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Research article

The drivers of plant turnover change across spatial scales in the Azores

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Beta diversity patterns are essential for understanding how biological communities are structured. Geographical and environmental factors, as well as species dispersal ability, are important drivers of beta diversity, but their relative importance may vary across spatial scales. In this study, we evaluate whether beta diversity changes across geographical scales and analyse how different drivers affect turnover patterns of native seed plants in an oceanic archipelago, the Azores (Portugal). Using a 500 × 500 m resolution grid, we selected cells that are covered by one of the following habitats: native forest, naturalized vegetation and seminatural pastures. We calculated species turnover at three spatial scales: 1) between islands, 2) between cells within each island, and finally 3) between cells of each of the habitats of interest in each island. We then calculated the contribution of dispersal syndromes (endozoochory, epizoochory, hydrochory and anemochory) to turnover at each of the scales. Lastly, we assessed the relationship between geographical and climatic distances and habitat type with turnover. Turnover was higher at the smallest spatial scale, particularly in seminatural pastures, and decreased with increasing spatial scales, a pattern potentially associated with the historical fragmentation and current patchy distribution of native forest and seminatural habitats in the Azores. Dispersal syndromes and habitat type had a negligible effect on turnover at all scales. Geographical distance had a positive effect on turnover at all scales, increasing its importance with scale. The relationship between turnover and climatic distance was only significant at the intermediate and small scales in specific islands and habitats. Therefore, scale plays an important role at determining the effect of the drivers of turnover, in particular geographical and climatic distance.

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These results highlight the need to carefully select the scale of analysis when studying turnover patterns, as well as identifying the potential drivers associated with each spatial scale.

Keywords: Azores, beta diversity, climatic distance, dispersal syndromes, geographic distance, island biogeography, spatial scale

Introduction

The study of beta diversity patterns is central to understanding how natural communities are structured, and how spatial and environmental factors affect them (Nekola and White 1999, Baselga 2010, Keil et al. 2012). Studying beta diversity also informs about how communities change in space and time, and at which scales these changes may occur (Keil et al. 2012, Hatosy et al. 2013), with patterns varying depending on the grain and spatial extent selected (Nekola and White 1999, Freestone and Inouye 2006, Soininen et al. 2007, Steinbauer et al. 2012, Otto et al. 2020). Grain refers to the minimum spatial resolution of data (e.g. cell size in a grid), while the spatial extent refers to the maximum size of the area studied (e.g. the whole grid). Variations in both are known to modulate beta diversity patterns even within the same group of organisms (Cacciatori et al. 2020). Specifically, strongest changes in the turnover component of beta diversity (i.e. compositional variations associated with species replacement; Baselga 2010) are achieved when decreasing the grain and increasing the extent (Nekola and White 1999, Soininen et al. 2007, Keil et al. 2012). Increasing the extent often involves including more distinct areas and/or habitats with possibly different species pools, which potentially can increase species turnover (McKinney 2005, Mouton et al. 2023). Conversely, larger grain sizes increase the chance of detecting rare species in each cell, and thus communities may appear as being more similar to each other (Keil et al. 2012).

Beta diversity can be driven by multiple factors. Environmental dissimilarity is one of them, as species persistence may change under different environmental conditions, which in turn affects species distribution and associated diversity patterns. Higher environmental dissimilarity can affect community composition conditioning competition and coexistence dynamics (Soininen et al. 2007). Habitat patchiness can also affect beta diversity, as the species pool of each habitat may be different, thus increasing beta diversity (Nekola and White 1999). Geographical distance, which is tightly related to dispersal limitations, can heavily affect community composition through its effect on species distribution ranges and spatial connectivity (Freestone and Inouye 2006, Keil et al. 2012). Complementarily, dispersal limitation may have important effects on beta diversity, since differences in dispersal ability among species can condition their distribution and thus affect community assembly (Carvalho and Cardoso 2014, Lowe and McPeck 2014, Borda-de-Água et al. 2017, Mouton et al. 2023). This is particularly important on islands, where some taxonomic groups are under-represented compared with their mainland pools (König et al. 2021), a pattern potentially driven by traits associated with long

distance dispersal (Gillespie et al. 2012, Heleno and Vargas 2015, Leo et al. 2021).

Dispersal is indeed a central factor explaining beta diversity patterns across spatial scales (Qian 2009, Wu et al. 2017), as communities with organisms with higher dispersal abilities should present lower beta diversity values due to their higher ability to reach environmentally suitable places (Nekola and White 1999, Jiménez-Valverde et al. 2010, Soininen et al. 2018). However, measuring dispersal ability and quantifying its role in any biological pattern is challenging at any scale of analyses (Burns 2019). For example, often there is only indirect evidence of dispersal events at long distances (Gillespie et al. 2012). In plant studies, the most widely used approach to study dispersal events has been assigning species into different dispersal syndromes, particularly to address the role of long-distance dispersal (LDD) on the assembly of island floras (Carlquist 1966, Howe and Smallwood 1982, Schaefer 2002, Gillespie et al. 2012, Heleno and Vargas 2015, Arjona et al. 2018, Fajardo et al. 2019, Walentowitz et al. 2022). Dispersal syndromes refer to a combination of seeds and/or fruits traits (in most cases morphological) that allows relating plant species to specific dispersal vectors such as animals, water or air (Gillespie et al. 2012). Species that are dispersed by animals are called endo- or epizoochorous (depending on if they are dispersed internally or externally), hydrochorous if dispersed by water, and anemochorous if dispersed by wind. Unassisted or self-dispersed diaspores are called autochorous. By applying this approach, several studies have found a larger representation of zoochorous (Gillespie et al. 2012, Arjona et al. 2018, Walentowitz et al. 2022) and hydrochorous species (Heleno and Vargas 2015, Arjona et al. 2018) on islands. However, the role LDD syndromes play in structuring communities is still under debate at both large (König et al. 2021) and small spatial scales (e.g. within islands, Leo et al. 2021).

Although understanding diversity patterns is a key priority on island research (Patiño et al. 2017), the number of studies focusing on beta diversity patterns in island settings is still limited. Available results support a stronger influence of environmental dissimilarity on beta diversity compared to geographical distances (König et al. 2016, Matthews et al. 2020, Mouton et al. 2023), although other spatial variables such as island age, area, elevation and number of islands in the archipelago might also affect beta diversity patterns (Cabral et al. 2014, Arjona et al. 2018, König et al. 2021, Walentowitz et al. 2022, Mouton et al. 2023). In particular, a recent study in Macaronesia identified precipitation as one of the main drivers of turnover for several groups of land plants (Mouton et al. 2023), which goes in line with other studies conducted in the mainland (Freestone and Inouye 2006, Baselga 2010) that indicate an increase in turnover

with increasing environmental dissimilarity. Here, we evaluate beta diversity patterns of the Azorean flora, focusing particularly on native seed plants. Most beta diversity studies developed on this archipelago have dealt with animal groups, particularly arthropods (Cardoso et al. 2010, Carvalho and Cardoso 2014, Matthews et al. 2019). However, some studies have addressed beta diversity patterns for plant species in the Azores both between and within islands (Aranda et al. 2013, Henriques et al. 2017, Borges et al. 2018a, Mouton et al. 2023), showing that different patterns emerge when comparing groups with different dispersal abilities. Specifically, seed plants tend to show higher values of turnover than bryophytes and pteridophytes (Aranda et al. 2013, Mouton et al. 2023). These results coincide with those obtained in other archipelagos (Mouton et al. 2023) and continental areas (Nekola and White 1999, Freestone and Inouye 2006, Soininen et al. 2007), supporting the important role of dispersal at shaping beta diversity patterns.

In this study, we assess whether species turnover of native seed plants of the Azores varies across three different spatial scales (between islands, within islands and within habitats within islands), and further evaluate whether these changes are associated with plant dispersal syndromes – used as a proxy of dispersal ability – climatic and geographical distances and habitat types. We focus on the turnover component of beta diversity, using beta diversity and turnover as equivalent terms, and assuming that higher beta diversity implies higher turnover, that is, higher dissimilarity between communities (Keil et al. 2012). The Azorean Islands are a homogeneous archipelago, composed by young, small, environmentally stable and similar islands, that host a widespread endemic flora (Carine and Schaefer 2010, Triantis et al. 2012). We foresee that these similarities between the Azorean Islands might cause a wide distribution of not only endemic but also non-endemic native flora across the archipelago, which leads to a homogenization of island communities and lower beta diversity patterns at large spatial scales (i.e. between islands). This hypothesis is also supported by the lower number of Azorean endemic seed plants compared with the other Macaronesian archipelagos, but with a widespread distribution across the archipelago, a characteristic of the flora that has been subject of a long scientific debate (Carine and Schaefer 2010, Triantis et al. 2012).

Although most islands host similar habitats, human disturbance in the Azores led to a dominance of anthropized landscapes, which created a complex combination of natural and semi-natural habitats patches within the islands (Borges et al. 2019). This heterogeneous landscape can affect species distribution, leading to higher values of beta diversity within islands. Regarding the role of dispersal syndromes, and based on the evidence described above, we hypothesize that species bearing dispersal syndromes typically associated with greater dispersal ability in island contexts (zoochorous and hydrochorous; Gillespie et al. 2012, Arjona et al. 2018, Leo et al. 2021) will be more ubiquitous and present lower beta diversity than the species with allegedly more limited dispersal potential (anemochorous). We also predict that the

importance of dispersal syndromes will be higher at large scales: as dispersal events are rarer at large scales, any trait that increases the chance of a successful dispersion will have an effect on diversity patterns (Nathan 2005, Gillespie et al. 2012). Finally, we predict that geographical distances will show stronger correlation with beta diversity at larger scales, while we do not expect a strong dependency between climate and beta diversity at any scales due to the climatic homogeneity of the archipelago (Borges et al. 2020).

Material and methods

Species and habitat distribution

This study focuses on the native seed plant flora of the Azorean archipelago. The Azores are an oceanic archipelago located close to the mid-Atlantic ridge in the North Atlantic Ocean, composed of volcanic islands of recent origin. It is one of the most remote archipelagos in the world, being separated by 1376 km from the closest shore in the Iberian Peninsula (Florencio et al. 2021). Its islands are located along a NW – SE axis, with the oldest island, Santa Maria, being located in the southeast, whereas the youngest, Pico, is located in the central region of the Azores (Fig. 1). The climate is temperate and wet with mild summers according to the Köppen Climate classification (Borges et al. 2020).

Species occurrences were extracted from the 'ATLANTIS initiative in the Azores' Global Biodiversity Information Facility (GBIF) dataset (GBIF.org 2019). This dataset comprises a total of 1 338 102 georeferenced records (Borges et al. 2018b), including native and non-native species. Species nomenclature was homogenized according to the Azores Biportal, the reference for biodiversity data in the Azores (Silva et al. 2023). We kept only the records for seed plant species that were classified as either native or endemic according to the Azores Biportal, filtering those with the most precise geographical information (500 × 500 m cell resolution), and that were registered later than 2000, since many older records were not properly georeferenced (missing or inexact coordinates). Introduced species, which represent ca 80% of the total seed plant flora, were discarded from the dataset, as well as duplicated records per grid cell. This curation process led to a large decrease in the available information, and the final dataset comprised 159 411 suitable records of native seed plants.

As introduced species dominate the Azorean flora, the native habitats occupy only a small fraction of the archipelago (Borges et al. 2020). In this study we focused on the three least disturbed habitats, where most species are native (following Picanço et al. 2017, based on a previous work of Cardoso et al. 2013), namely: 1) native forests, characterized by a dense tree and shrub cover of small stature and currently restricted to high elevations in the islands (detailed description of the current types of native forest can be found in Elias et al. 2016); 2) naturalized vegetation patches mostly composed of native plants and located outside the native

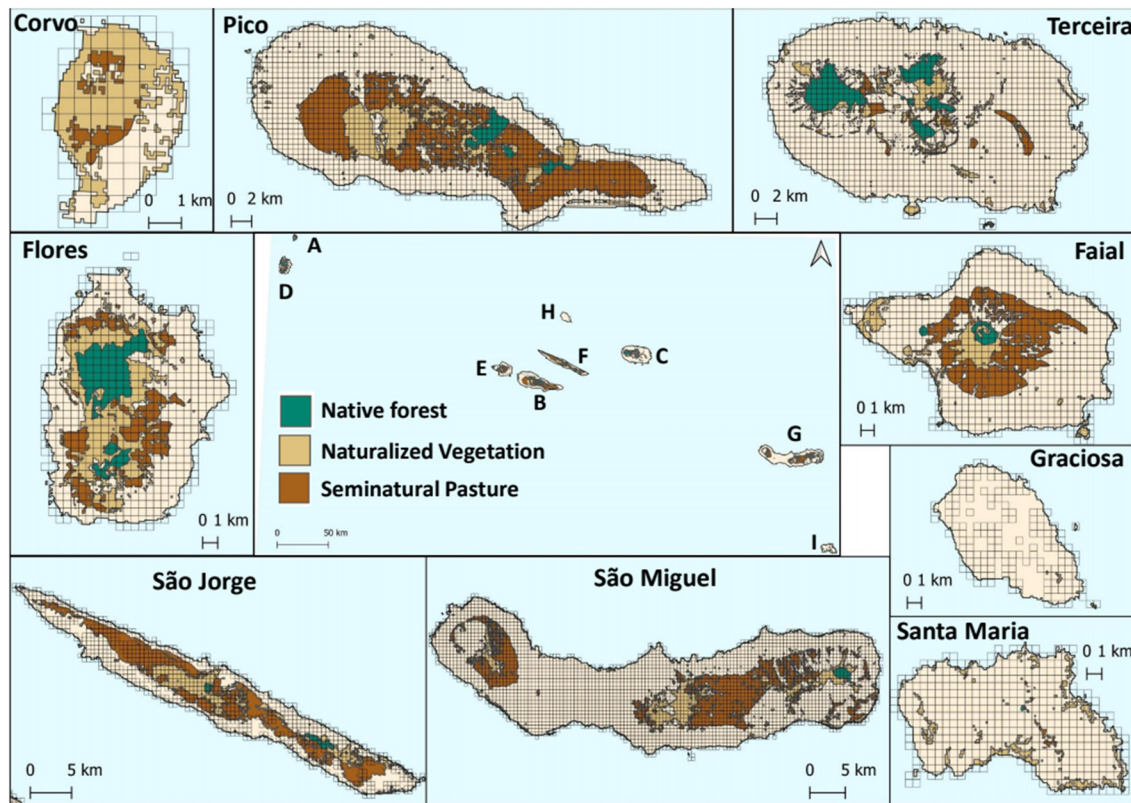


Figure 1. Azorean islands and habitat distribution within them. The location of each island in the archipelago is depicted in the central panel, with letters corresponding to each of the six islands. Corvo and Flores (A and D) are located in the westernmost part of the archipelago, Pico (B), Terceira (C), Faial (E), São Jorge (F) and Graciosa (H) constitute the central cluster of the archipelago; and São Miguel (G) and Santa Maria (I) are located in the east of the archipelago. Grid has a 500 m cell width resolution. Selected habitats correspond to: native forests in green, naturalized vegetation in light brown and seminatural pastures in brown.

forest; and 3) seminatural pastures, which are mid- and high-elevation pastures that maintain some native plants and are subject to short-term cattle grazing activity and low inputs of fertilizers (Fig. 1). For the island of Terceira, the spatial extent of the categories ‘native forests’ and ‘naturalized vegetation patches’ was delimited as in Picanço et al. (2017). Due to the high similarity of habitats that exists between islands (Triantis et al. 2010), we extended their approach to the other islands. ‘Seminatural pastures’ were defined as the areas of pastures located above 400 m. Altitudinal data were extracted from a digital elevation model with a 25 m spatial resolution of the islands (EU-DEM 2021). Then, we calculated the area and percentage of each habitat type for each 500 × 500 m cell of the occurrences grid; in the case of seminatural pastures this was done by intersecting the altitudinal and pasture shapefiles. These analyses were performed using the QGIS Development Team software (2020). To evaluate if there were any differences in species richness between habitats, we built species accumulation curves for each habitat type considering only cells covered with at least 50, 75 or 99% of the focal habitat (Supporting information). Since the curves at 50 and 75% stabilized at larger richness than at 99%, we used this latter threshold to assign a cell to a specific habitat. We set the threshold at 99% cover to consider a 1%

of disagreement due to variation of areas associated with the projection. Thus, cells with less than 99% of a specific unique habitat were discarded from the analyses. Due to the absence of cells matching this criterion in Santa Maria and Graciosa, and also the low number of cells identified in Corvo for at least one habitat, we excluded these three islands from this study (Fig. 1). The number of cells retrieved from each island and for each habitat within islands is given in the Supporting information.

Beta diversity at different scales

Three distinct spatial scales were considered in this study: large (archipelago scale), intermediate (island) and small (habitats within an island) scales. At the large scale, beta diversity was calculated among all selected islands, merging all selected cells within an island and using the island as grain size (Supporting information). In the case of the intermediate and small scales, grain size corresponded to cells of 500 × 500 m. At the intermediate scale, beta diversity was calculated within each island, among all grid cells of the three selected habitats, irrespective of each cell’s habitat type (Supporting information). At the smallest scale, beta diversity was calculated among all cells of each habitat within an

island (e.g. cells covered with native forest in Terceira Island) (Supporting information). At this scale, each habitat patch was only considered in the analyses when there were more than 20 contiguous cells occupied by the same habitat at > 99% cover (Supporting information). Therefore, we could only consider native forest patches from Flores and Terceira islands, naturalized vegetation patches from Pico, São Jorge and São Miguel, and seminatural pastures patches from Faial, Pico, São Jorge and São Miguel.

Turnover was estimated in each of these scales using the multiple site Simpson's index (β_{SIM} , Baselga et al. 2018). We used multiple site β_{SIM} instead of average pairwise β_{SIM} between units because we were interested in quantifying the heterogeneity in species composition among several spatial units at a given scale (e.g. islands for large scale or cells for intermediate and small scales). This way, beta diversity is interpreted as an attribute of the whole scale and not an attribute of a given pair of units. Multiple site β_{SIM} was calculated using the *beta.multi* function from the R package 'betapart' (Baselga et al. 2018). Multiple site β_{SIM} was then computed at the archipelago scale, within islands and within habitats in islands. We complemented our analyses by calculating pairwise β_{SIM} implemented in the *beta.pair* function to estimate the turnover between pairs of islands, between pairs of habitats within islands, and thus address the similarity in native plant composition between Azorean islands. Finally, to correlate climatic and geographical distance to beta diversity, we also computed pairwise β_{SIM} between cells within islands.

Because islands and habitats had a different number of cells, we re-calculated all measures of multiple β_{SIM} by standardizing the number of cells to 20 to deal with a similar sampling effort. We then repeated this procedure 1000 times with replacement to obtain the mean and 95% confidence interval of each β_{SIM} . The significance of the differences in the multiple site β_{SIM} was estimated as the degree of overlap between the 95% confidence interval obtained from the bootstrapping procedure. This procedure was not implemented for multiple β_{SIM} at the large scale (between islands) since we only considered six islands. All results presented correspond to the standardized values.

Drivers of turnover

Each species, of a total of 112 species, was assigned to a dispersal syndrome following the classification of Schaefer et al. (2011) (Supporting information). This classification is based on field observations made throughout the years by botanists experts on the Azorean flora, rather than being based just on morphological traits, which can be considered as a more accurate description of the dispersal process (Green et al. 2022). It refers to the main mean of dispersal for each species in the Azores and includes seven dispersal categories: anemochorous, hydrochorous, endozoochorous, epizoochorous, anthropochorous, myrmecochorous and autochorous (28, 41, 19, 50, 1, 1 and 3 of our species respectively; the three last categories were discarded due to the low number of species).

Seventeen climatic variables were obtained from the CIELO model (Azevedo 1996, de Azevedo et al. 1999), corresponding to the WorldClim variables (www.worldclim.org/bioclim) but with a higher resolution for the Azorean islands (100 × 100 m cell resolution). We checked for autocorrelation among them, and selected the four least correlated variables that best represented the different features of climate (Leo et al. 2021): annual mean temperature, mean diurnal range (mean of the monthly difference between maximum and minimum temperatures), annual precipitation and precipitation seasonality (coefficient of variation). At the large spatial scale, climatic dissimilarity between islands was calculated by averaging Euclidean distance between islands, while at the intermediate and small scale climatic distances were simply the Euclidean distance between the cells. We constructed a global Euclidean distance between all pairs of cells using the four selected climatic variables, which were first standardized with a mean of 0 and a standard deviation of 1.

For the large spatial scale, we used GoogleEarth to measure geographical distances in km from coast to coast between all pairs of islands. For the intermediate and small scales, geographical distances between cells were calculated as the distance between the coordinates of the centroids of the cells.

Statistical analyses

Contribution of dispersal syndromes to beta diversity

The effect of dispersal syndromes on beta diversity was estimated at all scales. For a given dispersal syndrome, we calculated the multiple site β_{SIM} values excluding those species that displayed that specific dispersal syndrome, and calculated the delta (Δ) as the difference between the multiple site β_{SIM} of the whole community and the multiple site β_{SIM} of the same community without the species bearing that dispersal syndrome (delta ranges from -1 to 1). Therefore, a negative Δ indicates that a specific dispersal syndrome contributes to homogenize the community, whereas a positive Δ shows an increase of the heterogeneity in the community. To test if the Δ value was higher or lower than expected by chance, we generated 1000 random values of Δ between the multiple site β_{SIM} of the whole community and 1000 values of random multiple site β_{SIM} created by removing randomly the same number of species bearing that specific dispersal syndrome. This null distribution of Δ was used to test whether the observed the Δ was lower or higher than expected using a two-tailed test.

Contribution of geographic and environmental distances, and habitats to beta diversity

We used values of turnover between islands and between cells within islands to test the effect of geographical and environmental distance on beta diversity across scales. The analyses were performed using multiple regression on distance matrices (MRM) with Pearson's correlation and 10 000 permutations (Lichstein et al. 2007). The MRM were calculated with the function *MRM* in 'ecodist' package (Goslee and Urban 2007). At the intermediate and small scales, we

also added a third distance matrix to account for the effect of habitats along with the effect of climatic and geographic distances. This distance matrix was computed as follow: two cells belonging to the same habitat were coded as 0, and two cells belonging to different habitat where coded as 1 (following [Carvalho and Cardoso 2014](#)). To determine the relative contributions of geographical and climatic distances, as well as habitat type, we further used hierarchical variance partitioning to partition the global R^2 into its geographical, and climatic and habitat components using the function *hier.part* of the R package 'hier.part' ([Mac Nally and Walsh 2004](#)). All statistical analyses were implemented within R (www.r-project.org).

Results

Beta diversity across scales

Overall, turnover (Multisite β_{SIM}) was lower at the archipelago scale (large scale, 0.23) than within islands and within habitats within islands (intermediate and small scale respectively, [Fig. 2](#)).

Regarding the within islands scale, multisite β_{SIM} values ranged from 0.67 in Flores to 0.94 in São Miguel (mean = 0.82) ([Fig. 2](#)). Moreover, 95% confidence intervals from the standardization with 20 cells indicated that São

Miguel had the highest turnover, being significantly different from the rest of the islands except Terceira ([Fig. 3A](#)). Flores was the island with the lowest turnover, but it was also not significantly different from any other island except São Miguel and Terceira. Turnover calculated between pairs of islands (Pairwise β_{SIM}) was very low and ranged from 0.06 between Faial and São Jorge or Terceira, to 0.17 between São Miguel and São Jorge (mean = 0.11) ([Fig. 2](#)), supporting the results obtained with Multisite β_{SIM} at large scale.

Turnover (Multisite β_{SIM}) within habitats showed very contrasting patterns. In native forests, the turnover value in Terceira was twice the value as in Flores (0.81, and 0.39 respectively; [Fig. 2–3B](#)), and the 95% confidence intervals from the standardization at 20 cells indicated that this difference was significant ([Fig. 3B](#)). For naturalized vegetation, strong variations between islands were also found with turnover values ranging from 0.86 for São Miguel to 0.20 for São Jorge. Thus, the 95% confidence intervals from the standardization at 20 cells indicated that β_{SIM} of São Miguel was significantly higher than β_{SIM} of Pico and São Jorge ([Fig. 3B](#)). In contrast, turnover values for seminatural pastures were consistently high across all islands being 0.90 for São Jorge and Pico and slightly lower for São Miguel or Faial (0.8 and 0.7 respectively; [Fig. 2–3B](#)). Interestingly, as in the case of between pairs of islands, turnover between pairs of habitats (Pairwise β_{SIM}) was found to be very low within islands, as all β_{SIM} values were lower than 0.25 ([Fig. 2](#)).

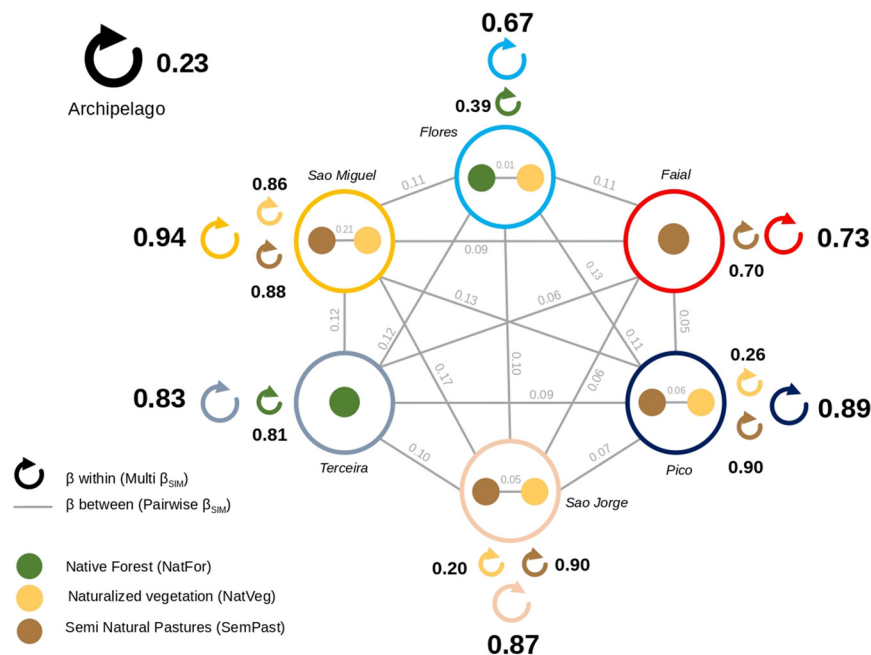


Figure 2. Turnover values across three different spatial scales. Values presented for the archipelago, island and habitat scales correspond to Multisite β_{SIM} (represented by the curved arrows), and those of the between islands and the habitats within islands scales correspond to Pairwise β_{SIM} (represented by the grey lines). Large colored circles depict the six islands considered in this study, each color corresponding to an island: light blue corresponds to Flores, red to Faial, dark blue to Pico, pink to São Jorge, grey to Terceira and yellow to São Miguel. Full circles within islands depict the three habitats considered, each color relating to an habitat: dark green for native forest, light green for naturalized vegetation and brown for seminatural pastures. Values of Multisite β_{SIM} are marked with a curved arrow in black for the whole archipelago (large scale), for each island in the respective color (intermediate scale), and for each habitat (small scale) also in the respective habitat colour.

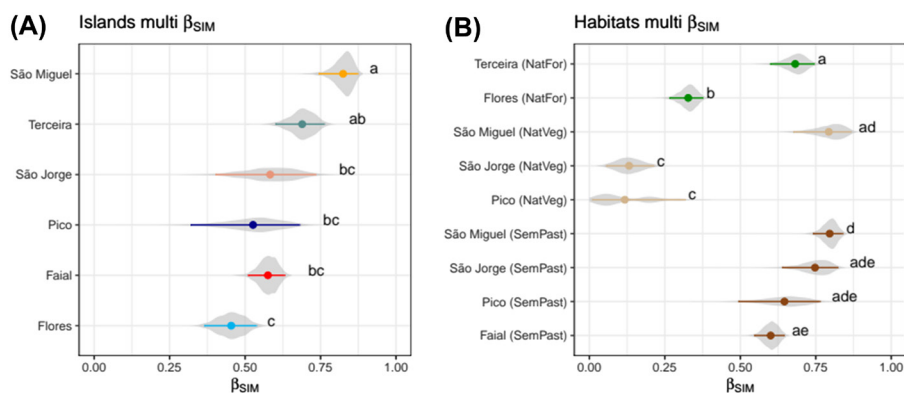


Figure 3. Multisite β_{SIM} turnover values at different scales: (A) intermediate scale (within islands, independently of habitat type) for the six islands considered (light blue corresponds to Flores, red to Faial, dark blue to Pico, pink to São Jorge, grey to Terceira and yellow to São Miguel), and (B) small scale (within each of the habitats present in an island) for the three habitats considered (dark green to native forest – NatFor, light green to naturalized vegetation – NatVeg, and brown for seminatural pastures – SemPast). Grey violins represent the distribution of the 1000 β_{SIM} generated by the random selection (with replacement) of 20 cells within each island or within each habitat within islands. The dots correspond to the mean of the 1000 β_{SIM} values while the line depicts the 95% confidence interval. Islands and habitats presenting a different letter are significantly different from each other ($p < 0.05$).

Contribution of dispersal syndromes to beta diversity

The sign (positive or negative effect) of the contribution of dispersal syndromes to turnover was consistent for most scales, but its value changed depending on the scale (Fig. 4). None of the habitats studied showed a consistent pattern regarding the effect of dispersal syndromes. In most cases, the effect of dispersal syndromes on turnover was not significant, and its absolute contribution ranged between 0.1 to less than 0.3. Endozoochorous species consistently decreased turnover at the three scales analyzed when they had a significant effect. On the other hand, epizoochorous species increased turnover at all scales, but the effect was significant in very few cases. Anemochorous species only had a significant effect at the small scale in Flores naturalized vegetation and at the intermediate scale in Faial, while hydrochorous had almost no significant contribution to turnover at any scale but in Flores at the intermediate scale.

Relationship between geographical distance, climatic distance, habitat type and beta diversity

At the largest scale, geographic and climatic distances did not show any significant relationship with turnover (Fig. 5A). In the case of the intermediate scale, all islands showed a positive relationship between geographical distance and turnover ($R^2 = 0.27, 0.22, 0.03, 0.11, 0.04$ and 0.09 for Faial, Flores, Pico, São Jorge, São Miguel and Terceira, respectively; Fig. 5B). At the smallest scale, the relationship between geographical distance and turnover was also positive and significant in most islands except in naturalized vegetation of São Jorge (Fig. 5C), although all significant R^2 values were small and ranged between 0.06 and 0.19. Overall, the effect of climatic dissimilarity on turnover was weaker than that of the geographical distance. A positive and significant effect of

climate was detected at intermediate scale for Pico, Faial, and São Jorge ($R^2 = 0.01, 0.03$ and 0.10 , respectively; Fig. 5B). At the smallest scale, climatic dissimilarity only had a significant positive effect for the naturalized vegetation of São Jorge ($R^2 = 0.45$), and in the seminatural pastures in São Jorge and São Miguel ($R^2 = 0.11$ and 0.12 ; Fig. 5C). Finally, there was no significant effect of habitat type on turnover at the intermediate scale (Fig. 5B).

Discussion

Beta diversity across scales

In this study we found that species turnover patterns and associated drivers vary according to the scale considered, being in line with a growing body of research that stresses the importance of carefully selecting the scale when studying beta diversity (Nekola and White 1999, Keil et al. 2012, Steinbauer et al. 2012, Cabral et al. 2014, Cacciatori et al. 2020). Islands are intuitive to use as grain size when studying diversity patterns within an archipelago since they are easy to delimit, with distinct boundaries separating the land from the sea. However, there are several barriers within islands that could also affect species distribution, and hence beta diversity, such as mountains, volcanic craters, water bodies, human structures such as cities or roads, or even the presence of different habitats, each of which may have its own environmental conditions. Therefore, islands might sometimes represent a grain size that is too coarse to capture certain variations in community composition (Nekola and White 1999, Keil et al. 2012, Cacciatori et al. 2020).

We found the lowest values of turnover at the island scale, which corresponds to the largest scale considered. These results suggest that community composition is more similar

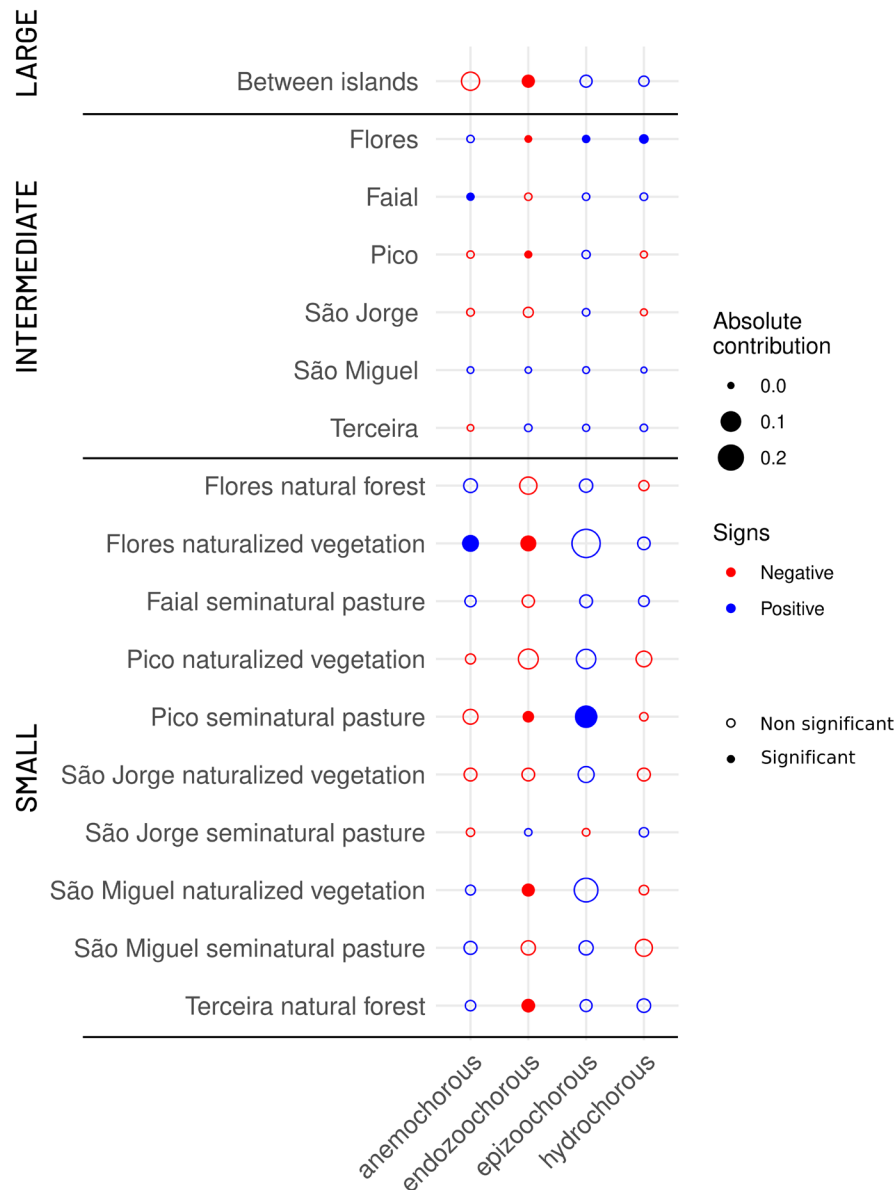


Figure 4. Effect of dispersal syndromes on Multisite β_{SIM} at the three scales analyzed (archipelago, islands and habitats within islands). Colors indicate the sign of the effect (whether a dispersal syndrome increases, in blue, or decreases, in red, Multisite β_{SIM}), and size reflects the value of the absolute contribution of the dispersal syndrome (i.e. anemochorous, endozoochorous, epizoochorous and hydrozoorous) to the Multisite β_{SIM} at a given scale. Non-significant values ($p > 0.05$) are shown without fill color. The largest scale corresponds to archipelago ('between islands'), island name corresponds to the intermediate scale (within islands) and the remaining categories belong to the smallest scale (within habitats in an island, namely, native forest, naturalized vegetation and seminatural pastures).

when comparing islands than habitats or areas within them, as already suggested by König et al. (2016). They also coincide with other studies conducted in the mainland (Soininen et al. 2007, Keil et al. 2012), which showed a decline in turnover with increasing grain size and reinforce the idea that ecological patterns may change for the same group of organisms depending on the scale considered (Cacciatori et al. 2020). However, these results contradict the findings of Mouton et al. (2023), who described an increase in turnover from intra to inter-archipelago comparisons in Macaronesian

archipelagos, probably related to the fact that many plants are endemic to each of the archipelagos.

At the intermediate scale (i.e. within islands), turnover values between the cells of each island vary greatly depending on the island considered. For example, Flores corresponds to the island with the lower values of turnover, being also one of the most habitat-homogeneous islands (Schaefer 2002, Borges et al. 2020), harbouring the highest proportion of native forest of all of the Azores (Florencio et al. 2013). These native forests, together with the naturalized vegetation, form

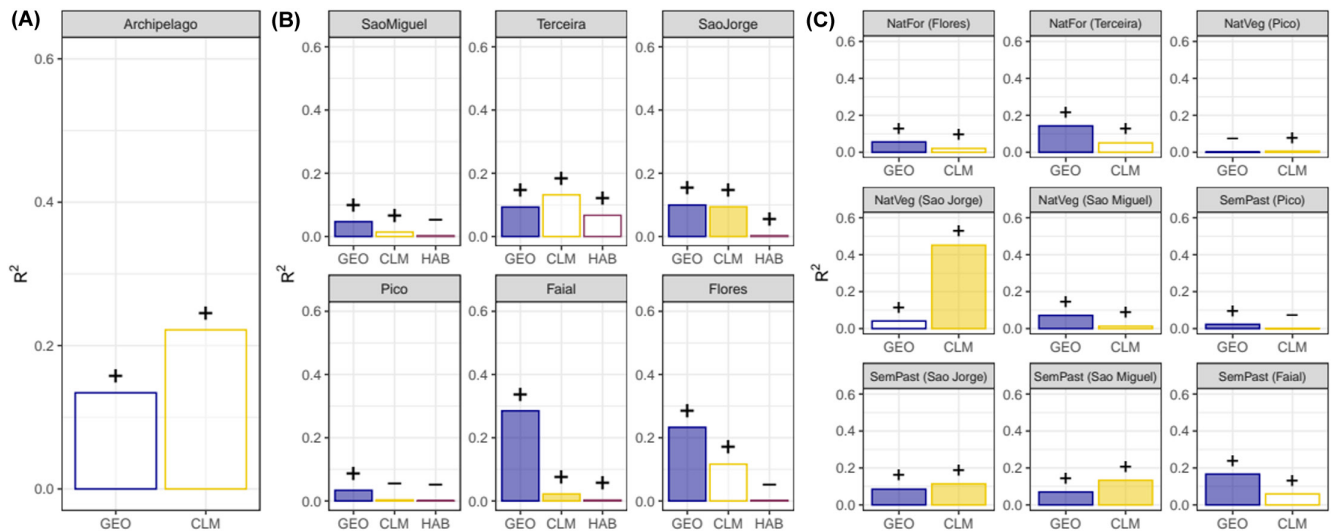


Figure 5. Effect of geographical distance (GEO), climatic distance (CLM) and habitat (HAB; only for the island scale) on pairwise β_{SIM} at large (A), intermediate (B) and small (C) spatial scales. R^2 for geographical, climatic distances and habitat (this latter only for the island scale) were obtained from a hierarchical partitioning of the global R^2 , while the significance and sign of the relationships were obtained from multiple regressions on distance matrices (MRM). Sign of the relationship is indicated above the bars, + for positive relationships and – for negative ones. Filled bars indicate significant effect ($p < 0.05$), while empty ones indicate non-significant effect ($p > 0.05$). At the small scale (C), habitats correspond to native forests (NatFor), naturalized vegetation (NatVeg) and seminatural pastures (SemPast).

a continuum of vegetation (Fig. 1) in which different habitat types present a similar species composition, but with differences in the relative abundance of the main species present (Elias et al. 2016). This can facilitate species expansion across the island, and consequently plants may have wider distributions (which leads to lower turnover). On the other hand, São Miguel presents the highest values of beta diversity. This is the largest island of the archipelago, in which the distribution of the habitats under evaluation is polarized towards the two volcanic craters located in the eastern and westernmost parts of the island (Fig. 1). Thus, naturalized vegetation and semi-natural pastures are found on both ends of the island, separated by a large, highly disturbed area associated with human land uses, located in the more central region of the island, showing a fragmented pattern widely extended in the Azores (Triantis et al. 2010). This spatial configuration can potentially be limiting species dispersal within this island, which in turn can result in a very differentiated community composition and thus the observed higher turnover.

Regarding the smallest scale, i.e. considering cells of the same habitats in each of the islands, there is a consistent trend in which seminatural pastures, mostly dominated by herbs, display the largest values of turnover in all the islands where this habitat occurs. Seminatural pastures are abandoned fields often recolonized by endemic species from the remaining patches of native forest (Cardoso et al. 2013), in a process that may have resulted in more complex assemblages than the native communities they came from. Previous findings reported by König et al. (2016), showed that distance decay rate of herbs was lower than for trees or shrubs, unlike this study where these are comparable to native forests (trees) and naturalized vegetation (shrubs).

This can be related to the grain selected for the analysis; while König et al. (2016) focused on patterns at a global scale using grains that ranged between 1 and 500 000 km², our analysis has a smaller extent and grain size that may be capturing heterogeneity-related processes that are not very determinant at larger scales (Barton et al. 2013). Also, the size of the organisms has to be taken into consideration. In the case of seminatural pastures, a cell of 500 m width resolution can harbor more diversity of grasses and herbs than of shrubland or trees, just because of the smaller size of the organisms, and such differences may dilute as the scale of analysis increases. Thus, although we are using the same unit for all habitats (cells of 500 × 500 m size), this resolution might not be functionally equivalent for the three of them, and assembly processes might differ.

Beta diversity and dispersal syndromes

Although dispersal is considered an important driver of turnover patterns among islands and archipelagos (Carvalho and Cardoso 2014, Mouton et al. 2023), in this study dispersal syndromes fail to support this claim. At large scales, dispersal syndromes show a small and almost negligible contribution to beta diversity patterns, and although their importance increases at small scales, their effect is still minor. Hydrochory does not influence turnover at any of the scales considered, and anemochory has only a small effect in Flores naturalized vegetation, which is an unexpected result. On the one hand, wind and water can transport seeds and fruits across long distances, but they do so following air and water currents that usually have a fixed, continuous direction – with the exception of rare, extreme events such as hurricanes or

other non-standard dispersal vectors (Nathan et al. 2008). Trade winds in the Azores may disperse plants along a NE direction for the easternmost islands (Santa Maria and São Miguel), and N, NW and SW directions for the remaining islands, while winds from the E are rare in this archipelago (Schaefer 2002). Consequently, not all anemochorous species may reach all the islands.

Both water and wind are dispersal agents for most plant species in the Azores at small scales (Schaefer 2002). This means that within an island, traits associated with each of these dispersal syndromes may not be important since all species might be dispersed by both wind and water, regardless of their dispersal syndrome. This result could also be explained by the heterogeneity of traits that are encompassed within these two categories, which include traits that enhance dispersal at long, small, or all distances, as suggested in other studies (Fajardo et al. 2019, Leo et al. 2021), and that could be acting in opposite ways. For example, anemochorous species encompass those with tiny, minute seeds highly efficient in LDD (Fajardo et al. 2019), and seeds with pappi that may fly for small distances under dry conditions, but that rapidly collapse in the Azores due to the high humidity atmospheric values registered in these islands (Schaefer 2002), thus not being very efficient at long distance anemochory dispersal. Thus, species grouped under the same category of dispersal syndromes may display very different patterns of dispersal.

Epizoochory and endozoochory show a significant but small effect on turnover, with an opposite trend: epizoochorous species consistently increase species turnover, while endozoochorous tend to homogenize communities. Epizoochory, which consists on the dispersal of seeds and fruits attached externally to the animal, displays high, unpredictable chances of both seeds and fruits falling during the dispersal process (Will and Tackenberg 2008). These random falls are likely to contribute to species turnover, but also may limit their ability to have strong effects. In the case of endozoochorous species, previous studies in the Azores already suggested they have broader distributions (Heleno and Vargas 2015), which would contribute to reduce turnover between communities. Moreover, birds, which are the main zoochorous dispersers in the Azores, tend to move between similar habitats. These directional movements disperse endozoochorous species between patches of the same habitat, either within or between islands, which homogenizes the communities found in the archipelago.

We expected that dispersal syndromes would play a larger role at the largest scale, since limitations to dispersal appear to be more critical at this scale. Indeed, even poor dispersers can disperse within a few meters radius just by chance (Nathan et al. 2008), but crossing the open sea towards the next island can be a major challenge that requires more than chance events (Gillespie et al. 2012, Heleno and Vargas 2015). This expectation was also in accordance with the study by Mouton et al. (2023), which found differences in plant turnover patterns in the Macaronesian archipelagos between two groups with contrasting dispersal ability (bryophytes

and spermatophytes), although not evaluating the influence of dispersal syndromes per se. One possible explanation for the marginal role played by dispersal syndromes on turnover could be that they are not good proxies of plant dispersal ability (König et al. 2021, Leo et al. 2021). This is reinforced by the relationship between geographical distance and turnover we reported at all scales, except at the larger one, since the presence of a strong spatial signal in beta diversity pattern is considered an indication of dispersal limitation (Barton et al. 2013, König et al. 2016).

Beta diversity, geographical and climatic distances, and habitats

Beta diversity is often interpreted as the result of the shared effects of spatial configuration and environmental dissimilarities (Soininen et al. 2007). We found a positive relationship between geographical and climatic distances and turnover at the intermediate and small scales, with a stronger effect occurring at the intermediate scale (i.e. within island, independently of the habitat type). Multiple studies have shown that increasing distance reduces community similarity (Nekola and White 1999, Freestone and Inouye 2006), which is often explained by the fact that increasing geographical distance tends to increase environmental dissimilarity. However, this is not the case in our study, which points towards other factors such as limitations to dispersal as potential drivers of turnover (Freestone and Inouye 2006, Soininen et al. 2007, König et al. 2016). Other distance metrics, such as the distance to the oldest island or stepping-stone distance might be also important when interpreting beta diversity patterns, as suggested for species richness (Weigelt and Kreft 2013, Carvalho et al. 2015).

Similarly, climatic distance is not related with turnover at the largest scale. Turnover has been reported to be more associated with environmental variables than with geographical distance on islands and island-like systems (Freestone and Inouye 2006, König et al. 2016, Mouton et al. 2023). Indeed, previous studies on islands have suggested that higher environmental heterogeneity was associated with higher turnover, highlighting the role of elevation, area, temperature and precipitation, among other factors, on species distribution patterns (Cabral et al. 2014, König et al. 2016, Mouton et al. 2023). In particular, in the study of Mouton et al. (2023), turnover in the Azorean flora was lower than in other Macaronesian archipelagos, which may be related with the homogeneity of the Azorean climate, with high precipitation and mild temperatures throughout the year (Borges et al. 2020). At the intermediate scale, Faial, Pico and São Jorge were the only islands in which climatic distance showed a significant relationship with beta diversity. These three islands have a complex topography that may create heterogeneous climatic conditions at small and intermediate scales, that in turn can be affecting turnover. In addition, we have only addressed communities in the remaining patches of native plants across the archipelago, which may be also increasing community similarity between islands.

The absence of effect of habitat type on turnover may be related to the low number of units we have considered, but also that the categories used are broad enough to have more variation within habitat than between them. For example, seminaturalized vegetation includes a wide variety of shrublands (Schaefer 2002) that present very different species compositions; *Erica azorica* dominated shrublands harbour different species compared with *Calluna vulgaris* ones (Elias et al. 2016). Also, because the habitats are spatially structured (native forest mainly at high elevations, seminatural pastures at intermediate elevations) and climatically different, we cannot exclude that the effect of habitat type is somehow captured by geographical and climatic distances.

There are also other factors, such as soil heterogeneity or human influence, that we have not considered in this study that might be limiting species distributions, and thus affecting turnover patterns. At small scales, soil characteristics are often considered an important driver of beta diversity (Barton et al. 2013). In the Azores, there are three types of andosoles, but one of them occurs mostly in areas occupied by agriculture and thus was excluded from this study (Schaefer 2002). The other two soil types (typical andosoles and ferruginous soils) are both very fertile and not very different from each other within this archipelago, that combined with the fact that we have restricted our analysis to the few well-conserved areas in the archipelago (Borges et al. 2006, 2020, Picanço et al. 2017), indicates that the patterns found are most probably not affected by soil heterogeneity. Regarding human influence, the Azores is a highly disturbed archipelago whose original vegetation is actually restricted to small areas located above 500 m of altitude (Borges et al. 2020). Native vegetation forms patches with different degrees of connectivity between them, and thus landscape discontinuity could also be affecting our results. However, by selecting only the remaining least affected areas and just the native species of the Azorean flora, we believe the patterns found in this study are solid and are not particularly conditioned by human influence.

In summary, our results show that plant beta diversity patterns in the Azores change depending on the scale considered. The main drivers of turnover change also across scales, with geographical and climatic distance being only important at the intermediate and small scales and in certain islands. Dispersal syndromes play a minor role in structuring beta diversity patterns at all scales. This finding is in contradiction with the significant effect of geographical distance we reported at intermediate and small scales, suggesting that dispersal syndromes are not a good proxy of dispersal ability, at least in this study system and scales considered. Environmental and spatial factors are two main groups of factors driving beta diversity patterns in any ecosystem (Soininen et al. 2018), but understanding the preeminence of one group over the other is still a work in progress. More studies on beta diversity in oceanic archipelagos are necessary to help discriminate if the pattern we have found is specific of the Azores or is comparable in other islands, and thus improve our knowledge of how communities assembly across scales.

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Author contributions

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Data availability statement

Data are available from Zenodo: <https://doi.org/10.5281/zenodo.10624995> (Leo et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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