RESEARCH ARTICLE

Dispersal syndromes are poorly associated with climatic niche differences in the Azorean seed plants

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Abstract

Aim: Environmental niche tracking is linked to the species ability to disperse. While well investigated on large spatial scales, dispersal constraints also influence small-scale processes and may explain the difference between the potential and the realized niche of species at small scales. Here we test whether niche size and niche fill differ systematically according to dispersal syndrome within isolated oceanic islands. We expect that species with higher dispersal abilities (anemochorous or endozoochorous) will have a higher niche fill, despite their environmental niche size.

Location: Azores archipelago.

Taxon: Native seed plants.

Methods: We combined a georeferenced database of the species distribution within the archipelago (Azorean Biodiversity Portal/GBIF) with an expert-based dispersal syndrome categorization and a high-resolution climatic grid (CIELO model). Using four climatic variables (Annual Mean Temperature, Mean Diurnal Range, Annual Precipitation, Precipitation Seasonality), we calculated a four-dimensional hypervolume to estimate the niche size of each species. Niche fill was quantified as the suitable climatic space of the island that was occupied by the focal species.

Results: We found a significant relationship between dispersal syndromes and niche size, and also between dispersal syndromes and niche fill. Such relationships presented no phylogenetic signal. Endozoochorous species display higher niche fill compared to

epizoochorous and hydrochorous species, and larger niches than anemochorous and epizoochorous. Differences among the remaining groups are not significant for either niche size or for niche fill.

Main conclusions: The ability of a species to track its niche at small scales is not tightly related to its dispersal syndrome, although endozoochorous species track their niche more efficiently than the rest of groups. Despite being intuitively appealing, dispersal syndrome classifications might not be the most appropriate tools for understanding dispersal processes at small scales.

1 | INTRODUCTION

Linking niche dynamics and dispersal potential is central to understanding species distributions (Bridle & Vines, 2007; Pulliam, 2000) and these concepts have been integrated into a single framework—BAM (Peterson et al., 2011; Soberón & Peterson, 2005), which has proven useful to relate ecological niches (i.e. environmental space) and geographical distributions (i.e. geographical space) (Colwell & Rangel, 2009; Jiménez-Valverde et al., 2008; Peterson et al., 2011; Sales et al., 2021). BAM accounts for the joint effects of biotic (B) and abiotic (A) factors, and dispersal (M, for Movement) on the distributional range of a species. The set of all environmental states, both biotic and abiotic, where species populations maintain a positive growth rate is called the fundamental niche (Peterson et al., 2011), whereas the intersection of A, B and M corresponds to the geographical area where the species actually holds viable populations (Jiménez-Valverde et al., 2008; Peterson et al., 2011). Note that A resembles the potential niche as defined by Jackson & Overpeck (2000), being A the part of the fundamental (abiotic) niche that actually exists in the region and/or period of time of interest, whether it is occupied by the species or not. The realized niche was defined more precisely by Peterson et al. (2011; p. 278) as 'the set of all environmental states that would permit a species to exist in the presence of competitors or other negatively interacting species and restrictive factors', but niche concepts have been widely discussed in the literature and other definitions for realized niche have been proposed (see, e.g. Sales et al., 2021; Soberón, 2007; Soberón & Nakamura, 2009). Here we follow the definition proposed by Soberón and Nakamura (2009), in which the realized niche is considered as the part of the potential (abiotic) niche that the species actually uses—after considering the effects of competitors and predators—and that can be estimated from the species distribution (Colwell & Rangel, 2009; Sales et al., 2021) as the intersection between A and M. The ability of a species to track its potential (abiotic) niche, and thus fill it, can be related to its dispersal ability (Rumpf et al., 2019).

The relationship between dispersal ability and range size (and thus realized niche) is not straightforward (Lester et al., 2007), as the

observed species distributions may be the outcome of contrasting processes. At large scales, high dispersal ability may result in a high migration potential, allowing species to overcome dispersal barriers and to track their potential niche (e.g. Alsos et al., 2007; Angert, 2009; Svenning et al., 2008). In many cases, high dispersal potential can even result in larger realized niches (Lester et al., 2007), or range/niche filling (Dullinger et al., 2012; Munguía et al., 2008). However, such a pattern is not general, and there might be mismatches between dispersal ability and the size of the realized niche, as demonstrated by migration lags that occurred in the temperate flora following climate change since the last glacial maximum (e.g. Alexander et al., 2018).

At small scales, dispersal constraints may pose a competitive disadvantage, particularly for short-lived species or following disturbance events or changing environmental conditions. Limited niche tracking at small scales has been attributed to dispersal characteristics for different plant groups (Angert, 2009; Primack & Miao, 1992), resulting in a discrepancy between range size and niche fill (Angert, 2009). In general, studies at small scales indicate an inconsistent relationship between dispersal and range size in plants (Lester et al., 2007; Primack & Miao, 1992) and animals (Angert, 2009; Dapporto et al., 2019; Iversen et al., 2013; Lester et al., 2007). Differentiating and understanding the effect of dispersal on small and large spatial scales and how this translates into long-term survival constitute key aspects for understanding the processes that shape and maintain biodiversity.

Oceanic islands are one of the best settings available for evaluating the effect of dispersal constraints on the ability of species to track and fill their niche. Oceanic islands are self-contained units that have always been isolated from the mainland. As a result, the island's indigenous species must be the outcome of either colonization or speciation events (Carlquist, 1967; Price & Wagner, 2004). While within-island dispersal has rarely been studied, there is a large body of literature reporting mixed results on the relationship between colonization success and dispersal characteristics (e.g. Fajardo et al., 2019; Gillespie et al., 2012; Heleno & Vargas, 2015; Price & Wagner, 2004). Island colonization occurs after the propagules overcome large distances, a process that is enhanced

by the presence of specific traits that allow them to travel—above or through the water—for long distances (Gillespie et al., 2012). These traits have been used to categorize species into different dispersal syndromes (Carlquist, 1967; Ridley, 1930) that are linked with different dispersal agents. Usually, species are classified as anemochorous (dispersed by wind), hydrochorous (dispersed by water), endo- and epizoochorous (dispersed by animals- either internally or on the outside of their bodies) or autochorous (self-dispersed) (Carlquist, 1967; Ridley, 1930). These different dispersal syndromes have been compared in several studies conducted in mainland areas, showing heterogeneous results regarding its efficiency in long-distance dispersal (LDD). Some authors proposed that endozoochorous species are the best dispersing organisms, followed by anemochorous and epizoochorous and lastly, hydrochorous and autochorous plants (Engler et al., 2009; Vittoz & Engler, 2007). These studies are in line with early works on LDD potential on islands (Carlquist, 1967), but contradict others that indicate that wind-dispersed seeds are the best dispersers on mainland areas (Higgins et al., 2003), or that claim no differences among dispersal syndromes on islands at large biogeographical scales (Fajardo et al., 2019). While the processes of LDD for island colonization are thus well investigated with mixed results (e.g. Fajardo et al., 2019; Gillespie et al., 2012; Heleno & Vargas, 2015; Price & Wagner, 2004), our understanding of within-island dispersal is limited by a lack of studies (see Kelly et al., 2001; McConkey & Drake, 2015).

Independently of the LDD vector associated with arrival on a new territory, the second step of the colonization process involves establishing viable populations. To achieve this, individuals must track their fundamental niche. Translated to an island context, this is only possible if there are no major dispersal constraints within each island. In fact, the ability to track suitable habitats within dynamic oceanic islands may be more important for the successful establishment of island lineages than adaptations to the initial LDD event that would allow its colonization. The dispersal syndromes that allow species to colonize an isolated archipelago might thus lose importance when considering within-archipelago (see Arjona et al., 2020; García-Olivares et al., 2017) or within-island dispersal, as dispersal filters acting at this scale will most probably differ from those present at larger scales. For example comparing within-island dispersal to LDD, hydrochory might be a less important syndrome, as water bodies are not so well represented within an island compared to the open sea. The fact that some populations of the same species present genetic differences within an island (Gillespie et al., 2012; Price & Wagner, 2004) is indicative of reduced gene flow and thus the existence of dispersal constraints even on a small oceanic island.

Here, we evaluate whether dispersal syndromes are associated with distribution patterns at the within archipelago level, using as a study system the native vascular flora of the Azorean islands, one of the most isolated archipelagos. We investigate the link between niche dynamics and dispersal by contrasting the size of the realized niche, the niche fill and their relationship with different dispersal syndromes. Specifically, we model the climatic realized niche (hereafter *realized niche*) and estimate the potential climatic niche (hereafter *potential niche*), showing how a species responds to its physical and biotic environment (Barve et al., 2011; Jackson & Overpeck, 2000), and also its ability to track its niche (Alsos et al., 2007). Regardless of niche size, we expect a larger niche fill in endozoochorous and anemochorous species given these dispersal syndromes are usually considered more efficient. As for niche size, we expect that species with small niches are highly dependent on re-colonization processes, and so their long-term survival on islands is greatly determined by their dispersal ability; therefore, small niche size and larger niche fills will be more typical in endozoochorous or anemochorous species than in other groups (Figure 1).
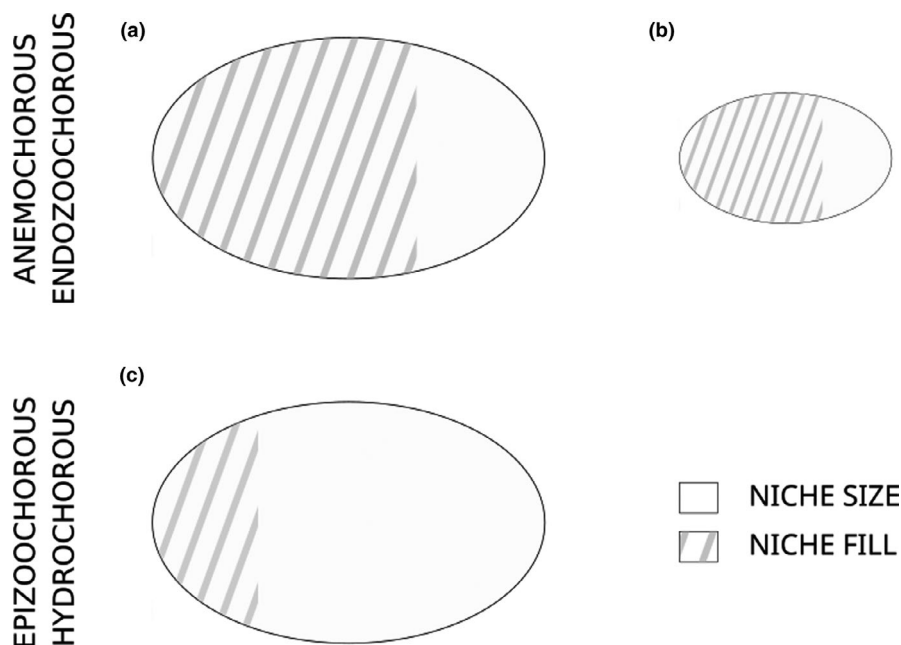

FIGURE 1 Conceptual figure of the potential relationships between niche size and niche fill of different dispersal syndromes. Anemochorous and endozoochorous species are expected to display large niche fills independently of niche size (a and b), whereas epizoochorous and hydrochorous species are expected to have large niches and small niche fills (c)

2 | MATERIALS AND METHODS

2.1 | Study area

This study focuses on the native vascular flora of the Azorean islands. The Azores is an archipelago of volcanic origin, located in the North Atlantic near the mid-Atlantic ridge. It includes nine islands distributed in three clusters, the highest being Pico with a maximum altitude of 2351 m a.s.l., and the lowest being Graciosa, reaching just 405 m a.s.l. The closest continental shore is Portugal, at about 1641 km, whereas North America sits at almost 3000 km westwards, making it one of the most isolated archipelagos in the world (Borges et al., 2020). In line with many other oceanic islands, native ecosystems have been dramatically reduced during the last 600 years of human occupation (Borges et al., 2020). According to the Köppen Climate classification, the prevalent climate in the Azores is temperate with no dry seasons and mild summers (Borges et al., 2020). The indigenous flora has been widely studied (Carine & Schaefer, 2010; Heleno & Vargas, 2015; Schaefer, 2002; Schaefer et al., 2011) and includes about 149 indigenous species, 59 of them being endemic (Schaefer et al., 2011).

2.2 | Data gathering

Data on species occurrences were downloaded as a dataset from GBIF in April 2019, at a 500 × 500 m grid resolution (Borges et al., 2018) and included 1.338.102 georeferenced localities. The data were largely assembled by the ATLANTIS initiative in the Azores and provide species occurrence information with very high spatial resolution and taxonomic completeness for many of the islands (Borges et al., 2010). Records in the dataset with a date prior to the year 2000 were discarded because many of them were not properly georeferenced. Species nomenclature was homogenized using TNRS, a free tool for correcting and standardizing plant names (Boyle et al., 2013), and then reviewed for potential errors. Introduced species, which represent *c*. 80% of the total seed plant flora, were discarded from the dataset. The remaining species occurrences were checked to assure a maximum of a data point per grid cell for each species, which resulted in a final number of 107.019 records after the removal of 1.230.993 records. Dispersal syndrome classification follows the one proposed by Schaefer et al., (2011), which is based on expert criteria by studying the species in the field. All species were categorized as anemochorous, hydrochorous, endozoochorous or epizoochorous. Autochorous species were discarded due to the low number of species in this category (three species).

Climatic data were obtained from the CIELO model (Azevedo, 1996; Azevedo et al., 1999). The model has been developed in order to produce high-resolution fields of the elemental climatic variables (pressure, temperature, rainfall, relative humidity, etc.), which can be combined statistically in order to produce spatially detailed distributions for climatic indicators or climatic-dependent outputs (evapotranspiration, bioclimatic indices, etc.). Seventeen CIELO variables were selected for analysis, using a grid resolution of 100 × 100 m cell size, which correspond to the WorldClim variables (www.worldclim.org/bioclim) but with a more accurate and reliable resolution for islands (Azevedo & Reis, 2016). After checking for autocorrelation among the 17 variables with a Pearson correlation test, we selected the four that best represented different features of the climate and that were not correlated among them (Figure S1, Supplementary Material): Annual Mean Temperature, Mean Diurnal Range (mean of the monthly difference between the maximum and minimum temperatures), Annual Precipitation and Precipitation Seasonality (coefficient of variation).

2.3 | Statistical analyses

The fundamental niche can be defined as an *n*-dimensional hypervolume where each point corresponds to a state of the environment which would allow a species to persist indefinitely (Hutchinson, 1957). Due to the intrinsic difficulties of measuring a species' fundamental niche (Guisan & Thuiller, 2005; Peterson et al., 2011), studies often focus on the potential niche, which corresponds to the portion of the fundamental niche that includes the realized combinations of the environmental variables at a given time (Jackson & Overpeck, 2000). The subset of conditions of this potential niche in which the species is actually found is known as the realized niche (Soberón & Nakamura, 2009). In many studies, the niche is defined considering only its abiotic dimension (*Grinellian niche* according to Soberón, 2019), particularly climatic data (Barve et al., 2011; Soberón & Peterson, 2005). Species' climatic realized niches were calculated following the approach described in Blonder et al. (2014), where the niche size is estimated as an *n*-dimensional hypervolume (see more details below). Following Blonder et al. (2018), we only considered those species that had at least 10 valid occurrence records. Since the exploratory analysis revealed a direct relationship between the number of occurrences and hypervolume size, we calculated the hypervolume size with 13 different thresholds for a minimum number of occurrences: 10, 25, 50, 75, 100, 150, 250, 350, 500, 750, 1000, 2500 and 5000 (Figure S2, Supplementary Material). We then selected a minimum of 25 occurrences per species as threshold for the subsequent analyses, to retain as many species as possible from the original dataset of 149 native species while keeping an adequate number of valid records. We retained 109 species with a minimum of 25 occurrences (73.1% of the total number of native species, 96.6% of the total number of endemic species).

The four-dimensional hypervolume, that corresponds to the realized niche size, was calculated using the *hypervolume_svm* function from the R package *hypervolume* (Blonder et al., 2014, 2018) with default values $\nu = 0.01$ and $\gamma = 0.5$. The axis of the hypervolume corresponded to the four above-mentioned climatic variables centred and re-scaled, since multidimensional niche estimations are highly sensitive to the use of different units in each axis (Blonder et al., 2018; Mammola, 2019). Spurious relationships were eliminated by performing a bootstrap approach, where the hypervolume size was

calculated 100 times per species. Each time, the hypervolume was calculated by sampling 25 random occurrences of the total number and the final volume size was the mean of all 100 randomizations.

Niche fill was calculated to evaluate the ability of a species to track its niche in the archipelago. A climatic space was built for the archipelago for all existing combinations of the climatic variables. The *hypervolume_inclusion_test* function from the package *hypervolume* (Blonder et al., 2018) was used to compare the hypervolume size of each species with the climatic hypervolume built for the archipelago. We considered the potential niche in the Azores for a particular species as the conditions that would allow the species to exist, regardless of its occupancy, and thus, it could be estimated by the intersection of both hypervolumes. As a result, a species could occupy all suitable cells in the archipelago (niche fill = 100%, total occupation of the niche) or be absent from some of them (100%<niche fill <0%). This percentage provides an estimation of the potential niche the species occupies (Blonder, 2018; Peterson et al., 2011). Exploratory analysis performed to select the function parameters provided similar results for the algorithms *fast* and *accurate*, so the algorithm *fast* was preferred to reduce computation time. Final parameters employed were a reduction factor of 1 and a distance factor of 1.

Generalized linear models (GLMs) using "gaussian" as family were used to evaluate whether the realized niche size or niche fill were related to the dispersal syndrome classification. Residuals were checked to confirm they met the normality, homoscedasticity and

linearity required. Post hoc differences between groups were calculated using the Tukey honestly significant difference (HSD) test (significance set to α = 0.05). To assess if there was any phylogenetic autocorrelation among species that could be biasing our results, we performed a Phylogenetic Generalized Least Square (PGLS) analysis using the ultrametric phylogeny for the native Azorean seed plant species from Schaefer et al. (2011). PGLS were calculated using the *pgls* function from the *caper* package (Orme, 2013) and value of lambda was assessed with the *fitDiscrete* function from the *geiger* package (Pennell et al., 2014). All analyses were performed in R (version 3.6.1, cran.r-project.org). The code used to perform these analyses can be found in https://github.com/neckera/niche-Azores.

3 | RESULTS

Our dataset comprised 109 species of 80 genera and 39 plant families, being 42 species classified as epizoochorous, 17 as endozoochorous, 31 as hydrochorous and 19 as anemochorous (see Table S1, Supplementary Material).

Niche size shows a significant relationship with dispersal syndromes (Figure 2; GLM F = 4.297, p = 0.007, d.f. = 3). Extreme values ranged from 0.01 (*Potamogeton nodosus*, epizoochorous) to 17.81 (*Lysimachia azorica*, hydrochorous). Tukey post hoc comparisons confirmed that endozoochorous species have slightly larger niches than anemochorous and epizoochorous species (p < 0.05), but no
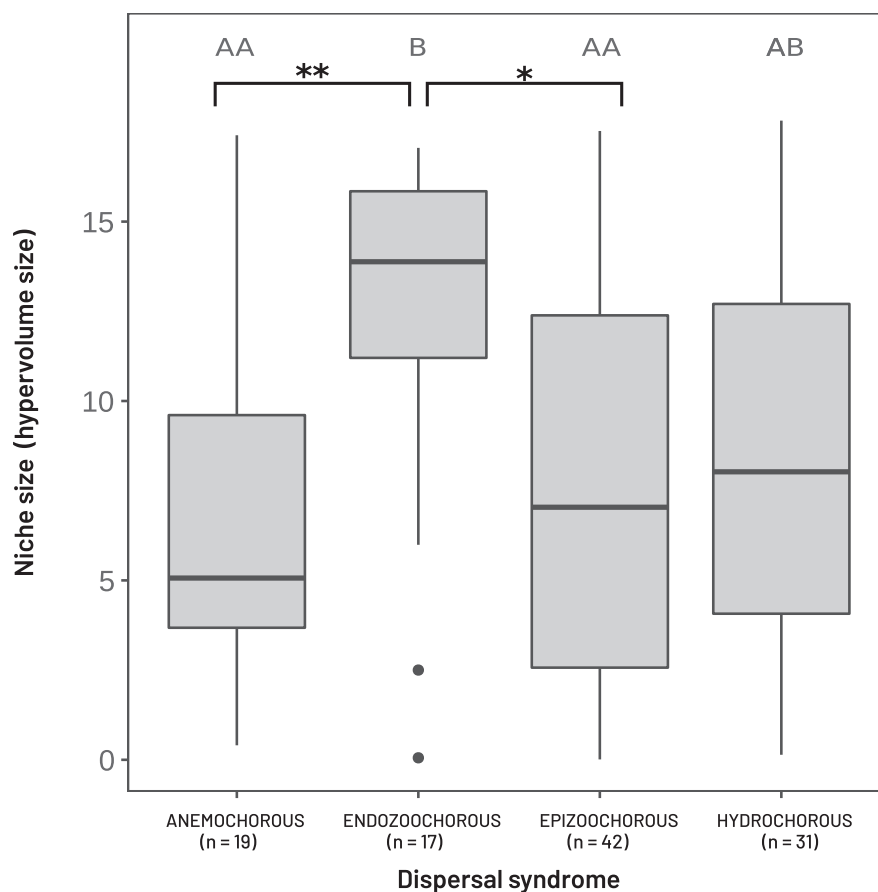
FIGURE 2 Niche size of the native seed plant species of the Azores grouped within each dispersal syndrome. Lines dividing the box represent the median of the data, top and bottom of the box show the upper (Q3) and lower quartile (Q1), and whiskers represent the highest and lowest value excluding outliers, which are represented by a dot. Asterisks represent statistically significant differences (**p < 0.01, *p < 0.05). Different letters (A, B and AB) above the boxes represent post hoc contrasted differences between dispersal syndromes

differences with hydrochorous species. There are no significant differences among anemochorous, epizoochorous and hydrochorous species. No phylogenetic signal was found for this relationship (Pagel's λ = 0.000, *p* < 0.001), so the PGLS results are equivalent to the GLM and are not discussed further.

Niche fill ranges from 7.6% (*Elatine hexandra*, epizoochorous) to 63.4% (*Galium saxatile*, epizoochorous). There is a significant relationship between niche fill and dispersal syndromes (Figure 3; GLM: *F* = 4.992; *p* = 0.0032, d.f. = 3). Tukey post hoc comparisons show that endozoochorous species display a larger niche fill than hydrochorous and epizoochorous species (*p* < 0.05), but no difference with anemochorous species. Anemochorous, hydrochorous and epizoochorous species do not show significant differences either. No phylogenetic signal was found for this relationship (Pagel's λ = 0.000, *p* < 0.001), so the PGLS results are equivalent to the GLM and they are not discussed further.

4 | DISCUSSION

Plants are sessile organisms whose survival depends on their capacity to track or fill environmentally suitable areas, which in turn relies on their ability to disperse and compete successfully with other plant species. Dispersal syndromes, which classify essential strategies for seed dispersal (Carlquist, 1967; Ridley, 1930), have been widely used as a proxy of dispersal ability (Engler et al., 2009). We found that the ability of species to occupy available suitable environmental conditions (i.e. niche fill) is somewhat related to dispersal syndromes in the Azorean islands, as endozoochorous species present higher niche fill and niche size than some of the other dispersal syndromes. However, differences among dispersal groups in both niche characteristics are not consistent and not mutually exclusive, indicating that the use of this classification might not always be appropriate. Endozoochorous species have larger niche fills compared to epizoochorous and hydrochorous species, but do not exhibit significant differences with anemochorous species, that in turn do have larger niche fills than the other two groups. In respect to niche size, there are differences among endozoochorous species and a group formed by epizoochorous and anemochorous species, that in turn do not differ from hydrochorous species. Indeed, previous studies conducted in continental areas found a small effect of dispersal syndromes on explaining dispersal at small scales (e.g. Dullinger et al., 2012; Rumpf et al., 2019), and some indicate that dispersal processes at small scales seem to be filtered by environmental heterogeneity (Jara-Guerrero et al., 2015). Also, it has been suggested that dispersal ability may be more related with niche fill than with niche size, as
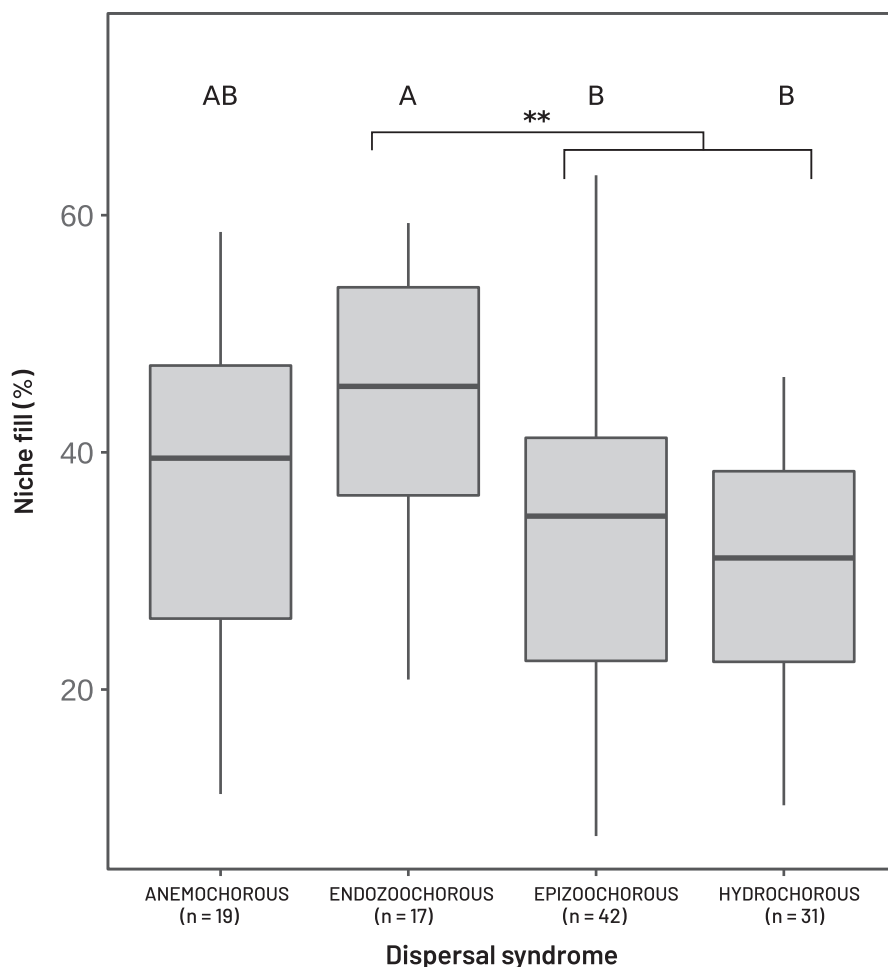

FIGURE 3 Niche fill (in percentage) of the native seed plant species of the Azores grouped within each dispersal syndrome. Lines dividing the box represent the median of the data, top and bottom of the box show the upper (Q3) and lower quartile (Q1), and whiskers represent the highest and lowest value excluding outliers. Asterisks represent statistically significant differences (***p < 0.01, *p < 0.05). Different letters (A, B and AB) above the boxes represent Tukey post hoc contrasted differences between dispersal syndromes

movement is intrinsically related to the ability of a species to track its niche, whereas the realized niche may be constrained by other factors, such as biotic interactions (e.g. absence of an essential symbiont or presence of predators and competitors) (Chase & Liebold, 2003; Peterson et al., 2011; Soberón & Nakamura, 2009; Soberón & Peterson, 2005).

This lack of consistent differences in niche size and niche fill of species presenting different dispersal modes may be due to similar suitability of these different strategies to disperse seeds at small scales, at least in the Azores. For example dispersal by animals, which includes endo- and epizoochory, has generally been considered a highly efficient dispersal mechanism (Vittoz & Engler, 2007), since it is directional—at least at small scales—and often takes place only among suitable habitats for both animals and plants, which increases plants ability to track its niche. Importantly, isolated island biotas (such as the Azores) are characterized by an absence of indigenous terrestrial mammal species (Masseti, 2010), likely increasing the importance of bird-related zoochory. We found that endozoochorous species have larger niches than epizoochorous and anemochorous species, and larger niche fills than epizoochorous and hydrochorous, which might indicate that birds not only disperse seeds further, but may also enhance seed germination in not perfectly suitable situations via the passing through the gut and latter deposition (Traveset et al., 2007). Faeces surrounding the seeds can have a fertilizing effect, promoting seedling growth and thus establishment (Traveset et al., 2007; Willson & Traveset, 2000). Indeed, on lava soils of oceanic islands, bird's feces are known to act as fertilizer, stimulating plant development and soil formation (Fridriksson, 1987). This biotic interaction may be enabling these species to thrive in otherwise suboptimal environments (Traveset et al., 2007), which may explain the larger niches we found in endozoochorous species compared to other dispersal syndromes. This would also coincide with a previous study that suggested that endozoochorous traits may have a positive influence on endozoochorous species distributions across the Azores archipelago (Heleno & Vargas, 2015). Although some of the arguments presented above could also apply for epizoochorous species, as they all are animal-dispersed, there is more randomness associated with epizoochory than with endozoochory. In epizoochory, the seeds and fruits are dispersed attached to the animal, which increases the chances that these will be lost and land in non-suitable habitats (Will & Tackenberg, 2008). This dispersal to non-suitable habitats is also a likely outcome of wind dispersal processes, which may explain why both anemochorous and epizoochorous species do not differ significantly in terms of niche filling.

Indeed, we expected anemochorous species to show significantly larger niche fills than any other dispersal type, apart from endozoochorous species, as wind and air currents are also often described as very efficient dispersal vectors at long distances (Engler et al., 2009; Gillespie et al., 2012; Schaefer, 2002). However, since we found that niche fill of anemochorous species does not differ from that of the other dispersal syndromes, these results suggest that the importance of anemochory at local scales may be variable.

Wind dispersal potential depends not only on seed size and other traits associated with anemochory (pappus, samaras, etc.), but also on weather conditions (Tackenberg et al., 2003). Wind dispersal in unstable atmosphere is more successful than dispersal in high wind, stormy weather due to the occurrence of long-lasting vertical updrafts caused by convection currents (Tackenberg et al., 2003). Besides, stormy weather—a common phenomenon in the Azores—is often associated with high air humidity and rain, which hinders dispersal even at small scales (Schaefer, 2002; Tackenberg et al., 2003). In fact, in the Azorean archipelago there is evidence that the hairy pappus of many Asteraceae collapses rapidly due to the high humidity of the air (Schaefer, 2002), which should hinder their ability to disperse. Altogether, these factors may explain why the well-documented efficiency of anemochory at LDD is not strongly reflected at small scales in the Azores.

Thalassochory—a specific type of hydrochory that can be defined as dispersal by oceanic currents—has been previously identified as an important LDD process in the Azores colonization (Heleno & Vargas, 2015). However, and contrary to our initial expectations, our results suggest that hydrochory (including not only thalassochory but also fresh water hydrochory) is also important for small-scale dispersal in this archipelago, because hydrochorous species do not show significantly smaller niches than any other group. Indeed, Schaefer (2002) indicates the importance of hydrochory for local within-island dispersal even in the absence of large water bodies, as almost all plant species in Azores are dispersed by freshwater or wind at least at small distances. This could explain why hydrochorous species are particularly abundant in humid regions of some of the Azorean islands, such as Flores and Faial (Schaefer, 2002), and are not restricted to coastal areas, occupying different environments across the archipelago. It is also possible that climatic conditions in the Azores, which is the most humid archipelago within Macaronesia (Fernández-Palacios & Dias, 2001), provide a favourable scenario for hydrochory and thus plants dispersed by water do not show smaller niches than any other dispersal type.

The apparent absence of a consistent link between dispersal syndromes and niche dynamics at small spatial scales may indicate that the use of such categorization is not as adequate at this level (i.e. within island level), as it could be for large spatial scales (Fajardo et al., 2019). It may, however, also reflect that dispersal syndrome classifications have been developed for studying LDD across large spatial scales (Carlquist, 1967; Ridley, 1930) and they should not be downscaled since dispersal processes at small scales are modulated by other factors. Moreover, the traits used to classify a species within the same category of dispersal may be operating at different scales. For example, Fajardo et al. (2019) point out that two groups can be defined under the category of anemochory: a group presenting medium to large seeds with pappus and other structures that favour wind dispersal, and another group presenting tiny dust seeds, which are more likely to be dispersed at long-distances than the first group. Thus, even if both groups bear traits that enhance wind dispersal, the outcome of this process is unlikely to be equivalent. The same

applies to zoochorous species, where the high variability of potential dispersers (i.e. reptiles, mammals, birds—that can be migratory or non-migratory, among other characteristics) will disperse seeds at very different distances. Another possibility is that non-standard dispersal mechanisms—such as mega-landslides, rare rafting events, or even secondary dispersal via predators who eat a frugivore that has previously eaten the seed—play a more important role than expected (García-Olivares et al., 2017; Gillespie et al., 2012; Higgins et al., 2003; Nogales et al., 2012), and potential patterns related with dispersal-syndromes may be blurred. Besides, dispersal processes imply high randomness, and despite that certain traits may favour dispersal through a specific vector, they can also benefit other means of dispersal (i.e. samaras in the genus *Acer* favours both wind and water dispersal), or even be irrelevant in certain dispersal events. Lastly, although we tend to categorize species within a single category of dispersal, species may be dispersed by multiple mechanisms (Higgins et al., 2003; Ridley, 1930), which can be responsible for enlarging or reducing the niche (Higgins et al., 2003).

It is important to take into account that the Azores is a highly disturbed archipelago (Borges et al., 2020), with very few pristine habitats and a high proportion of introduced species (*c.* 80% of the current flora), which could have caused the extinction of probably several bird species that might have been important dispersal agents (Rando et al., 2017). Both our estimations of the potential and the realized niches are very likely a subset of the original one. However, we have no *a priori* information to suspect that human actions have restricted the niche of species bearing a particular dispersal syndrome more than the others, nor that they have had a more pronounced effect on a certain dispersal syndrome.

The few studies that have addressed dispersal syndromes when studying multiple ecological processes—such as elevational range shifts (Rumpf et al., 2018), extinction and colonization debts (Rumpf et al., 2019), range filling (Dullinger et al., 2012) or ISAR (Aranda et al., 2013)—showed little or no difference in the patterns exhibited by the species presenting different dispersal syndromes. These works, together with the inconsistent pattern found in this study, suggest that dispersal syndromes may not be the best tool to study how dispersal contributes to biodiversity structuring, at least at small spatial scales. Although the study of dispersal syndromes has been a topic of interest in biogeography, recent studies are questioning long-assumed ideas such as the role they play in dispersal processes or the loss of dispersal ability in islands (Burns, 2018, 2019; Fajardo et al., 2019; García-Verdugo et al., 2017; Heleno & Vargas, 2015), whereas an effort is also being made towards integrating dispersal-related processes in ecological theory (Barve et al., 2011; Soberón & Peterson, 2005). Still, the main focus of dispersal-related studies continues to be on LDD and large-scale processes. Studies such as ours show that more attention should be given towards small scales processes in order to fully understand how dispersal shapes biodiversity patterns. Indeed, future research should identify and explore other surrogates of dispersal ability at small spatial scales,

acknowledging that they might be idiosyncratic. Dispersal kernels based on traits associated with life history and dispersal characteristics, such as number of seed produced or size of the dispersal unit (fruit or seeds), as well as species-specific dispersal models, are promising tools for understanding dispersal at small scales that should be further explored.

DATA AVAILABILITY STATEMENT

Biodiversity data were collected from GBIF (Global Biodiversity Information Facility, www.gbif.org, doi https://doi.org/10.15468/j0iceo). Climatic and biodiversity data used in this study are available for download from the Dryad data repository at https://doi.org/10.5061/dryad.v15dv41w0. R scripts can be found in https://github.com/neckera/nicheAzores.

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BIOSKETCH

María Leo is a PhD candidate in the National Museum of Natural Sciences (MNCN—CSIC, Spain). This paper is part of her PhD thesis, in which she addresses the role of plant dispersal syndromes in island biogeography. She is particularly interested in how biodiversity assembles across scales and the underlying factors that guide these processes. Her work is mainly focused on plants as model organisms.

Authors' contributions: M. L., M. J. S. and A. M. C. S. conceived the ideas; M. L. collected the data; M. L. and H. S. revised the data; M. L. and M. J. S. analysed the data, M. L. and A. M. C. S. led the writing, all authors contributed to the manuscript.

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