Spatial scaling of functional and taxonomic diversity across ecosystems on an island

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ABSTRACT

Spatial scale influences how we perceive, quantify, and conserve multiple biodiversity facets. Like other facets of biodiversity, functional diversity is scale-dependent and varies non-linearly with taxonomic diversity. Yet, studies commonly rely on single-scale analyses, limiting our understanding of the role of spatial scale in biodiversity patterns. Here, we assessed how spatial grain and extent modulate plant functional and taxonomic diversity of an oceanic island ecosystems. We found that grain alters the rate at which functional and taxonomic diversity accumulate across space, leading to shifts in ecosystem diversity rankings. We also found that the spatial aggregation of species and ecosystems environment likely underpin cross-grain differences in the spatial turnover of functional and taxonomic diversity, causing the grain-dependent shifts at the ecosystem level. Our study shows how ecosystem diversity and the environment shape different biodiversity facets at the island level,

highlighting how anthropogenic impacts on functionally unique ecosystems may disproportionately affect island biodiversity.

INTRODUCTION

Biodiversity is inherently scale-dependent, which implies that its patterns and underlying processes vary depending on the spatio-temporal scale considered (Arrhenius 1921; Crawley & Harral 2001). Across space, detecting spatial patterns of biodiversity relies on how well the scale inherent to a given ecological phenomenon matches the scale researchers use (Spake *et al.* 2022). Furthermore, as the ecological processes and mechanisms shaping diversity operate differently at small, intermediate, and large scales, taxonomic and functional diversity changes are often inconsistent across spatial grains and extents (Chase & Knight 2013; Keil & Chase 2019). For example, at regional scales, abiotic conditions and biogeographical history shape ecosystem diversity (Kreft & Jetz 2007), including trait variation and species pools (Sanmartín 2012). At local spatial scales, biotic interactions and ecological drift play a stronger role in determining diversity patterns (Chesson 2000; Siqueira *et al.* 2020; Vellend 2016). Environmental heterogeneity further shapes the spatial structure of biodiversity (Stein *et al.* 2014; Tamme *et al.* 2010), affecting the link between local and regional diversity, i.e., the spatial turnover of diversity. To account for the spatial dependence of biodiversity, a multi-scale approach that includes various spatial grains is essential for elucidating how diversity patterns emerge across space (Crawley & Harral 2001; Suárez-Castro *et al.* 2022), thereby facilitating cross-scale monitoring of multiple facets of biodiversity globally (Kissling *et al.* 2018). A major challenge in developing such an approach is the lack of quantitative assessments on the scale dependence of biodiversity facets beyond taxonomic diversity, such as functional diversity.

Studying ecosystem diversity across space helps understand how different environments shape biodiversity (Levin 2000). Key factors such as geographical isolation (Burns 2019; MacArthur & Wilson 1969) and environmental heterogeneity (Bruelheide *et al.* 2018; Pavoine & Bonsall 2011) additionally explain patterns of biodiversity facets (Suárez-Castro *et al.* 2022; Triantis *et al.* 2006). Resource-limited, isolated, and homogeneous environments generally limit diversity, leading species to share similar ecological attributes, such as functional traits, which reflect common strategies for persisting in a given environment (Barajas Barbosa *et al.* 2023; Spasojevic *et al.* 2014). High-elevation ecosystems exemplify this, as they exhibit limited diversity due to low temperatures, scarce precipitation, which require species to develop physiological and anatomical adaptations that facilitate their persistence (Körner 2003; Zanne *et al.* 2014). Similarly, arid ecosystems represent challenging environments, in which limited water availability requires an array of traits to cope with drought, such as an increase in wood density and reduced plant height (Dória *et al.* 2018; Maestre *et al.* 2021; Santini *et al.* 2024). Contrastingly, ecosystems with readily available resources, such as water and soil nutrients, and high environmental heterogeneity, are expected to support higher species diversity, a wider variety of functional traits, and greater spatial turnover (Alexander *et al.* 2011; Hanz *et al.* 2022).

Two components of spatial scale —grain, the size of the sampling unit, and extent, the total area sampled— are crucial for understanding shifts in species diversity patterns from local to regional scales (Scheiner *et al.* 2011; Viana & Chase 2019), as both affect diversity estimations locally and local site turnover (Whittaker 1972). Within the diversity partitioning framework (*sensu* Whittaker 1972), regional or gamma diversity is determined by alpha and beta diversity, highlighting how different factors, such as spatial heterogeneity, local resource availability, and area affect biodiversity across multiple spatial scales (Chase & Knight 2013). Investigating different spatial grains within this framework helps to disentangle the underlying drivers of diversity's scale dependence.

Despite growing interest in the interconnections and factors governing patterns of diversity across space (Chase *et al.* 2019; Hart *et al.* 2017; Jarzyna & Jetz 2018), the traditional focus on taxonomic diversity of mainland ecosystems commonly relies on one spatial grain (McGill *et al.* 2015; Willis & Whittaker 2002). As a result, further research is necessary to understand the effects of spatial grain on diversity, the interplay between local and regional functional diversity, and the parallels between taxonomic and functional diversity (Karadimou *et al.* 2016; Kraemer *et al.* 2022). Studying scale dependency of multiple biodiversity facets in parallel is particularly critical because spatial effects on diversity may not always be detectable using taxonomic diversity alone (Cadotte *et al.* 2011; Suárez-Castro *et al.* 2022). The level of functional similarity within a region or ecosystem (Eisenhauer *et al.* 2023), often influenced by environmental heterogeneity, can lead to different responses between functional and taxonomic diversity. For example, taxonomic diversity may progressively accumulate, whereas functional diversity may saturate more quickly due to environmental conditions driving functional similarity among species. The extent to which communities are functionally dissimilar and accumulate functional diversity in space is key to identifying the sensitivity of ecosystems to anthropogenic pressures such as agricultural expansion, tourism and biological invasions. These pressures are relevant in island ecosystems, which are experiencing high rates of biodiversity loss globally (Fernández-Palacios *et al.* 2021; Llorente-Culebras *et al.* 2024).

Using the oceanic island, Tenerife (Canary Island, Spain) as a natural laboratory, we disentangle shifts in functional and taxonomic diversity patterns of Tenerife native flora across spatial scales. We aim to understand the links between local and regional spatial patterns that determine the spatial structure and the emergence of plant functional and taxonomic diversity across the island's ecosystems, and how the diversity of different ecosystems contributes to shaping the overall diversity of the island. Due to the combination of a steep elevational gradient and the trade-wind system, Tenerife's ecosystems have highly variable climatic conditions (Fernández-Palacios & Nicolás 1995), ranging from arid and warm in the lowlands to humid mid-elevations, and arid and cold in the highlands (Fig. 1a). This along with the extensive *in-situ* functional trait data of the island (Barajas Barbosa *et al.,* 2023), makes it an ideal setting for investigating different facets of biodiversity across contrasting ecosystems.

Here, we address the following questions: i) How functional and taxonomic plant diversity patterns emerge from local to ecosystem and island scales? We expect that functional diversity will saturate more rapidly than taxonomic diversity because the probability of encountering unique trait combinations will decrease with increasing spatial extent. Spatial grain should also play a role in the accumulation rate of the different biodiversity facets. ii) How do diversity and spatial turnover vary across ecosystems, and to what extent are these variations influenced by total ecosystem area and the ecosystem's environment (e.g., arid, humid, or cold) and environmental heterogeneity? If differences in functional and taxonomic diversity are shaped by the environment, which facilitates the coexistence of species and functional groups, rather than by ecosystem area (Chase *et al.* 2020), we expect that ecosystems with greater environmental heterogeneity will have higher diversity at the ecosystem scale and high spatial turnover (Cadotte & Tucker 2017). At the island scale, however, diversity may emerge due to a combination of environmental heterogeneity within and across ecosystems. While contrasting environmental conditions across ecosystems impose different biophysical constraints, which can increase functional dissimilarity across ecosystems, plants may also converge on similar trait combinations in response to different abiotic filters. We therefore ask iii) how ecosystem diversity (i.e., the number of ecosystems) impacts the accumulation of taxonomic and functional diversity at the island scale. We expect that island-scale diversity across grains and biodiversity facets will increase non-linearly with ecosystem diversity. By addressing these questions, we evidence how spatial extent and grain influence plant diversity across insular ecosystems with distinct environments.

MATERIALS AND METHODS

Island ecosystems and their environment

Our study was conducted on Tenerife (2058 km²) (Fig. 1a), a heterogeneous island dominated by a semi-arid climate (Sperling *et al.* 2004; Whittaker & Fernández-Palacios 2007). Tenerife's floristic composition changes along a steep climatic and elevational gradient, and includes five major zonal vegetation belts (del Arco Aguilar & Rodríguez Delgado 2018), which we treat here as ecosystems. Ecosystems distribution differs from potential (Fig. 1a) to reduced actual area due to land use: coastal scrub (618 km² and 189 km², > 19°C, 50-300 mm y^{-1}), thermophilous woodlands (335 km² and 29 km², 15-19°C, < 250-450 mm yr^{-1}), laurel forest (327 km² and 106 km², 13–16°C, 1000 mm yr^{-1}), pine forest (519 km² and 386 km², 10–15°C, 400–1000 mm y^{-1}) and summit scrub (159 km² and 155 km², 5–10°C, 400 mm y^{-1}) (Fernández-Palacios & Nicolás 1995; del Arco Aguilar & Rodríguez Delgado 2018). We also treat ecosystem as the regional scale containing a species pool adapted to similar environmental conditions (Pärtel *et al.* 1996; Zobel *et al.* 2011). We assessed ecosystem's environmental heterogeneity by calculating ecosystem-level mean value of roughness for mean annual precipitation and mean annual temperature using CHELSA Climatologies (Karger *et al.* 2017). We obtained the roughness data from previously published heterogeneity rasters for oceanic archipelagos (Barajas-Barbosa *et al.* 2020) (Fig. S1).

Plant community data

We obtained species occurrence information for native seed plants at two spatial grains, 100 m^2 and 1 km^2. Small spatial grain data stem from a network of 200 10 m x 10 m plots that cover all ecosystems and elevational belts of the island (Fig. S2; Fernández-Palacios 1992) and contains 139 species, representing 31% of Tenerife's native flora (del Arco Aguilar & Rodríguez Delgado 2018). Large spatial grain data were taken from the *Banco de Datos de Biodiversidad* (www.biodiversidadcanarias.es/biota, version 3.1), from which we obtained species composition data for 500 m × 500 m cells. Large spatial grain data includes 348 native plant species, representing ca. 80% of Tenerife's native flora (Acebes Ginovés 2010). We used cells with the highest precision (levels 1 and 2), where species are identified and recorded within the cell. As the sampling effort varies across cells due to accessibility (Steinbauer *et al.* 2016), we aggregated cells at 1 km². We assigned each plot and cell to an ecosystem based on the vegetation map for the Canary Islands (*sensu* del Arco Aguilar *et al.* 2006). To avoid areas with high anthropogenic pressures and assess the natural patterns as accurate as possible, we removed cells located in urban areas and keep cells that fall within the current distribution of Tenerife ecosystems, following the map of the actual current distribution of Tenerife's ecosystems (*sensu* del Arco Aguilar *et al.* 2010). We additionally removed 878 1 km^2 cells that overlapped with two or more neighbouring ecosystems, using a 500 m buffer around ecosystems. Lastly, we removed 10 100 m^2 plots that did not belong to any of the defined ecosystems. In total, we used the following number of sampling units for the small (n = 190) and large (n = 1164) spatial grains (Fig. S2) and per ecosystem: coastal scrub (60 plots, 380 cells), thermophilous woodlands (34 plots, 104 cells), laurel forest (39 plots, 166 cells), pine forest (42 plots, 391 cells) and summit scrub (15 plots, 123 cells).

Estimation of functional and taxonomic diversity

To estimate functional diversity, we used eight plant functional traits measured *in-situ* for approximately 80% Tenerife native seed plants, i.e., 348 species (Barajas Barbosa *et al.,* 2023): leaf area (mm^2), leaf dry matter content (mg/g; LDMC), leaf mass area (g/m$^{2;}$ LMA), leaf nitrogen content (mg/g; leaf N), leaf thickness (mm), stem specific density (mg/mm^3; stem density), seed mass (mg) and maximum plant height (m; H). Traits were collected across the entire island, from sea level to 2700 m.a.s.l and across all island ecosystems. We used the filled missing trait values (5 % of species by trait combinations; using Barajas Barbosa *et al.,* 2023 data) that used phylogenetic imputation (Penone *et al.* 2014) and random forest algorithm (Stekhoven & Bühlmann 2012) to impute missing values. Traits selected here relate to plant ecological strategies (Díaz *et al.* 2016) and signal responses to the environmental conditions of Tenerife ecosystems, such as water loss prevention and drought tolerance (Li & Prentice 2024; Barajas Barbosa *et al.* 2023), and species competition for light and water (Liu *et al.* 2019).

We estimated functional and taxonomic diversity at both spatial grains using effective number of species and effective number of functional groups (Chao *et al.* 2019), allowing for direct comparisons across biodiversity facets (Chao *et al.* 2021). Using Hill number 0, we quantified taxonomic diversity as species richness and functional diversity as the number of equally distinct functional groups. Functional diversity is calculated using species-pairwise distances derived from a trait matrix comprised of the eight plant traits (Chao *et al.* 2019). For the parameter *tau*, which is the threshold for distinctiveness among functional groups, we used the mean distance (hereafter *Dmean*) between any two individuals randomly selected from the pooled assemblage based on the distance matrix (Chao *et al.* 2019). To estimate taxonomic diversity, species richness, we set the parameter *tau* as the minimum distance (hereafter *Dmin*) between any two individuals randomly selected from the pooled assemblage based on the distance matrix (Chao *et al.* 2019). We estimated taxonomic and functional diversity using the 'FunD' function (Chao *et al.* 2019). Lastly, we inspected the degree of species and species trait combinations shared across island ecosystems at small and large spatial grains, by plotting the number of shared species and building a principal component analysis (PCA), based on the eight plant traits previously described.

Multi-scale functional and taxonomic diversity patterns

To analyse the spatial scaling of functional and taxonomic diversity across spatial extents (the total sampled area; Scheiner *et al.* 2011) for both spatial grains, we use sample-based rarefaction that accounts for sampling effort variation (Gotelli 2001; Gotelli & Colwell 2001). We performed sample-based rarefaction by successively selecting sample units, i.e., plots or cells, in increments of 1, 2, 3..., up to N (where N is all sample units) and calculated at each step diversity using the 'FunD' function using the *tau* parameter set as *Dmean* and *Dmin*. To obtain a robust estimate, we randomized each successive sampling 999 times with replacement and then calculated the average diversity of the combined units at each step of 1, 2, 3..., up to N sample units.

To evaluate the links of functional and taxonomic diversity between the ecosystem and grain, we used the multiplicative diversity partitioning framework *sensu* Whittaker (1972). Because larger ecosystems have more plots and cells, we accounted for ecosystem extend (i.e., area) by standardizing alpha and gamma diversity using a minimum common number of sample units for plots (n=13) and cells (n=100), where alpha diversity is the average diversity of 13 plots and 100 cells and gamma diversity is the total diversity of the same number of plots. Beta diversity is the ratio between estimated gamma and alpha, i.e., $\beta = \gamma/\alpha$. We randomly selected 999 times with replacement the minimum common sample units per ecosystem and on each step, we used the 'FunD' function with the *tau* parameter set as *Dmean* and *Dmin* to compute alpha and gamma functional and taxonomic diversity (Chao *et al.* 2019). We computed mean values and 95% confidence intervals from all samples to compare functional and taxonomic diversity estimates across ecosystems.

To examine the effect of ecosystem diversity, i.e., number of ecosystems, on functional and taxonomic diversity at the island scale, we performed a simulation approach in which we estimated diversity using sampling units from a range of ecosystem diversity values, i.e., from one ecosystem to five ecosystems. For each sampling unit, e.g., two ecosystems, we generated all the possible combinations. For one and five ecosystems, we sampled across individual ecosystems and from the total pool of ecosystems, respectively. To obtain robust diversity estimates from the selected combinations of ecosystems, we randomly sampled 999 times the minimum common number of plots (n=13) and cells (n=100). On each step, we used the 'FunD' function calculating *Dmean* and *Dmin* (Chao et al., 2019). We then estimated diversity as the mean value and 95% confidence intervals for each across all replicates for each sampling unit, i.e., ecosystem number.

Finally, to examine how multiple components of ecosystem-level taxonomic and functional diversity (i.e., alpha, beta and gamma) are influenced by ecosystem area (both potential and actual), ecosystem's climatic conditions (i.e., ecosystem-level mean value of precipitation and temperature), and environmental heterogeneity (i.e., ecosystem-level mean value of precipitation and temperature roughness), we estimated person correlation coefficients among ecosystems' variables. We used R v. 4.1.0 for all analyses (R Core Team, 2024).

RESULTS

Ecosystem biodiversity facets varied across grain and extent (Fig. 1 b-e). At the small grain (Fig. 1b, d), laurel forest had the highest taxonomic diversity across extents, while coastal scrub and thermophilous woodlands had the highest functional diversity, with the latter ecosystem having the highest precipitation heterogeneity (Table S1). Laurel forests had intermediate functional diversity (Fig. 1d), while pine forests and summit scrub consistently had the lowest functional and taxonomic diversity values across extents (Fig. 1b, d). At the large grain, ecosystem diversity rankings changed (Fig. 1c, e). Coastal scrub, thermophilous woodlands, and laurel forest had the highest taxonomic diversity across spatial extents (Fig. 1c), while coastal scrub had the highest functional diversity across space (Fig. 1e). Laurel forest had the lowest functional diversity at the large grain (Fig. 1e) and summit scrub generally had low diversity (Fig. 1b-e), except for functional diversity (Fig. 1e).

Some ecosystems showed shifting trends across grains, laurel forest had higher functional diversity than the pine forest at the small grain (Fig. 1d), but pine forest surpassed it at the large grain (Fig. 1e). Diversity accumulation patterns varied with spatial grain. At the small grain, taxonomic and functional diversity increased steadily without reaching an asymptote (Fig. 1b, d), while at the large grain, diversity increased abruptly and quickly reached an asymptote (Fig. 1c, e). We found that fewer species and trait combinations were shared at the small grain than at the large grain, where overlap is greater (Fig. S3 and S4).

Our diversity partitioning framework showed differences across ecosystems and grains (Fig. 2). At the small grain, laurel forest had the highest alpha and gamma taxonomic diversity (Fig. 2a, e), while coastal scrub had the highest alpha and gamma functional diversity (Fig. 2b, f). Pine forest and summit scrub showed the lowest alpha and gamma diversity across both facets (Fig. 2a, e, b, f). At the large grain, thermophilous woodlands had the highest alpha and gamma taxonomic diversity (Fig. 2g, k) while pine forest and summit scrub remained lowest (Fig.2g, k). Functional alpha diversity was highest for thermophilous woodlands (Fig. 2h), while coastal scrub had the highest gamma functional diversity and laurel forest the lowest (Fig. 2l).

Ecosystems beta diversity also varied by biodiversity facet and grain (Fig. 2). At the small grain, thermophilous woodlands, laurel forest, and pine forest had the highest taxonomic beta diversity (Fig. 2c), while functional beta diversity was highest in thermophilous woodlands (Fig. 2d). At large grain, coastal scrub and pine forest had the highest beta diversity for both facets (Fig. 2i, j), while thermophilous woodlands, laurel forest and summit scrub had intermediate to low values (Fig. 2i, j).

Ecosystem diversity, i.e., the number of ecosystems, increased island-level taxonomic and functional diversity at both spatial grains (Fig. 3). While functional and taxonomic diversity showed low values for a single ecosystem (Fig. 3), they increased rapidly and non-linearly with increasing ecosystem diversity. At the small grain, the accumulation curves began to saturate when ecosystem diversity was greater than four (Fig. 3a, b). At the large grain, island-level taxonomic and functional diversity increased rapidly and non-linearly with increasing ecosystem diversity, with neither reaching their asymptote at the highest value of ecosystem diversity (Fig. 3c, d).

Ecosystem-level taxonomic and functional diversity varied with environmental heterogeneity and ecosystem area (Fig. S5). At small grain, most diversity components correlated positively with temperature and some with precipitation heterogeneity (e.g., beta diversity) (Fig. S5a). At the large grain, correlations varied, e.g., alpha and gamma taxonomic diversity correlated positively with temperature and precipitation heterogeneity while beta diversity showed a negative correlation with temperature heterogeneity (Fig. S5b). At small grain, diversity components correlated negatively with actual ecosystem area but positively with potential area (Fig. S5a), and at the large grain, alpha and gamma taxonomic diversity were negatively correlated with actual area (Fig. S5b).

DISCUSSION

The different shapes of the accumulation curves between the two spatial grains demonstrate the consistent scale dependence of the estimation of biodiversity facets. The large grain area allows for a rapid increase in functional and taxonomic similarity with increasing extent, leading to a quicker saturation of diversity, particularly for functional diversity (Fig. 1e). Contrastingly, the non-saturating increase of diversity at the small grain suggests a less similar (or less even; Chase *et al.* 2018) species and functional composition across extents. Even after accounting for differences in ecosystem area (i.e., spatial extent), the differences in our diversity partitioning analysis between the two grains (Fig. 2) suggests that grain-dependent changes in evenness, within-species spatial aggregation, or both underpin variation in functional and taxonomic diversity across ecosystems (McGlinn *et al.* 2019). This result also suggests that abiotic drivers, such as ecosystem environmental conditions and heterogeneity, may also be scale-dependent. We further show that ecosystems environmental heterogeneity and area relate differently to the different components of functional and taxonomic diversity across grains (Fig. S5); thus, locally and regionally, the effect of the environment acts differently on diversity.

Our results also show that the choice of spatial grain as well as the extent influences diversity estimations and drive shifts in ecosystems rankings (as observed between pine forests and laurel forests; Fig. 1e, d). Such shifts result from the large grain's extensive coverage and overlap in species and trait combinations (Fig. S3b and Fig. S4b), leading to fewer species locally but a higher species number at the pine forest ecosystem level. Conversely, the small grain plots (Fernández-Palacios 1992) have minimal overlap of species and traits across ecosystems (Fig. S3a and Fig. S4a), leading to different patterns. We attribute the lower taxonomic and functional similarity across ecosystems at the small grain to the apparently greater influence of dispersal limitation, environmental filtering, and biotic interactions than at the large grain (Whittaker & Heegaard 2003).

Scaling of island ecosystem diversity and ecosystems environment

Our results suggest that beyond ecosystems area, ecosystems' climate and environmental heterogeneity, driven by the Tenerife’s steep environmental gradient (Otto *et al.* 2012), are responsible for the contrasting and shifting spatial patterns of diversity across the island ecosystems (Fig. 1).

The generally high functional diversity of the arid to semi-arid ecosystems of the island, i.e., the coastal scrub and thermophilous woodlands, indicates a large array of trait combinations in both ecosystems at both grains; likely shaped by within-ecosystem environmental variation from (coastal) arid to more mesic conditions (del Arco Aguilar & Rodríguez Delgado 2018). Low precipitation and saline soils in the coastal scrub ecosystem may promote diverse trait combinations, including salt-tolerant succulents with small-round leaves (e.g., *Tetraena fontanesii*), large thick leaves (e.g., *Astydamia latifolia*), and bush-like plants with xerophilic leaves (e.g., *Neochamaelea pulverulenta*). The high environmental heterogeneity of the thermophilous woodlands ecosystem (Table S1) likely drives the high trait diversity turnover at the small grain (Fig. 2d), as locally the ecosystem can host different plant communities, from small succulents, to xerophytic plants (e.g., *Euphorbia* species), to intermediate-size shrubs with high stem density (e.g., *Juniperus turbinata*), and palm trees (e.g., *Phoenix canariensis*). These species have different trait adaptations to optimize water use in dry habitats or thrive in more mesic habitats (Fernández-Palacios *et al.* 2020).

The mild temperatures and high rainfall of the laurel forest ecosystem (del Arco Aguilar & Rodríguez Delgado 2018) support high taxonomic diversity, particularly for trees, but only intermediate functional diversity. The dominance of tree species (e.g., *Persea barbujana*, *Laurus novocanariensis*) with similar traits (high stature and stem density, and intermediate leaf area) explains the lower functional diversity of the laurel forest relative to its taxonomic diversity across grains. The dominance of a functional group is even more pronounced in the pine forest ecosystem because its canopy is dominated by a single tree species, the Canarian pine (*Pinus canariensis;* a tall, large-seeded plant) (De Nascimento *et al.* 2009), which explains the ecosystem's low functional diversity patterns at the small grain. Tree dominance in the pine forest can be attributed to the local climatic conditions and species competition, where cooler annual temperatures and semi-arid to mesic conditions (Arco Aguilar & Rodríguez Delgado 2018) favour the dominance of the Canarian pine and its adaptation to fire resistance prevents local coexistence with other plants (Barabás *et al.* 2022; Kraft *et al.* 2014). At the large grain, functional and taxonomic diversity patterns varied for pine forest, particularly for beta diversity, suggesting a high spatial turnover of species and trait combinations.

The low functional and taxonomic diversity of the summit scrub ecosystem across grains reflects the challenging environmental conditions of high-elevation ecosystems, such as freezing temperatures, low precipitation, and geographical isolation. These conditions hinder species colonization (Irl *et al.* 2015) and impose strong environmental filtering that limits species and trait diversity (Cadotte & Tucker 2017; Laughlin & Joshi 2015), as seen in the absence of some functional groups, e.g., tall or succulent plants. High-elevation floras are commonly dominated by short, woody plants with high stem densities (e.g., *Cytisus supranubius*, *Argyranthemum teneriffae*), which aid plant survival in drought, cold, and nutrient-poor soils (Sumner & Venn 2021). These trait adaptations contribute to a functional similarity of species in the summit scrub. The abrupt increase of functional diversity of the summit scrub at the large grain (Fig. 1e) is driven by the large overlap of trait diversity at this grain (Fig. S4).

Additional factors such as the biogeographical history of insular ecosystems (Martín-Hernanz *et al.* 2023), which we did not test here, may also influence our observed diversity patterns. For example, the expansion of arid environments in Tenerife (~7 Ma ago; van Huysduynen *et al.* 2021) has likely increased the taxonomic and functional diversity of semi-arid ecosystems by providing more niches for species and functional groups to occupy, and the long-term presence of the laurel forest ecosystem on the island and Europe (~2 million years; Fernández-Palacios *et al.* 2017) promotes lineages to converge into similar trait combinations, fostering the low functional diversity.

Spatial links between local, regional, and island diversity

Our results reveal how differences in local (alpha) and regional (gamma) diversity determine the spatial differentiation of diversity (beta diversity), where different/similar species and functional groups occur across sites within island ecosystems (Fig. 2). Heterogeneous environments, such as thermophilous woodlands ecosystem (Table S1) (Fernández-Palacios *et al.* 2020), promote spatial aggregation of species and traits as a response to their habitat preferences (Chase *et al.* 2018; McGill *et al.* 2015). Thus, the combination of low alpha and high gamma functional diversity at the small grain for thermophilous woodlands suggests that distinct plant communities and functional groups occur locally, where succulents aggregate in arid to semi-arid areas, while taller plants like palms and shrubs occur in mesic habitats. This drive spatial turnover of trait diversity (Loreau *et al.* 2003; Otto *et al.* 2012) and explains the high beta diversity of the thermophilous woodlands at the small grain. In contrast, the low beta diversity of summit scrub reflects low environmental heterogeneity and strong environmental filtering, leading to more homogeneous plant communities dominated by few functional groups adapted to high-elevation conditions.

Our simulation analysis of functional and taxonomic diversity accumulation across ecosystems (Fig. 3) highlights the unique contribution of each ecosystem to the overall diversity of the island. As ecosystem diversity increases, so does island-level taxonomic and functional diversity, highlighting that most ecosystems on the island make distinct contributions as a result of their functional dissimilarity. These unique contributions of most ecosystems to Tenerife’s diversity arise from the varying biophysical constraints that have shaped plant diversity in response to specific environments, indicating a relatively low taxonomic and functional overlap across ecosystems (Fig. S3 and S4). The uniqueness of each ecosystem's functional and taxonomic diversity has important implications for conservation efforts and management of island biodiversity threats, such as invasive species, agricultural expansion and tourism infrastructure (Otto *et al.* 2012). In particular, arid and mesic ecosystems are among the most affected ecosystems on the Tenerife, with the highest modified community composition (Otto *et al.* 2007; Otto *et al.* 2012). Our findings offer insights and open future questions about which insular ecosystems might be more vulnerable to ongoing global change drivers that threaten native plant diversity. Further research investigating the specific drivers of insular biodiversity loss will improve the understanding and identification of ecosystem vulnerabilities.

Overall, we showed how insular plant diversity across different spatial scales is shaped by the environmental conditions of its ecosystems. Habitat-diverse areas exhibit high species and functional diversity at both local and regional scale. In contrast, high-elevation ecosystems are low in diversity across spatial extents and grains. These patterns may be tightly related to the climatic conditions, environmental heterogeneity, and area, along with the unique biogeographical histories of the island ecosystems, which influence the spatial turnover of plant diversity and its structure across space. Our results also show that taxonomic and functional diversity patterns do not always mirror each other. Depending on the level of functional similarity within an ecosystem, parallels between biodiversity facets vary greatly, resulting in these two facets scaling differently across space. We also found that diversity estimates vary markedly across spatial grains, as grain influences the levels of similarity among ecosystems or regions. Lastly, we provide a broaden understanding of the relationship between local and regional functional and taxonomic diversity and their relation to larger scale diversity patterns of an oceanic island, which is crucial for identifying processes maintaining island biodiversity.

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FIGURES

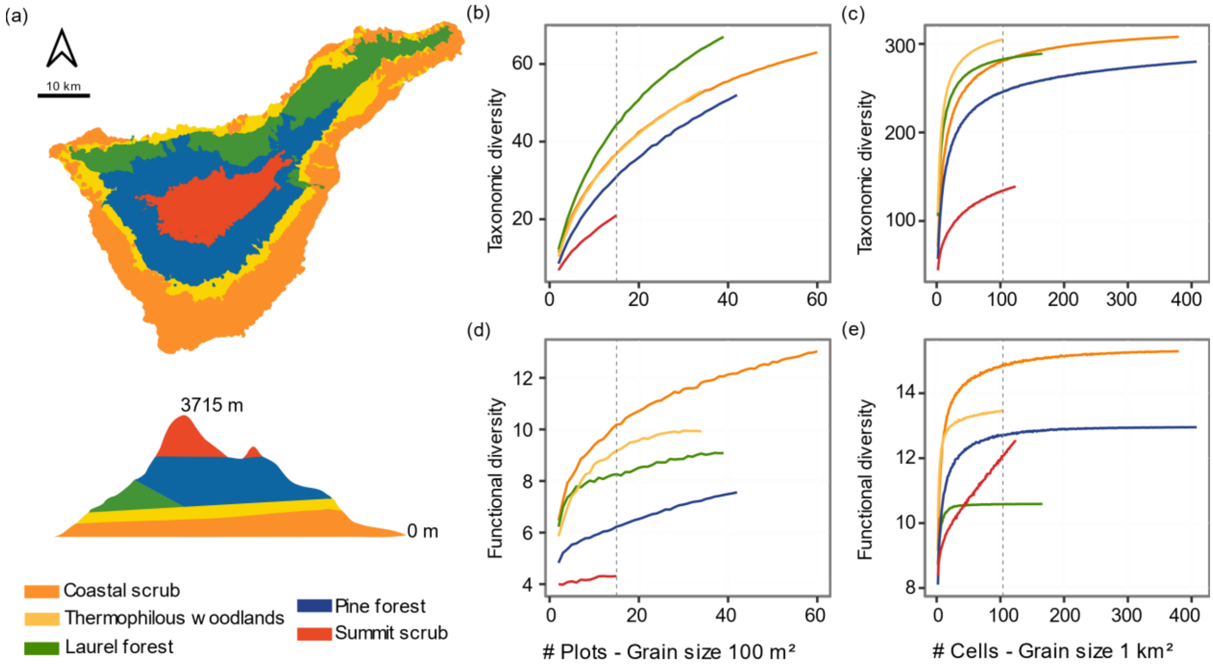


Figure 1. Spatial scaling of plant functional and taxonomic diversity of the five ecosystems of Tenerife Island (Canary Islands, Spain). Potential spatial distribution and altitudinal gradient (del Arco *et al*. 2006) of the island's five major ecosystems (a). The effective number of native plant species, i.e., taxonomic diversity (b and c), and the effective number of functional groups, i.e., functional diversity (d and e), with increasing extent or sampled area for each ecosystem. We estimated diversity at two spatial grains, 100 m² (b and d), and 1 km² (c and e). The different colours (b-e) correspond to an ecosystem following the colour legend (a) and the dotted vertical lines (b-e) represent the smallest number of plots or cells at small (15 plots) and large (104 cells) spatial grains.

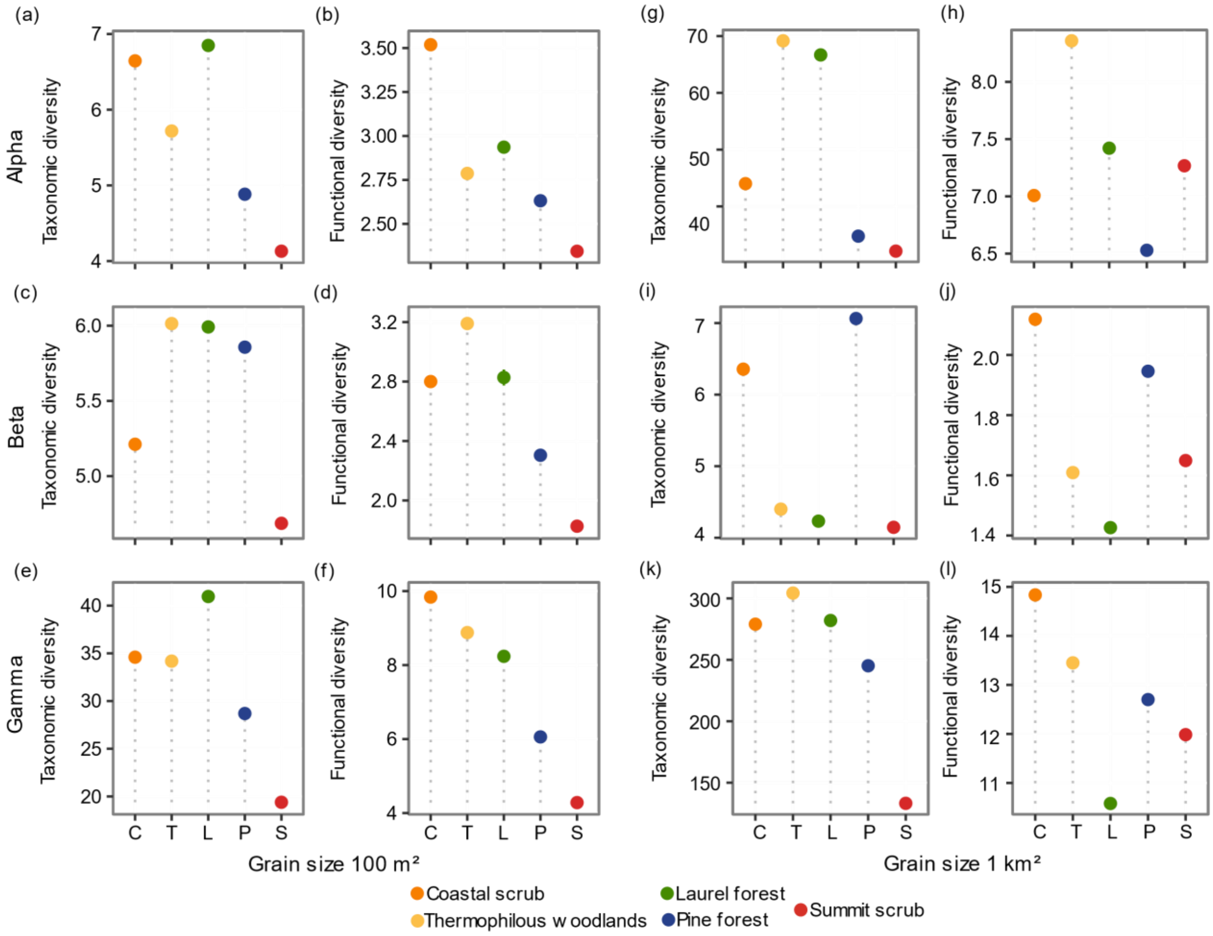


Figure 2. Functional and taxonomic diversity from local (alpha) to the differences between local and regional ecosystem (gamma) scales (beta) across ecosystems and spatial grains. On the x-axis, ecosystems are represented as follows: C for coastal scrub, T for thermophilous woodland, L for laurel forest, P for pine forest, and S for summit scrub, and are organized from low to high-elevation ecosystems. Functional and taxonomic diversity are estimated at the local scale, using either a small 100 m^2 grain (a-f) or a large 1 km^2 grain (g-l). Functional and taxonomic diversity values were calculated for a similar number of plots (n = 13) or cells (n = 100) within each ecosystem, which were randomly sampled with replacement 999 times plots or cells. Dots and error bars correspond to mean values and 95% confidence intervals, respectively.

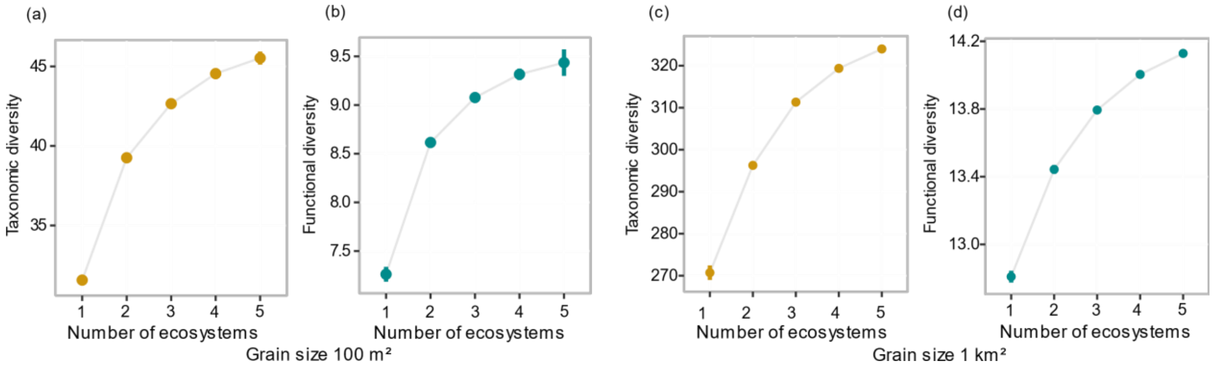


Figure 3. Accumulation of taxonomic and functional diversity across island ecosystems, representing island-level ecosystem diversity. On the x-axis 1 to 5 refers to the amount of randomly (sampled) accumulated island ecosystems. Functional and taxonomic diversity were calculated by controlling for differences in the number of plots and cells across ecosystems, that is, for a fixed number of cells (n = 13) and cells (n = 100) across 999 bootstrap samples for each number of ecosystems. Dots and error bars correspond to the mean values and 95% confidence intervals, respectively.

SUPPLEMENTARY MATERIAL

Spatial scaling of functional and taxonomic diversity across ecosystems on an island

Appendix S1

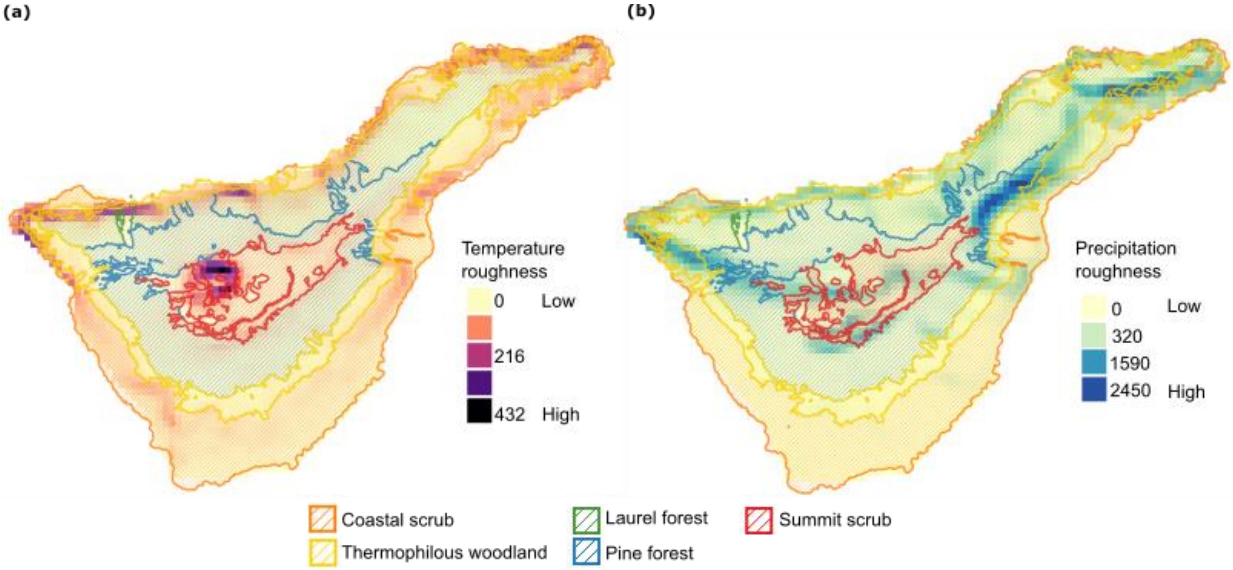


Figure S1. Environmental heterogeneity estimated as roughness, that is, the largest inter-cell difference within a focal cell and its surrounding cells in a specified window size of 12 × 12 pixels using mean annual temperature (°C; a) and mean annual precipitation (mm; b), from the Climatologies at High resolution for the Earth's Land Surface Areas (CHELSA) dataset at a spatial grain of 1 km (Karger et al., 2017). Roughness data was retrieved from published heterogeneity rasters from Barajas-Barbosa et al (2020).

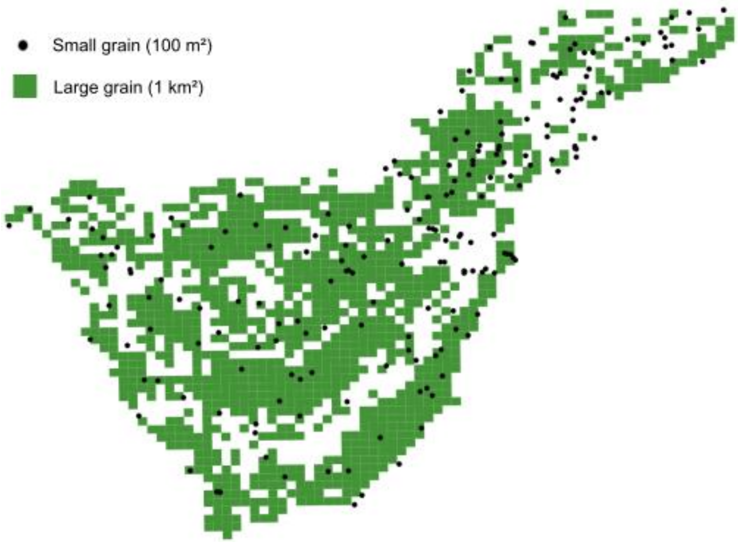


Figure S2. Spatial grains at which we examined plant functional and taxonomic diversity patterns on Tenerife. We assessed plant diversity using two spatial grains, plot (n= 190), and cell (n=1164).

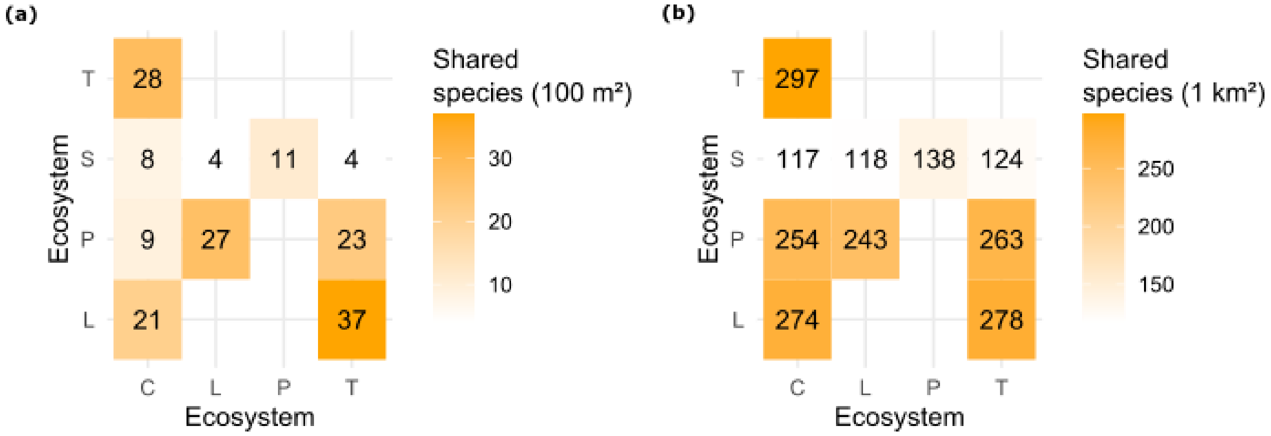


Figure S3. Number of species shared across island ecosystems at small (a) and large (b) spatial grain. Ecosystems are represented as follows: C for coastal scrub, L for laurel forest, T for thermophilous woodlands, P for pine forest and S for summit scrub.

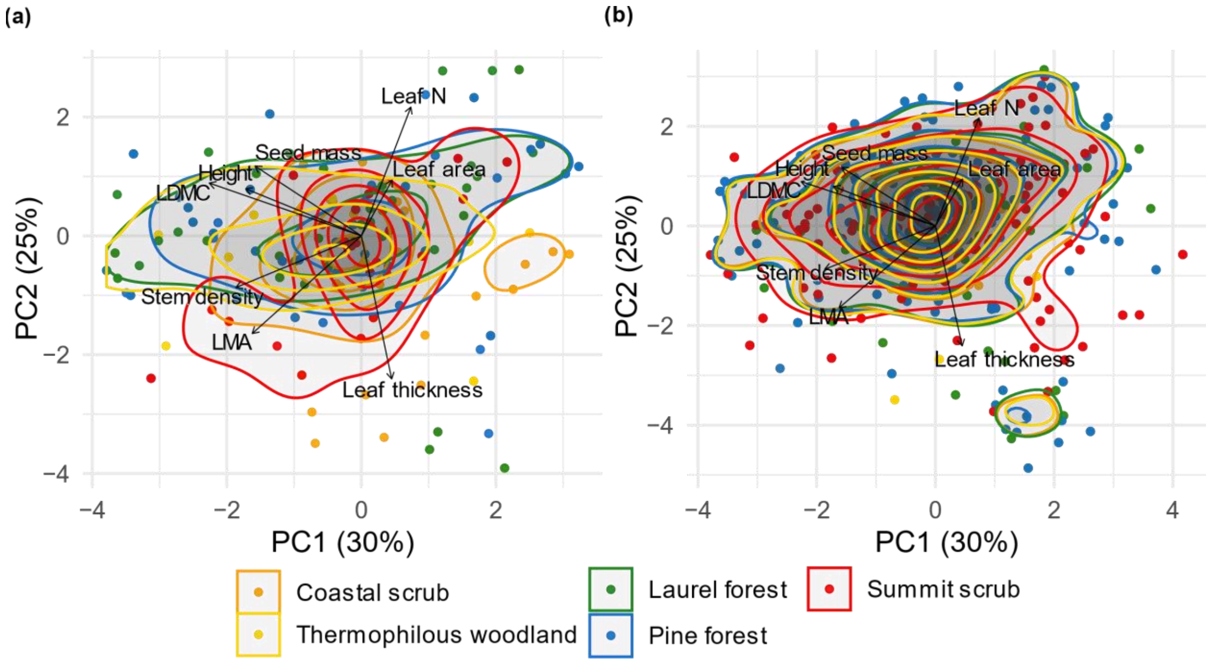
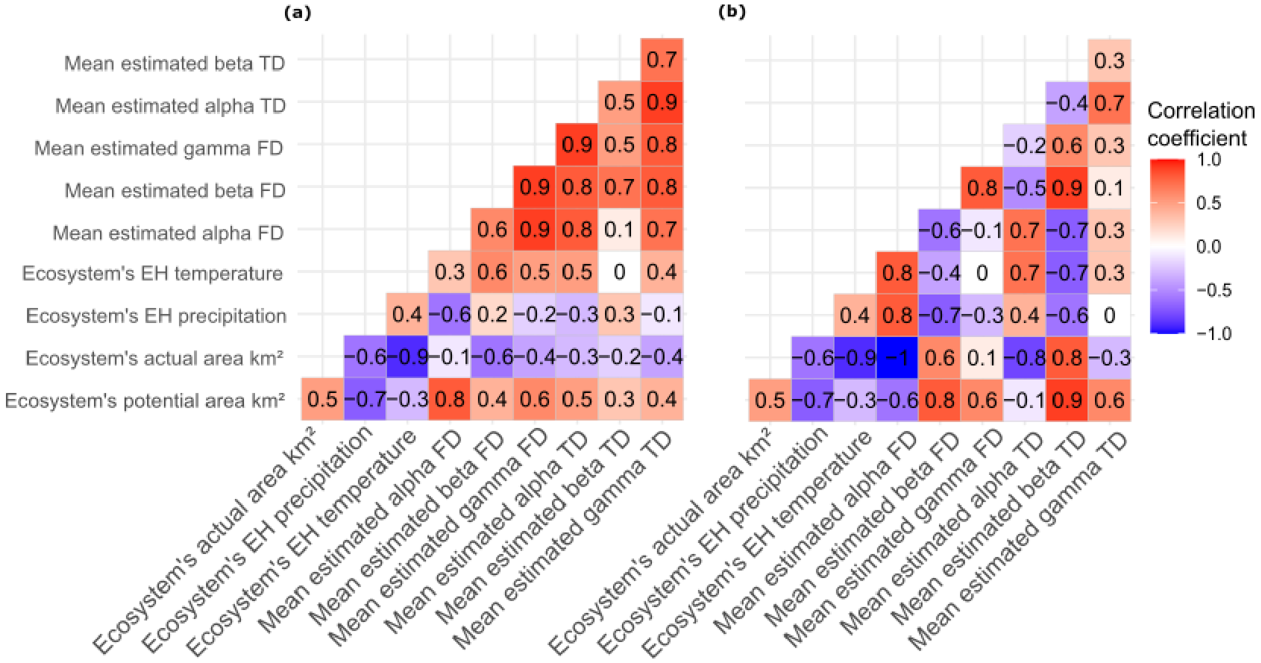


Figure S4. Degree of species trait combination shared across island ecosystems at small (a) and large (b) spatial grain. Each colour dot represents a species belonging to a given ecosystem. The position of the species in the PCA is driven by its trait combinations. 348 native plant species of 139 plant species



(a)

	Ecosystem's actual area km²	Ecosystem's EH precipitation	Ecosystem's EH temperature	Mean estimated alpha FD	Mean estimated beta FD	Mean estimated gamma FD	Mean estimated alpha TD	Mean estimated beta TD	Mean estimated gamma TD
Mean estimated beta TD									0.7
Mean estimated alpha TD								0.5	0.9
Mean estimated gamma FD							0.9	0.5	0.8
Mean estimated beta FD						0.9	0.8	0.7	0.8
Mean estimated alpha FD					0.6	0.9	0.8	0.1	0.7
Ecosystem's EH temperature				0.3	0.6	0.5	0.5	0	0.4
Ecosystem's EH precipitation			0.4	−0.6	0.2	−0.2	−0.3	0.3	−0.1
Ecosystem's actual area km²		−0.6	−0.9	−0.1	−0.6	−0.4	−0.3	−0.2	−0.4
Ecosystem's potential area km²	0.5	−0.7	−0.3	0.8	0.4	0.6	0.5	0.3	0.4

(b)

	Ecosystem's actual area km²	Ecosystem's EH precipitation	Ecosystem's EH temperature	Mean estimated alpha FD	Mean estimated beta FD	Mean estimated gamma FD	Mean estimated alpha TD	Mean estimated beta TD	Mean estimated gamma TD
Mean estimated beta TD									0.3
Mean estimated alpha TD								−0.4	0.7
Mean estimated gamma FD							−0.2	0.6	0.3
Mean estimated beta FD						0.8	−0.5	0.9	0.1
Mean estimated alpha FD					−0.6	−0.1	0.7	−0.7	0.3
Ecosystem's EH temperature				0.8	−0.4	0	0.7	−0.7	0.3
Ecosystem's EH precipitation			0.4	0.8	−0.7	−0.3	0.4	−0.6	0
Ecosystem's actual area km²		−0.6	−0.9	−1	0.6	0.1	−0.8	0.8	−0.3
Ecosystem's potential area km²	0.5	−0.7	−0.3	−0.6	0.8	0.6	−0.1	0.9	0.6

Figure S5. Correlation analysis for small grain (a) and for large grain (b) including ecosystem values for functional diversity (FD), taxonomic diversity (TD) for all alpha beta and gamma scales, and ecosystem environmental heterogeneity (EH) in terms of precipitation and temperature, and ecosystem area. Both actual (or current) and potential area of ecosystems are included.

Ecosystem	Environmental heterogeneity in terms of precipitation, i.e., mean roughness value of mean annual precipitation (mm)	Environmental heterogeneity in terms of temperature, i.e., mean roughness value of mean annual temperature (°C)	Potential area (km²)	Actual current area (km²)
Coastal scrub	179.56	39.357	618	189
Pine forest	252.15	17.031	519	29
Laurel forest	286.19	42.825	327	106
Summit scrub	322.40	36.180	158	386
Thermophilous woodlands	402.66	45.152	335	155

Table S1. Environmental heterogeneity, potential area and actual current area of Tenerife's principal ecosystems. Environmental heterogeneity values correspond to the mean value of roughness of mean annual temperature and mean annual precipitation at the ecosystem level. FD stands for functional diversity and TD for taxonomic diversity.