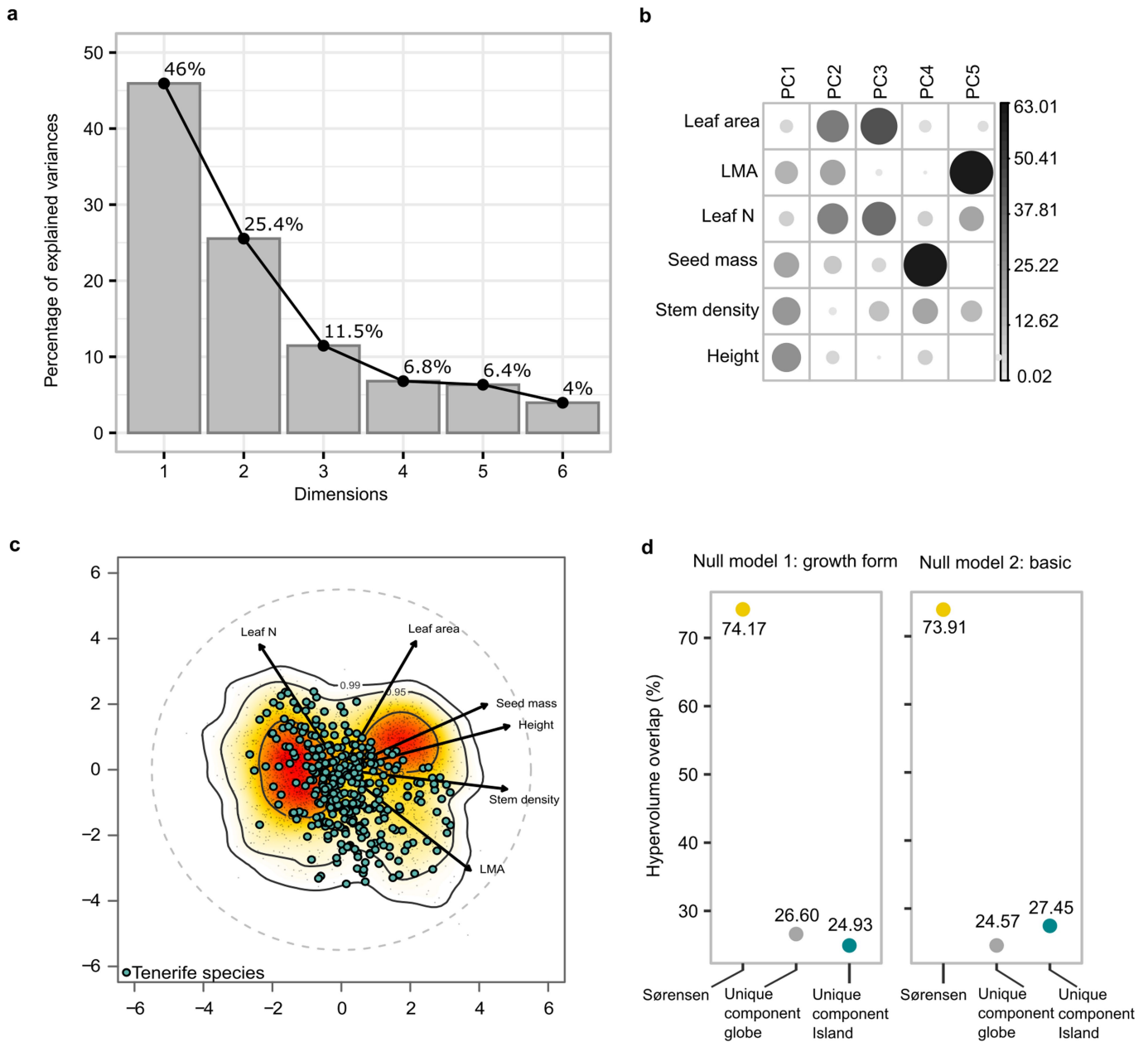
Extended Data Fig. 2 | Overview of the principal components explained variance of both island and global trait data, and hypervolume overlap. a. Percentage of explained variance of the six dimensions of the principal component analysis (PCA) based on six plant functional traits of Tenerife's native seed plants and seed plants from across the globe (348 Tenerife and 2,274 global species). **b.** Percentage of contributions of each trait to each dimension of the PCA. Trait values were z- and log-transformed prior to the PCA. **c.** Tenerife species projected onto the global spectrum of plant form and function[21], contour lines indicating 0.5, 0.95 and 0.99 quantiles using kernel density estimation; PCA protection following[74]. Note that Tenerife native flora falls within the 99% isoline space of the global trait space. **d.** Estimated overlap,

i.e., Sørensen index, between the island and global trait space estimated via null model (where n = 300 species randomly sampled, from island and global data separately, with replacement 999 times) based on hypervolume approach (see details in Methods). Null model 1 controls for a potential underrepresentation of shrubs in the global trait space by sampling the current proportions of growth form *sensu*[72] (see Methods) and for the species richness difference between datasets. Null model 2 controls only for the species richness difference between both global and Tenerife datasets. In **d**. dots and error bars (not visible here as they are close to the mean) correspond to the mean values and 95% confidence intervals.
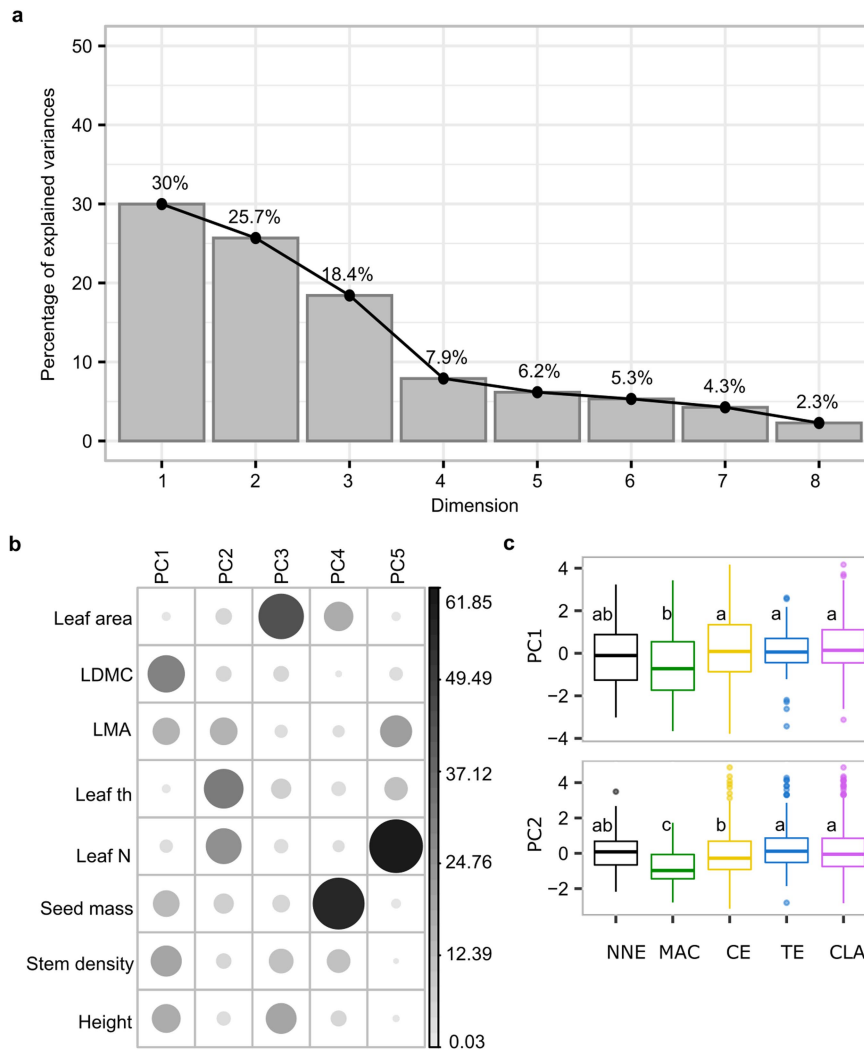
Extended Data Fig. 3 | Overview of principal components analysis (PCA) for eight plant functional traits (n = 348 species) of Tenerife native seed plants. a. Percentage of explained variance of the eight dimensions of the PCA. **b**. Percentage of contributions of each trait to each dimension of the PCA. Trait values were log- and scaled. **c**. Differences among the first and second principal component of the trait spaces of different biogeographical groups, Non-endemic native species (NEN), Macaronesian endemic species (MAC), Canary Islands endemic species (CE), Tenerife endemic species (TE) and cladogenetic species (CLA). Identical letters indicate no significant differences (Kruskal-Wallis text, P>0.05). Data are represented as boxplots where the middle line is the median, the lower and upper hinges correspond to the 25th and 75th percentiles, upper and lower whiskers extend from the hinge to the largest and lowest value, respectively, no further than 1.5*IQR from the hinge.
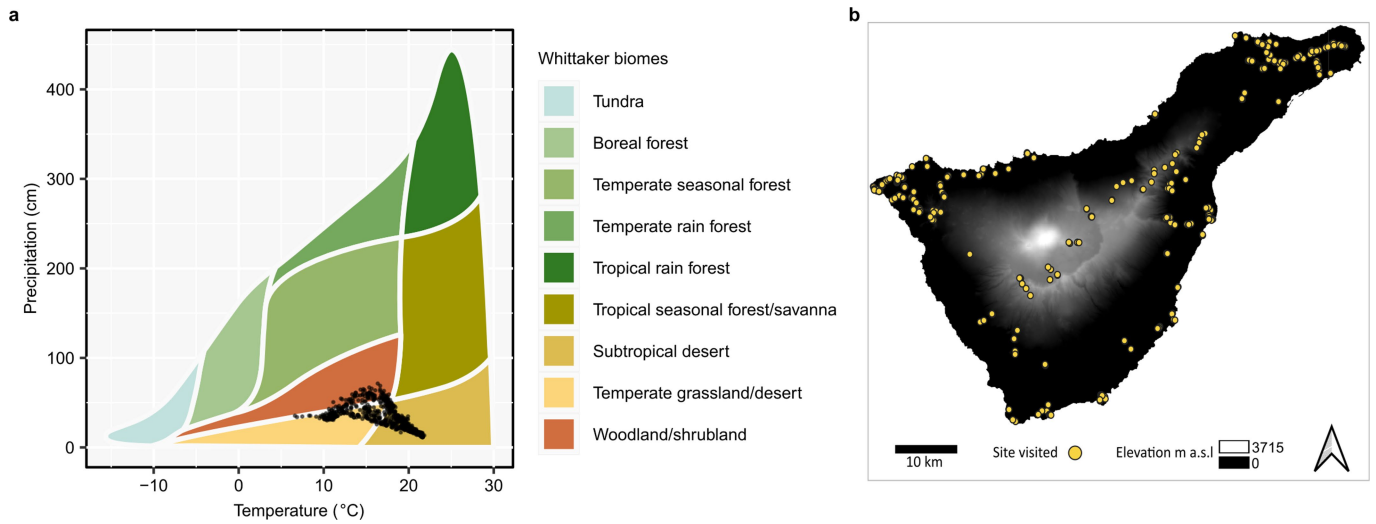
Extended Data Fig. 4 | Tenerife climatic representativity mapped on Whittaker biomes. a. and **b**. field sites visited in 2017 and 2018 (n = 500), where plant material was collected to measure plant functional traits for this study.
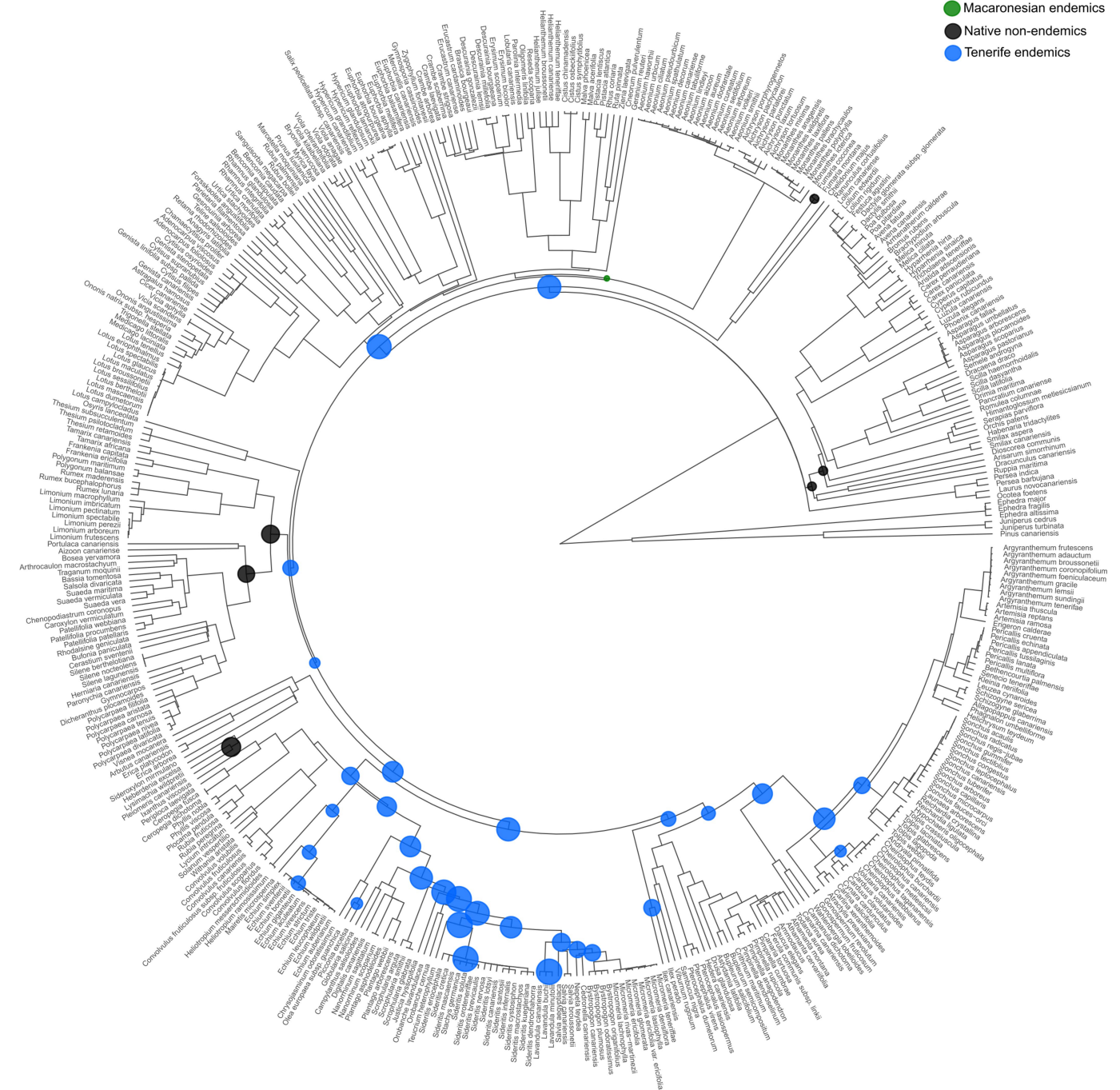
Extended Data Fig. 5 | Hot clades of endemic species of the Macaronesia (green), Tenerife (blue) and of native non-endemic species (black) are highlighted. Hot nodes indicate clades with more species than expected at random. Node corresponds to standard effect size and node transparency is scaled by the number of sample trees in which a node was significantly overdispersed. Nodes include at least 10 species and occur in at least 50 sample trees. Note that the vast majority of hot nodes are among Tenerife endemic species.
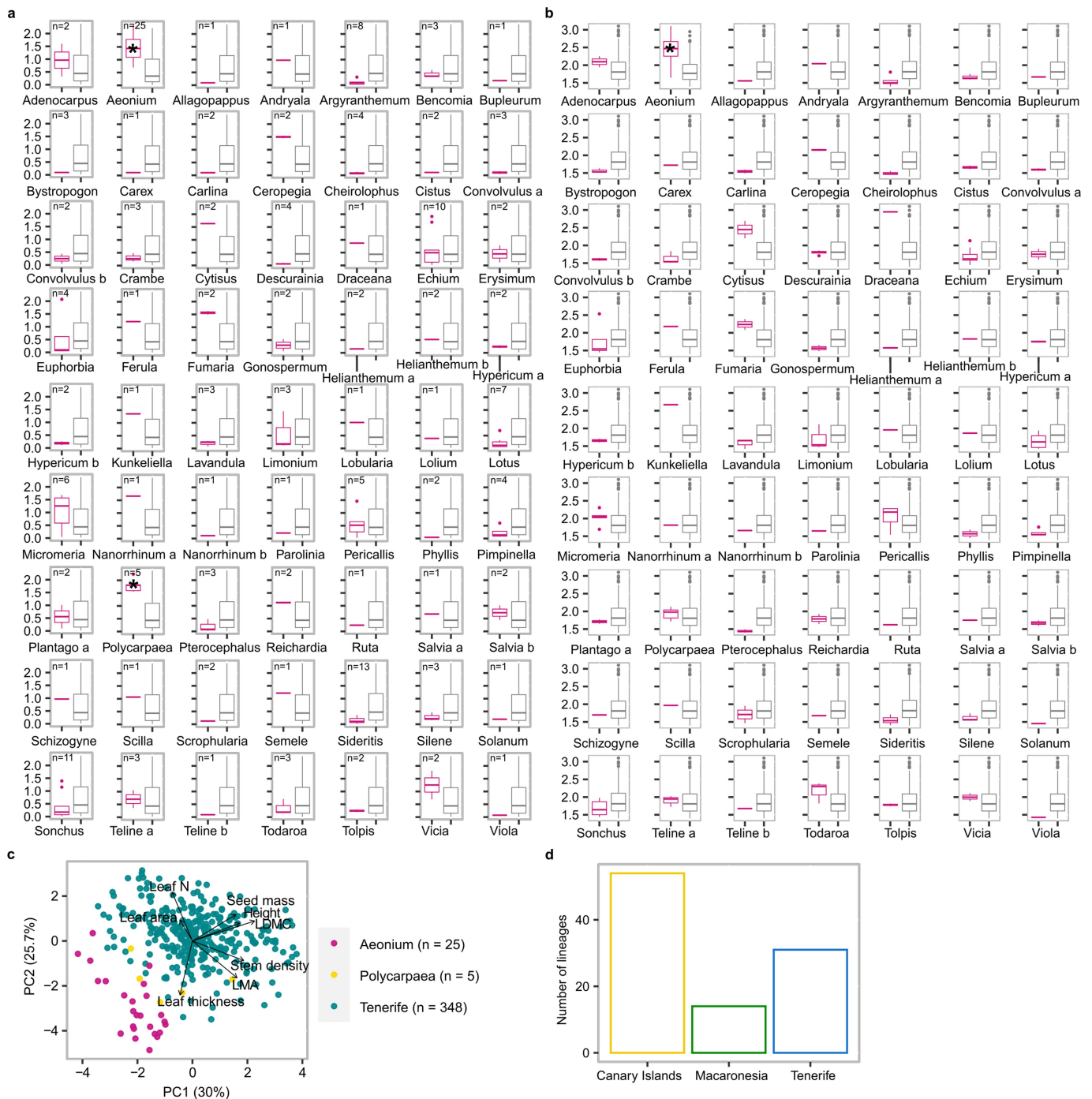
Extended Data Fig. 6 | Functional contribution and originality of the major radiated plant lineages present in Tenerife. a. Functional contribution and **b.** functional originality for the 63 radiated lineages. Note that only *Aeonium* alliance and *Polycarpaea* lineages (marked with *) are significantly contributing to the expansion of Tenerife trait space, as their functional contribution or originality are significantly different from other species that do not belong to the lineage (results based on Kruskal-Wallis, P < 0.05). Each box plot in magenta colour correspond to a lineage; number of species on a lineage (i.e., n numbers) are the same in **a-b**. Each box plot in grey colour corresponds to all island species, except for species included in the corresponding compared lineage. In **a**–**b** data

are represented as boxplots where the middle line is the median, the lower and upper hinges correspond to the 25th and 75th percentiles, upper and lower whiskers extend from the hinge to the largest and lowest value, respectively, no further than 1.5*IQR from the hinge. **c.** Location of *Aeonium* alliance and *Polycarpaea* species in the island trait space; lineages extend it towards high values of leaf thickness. **d.** Number of radiated lineages present in Tenerife (31), Canary Islands (54) and Macaronesia (14). The 63 major lineages are composed of 195 species or 56% of all species included in the main analysis. The 63 lineages are nested within the Macaronesia, Canary Islands and Tenerife.
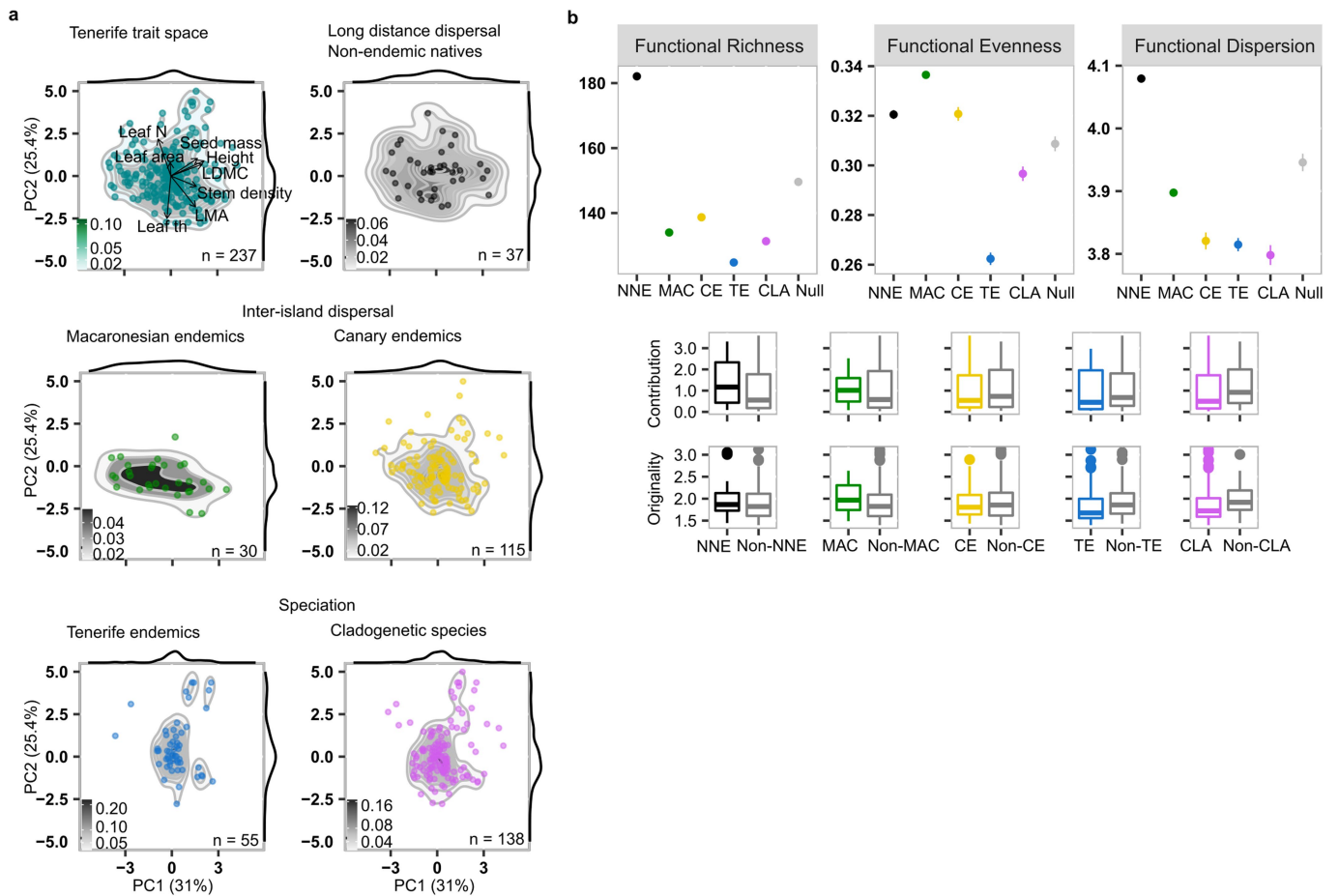
Extended Data Fig. 7 | Sensitivity analyses using only cases (n = 237 species) with complete empirical data for all 8 traits. a. Trait spaces for the native flora of Tenerife and dissected into five distinct species groups that illustrate the imprint of biogeography and evolution on the functional diversity of an oceanic island flora. **b**. Functional richness, functional dispersion and functional evenness were calculated using n-dimensional hypervolumes while controlling for the number of species richness for the five groups and for a null group in grey, where dots and error bars correspond to the mean values and 95% confidence intervals, based on null models (top). Functional contribution and originality of each group with respect to the rest of island species (bottom); data is represented as boxplots where the middle line is the median, the lower and upper hinges correspond to the 25th and 75th percentiles, upper and lower whiskers extend from the hinge to the largest and lowest value, respectively, no further than 1.5*IQR from the hinge. See details in Methods.

Extended Data Table 1 | Validation of trait values imputation

Imputed trait	OOB error with phylogenetically informed traits	OOB error with non-phylogenetically informed (naive) traits	Difference
Leaf area	44979719	47205974	-2226255
LDMC	4790.6	6627.05	-1836.45
LMA	3135.5	3210.21	-74.66
Leaf th	0.425	0.488	-0.06372
Leaf N	29.26	37.037	-7.779
Seed mass	2219.98	2418.79	-198.82
Stem density	0.0172	0.0203	-0.003129
Height	4.805	6.515	-1.7055

Out-of-Bag (OOB) scores are shown in units of the trait they correspond to. The lower the value, the better the random forest algorithm performed. Note: Trait values predicted with phylogenetic information had, in almost all cases, lower OOB scores, except for LMA predictions.

Extended Data Table 2 | Phylogenetic signal of empirical trait values and phylogenetic signal of missing trait values

Trait	n	Lambda (λ)	Trait (complete cases)	D statistic
Height	421	0.98	Height	0.73
Leaf area	350	0.20	Leaf area	0.83
LDMC	345	0.99	LDMC	0.85
LMA	345	0.64	LMA	0.85
Leaf th	345	0.64	Leaf th	0.85
Leaf N	348	0.79	Leaf N	0.82
Seed mass	322	1.00	Seed mass	0.75
Stem density	330	0.88	Stem density	0.78

A trait has a strong phylogenetic signal if λ>0.80: n refers to the number of species. The D statistic tests whether missing trait values are independent of the phylogeny (D =1) or if they follow a distribution expected under a Brownian motion model of evolution (D = 0).

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Corresponding author(s):   Martha Paola Barajas Barbosa

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n/a	Confirmed	
☐	☒	The exact sample size (n) for each experimental group/condition, given as a discrete number and unit of measurement
☐	☒	A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☐	☒	The statistical test(s) used AND whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
☐	☒	A description of all covariates tested
☐	☒	A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
☐	☒	A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☐	☒	For null hypothesis testing, the test statistic (e.g. F, t, r) with confidence intervals, effect sizes, degrees of freedom and P value noted *Give P values as exact values whenever suitable.*
☒	☐	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☒	☐	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☒	☐	Estimates of effect sizes (e.g. Cohen's d, Pearson's r), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	We obtained plant trait data from fieldwork campaigns in 2017 and 2018 in Tenerife. Our collecting permits, no. 33189 and 65306, were issued by Cabildo de Tenerife, the governing body of the island of Tenerife.
Data analysis	We performed all statistical analysis and data visualization using open source R software version 4.1.0. Main R packages used are plotbiomes, V.PhyloMaker, MissForest, phytools, caper, ggplot2, Hypervolume, BAT, Agricolae. We used the software WinFOLIA (Version 2016b Pro, Regent Instruments Canada, 2016) to estimate leaf area. We estimated Leaf Nitrogen content with a C/N elemental analyser (Vario EL III, elementar, Hanau, Germany).

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio guidelines for submitting code & software for further information.

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Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:
- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
- For clinical datasets or third party data, please ensure that the statement adheres to our policy

Plant trait data for Tenerife and floristic information of the species that support the findings of this study are available in Figshare repository: https://doi.org/10.6084/m9.figshare.22355065.v1. We further used TRY database (requested May 2022) https://www.try-db.org/TryWeb/Home.php, GIFT database (requested May 2022) https://gift.uni-goettingen.de/home and Tenerife interpolated mean values for temperature and precipitation (accesed May 2022) https://datadryad.org/stash/dataset/doi:10.5061/dryad.qrfj6q5fs

Research involving human participants, their data, or biological material

Policy information about studies with human participants or human data. See also policy information about sex, gender (identity/presentation), and sexual orientation and race, ethnicity and racism.

Reporting on sex and gender	not applicable
Reporting on race, ethnicity, or other socially relevant groupings	not applicable
Population characteristics	not applicable
Recruitment	not applicable
Ethics oversight	not applicable

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences   ☐ Behavioural & social sciences   ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	We study the functional diversity and its assembly of 80% of native seed plant of the oceanic island Tenerife. We quantified functional diversity using eight plant traits.
Research sample	Seed native flora, i.e., 348 seed plant species described as certainty native
Sampling strategy	Field work campaign across the entire island, covering all elevation gradients of Tenerife.
Data collection	Plant traits were collected in-situ following standard protocols. Plant material were collected by M. Paola Barajas-Barbosa, Rudigger Otto and student assistants
Timing and spatial scale	Data collection time were July 2017 and Feb-Jun 2008. on the entire Tenerife island.
Data exclusions	We excluded Tenerife species with low trait data coverage (i.e., species with minimum 5 traits)
Reproducibility	Data and analysis is reproducible, with the data and R code we make available with this submission via Figshare
Randomization	We performed Null models assessing island and global trait spaces overlap. As well as Null model results for functional diversity indices that test for convergence or divergence. Using the null models resuts, we estimated confidence intervals (alpha level 0.05) to assess difference among groups.
Blinding	Our analysis did not required blinding

Did the study involve field work?   ☒ Yes   ☐ No

Field work, collection and transport

Field conditions	We collected plant materials following the phonological calendar, in order to obtain plant traits of fully developed individuals
Location	Tenerife, canary Islands, Spain
Access & import/export	We obtained plant trait data from an extensive fieldwork campaigns in 2017 and 2018 in Tenerife. Our collecting permits, no. 33189 and 65306, were issued by Cabildo de Tenerife, the governing body of the island of Tenerife. Plant materials were exported to Germany in the EU framework.
Disturbance	We collected adjacent / non-vital organs of plants to avoid damage

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☐	☐ Antibodies
☐	☐ Eukaryotic cell lines
☐	☐ Palaeontology and archaeology
☐	☐ Animals and other organisms
☐	☐ Clinical data
☐	☐ Dual use research of concern
☐	☐ Plants

Methods

n/a	Involved in the study
☐	☐ ChIP-seq
☐	☐ Flow cytometry
☐	☐ MRI-based neuroimaging

Antibodies

Antibodies used	not applicable
Validation	not applicable

Eukaryotic cell lines

Policy information about cell lines and Sex and Gender in Research

Cell line source(s)	not applicable
Authentication	not applicable
Mycoplasma contamination	not applicable
Commonly misidentified lines (See ICLAC register)	not applicable

Palaeontology and Archaeology

Specimen provenance	not applicable
Specimen deposition	not applicable
Dating methods	not applicable

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Ethics oversight	not applicable

Note that full information on the approval of the study protocol must also be provided in the manuscript.

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Laboratory animals	not applicable
Wild animals	not applicable
Reporting on sex	not applicable
Field-collected samples	not applicable
Ethics oversight	not applicable

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Clinical data

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Clinical trial registration	not applicable
Study protocol	not applicable
Data collection	not applicable
Outcomes	not applicable

Dual use research of concern

Policy information about [dual use research of concern](#)

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Could the accidental, deliberate or reckless misuse of agents or technologies generated in the work, or the application of information presented in the manuscript, pose a threat to:

No | Yes
☐ | ☐ Public health
☐ | ☐ National security
☐ | ☐ Crops and/or livestock
☐ | ☐ Ecosystems
☐ | ☐ Any other significant area

Experiments of concern

Does the work involve any of these experiments of concern:

No | Yes
☐ | ☐ Demonstrate how to render a vaccine ineffective
☐ | ☐ Confer resistance to therapeutically useful antibiotics or antiviral agents
☐ | ☐ Enhance the virulence of a pathogen or render a nonpathogen virulent
☐ | ☐ Increase transmissibility of a pathogen
☐ | ☐ Alter the host range of a pathogen
☐ | ☐ Enable evasion of diagnostic/detection modalities
☐ | ☐ Enable the weaponization of a biological agent or toxin
☐ | ☐ Any other potentially harmful combination of experiments and agents

Plants

Seed stocks	Plant specimens were collected on across the entire island of Tenerife following protocols (Pérez-Harguindeguy et al 2016).
Novel plant genotypes	not applicable
Authentication	not applicable

ChIP-seq

Data deposition

☐ Confirm that both raw and final processed data have been deposited in a public database such as GEO.

☐ Confirm that you have deposited or provided access to graph files (e.g. BED files) for the called peaks.

Data access links *May remain private before publication.*	not applicable
Files in database submission	not applicable
Genome browser session (e.g. UCSC)	not applicable

Methodology

Replicates	not applicable
Sequencing depth	not applicable
Antibodies	not applicable
Peak calling parameters	not applicable
Data quality	not applicable
Software	not applicable

Flow Cytometry

Plots

Confirm that:

☐ The axis labels state the marker and fluorochrome used (e.g. CD4-FITC).

☐ The axis scales are clearly visible. Include numbers along axes only for bottom left plot of group (a 'group' is an analysis of identical markers).

☐ All plots are contour plots with outliers or pseudocolor plots.

☐ A numerical value for number of cells or percentage (with statistics) is provided.

Methodology

Sample preparation	not applicable
Instrument	not applicable
Software	not applicable
Cell population abundance	not applicable
Gating strategy	not applicable

☐ Tick this box to confirm that a figure exemplifying the gating strategy is provided in the Supplementary Information.

Magnetic resonance imaging

Experimental design

Design type	not applicable
Design specifications	not applicable
Behavioral performance measures	not applicable

Acquisition

Imaging type(s)	not applicable
Field strength	not applicable
Sequence & imaging parameters	not applicable
Area of acquisition	not applicable

Diffusion MRI ☐ Used ☐ Not used

Preprocessing

Preprocessing software	not applicable
Normalization	not applicable
Normalization template	not applicable
Noise and artifact removal	not applicable
Volume censoring	not applicable

Statistical modeling & inference

Model type and settings	not applicable
Effect(s) tested	not applicable

Specify type of analysis: ☐ Whole brain ☐ ROI-based ☐ Both

Statistic type for inference (See Eklund et al. 2016)	not applicable
Correction	not applicable

Models & analysis

n/a	Involved in the study
☐	☐ Functional and/or effective connectivity
☐	☐ Graph analysis
☐	☐ Multivariate modeling or predictive analysis

Functional and/or effective connectivity	not applicable
Graph analysis	not applicable
Multivariate modeling and predictive analysis	not applicable