

Towards a mechanistic explanation of Island biogeography using subterranean animal communities

Alejandro Martínez¹, Stefano Mammola¹, Antonio Pérez-Delgado², Rafael García³, Heriberto López⁴, Diego Fontaneto¹, and Pedro Oromí⁵

¹Consiglio Nazionale delle Ricerche

²IPNA-CSIC

³Affiliation not available

⁴IPNA-CSIC

⁵University of La Laguna

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Abstract

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Alejandro Martínez (1), Stefano Mammola (1,2), Antonio J. Pérez-Delgado (3), Rafael García (4), Heriberto López (3), Diego Fontaneto (1), Pedro Oromí (5)

1. Molecular Ecology Group (MEG), Water Research Institute (IRSA), National Research Council of Italy (CNR). Largo Tonolli, 50. 28922. Verbania, Italy
2. Laboratory for Integrative Biodiversity Research (LIBRe), Finnish Museum of Natural History (LUOMUS), University of Helsinki, Helsinki, Finland
3. Island Ecology and Evolution Research Group, Institute of Natural Products and Agrobiology (IPNA-CSIC). 38206 La Laguna, Tenerife, Spain
4. C/. San Miguel 9, 38700 Santa Cruz de La Palma, La Palma, Canary Islands
5. Department of Animal Biology and Edaphology and Geology, University of La Laguna (ULL), La Laguna, Spain

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Corresponding author: Alejandro Martínez. alejandro.martinezgarcia@cnr.it

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Data accessibility. All data and scripts will fully available at the Dryad repository upon publication

Abstract [150 words]

Using subterranean fauna in the Canary Islands as a simplified natural laboratory, we explored how the interplay of eco-evolutionary processes shape taxonomic and functional diversity patterns in oceanic archipelagos through geological times. First, we demonstrated an overall convergence in the trait spaces of subterranean communities across islands, yet with variability according to each island’s ontogenetic state—young, mature, or senescent. Next, we showed that the reduced species contribution to the island’s traits space in mature islands is a consequence of an optimisation of the use of the available niche space driven by species interactions. Finally, we link those lines of evidence showing that species interactions select a non-random combination of traits in mature islands. Collectively, our results provided a mechanistic description of the drivers of diversity in oceanic islands by suggesting causal relationships between species functional properties and island diversity metrics accounting for their geological age.

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Introduction

Oceanic islands have been the all-time favourite natural laboratory to test predictions about evolution of biota through time (Warren et al. 2015; Whittaker et al. 2017). The theory of island biogeography, a conceptual model to predict species richness on islands, is at the core of many of those advances (Warren et al. 2015). In its original formulation, the theory assumes that the number of species in a given island represents an equilibrium between immigration and extinction rates, both dependent on the island surface and the distance from the nearest continent acting as species pool (MacArthur & Wilson 1967).

The inclusion of geological and climatic processes added more nuance to these assumptions. Oceanic islands change in size, configuration, and isolation through time with comparable geodynamic cycles, in which a sequence of islands is produced as the plate moves over a volcanic hotspot. Each island subsequently erodes and eventually subsides as it is carried away from the hotspot. By incorporating such geodynamic information, the general dynamic model of oceanic island biogeography (Whittaker et al. 2008) has successfully predicted an increase of the number of species in a given island during the emergence and building phases, driven by immigration and *in situ* speciation. The model predicts subsequent decay of the number of species, as erosion and gravitational collapses reduce the extension and habitat heterogeneity. At the point of the highest geological heterogeneity within each cycle, the total number of species in an island achieves its maximum relative to the carrying capacity. Accordingly, islands with higher altitudes and larger surface will sustain more species as they offer more opportunities for local adaptation and diversification.

This island dynamic model has successfully predicted the number of species at a large set of oceanic archipelagos based on the roles of immigration, speciation, and extinction (Warren et al. 2015). Nevertheless, the model does not explicitly inform on how species interactions interplay with the processes driving diversity within each island at the community level (Rosindell et al. 2017). It has been proposed that immigration-speciation dynamics mostly drive diversity in young islands where low competition and empty niche space

provide increased ecological opportunities. However, as the island approaches the carrying capacity, species interactions within established communities might gain importance, with niche segregation and ecological speciation playing an important role in optimising ecological networks to better exploit the available niche space (Gillespie et al. 2020). Ultimately, as the island approaches senescence and gets eroded under the sea, diversity is driven—more or less randomly—by extinction.

The specific role of species interactions has been difficult to quantify, particularly in archipelagos formed by several islands, in which dispersal favours colonisation across them even allowing for the presence of metacommunities (Lawson et al. 2019). These problems can be alleviated by focusing on a subset of habitats that, due to their particular ecological conditions, filter their potential colonisers to lineages evolving *in situ*, because the habitats impose strong constraints that limit the likelihood of arrival and survival of immigrants from other islands (Patiño et al. 2017). Yet, most habitats potentially fulfilling these requisites, such as mountain summits or lakes (Itescu et al. 2019), are not present through the entire island’s life cycle since they depend on the island’s geological state. Because of this dependency of most habitats to geological history of an island, it is unlikely to find a whole habitat-specific animal community throughout the whole history of an island, if not considering that oceanic volcanic islands host an impressive diversity of subterranean habitats. Subterranean habitats impose strong constraints against the arrival and survival of immigrants from other islands, favour *in situ* speciation, and can be found across all the geological history of the island.

Subterranean adapted fauna importantly contributes to the pool of endemic species in many archipelagos (Naranjo et al. 2020). Lava tubes are the most iconic example amongst their caves (Sauro et al. 2020). However, caves are just a small, human-accessible fraction of the subterranean habitats available to potential colonisers. Due to their small body size, most subterranean animals dwell in the labyrinthic network of pores and small fissures forming within volcanic rocks and clasts—a habitat termed *Milieu Souterrain Superficiel* (MSS; Oromí et al. 1986; Mammola et al. 2016). Collecting ecological data in these environments is notoriously challenging (Mammola et al. 2021a). However, once the exploration and sampling impediments are overcome, our efforts are compensated by the set of unique properties that make subterranean habitats ideal laboratories for eco-evolutionary research (Mammola & Martinez 2021)—including their discrete nature largely preventing long-range migration (Mammola, 2019) and the presence of relatively simple communities showing high trait convergence (Gibert & Deharveng 2002; Trontelj et al. 2012; Mammola et al. 2022). Given that subterranean habitats in oceanic islands are *de facto* “islands within islands” (Esposito et al. 2015), they should represent the perfect model system to explore broad questions within the realm of island biogeography (Culver 1970, 1971; Fattorini et al. 2016; Balog et al. 2020).

The aim of this paper is to investigate how the interaction between ecological and evolutionary processes shape the diversity patterns in oceanic archipelagos. Our goal was to derive the expectation in species diversity predicted from the island biogeographic theory from the relative contribution of speciation, community-level interactions, and extinction at different stages of their ontogenetic cycle. We accomplished our objective in four steps, each of them associated with a specific hypothesis. (1) Firstly, we described the trait space of all the subterranean species in each island. We expected it to converge due to the ecological filtering exerted by the colonisation of subterranean habitats, yet exhibiting a certain degree of variation according to each island’s ontogenetic state. (2) Secondly, we explored how this overall convergence in the trait space might be explained by the different contributions of each species to their overall trait space of islands with different ages. We expected that species contribute progressively less as an island approaches its maximum geological complexity, reflecting increasing niche occupancy and a progressive reduction of ecological opportunity. The contribution of individual species might increase as an island approaches its senescence and extinction reduces its species richness. (3) Third, we hypothesised that the reduction in species contribution is a consequence of an optimised use of the available niche space driven by species interactions. Under this assumption, we expect that functionally similar species will experience a stronger ecological and geographical isolation in mature islands; whereas the distribution of species and their niche occupancy will be more random in senescent or young islands (4) Finally, we proposed that species interactions might select a non-random combination of traits in each island, leading to trait spaces with smaller volume and higher degree of order in mature islands than those expected by chance from a sample of the archipelago’s species pool. By confirming these

hypotheses, we could provide a mechanistic description of the drivers of diversity in oceanic islands (Wilson 1969; Losos et al. 2010) by establishing causal relationships between species functional properties and island diversity metrics accounting for each island’s age.

Material and methods

Model system and rationale

We selected the Canary Islands as a study system for two reasons: first, we have a nearly complete knowledge of their terrestrial cave-adapted diversity (Oromí et al. 2021); second, they cover a time span of 21 Ma (Gillespie & Clague 2009), being the only studied volcanic oceanic archipelago in the world with such a broad range of ages (Borregaard et al. 2017). The eastern islands (Lanzarote and Fuerteventura) are very close to each other and about 100 km from the continent; the remaining five islands span towards the West over ca. 400 km. Except for Lanzarote and Fuerteventura, each island represents an independent volcanic building separated by oceanic depths, so they were never superficially connected to one another or to Africa (Troll & Carracedo 2016). Therefore, the Canary Islands can be regarded as oceanic islands that have been biologically colonised across the ocean, mainly through the marine channel separating the islands from North Africa (Florencio et al. 2021). Most subterranean species in the Canary Islands are single-island endemics, with speciation trajectories that happened *in situ* from surface ancestors (Arnedo et al. 2007). All islands harbour extensive subterranean habitats, including caves, lava tubes, and MSS (Oromí et al. 2021). Regarding age, Lanzarote and Fuerteventura are the oldest islands, having undergone a long erosive period only interrupted by two historical volcanic episodes in Lanzarote. They are here considered in their senescent ontogenetic stage. The central islands of Gran Canaria, Tenerife, and La Gomera represent the islands with the highest structural complexity, although La Gomera and Gran Canaria have fewer caves than Tenerife, which might imply a smaller carrying capacity than expected by their altitude (Oromí et al. 2021). Lava tubes usually become destroyed within a few hundred thousand years only persisting in relatively young parts of the islands, thus being very few on Gran Canaria and La Gomera where volcanism has been scarce or even absent in the last 2 Ma (Oromí, 2004). These three islands are considered as geologically mature. La Palma and El Hierro are the youngest islands, and those that have concentrated most of the volcanic episodes in historical times (Longpré & Felpeto, 2021). A summary of the most relevant features of each island is in Table S1.

Dataset assembly

The assembled dataset is a synthesis of the last 40 years of research in the subterranean terrestrial fauna of the Canary Islands (Oromí et al. 2021), consisting of arthropods. The sample effort during this time was comparable across islands. The lack of records in Lanzarote (including La Graciosa) corresponds to a real absence of such subterranean fauna. The database includes all published and unpublished records of subterranean species from both cave and MSS habitats. We collected functional traits from the original description or relevant references and, if needed, completed from newly measured specimens. A complete list of the occurrences, as well as the definition of each trait, the methodology followed for its measurements, their values and the employed sources the sources can be found in [Dryad repository].

Hypotheses testing

Our goal was to derive the predictions of the island biogeographic theory from the different roles that community-level processes—speciation, community-level interactions, and extinction—might have at each island given their ontogenetic state (young, mature, senescent) (Figure 1A). In our system, the role of immigration is negligible, given that almost all Canarian subterranean species are single-island endemic species that have evolved within each island (Oromí et al. 1991).

Our approach was to first provide a description of the trait space of each island using n-dimensional hypervolumes. We described those hypervolumes in terms of functional richness, which we used as a proxy of total niche occupancy, and functional evenness, which reflects the homogeneity of the distribution of species within this niche space. Then, we looked at the role of individual species in each island. First, we estimated

each species contribution to the islands’ hypervolume; second, we explored the relationship between species’ functional distances and niche/geographical occupancy using partial mantel permutational tests. Lastly, we explored whether the presence of strong species interactions leads to a non-random distribution of functional traits in each island using null modelling. In this last step, we connected the macroscopic description of the island states from step 1, with the community-level processes disentangled in steps 2 and 3. The hypotheses specifically tested at each of the four steps are provided below, along with a detailed description of the methods.

Hypothesis 1. Island trait spaces converge across islands

First, we explored the functional diversity patterns of the subterranean communities in the Canary Islands relating the properties of each trait space to the age and stage of the geological cycle for each island. Since the subterranean environment imposes a similar ecological filter across islands (i.e., permanent darkness and scarcity of food), we expected a functional convergence of trait spaces across islands (Gibert & Deharveng 2002; Trontelj et al. 2012; Mammola et al. 2022). Yet, we expect some degree of polarisation of the trait space according to the ontogenetic stage—young (La Palma and El Hierro), mature (La Gomera, Tenerife, and Gran Canaria), and senescent (Fuerteventura and Lanzarote) islands. We represented the subterranean trait space of each island using geometrical n -dimensional hypervolumes (Blonder et al., 2014). Since some of the traits were categorical, we applied a Gower dissimilarity measure to the complete trait matrix and extracted orthogonal morphological axes through principal coordinate analysis (Carvalho & Cardoso 2020). We delineated the hypervolumes using a gaussian kernel density estimate (Blonder et al., 2014, 2018), the first four principal coordinate axes (cumulatively 89% variance explained), and a default bandwidth for each axis as implemented in the function `kernel.build` of the R package BAT version 2.7.0 (Cardoso et al. 2015, 2021). We opted for a gaussian kernel density estimation instead of more frequently used techniques such as functional convex hull (Mouillot et al. 2021) because we were interested in a probabilistic characterisation of the trait space, allowing us to identify gaps and areas of higher trait density (Blonder 2016; Mammola et al. 2021b). Furthermore, hypervolumes are less sensitive to outliers than other techniques for functional estimation (Mammola et al. 2021b), an important property given the wide taxonomic coverage of our dataset. We expressed the properties of the hypervolume within each island using functional richness (`kernel.alpha` function) and regularity (`kernel.evenness`) (Mammola & Cardoso 2020).

We investigated the functional differences among islands compared to their taxonomic differences using the BAT functions `kernel.beta` and `beta`, respectively. We expected the values of beta functional diversity among islands to be low (around ca. 0.5), compared to the values of beta taxonomic diversity, which we expected to tend to 1.

Hypothesis 2: Differences in trait spaces are explained by different species contribution

Our second goal was to characterise the contribution of each species to the island’s trait space. If there is convergence of all islands’ trait space with variations according to the ontogenetic state, we expected that species contribution will be minimal in mature islands (Tenerife, La Gomera, and Gran Canaria), and larger both in young (La Palma and El Hierro) and senescent (Fuerteventura and Lanzarote) islands.

We expressed the contribution of each individual species to the functional hypervolume of each island using the functional species contribution metric, calculated using the BAT function `kernel.contribution` and the “neighbor” approach. Contribution is a measure of the functional rarity (Violle et al. 2017; Carmona et al. 2017), which allows mapping the impact of each species to the richness component of the functional diversity (i.e. the volume of the island’s trait space). The distribution of the contribution values was then represented as a density plot for each island.

Hypothesis 3: Species interactions are stronger in mature islands

Our third goal was to investigate the relative importance of species interactions in islands of different ages. Our overall hypothesis was that species interactions, and not the mere accumulation of species, reshape the community structure in mature islands leading to an optimised use of the available niche space—explaining

why the contribution of individual species might be reduced in mature islands. In this scenario, we would expect that functional distance across pairs of species will exert a stronger effect on both ecological and geographical niches in mature islands. We do not expect to find such a strong effect in young islands whose diversity dynamics are dominated by speciation and where species interactions play a weaker role shaping their diversity; nor in senescent islands, where species interactions might play a marginal role, depending on how extinction affects different communities.

To analyse the extent of functional differentiation between coexisting species, we modelled the functional distance of each pair of species co-occurring in the same island as a function of their geographical and ecological range overlap. We calculated the geographical range overlap as the distance between the centroids of the distribution area of each pair of species. For environmental niche overlap, we extracted seven bioclimatic variables from WorldClim 2 database (Flick et al. 2017) using the values at the coordinates of the cave entrance or MSS traps (see Supplementary methods). All extracted variables were highly correlated with altitude (all Pearson r correlation $> \pm 0.7$), and therefore we used the overlap of the altitudinal range of each species as a proxy for niche overlap. We modelled the correlation between the ecological and geographical distances and the functional distance between pairs of species within each of the islands using partial Mantel tests using the function `mantel.partial` in the R package `vegan` version 2.5 (Oksanen et al. 2020),

Hypothesis 4: Species interactions lead to the presence of non-random combinations of traits, hence defining the properties of the island trait spaces

We compared the observed metrics for each island’s trait space with the values obtained from a random sample of the species from the Canary Islands’ subterranean species pool. We hypothesised finding larger differences between observed and random values on mature islands, where community and evolutionary processes have optimised the use of the trait space via the establishment of stronger species interactions (Wilson 1969; Borregaard 2016; 2017). Therefore, we expected that functional richness and evenness would resemble the value expected by chance in young islands, as these offer more ecological opportunities for speciation and new species will evolve occupying all the vacant niche space. However, as the island reaches its maximum topological complexity and the species richness gets to its equilibrium, we expected functional richness to decrease and functional evenness to increase, reflecting how the establishment of more interactions among species at the community level will promote a reorganisation the use of the island’s trait space in a non-random manner. In senescent islands where extinction dominates the island dynamics, we expected the strength of species interactions to relax, leading to values of functional richness and evenness again similar to those expected by chance alone.

We applied null modelling to test whether the hypervolume metrics for each island were different than expected from a random sample of species from the Canarian subterranean species pool. We expressed the observed value as the actual functional richness and evenness of the hypervolume for each island. Then, we repeatedly (999 times) randomly subsampled n species from the species pool, where n equalled the total species richness in each island, and extracted the same two functional metrics. For each permutation, we estimated standard effect sizes and associated p -values using the BAT function `ses` to assess the significance of the deviation from the null expectations.

Results

In agreement with hypothesis 1, we observed an overall convergence of the trait space occupied by subterranean communities in each island (Figure 1), although the centroids of each island’s hypervolume were grouped according to the island’s age. Interestingly, the largest trait space was exhibited by Fuerteventura, despite being the island with the lowest number of species (Table 1). When we compared the diversity across islands, we found that beta diversity approached 1 between pairs of islands (Figure 1), indicating full taxonomic replacement across islands. Once again, this was in contrast with the patterns of functional diversity, whose values ranged between 0 and 0.8, indicating greater functional similarity among islands.

In agreement with hypothesis 2, the distribution of individual contributions of species to the overall trait space of each island largely varied across islands (Figure 2). In general, the largest functional contribution

for each individual species was found in the senescent island Fuerteventura (average contribution per species = 67.196 ± 5.892), whereas the smallest was recorded in the mature island Tenerife (average contribution per species = 2.348 ± 0.205), compared to the remaining islands (Figure 2, Table 1). The distribution of the densities for the functional contribution values were unimodal in all the islands, except for Tenerife where they were markedly bimodal.

Regarding Hypothesis 3, partial mantel tests only yielded significant correlations for the island of Tenerife ($R = 0.207$, $p < 0.005$) between functional and geographical distances, with ecological distances included as a confounding factor (Table S1). However, the absolute values of the mantel r yielded the highest values for the mature islands, decreasing towards the young and the senescent islands (Figure 2).

Null modelling (Hypothesis 4) yielded larger values for functional richness than those observed in El Hierro (Observed, $obs = 0.0376$, estimated, $est = 0.0506 \pm 0.0006$), La Gomera ($obs = 0.0238$; $est = 0.0463 \pm 0.0007$), and Tenerife ($obs = 0.0320$, $est = 0.0482 \pm 0.0003$); smaller in La Palma ($obs = 0.0520$, $est = 0.0496 \pm 0.0004$), Gran Canaria ($obs = 0.0565$, $est = 0.0497 \pm 0.0003$), and Fuerteventura ($obs = 0.0531$, $est = 0.0425 \pm 0.0010$). Functional evenness exhibited the opposite pattern: predicted values exceeded observed values in La Palma ($obs = 0.2498$, $est = 0.2766 \pm 0.0011$), Gran Canaria ($obs = 0.2421$, $est = 0.2728 \pm 0.0010$), and El Hierro ($obs = 0.2755$, $est = 0.2955 \pm 0.0014$), whereas in Fuerteventura ($obs = 0.3913$, $est = 0.3526 \pm 0.0024$), La Gomera ($obs = 0.3536$, $est = 0.3118 \pm 0.0017$) and Tenerife ($obs = 0.2817$, $est = 0.2627 \pm 0.0008$) the observed values were larger than those expected by chance (Figure 3). Nevertheless, the differences between predicted and observed values were only significant for the functional richness in Tenerife ($SES = -2.0134$, $p = 0.022$; Table S2).

Discussion

Our results show, on the one hand, how age-dependent changes in carrying capacity affect the overall properties of the island's trait space and, on the other hand, how those changes are a consequence of species interactions. Those interactions increase in strength as the island niche space becomes filled through time, favouring the presence of a non-random combination of functions. This agrees with the idea that species interactions at the community level drive species diversity in island systems (Wilson 1969). Our work also aligns with recent studies on island biogeography, proposing to move beyond a strictly species richness-centred approach through the use of functional traits to infer the processes shaping island assemblages (Ottaviani et al. 2020; Schrader et al. 2021). We here show how, by assigning functional identities to each species in the island's assemblage, it is possible to derive the assumptions of island biogeographic theory—which, in essence, describes the macroecological state of an island in a given time—from the description of island's communities interactions. Through the test of time (Patiño et al. 2017; Whittaker et al. 2017), island biogeography theory proved to be a milestone idea in ecology and evolution, allowing us to understand the impact of ecological dynamics and historical contingencies on the biodiversity of a broad range of systems beyond islands (e.g., Dawson 2016; Ottaviani et al. 2020, Dunn et al. 2022). Given the essentially transferable nature of trait-based approaches (Weiss & Ray 2019), addressing island biogeography models through a mechanistic description of trait states is a key step to generalise these predictions even further.

Connecting macroscopic description of the island system with community processes using functional traits.

An emerging oceanic island represents an empty niche space susceptible to being colonised by individuals from different species, which will start competing for resources occupying empty niches and evolving there until, eventually, there will be no more niche space available for newcomers. In this process of colonisation and adaptation, species also establish networks of interactions that allow them to compress themselves through the niche space, optimising the flow of energy through the ecosystems. One might then predict that young islands, as they grow, will provide increasing levels of ecological opportunity facilitating the evolution of many species interacting loosely due to broad availability of resources. This is what we observe on the youngest islands of El Hierro and La Palma, where most of the available terrains are occupied by a network of lava tubes, fissures, and MSS-like habitats, with recent volcanic eruptions continually promoting the generation of new subterranean habitats. In those islands, we did not find a weaker correlation of ecological

and geographical distances over the functional distances between pairs of species.

However, once the island matures towards its maximum level of geological complexity, ecological opportunities reduce as no newer habitat is generated. At that point, species have occupied all the available niche space. This leads to a higher ecological redundancy determined by the available resources, also because the more heterogeneous geological structure of the islands favours processes of parapatric speciation (Arnedo et al. 2007). At this stage, species interactions gain importance in modulating niche spaces and determining species distributions. This is what we expected to observe in the mature islands of La Gomera, Tenerife, and Gran Canaria. However, we only obtained a significant correlation between functional and geographical distances in Tenerife. This was probably influenced by confounding factors derived from the specific geological features in each island. For example, La Gomera is a relatively small island that concentrates most of its suitable subterranean habitats at an altitude of 830–1170 m, yet fragmented by the network of ravines and mountains of the Garajonay National Park, hindering dispersal events across them. Tenerife, instead, is much larger and the lava fields once flowing from El Teide have generated potential habitats along the entirely altitudinal gradient of the island.

Eventually, in a senescent stage of the islands, surviving species might still evolve trying to optimise their occupation of the niche space, while competition becomes less important as fewer species remain. Indeed, in Fuerteventura we found only a weak effect of functional and geographical/ecological distances between pairs of species. Interestingly, the island of Lanzarote does not harbour any subterranean terrestrial species, with the young, exposed and arid volcanic terrains of the Timanfaya National Park being colonised by surface species only (Oromí et al. 2004).

Islands within islands: a frontier for eco-evolutionary studies?

The use of simplified subterranean ecosystems as a model allowed us to disentangle the role of interactions from that of confounding effects, such as the shift of traits related to ecological successions or trait-dependent extinction risk that has been described in other types of island habitats (Karadimou et al. 2018; Gray 2019). Conversely, given that the subterranean environment through time and across islands filters for simplified communities bearing a relatively narrow set of traits, we avoided problems associated with selecting meaningful traits across a large sample of organisms. However, the main advantage of our model system is that there is no migration across subterranean habitats between different islands, warranting that most changes that we observe in the trait space of each island depends on *in-situ* processes. In essence, subterranean habitats in each island are independent and only linked by the common geological history of the archipelago.

In a sense, including further archipelagos in our analyses would have increased the number of confounding factors, since different archipelagos across the world have largely different species pools with different evolutionary trajectories. Archipelagos consisting of non-oceanic islands, for example, are expected to follow different geological evolution generating different age-dependent diversity patterns (Whittaker et al. 2017). Furthermore, most oceanic archipelagos in the world are much younger than the Canary Islands and cover a shorter time span hindering comparability of results (Borregaard et al. 2017). There are few exceptions, such as Cabo Verde and Madeira (Florenco et al. 2021). However, very fragmentary data exists on the subterranean animals of Cabo Verde, whereas only non-specialized species have been found in the Selvagens and Porto Santo, the oldest island in Madeira (Oromí, 2004).

Applications of island biogeography theory beyond islands

Islands provide a powerful tool to address ecological questions because they represent discrete environments offering multiple replicates of comparable eco-evolutionary processes. Furthermore, there is a well-established theory that postulates a connection between the macroecological patterns observed in a set of islands and the identity and interactions between the species that integrate their species' assemblages (Wilson 1969). In its initial formulations, however, island biogeographical models were essentially neutral, insofar as they only relied on species identity and endemism, treating all species as functionally equivalent. This is analogous to say that the position of each species on the niche space is random and does not affect the properties of the overall island biodiversity. We now know this is a strong assumption, which can be relaxed by incorporating

a functional description of the species occurring in each island (Hubbell 2011; Rosindell et al. 2011). This way, the position of each species is defined in the n-dimensional overall trait space of each island, allowing us to make further assumptions on how the presence of different, non-random combinations of traits affect the macroecological status of the islands: a crucial step to connect community scale patterns with island-level observations.

Indeed, the results of null-modelling confirms that the combination of traits in each island is not random and can be linked to the predictions of the island biogeography model. In other words, our analysis suggests a causal relationship among the island age, the changes in the niche availability and the overall island's biodiversity. Our results indicate how in young islands functional richness and evenness approach the values expected by change for the same species richness, illustrating a multidirectional expansion of the trait space as a consequence of the species radiation and ecological opportunity. However, as an island matures, the traits space becomes smaller and more ordered when compared to the null-model, reflecting how the existence of a more connected network of species interactions optimizes the use of the available niche space. Subsequently, as an island is eroded and its niche space reduced, species will start to be extirpated. An initial stage of this phase can be seen in Gran Canaria, where the null-modelling reveals that the trait space functional richness is larger than expected by chance, whereas evenness approaches the randomly predicted values. Indeed Gran Canaria, despite being younger than Fuerteventura, has already undergone a long erosive period, characterized by a lack of volcanism and massive landslides dramatically affecting its geomorphology. The trait space of Fuerteventura resembles the values obtained by null-modelling, illustrating the collapse of the island's ecological network during its final ontogenetic stage, just before it will disappear under the ocean.

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Tables

Table 1. Descriptors and diversity metrics of each island. Surface is expressed in square kilometres. Altitude is expressed in metres above sea level. Age is written in million years. Species refer to the number of known cave exclusive species; Richness, Evenness, and Contribution (including the range of variation) refer to metrics of functional diversity. Contribution corresponds to the actual values multiplied by 10,000 to facilitate reading.

	Surface	Altitude	Age	Species	Richness	Evenness	Contribution
El Hierro	269	1501	1.1	22	0.0376	0.2755	12.125 ± 1.011
La Palma	708	2426	1.8	43	0.0520	0.2498	7.907 ± 0.599
La Gomera	370	1487	12	13	0.0238	0.3536	14.431 ± 1.931
Tenerife	2034	3718	11.6	79	0.0320	0.2817	2.348 ± 0.205
Gran Canaria	1560	1949	14.5	53	0.0565	0.2421	6.433 ± 0.601
Lanzarote	846	671	15.5	0	NaN	NaN	NaN
Fuerteventura	1660	812	20.6	7	0.0531	0.3913	67.196 ± 5.892

Table S1 . Summary of the partial mantel test statistics calculated for each of the islands. Functional distance was the response variable in all the tests, whereas the explanatory variable is included under the column “variable”. The being other variable as a confounding factor.

Island	Variable	Confounding	Mantel statistic r	p-value
El Hierro	geographic	ecological	0.0469	0.253
	ecological	geographic	-0.0202	0.575

La Palma	geographic	ecological	-0.0949	0.896
	ecological	geographic	-0.0219	0.615
La Gomera	geographic	ecological	-0.1694	0.813
	ecological	geographic	0.2394	0.110
Tenerife	geographic	ecological	0.2047	0.002**
	ecological	geographic	-0.1323	0.990
Gran Canaria	geographic	ecological	0.0582	0.157
	ecological	geographic	-0.0971	0.975
Fuerteventura	geographic	ecological	-0.0232	0.478
	ecological	geographic	0.0676	0.381

Table S2. Summary of null-modelling parameters calculated for functional richness and evenness of each island in order to test our hypothesis 4. Abbreviations: se, standard deviation; ses, standardized effect size.

Island	Metric	mean \pm se	ses	p-value
El Hierro	Richness	0.0506 \pm 0.0006	-0.6898	0.2451
	Evenness	0.2955 \pm 0.0014	-0.4472	0.3273
La Palma	Richness	0.0496 \pm 0.0004	0.2038	0.5807
	Evenness	0.2766 \pm 0.0011	-0.7487	0.227
La Gomera	Richness	0.0463 \pm 0.0007	-0.9355	0.1697
	Evenness	0.3118 \pm 0.0017	0.7711	0.7797
Tenerife	Richness	0.0482 \pm 0.0003	-2.0134	0.0220*
	Evenness	0.2627 \pm 0.0008	0.7182	0.7637
Gran Canaria	Richness	0.0497 \pm 0.0003	0.6294	0.7355
	Evenness	0.2728 \pm 0.0010	-0.9807	0.1633
Fuerteventura	Richness	0.0425 \pm 0.0010	0.3286	0.6287
	Evenness	0.3526 \pm 0.0024	0.5122	0.6957

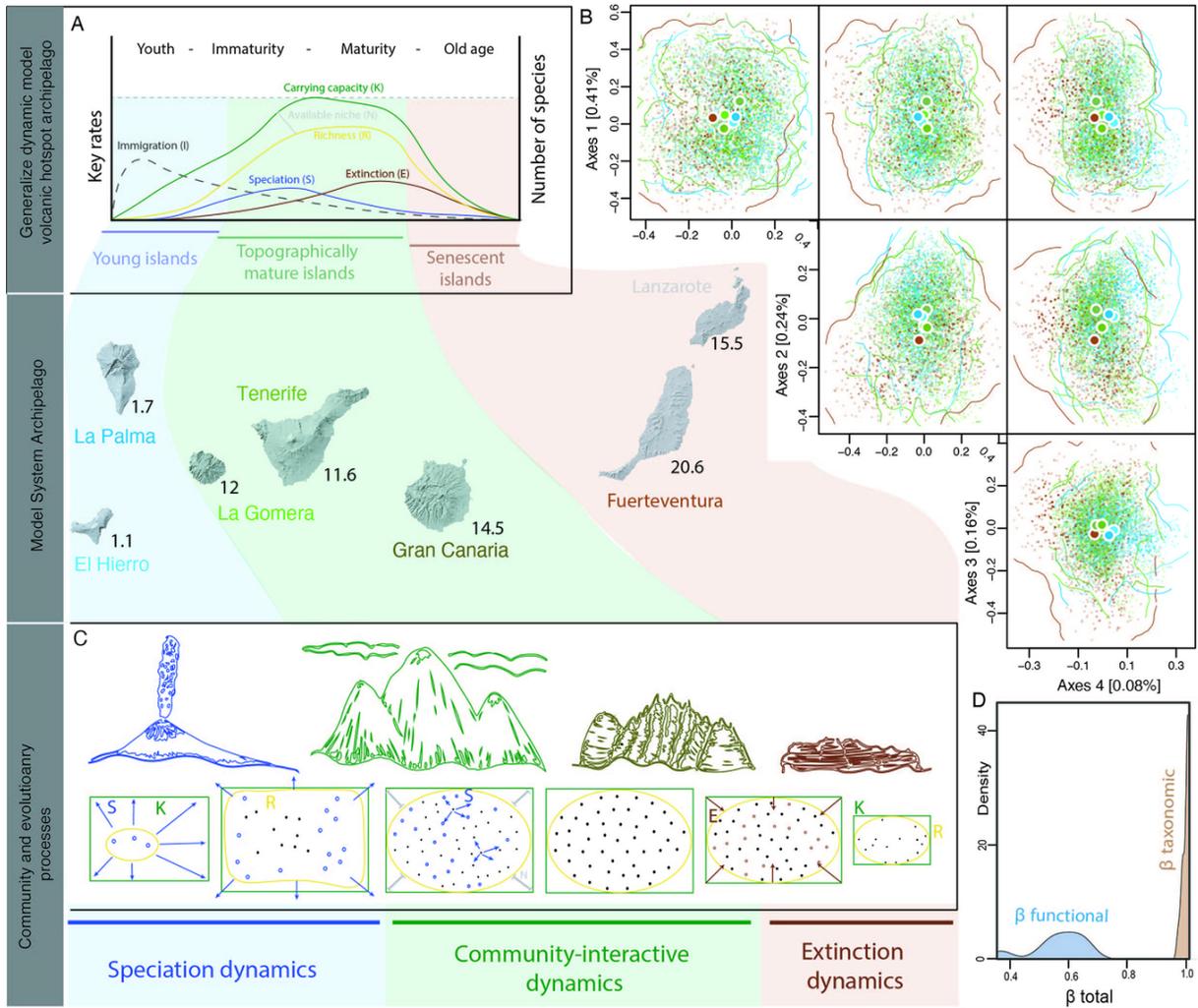


Figure 1: Island-based functional description of the Canary Islands terrestrial subterranean adapted fauna. (A) The number of species in each of the Canary Islands follows a generalised dynamic model for island biodiversity (Figure S1) (B) The functional hypervolumes ($n=6$) of each island converge, whose shape and boundaries are defined by 1000 random points; yet showing a certain segregation of the arrangement of the centroids (large points with white borders) according to island ages (represented by different colours) (Hypothesis 1). (C) Hypothesised contributions of speciation, community interactions, and extinction at islands at different stages. During early stages dominated by rapid speciation (S, blue arrows) and ecological opportunity, we expect a rapid increase of functional richness (R, yellow area) of new species evolving new combination of traits that allow them to explore the available niche space (K, green square). At some point during island maturity, island communities reach the carrying capacity. At that point, diversity is driven by community dynamics that optimize the use of the available niche space. Finally, at a late stages' dynamics are dominated by extinction (E, brown arrows), driven by a decrease of the available niche space. (D) Density plots show the distribution of beta taxonomical and functional values across islands. Whereas functional beta diversity varies from 0 to 0.8, taxonomical beta diversity is nearly 1, indicating nearly completely different species pools in each island

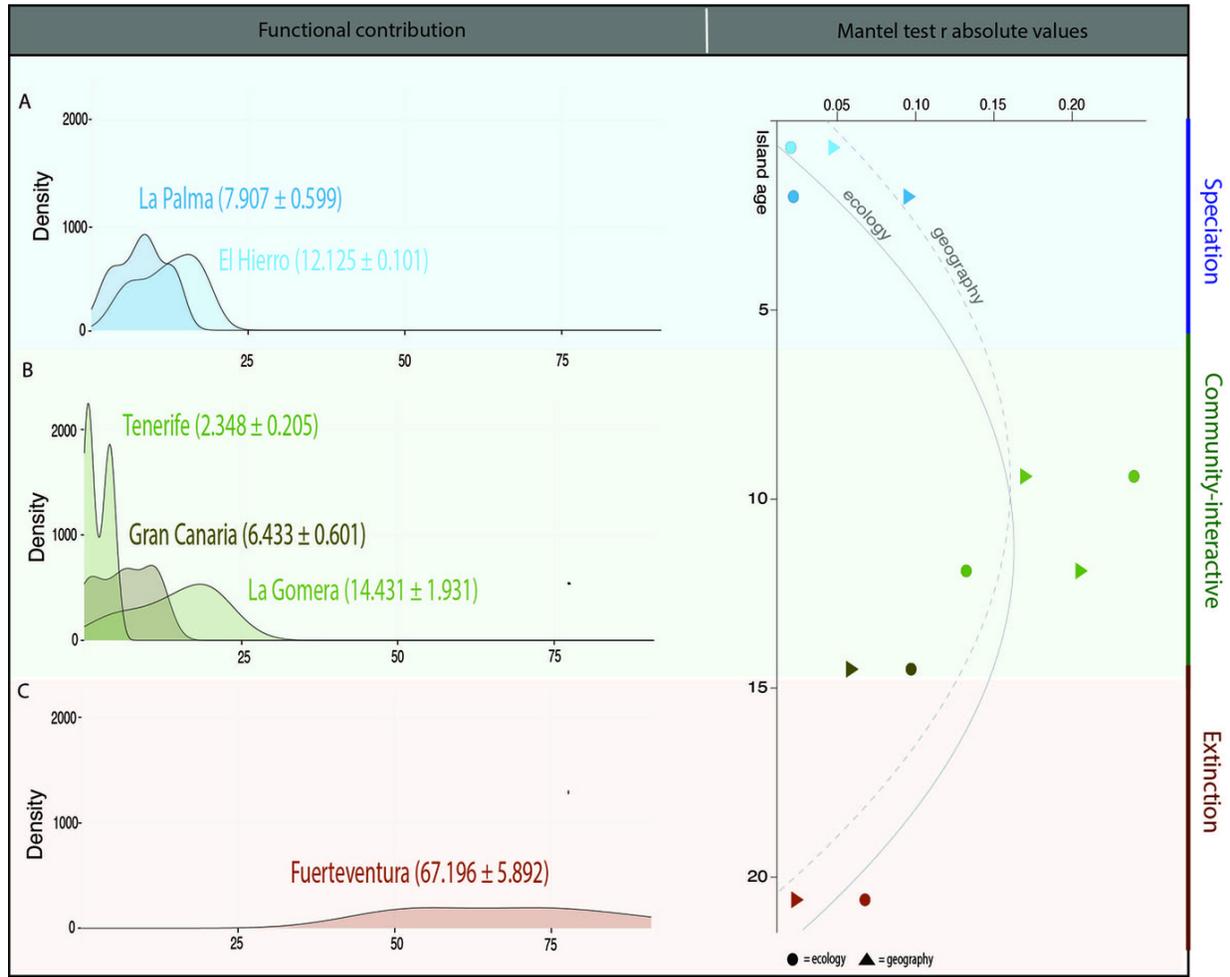


Figure 2: **Species-based functional description of the Canary Islands terrestrial subterranean fauna.** On the left, density plots of functional contribution of individual species to the functional hypervolume of each island grouped according to their ontogenetic state. The species functional contribution of each species is maximum in Fuerteventura and minimal in Tenerife. The rest of the islands exhibit a similar average contribution per species (Hypothesis 2). The average and standard deviation of the contribution values per island are in parenthesis. All values are multiplied by 1000 to facilitate comparisons. On the right, plot of the absolute mantel test r values for each island against the island's each. The curves have been obtained via quadratic approximation. Despite we only obtained significant values for the Mantel test in Tenerife, the mantel test r values indicate stronger species interactions in the mature islands.

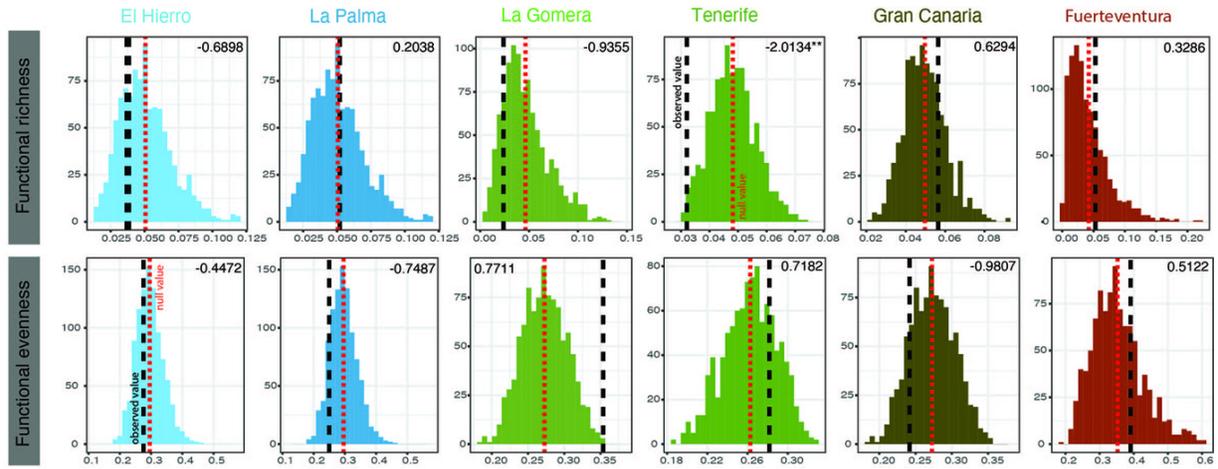


Figure 3: **Evaluation of the fit of the macroscopic ecological description of the island and the functional metrics based on null modelling-based.** Each histogram was calculated after 999 replicates with a sampling number equal to the island richness (Table 1, number of species). Black lines represent observed metrics. Red lines represent the mean value of the random sample for each island. The estimated standardised effect size is reported within each chart, being this test only significant for Tenerife. The results are complex and affected by the geological characteristics of each island. Nevertheless, observed values of evenness are larger than estimated values in the mature islands of La Gomera, Tenerife and Fuerteventura, where diversity is driven by community interactions, whereas they are smaller in those islands where extinction and speciation play a more important role. Estimated richness values are larger than observed values in mature islands

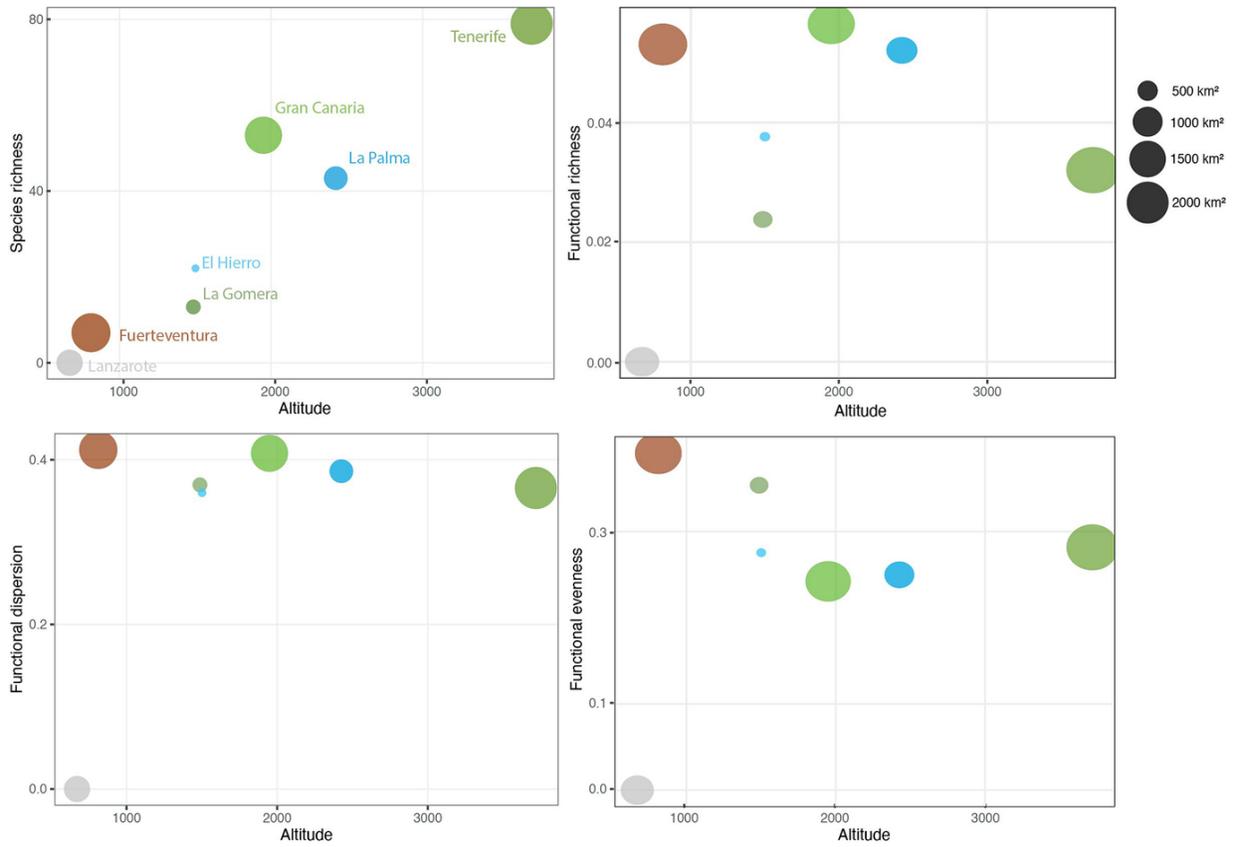


Figure 4: **Summary of the relationship amongst taxonomic and functional metrics of each islands plotted against altitude, surface, and age.** The size of the dots represents the surface of the islands. Blue represents young islands, green mature, and brown senescent islands. Lanzarote is represented in grey because no cave adapted species have been reported for the island