RESEARCH ARTICLE

Dispersal limitation shapes distance-decay patterns of European spiders at the continental scale

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Abstract

Aim: To assess the relative relevance of dispersal limitation and species sorting as drivers of spatial turnover between spider faunas of European territories.

Location: Continental Europe.

Time period: Present.

Major taxa studied: Spiders (Order Araneae).

Methods: We analysed how distance-decay patterns differ between northern and southern Europe (broadly, territories covered vs. not covered by ice sheets during the last glacial maximum, respectively) in 15 spider families, using standardized distances to allow a direct comparison between parameters (i.e. slope and intercept) of climatic and spatial distance-decay models. Thus, we assessed North–South differences in parameters of spatial and, independently, climatic distance-decay models, and whether those differences are explained by family-specific traits related to dispersal ability.

Results: Climatic and spatial distance-decay patterns are very similar in northern Europe, where climatic and spatial distances are highly correlated. In contrast, slopes are steeper in spatial than in climatic distance-decay curves in southern Europe, where climatic and spatial distances are decoupled. Moreover, family traits related to dispersal ability explained the North–South difference in spatial distance-decay slopes, as well as the amount of nestedness-resultant dissimilarity between southern and northern spider faunas.

Main conclusions: Our results suggest that differences in beta diversity patterns between northern and southern Europe reflect the strength of dispersal limitation in spiders, which varies across families and leads to different degrees of disequilibrium with current climatic conditions depending on the taxon. Moreover, in the South of Europe, where spatial and climatic distances are uncorrelated, spatial distance-decay models are steeper and have larger explanatory power than climatic distance-decay models, which suggests that dispersal limitation is the main factor shaping current beta diversity patterns of European spiders at the continental scale.

Andrés Baselga and Carola Gómez-Rodríguez contributed equally to this work.

1 | INTRODUCTION

Understanding the processes behind differences in species composition between sites (i.e. beta diversity) is a central question in ecology and biogeography. For this reason, beta diversity patterns have been widely studied across a wide range of territories, scales, times and taxa (e.g. Ávila et al., 2020; Pavlek & Mammola, 2020; Soininen et al., 2007; Steinbauer et al., 2012). At large scales, compositional differences between sites are commonly explained by two major processes, dispersal limitation and species sorting (Nekola & White, 1999; Soininen et al., 2007), which are not mutually exclusive (Gravel et al., 2006). Under dispersal limitation, even if areas with suitable conditions are available, species may not have the capacity to move across the required distances to colonize those areas, so their spatial distributions would not be in equilibrium with environmental conditions. As a result, the more spatially distant two sites are, the more dissimilar their communities are as well (Hubbell, 2001; Nekola & White, 1999). In turn, under species sorting, species are present or absent in a site depending on its biotic and abiotic characteristics (Leibold et al., 2004) and, in consequence, species distributions are constrained by environmental conditions (e.g. climate) and biotic interactions (e.g. competitive exclusion). In this case, the more different the biotic and abiotic characteristics of two sites, the more dissimilar their communities (Nekola & White, 1999).

The interplay between these two processes (dispersal limitation and species sorting) can lead to perdurable effects of past climatic events on present-day biodiversity patterns (Svenning et al., 2015). Pleistocene glaciations are one of the most important historical climatic events explaining the current distribution of species in Europe (Hewitt, 1996, 2000). During this period, northern Europe was covered by ice sheets, and most of the fauna and flora were restricted to glacial refugia, mainly in the Mediterranean region (Hewitt, 1999). When the ice sheets retreated, species were able to expand their ranges and colonize territories in northern latitudes. Consequently, the flora and fauna of northern Europe are the result of a postglacial recolonization process, which may be still ongoing for some taxa (Gómez-Rodríguez & Baselga, 2018; Svenning & Skov, 2007). Therefore, large-scale diversity patterns in Europe are expected to be driven by these two major processes, whose relative relevance would vary depending on the biological group: (i) species sorting, when species have recolonized all the regions where biotic and abiotic conditions are suitable for them, and (ii) dispersal limitation, when species have not been able to reach all the regions where conditions are suitable for them. This is because their distribution ranges are lagging behind the warming climatic conditions since the last glacial maximum, LGM (Svenning & Skov, 2007).

The effects of long-term dispersal limitation and species sorting in the spatial configuration of European biodiversity have been assessed in a wide range of organisms, especially vertebrates and plants (e.g. Astorga et al., 2012; Leprieur et al., 2009; Svenning et al., 2011). In invertebrates, these effects are less studied, but previous analyses suggest a major role of dispersal limitation. Specifically, Gómez-Rodríguez and Baselga (2018) showed that beta diversity patterns are markedly different between northern and southern Europe in beetle groups with low dispersal ability, evidencing the strong imprint of past climatic events in current diversity patterns. When the extension of the ice sheets during the LGM is considered, European territories can be classified in northern territories (>48° N) and southern territories (<48° N), broadly reflecting whether they were covered or not by ice sheets during LGM (Gómez-Rodríguez & Baselga, 2018; Hughes et al., 2016). Thus, Gómez-Rodríguez and Baselga (2018) modelled the decrease of community similarity with spatial distance, also referred to as 'distance-decay relationship' (Nekola & McGill, 2014; Nekola & White, 1999), in such beetle groups and compared the slopes of distance-decay models between northern and southern Europe. The observed North–South differences in distance-decay patterns suggested that, in beetle groups with low dispersal ability, most species were restricted to the South of Europe but a few species, that is, those with good dispersal ability, had been able to reach the North of Europe in a postglacial recolonization process. As a result, Gómez-Rodríguez and Baselga (2018) inferred that (i) the northern European fauna is a subset of the southern fauna, composed only of species with high dispersal ability able to colonize distant territories; and (ii) the species composition is similar across northern territories, resulting in a flat distance-decay curve within the northern region (i.e. high community similarity over long spatial distances, resulting in a weak longitudinal pattern). In contrast, the dispersal limited species would show narrower distributions and would be restricted to the South of the continent, resulting in steeper distance-decay curves in the South than in the North. In other words, dispersal limitation would play a major role in determining the beetle fauna of northern Europe but would not shape the longitudinal diversity pattern across this region (Gómez-Rodríguez & Baselga, 2018).

In addition to spatial distance-decay patterns, it is also possible to assess the decay of community similarity with climatic distance (Graco-Roza et al., 2022; Saito et al., 2015). Analyses of climatic distance-decay relationships aim to assess the effect of species sorting across climatic gradients, in an analogous way as analyses of spatial distance-decay patterns aim to assess the effect of dispersal limitation. Contrasting how well spatial and climatic distances explain community similarity has proven useful to discern the relative relevance of dispersal limitation and species sorting along climatic gradients in multiple biological systems (e.g. Baselga & Leprieur, 2015; Leprieur et al., 2009; Qian et al., 2005; Rodriguez-Artigas et al., 2016). However, because there is usually some degree of correlation between spatial and climatic distances, it is necessary

to account for their covariation either using variance partitioning (Borcard et al., 1992; Smith & Lundholm, 2010) or alternative approaches. Here, we standardized climatic and spatial distances in order to directly compare the slopes of spatial and climatic distance-decay models. Because the slopes of distance-decay models inform about the rate at which species are replaced with distance, using standardized distances allows comparing both rates.

A complementary approach to assess whether diversity patterns may be the result of incomplete postglacial colonization is to assess whether differences between northern and southern European faunas are related to nestedness (i.e. the northern fauna is a subset of the southern fauna) or spatial turnover (i.e. northern and southern faunas are constituted by unique sets of species) in community composition (Baselga, 2010). If northern faunas were nested within southern faunas, it would point to postglacial recolonization processes primarily constrained by dispersal limitation (Dobrovolski et al., 2012), while, on the contrary, spatial turnover would suggest species sorting processes along climatic gradients at continental scales. In other words, if dispersal limitation was the major factor shaping large-scale beta diversity patterns in Europe, the northern fauna would be a subset of the southern one. Therefore, dissimilarity between southern and northern faunas would be mainly due to nestedness, and groups with poor dispersal ability would show higher differences, as found in Dobrovolski et al. (2012) for New World vertebrates. In contrast, if species were not dispersal limited, but their ranges were constrained by climatic tolerances, we would expect a larger contribution of spatial turnover to dissimilarity between southern and northern faunas, as found by Svenning et al. (2011) for European mammals.

In this paper, we will focus on European spiders. Spiders are one of the most diverse arthropod groups (with ca. 50,000 species described to date, World Spider Catalog [2023] and are present in most terrestrial ecosystems [Wise, 1993]). Their long-distance dispersal ability depends on a method of passive aerial dispersal called ballooning, which is based on being carried by the wind supported by silk threads (Duffey, 1998). This method can be so efficient that some spiders have been found at altitudes up to 4 km (Freeman, 1946; Glick, 1939) and can travel more than 1000 km during a lifetime (Bell et al., 2005). Spiders are thus one of the first taxa to colonize islands (Edwards & Thornton, 2001; New & Thornton, 1988). Despite this high dispersal ability, the European spider fauna is expected to be in disequilibrium with climate, as not all species seem to have recolonized the climatically suitable northern territories (Koponen, 1991). Taxa with strong ballooning propensity might have reached the northern latitudes, but it is not clear how different spider groups have lagged behind the retreat of ice sheets (Koponen, 1991) and thus to which degree the legacy of past glaciations imprints the spatial structure of present-day assemblages. Ballooning tendency varies among spider families (Bell et al., 2005; Cardoso et al., 2011; Foelix, 2011; Szymkowiak et al., 2007), which also exhibit different ecological and morphological characteristics (e.g. preferred habitat/vertical stratum, web building behaviour or body size) that can condition ballooning propensity as well (Blandenier, 2009; Dean & Sterling, 1985;

Larrivée & Buddle, 2011). This variation in dispersal, morphological and ecological traits must affect the relative relevance of dispersal limitation and species sorting processes across taxa. As for species sorting processes, we focus on the climatic drivers of species composition but not on biotic factors, such as competitive exclusion or priority effects. This choice is based on two considerations. First, spider communities have been shown to be unsaturated. Natural communities usually harbour multiple species that exploit similar niches but are still able to coexist via spatio-temporal niche partitioning (Agnarsson et al., 2016; Mammola et al., 2020; Villanueva-Bonilla et al., 2019) and the addition of non-native species has been shown not to impact the abundances of native species (Burger et al., 2001). Second, the spatial scale at which we are analysing the variation in species composition (European countries) makes it even more unlikely for species interactions to play a relevant role in the observed patterns (Araújo & Rozenfeld, 2014). The role of both dispersal limitation and species sorting along climatic gradients in driving spider communities has been studied at small spatial scales (e.g. Baldissera et al., 2012; Carvalho et al., 2011; Fernandez-Fournier & Avilés, 2018; Zhang et al., 2018) but not at a continental scale, except for subterranean spiders (Mammola et al., 2019).

Here, we aim to study the role of dispersal limitation and climatic constraints in shaping current beta diversity patterns in European spider faunas at large spatial scales (both in terms of grain and extent), by assessing the decrease of faunistic similarity between European countries. To do so, we compared the parameters (intercept and slope) of spatial and climatic distance-decay curves of 15 spider families in northern and southern Europe (i.e. territories covered and non-covered by ice sheets during the LGM, Figure 1) to assess (i) how the relationship between compositional similarity and spatial or climatic distance differs between northern and southern Europe. We also assessed, for each spider family, (ii) whether the differences in species composition between northern and southern Europe are more related to nestedness or spatial turnover. We expect nestedness to be predominant if the North–South faunistic differences are caused by dispersal limitation, whereas turnover will be predominant if the differences are caused by species sorting. Finally, we analysed (iii) whether dispersal-related traits of spider families explained the differences in species composition and in distance-decay parameters between the North and South of Europe. We expect a significant relationship between the differences in distance-decay parameters and dispersal-related traits of spiders if dispersal limitation is the main process driving the composition of European spider assemblages.

2 | MATERIALS AND METHODS

2.1 | Distribution data

Presence/absence tables for 15 spider families (3075 species in total) in 39 continental European territories were compiled from araneae.nmbe.ch (Nentwig et al., 2022) (accession, July 2022). We
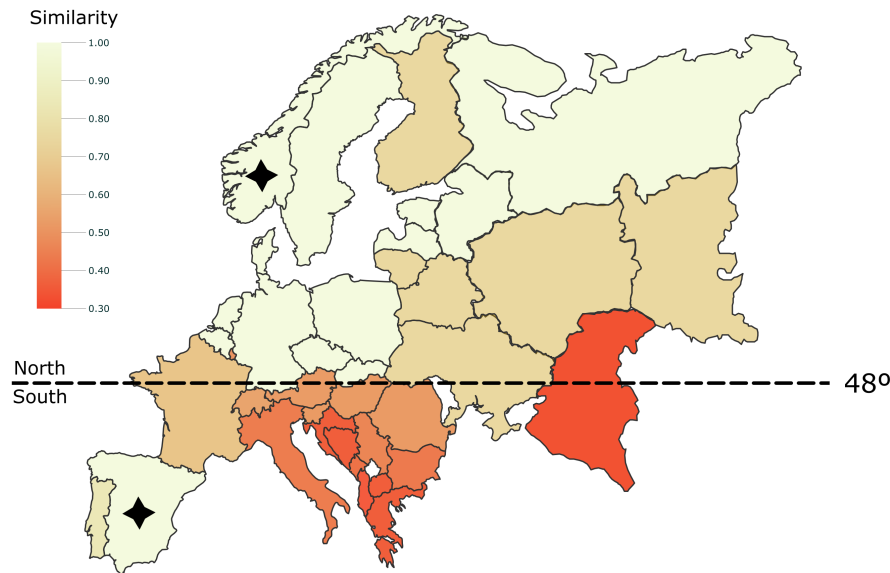
FIGURE 1 Example illustrating the decay of faunistic similarity with distance for Agelenidae using two territories, one in the North and one in the South, as reference. Thus, territory shades represent their faunistic similarity against a reference territory, Spain in the South and Norway in the North. The broken line (48° N) indicated the cut-off used to classify northern and southern territories.

selected families Agelenidae, Araneidae, Clubionidae, Dictynidae, Gnaphosidae, Hahniidae, Linyphiidae, Liocranidae, Lycosidae, Philodromidae, Pholcidae, Salticidae, Tetragnathidae, Theridiidae and Thomisidae because of their large number of species, which allowed the robust computation of community similarity indices, their wide distribution through continental Europe and their different biological characteristics. The source provides a list of species by country (except for Russia, subdivided into five regions: North, Centre, South, East and West) based on published observations. Thus, most of our territories correspond to European countries, with some remarks. Due to their different biogeographic characteristics, islands were excluded from this study. Countries with an area of less than 2000 km² (Monaco, Liechtenstein, San Marino and Vatican City) were excluded from our data set to avoid extreme differences in area and, for the same reason, we maintained the subdivision of European Russia into five territories (North, Centre, South, East and West). Bosnia-Herzegovina and Croatia were considered a single territory because the latter surrounds the former. Kosovo was excluded from the analyses due to the absence of data on some taxa that may cause bias in computing community similarity. We studied the species–area relationship of the remaining territories to detect if any of them have incomplete inventories. We fitted a linear model to the log(richness) ~ log(area) relationship, and identified influential cases based on Cook's distance (cut-off = 0.15, $F_{1,37}$, 30th percentile [Ayinde et al., 2015]). Moldova and European Turkey stood out (Figure S1), suggesting their inventories were largely incomplete, so both territories were also excluded from subsequent analyses.

2.2 | Faunistic similarity and distance-decay models

To assess the effect of dispersal limitation or species sorting along climatic gradients, we compared the decay of faunistic similarity between territories with spatial and, independently, with climatic distance for 15 spider families, and for northern and southern Europe separately. For each family, we constructed two presence/absence tables, one for northern (territories with centroids at >48°) and one for southern Europe (territories with centroids at <48°). A latitude of 48° has been chosen as cut-off reference because it is the approximate latitude at which the ice sheets covered the continent during the LGM (Hughes et al., 2016). Each presence/absence table was used to compute the pairwise similarity between territories using the Simpson's similarity index (1-β_{sim}) (Baselga, 2010; Simpson, 1943), with the function *beta.pair* of the R package *betapart* (Baselga et al., 2023; Baselga & Orme, 2012). Spatial distances between territories were computed as the geodesic distance between its centroids using the *geodist* function of the R package *geodist* (Padgham & Sumner, 2021). To compute climatic distances, we first extracted the mean value of six climatic variables for each territory from Worldclim (Hijmans et al., 2005): mean annual temperature (Bio1), maximum temperature of the warmest month (Bio5), minimum temperature of the coldest quarter (Bio6), annual precipitation (Bio12), precipitation of the wettest quarter (Bio16) and precipitation of the driest quarter (Bio17). These variables were submitted to a principal component analysis (PCA) with a varimax rotation and the first two dimensions (explained variance = 100%) were retained. We computed the climatic distances between territories as the Euclidean distance between their respective PCA scores (Figure S2). We also computed the correlation between spatial and climatic distances, both in northern and southern Europe, with a Mantel test using 1000 permutations. The degree to which spatial and climatic distances are correlated is relevant because, if correlation is low, the relationship between community similarity and spatial or climatic distance could be attributed to dispersal limitation or species sorting, respectively, and it would be independent of the alternative process.

To make the parameters of climatic and spatial distance-decay models directly comparable, we first standardized spatial and climatic distances between 0 and 1. This allows, for example,

assessing whether the slopes are steeper in spatial or climatic distance-decay models, pointing to the preponderance of dispersal limitation or species sorting, respectively. Each standardized distance value (d_s) was computed as $d_s = (d_i - \min(d))/(\max(d) - \min(d))$ where d_i is the original spatial or climatic distance value, and d is the vector of all original spatial or climatic distances. Standardized spatial and climatic distance-decay models were built fitting power-law, negative exponential and Gompertz functions (Martín-Devasa et al., 2022a) to the relationship between similarity and standardized spatial/climatic distances with the *decay.model* function of the R package *betapart*. The negative exponential model was selected for subsequent analyses as it showed the lowest AIC values in most cases (Tables S1 and S2 in Supplementary Material). The differences between spatial and climatic distance-decay parameters in each spider family were independently assessed for the North and the South with the z_{dep} statistic, a test specifically designed to compare parameters of models fitted with pairwise-dependent data (Martín-Devasa et al., 2022b), using the *zdep* function (with 1000 resamples) of the R package *betapart*. Additionally, to control for the evolutionary relationships of spider families, we also tested for the difference in the average of intercepts and slopes between standardized spatial and climatic distance-decay models with a phylogenetic paired *t*-test using the *phyl.pairedttest* of the R package *phytools* (Revell, 2012). To this end, a phylogenetic tree for the 15 spider families included in our analyses was obtained by pruning the phylogenetic tree in Macías-Hernández et al. (2020a), keeping only one species per family. We chose common species with a wide distribution across Europe (Table S3).

To compute the dissimilarity between northern and southern faunas as a whole, the territory-level presence/absence tables were collapsed into a new table coding the presence/absence of each species in two larger regions, northern (>48° N) and southern Europe (<48° N). This collapsed table was used to compute the pairwise dissimilarity between northern and southern faunas (β_{sor}), and the fractions of dissimilarity related to species turnover (β_{sim}) and nestedness (β_{sne}), following the beta diversity partitioning framework introduced by Baselga (2010). Whether spatial turnover or nestedness-resultant dissimilarity was the dominant fraction was determined using the β_{sim}/β_{sor} ratio (β_{ratio}). Thus, the higher the β_{ratio}, the higher the relative importance of turnover over nestedness.

2.3 | Relationship between beta diversity patterns and dispersal-related traits of spiders

To study whether dispersal-related traits explain beta diversity patterns of spiders in Europe, we assessed the relationship of these traits with (i) the North–South difference in intercepts of spatial and climatic distance-decay models, (ii) the North–South difference in slopes of spatial and climatic distance-decay models and (iii) the values of turnover (β_{sim}) and nestedness-resultant dissimilarity (β_{sne}) between the North and South of Europe. Ballooning is the main long-distance dispersal method of spiders, so spider families were

classified according to their ballooning tendency in frequent and infrequent ballooners. The assignation of each spider family to these categories was based on studies of ballooning behaviour and the proportions of different families observed in aerial samples (Bishop & Riechert, 1990; Blandenier, 2009; Blandenier & Fürst, 1998; Dean & Sterling, 1985; Greenstone et al., 1987; Pearce et al., 2005). Following Carvalho and Cardoso (2014), families that represent less than 1% of the total number of individuals in aerial samples were classified as infrequent ballooners, whereas families representing more than 1% of individuals were classified as frequent ballooners. We also incorporated into the analysis some additional traits that can influence the ballooning tendency and efficiency, and have also been used as proxies of spiders dispersal ability in previous papers (Carvalho & Cardoso, 2014; Jiménez-Valverde et al., 2010): maximum female body size, as bigger species tend to fall at shortest distances (Dean & Sterling, 1985); vegetation strata, as high strata inhabitants are easily carried by the wind (Blandenier, 2009; Platnick, 1976) and silk production, as not producing silk hampers ballooning (Bonte et al., 2004; Larrivée & Buddle, 2011). We estimated the maximum female body size of each family by obtaining a random sample of 50 species and averaging the maximum female body size across species. For families with less than 50 species, all species were considered. Female body size data were obtained from Nentwig et al. (2022), Esyunin and Sozontov (2016), Koch (1879), Tyschchenko (1965), Marusik and Koponen (1998), Ponomarev (2009), Ledoux (2014) and Macías-Hernández, Ramos, et al. (2020). We assigned each family a vertical strata category—soil, vegetation or both—based on the classification of Cardoso et al. (2011). Finally, we also classified spider families as web builders or non-web builders. The spider families' traits can be found in Table 1. We acknowledge that using trait data at the family level is a broad approximation. However, spider life-history traits (e.g. ballooning propensity, web building or web type, etc.) are generally well conserved within families (Cardoso et al., 2011; Carvalho & Cardoso, 2014), which has allowed many studies to successfully use family-level trait data in biogeographical studies (e.g. Jiménez-Valverde et al., 2010; Suárez et al., 2023; Wu et al., 2017). Thus, the use of family-level dispersal traits as proxies of dispersal ability is a reasonable approximation to assess cross-family differences in biogeographic patterns likely affected by dispersal ability, such as distance-decay patterns.

To assess whether the differences in spatial and climatic distance-decay parameters between northern and southern Europe are related to dispersal traits of spider families, we used phylogenetic generalized least square (PGLS) analyses with the *pgls* function of the R package *caper* (Orme et al., 2018), considering as dependent variable (i) the difference in intercepts (northern intercepts—southern intercepts), (ii) the difference in slopes (northern slopes—southern slopes) and (iii) the dissimilarity in species composition between northern and southern faunas due to (iii.a) turnover (β_{sim}) or (iii.b) nestedness (β_{sne}). Traits in evolutionarily related groups may present phylogenetic autocorrelation that can inflate type I (false positive) and type II (false negative) errors (Gittleman & Kot, 1990), so we used PGLS models to account for phylogenetic autocorrelation as inferred

TABLE 1 Classification of spider families according to dispersal traits.

	Ballooning	Web builders	Strata	Max size females (mm)
Agelenidae	Infrequent	Yes	Both	9.57
Araneidae	Frequent	Yes	Vegetation	11.70
Clubionidae	Infrequent	No	Vegetation	7.66
Dictynidae	Infrequent	Yes	Both	3.14
Gnaphosidae	Infrequent	No	Soil	7.83
Hahniidae	Infrequent	Yes	Soil	2.66
Linyphiidae	Frequent	Yes	Both	2.80
Liocranidae	Infrequent	No	Soil	5.95
Lycosidae	Frequent	No	Soil	10.03
Philodromidae	Frequent	No	Both	6.62
Pholcidae	Infrequent	Yes	Both	5.50
Salticidae	Frequent	No	Both	6.03
Tetragnathidae	Frequent	Yes	Vegetation	9.86
Theridiidae	Frequent	Yes	Both	3.83
Thomisidae	Frequent	No	Both	7.10

from the pruned phylogenetic tree based on Macías-Hernández et al. (2020a) (Figure S3). We computed 16 different PGLS models, considering all possible trait combinations, and selected the model with the lowest AIC as best.

3 | RESULTS

We first measured the correlation between spatial and climatic distances to know whether any relationship between community similarity and spatial or climatic distance could be attributed to dispersal limitation or climatic sorting, respectively, independently of the alternative process. Correlation between spatial and climatic distance was high in the North (Mantel test, Pearson $r = 0.72$, $p < 0.001$), but low in the South (Mantel test, Pearson $r = 0.14$, $p = 0.175$) (Figure S4).

In southern Europe, faunistic similarity markedly decreased with spatial distance (Figure 1 shows the decay of faunistic similarity against a reference territory, Spain, for illustrative purposes). As a result, spatial distance explained a relevant fraction of variation in community similarity in most families (pseudo-$R^2 > 0.3$ in nine families, see Figure 2), while climatic distance explained a negligible fraction (pseudo-$R^2 \leq 0.07$ in all families, Figure 2). On average, the intercept was significantly lower (phylogenetic paired t-test, $t_{12} = 3.41$, $p = 0.005$) for climatic (0.78 ± 0.08 [SD]) than for spatial models (0.86 ± 0.06 [SD]), and mean slope was significantly steeper ($t_{12} = -6.76$, $p < 0.001$) for spatial (-0.53 ± 0.29 [SD]) than for climatic (-0.08 ± 0.07 [SD]) models (Figure 3). When comparisons were made within each family using the z_{dep} statistic, the intercepts were also significantly lower for climatic curves in 10 of 15 families, and slopes were significantly steeper for spatial than for climatic distance-decay curves in 12 of 15 families (Table S4). All parameters are shown in Table S5.

In northern Europe, faunistic similarity hardly decreased with spatial distance (Figure 1 shows the decay of faunistic similarity against a reference territory, Norway, for illustrative purposes). As a result, spatial distance explained a small fraction of variation in community similarity (pseudo-$R^2 > 0.3$ in only three families, see Figure 4), and climatic and spatial distance explained a similar fraction of variation in most families (difference in pseudo-R^2 between climatic and spatial models ≤ 0.1 in all families but two, Figure 4). In the North, the average intercept was significantly lower (phylogenetic paired t-test $t_{12} = 3.25$, $p = 0.007$) for climatic (0.94 ± 0.04 [SD]) than for spatial models (0.96 ± 0.03 [SD]), and mean slope was significantly flatter (phylogenetic paired t-test $t_{12} = -4.17$, $p = 0.001$) for climatic (-0.18 ± 0.12 [SD]) than for spatial (-0.26 ± 0.11 [SD]) models (Figure 3), although the difference was much less marked than in the South (difference between mean slope of 0.08 in the North vs. 0.45 in the South). When comparisons were made within each family, spatial and climatic intercepts and slopes were significantly different only for one of the 15 families (Table S4). Taken altogether, these results evidenced that spatial and climatic distance-decay models are coupled in the North of Europe, but not in the South, where only spatial distance, but not climatic distance, is a relevant predictor of faunistic similarity.

When the relationship between family traits and the North–South difference in parameters of spatial distance-decay models was assessed, we found that southern slopes were steeper than northern slopes (Figure 3a) and the North–South difference in slope was explained by all dispersal traits, as the best model included ballooning tendency (smaller difference in frequent ballooners), vegetation strata (smaller difference in higher strata) and maximum female size (larger difference in bigger families) of the spider families ($R^2 = 0.57$, $F_{4,10} = 3.29$, $p = 0.06$) (Tables S6 and S7). In turn, the best model of the North–South difference in intercept included only vegetation strata
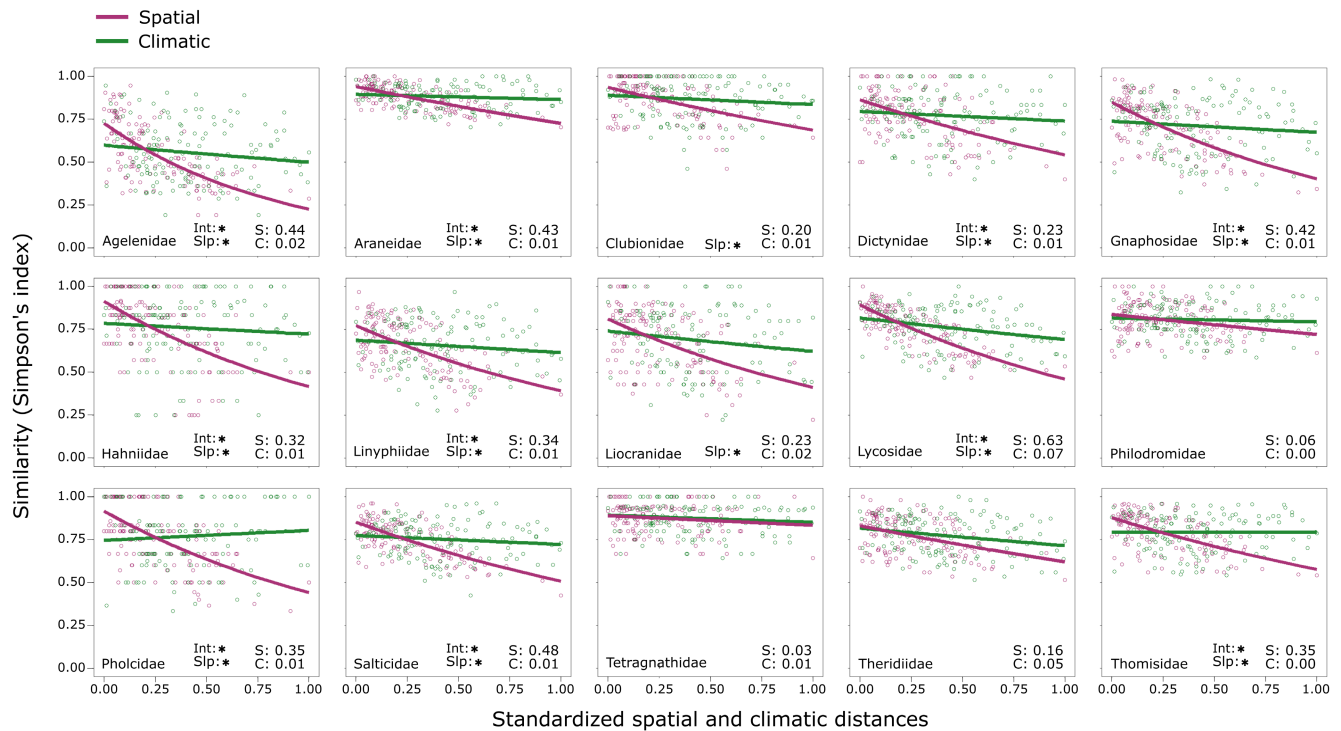
FIGURE 2 Distance-decay models (fitted with a negative exponential function) using standardized spatial and climatic distances for 15 spider families in southern Europe. Spatial and climatic distances were scaled to [0, 1] range to allow a direct comparison of model parameters. S and C indicate the pseudo-R^2 of the spatial and climatic distance-decay models, respectively. Int: * indicates significant differences between intercepts and Slp:* indicates significant differences between slopes according to the z_{dep} statistic.

and was not significant ($R^2 = 0.25$, $F_{2,12} = 2.00$, $p = 0.18$) (Tables S6 and S8). Regarding climatic distance-decay models, we found that intercepts were higher in the North than in the South (Figure 3b), and that the best supported model for the North–South difference in intercept explained a large fraction of variance and, as predictors, included ballooning tendency (smaller difference in frequent balloners), vegetation strata (smallest difference observed in higher strata, see Table S9) and maximum female size (positive effect) of the spider families ($R^2 = 0.64$, $F_{4,10} = 4.45$, $p = 0.02$) (Tables S6 and S9). However, the best model of the North–South difference in climatic distance-decay slope was not significant ($R^2 = 0.28$, $F_{2,12} = 2.32$, $p = 0.14$) (Tables S6 and S10). It should be noted that alternative models were also equally plausible ($\Delta AIC < 2$) and they are reported in Table S6.

When the dissimilarity between the northern and southern European spider faunas was assessed, nestedness-resultant dissimilarity (β_{sne}) was the largest component of compositional differences between northern and southern Europe for 10 of the 15 families studied ($\beta_{ratio} < 0.5$). In contrast, species turnover was the largest component in the families Clubionidae, Dictynidae, Linyphiidae, Lycosidae and Thomisidae ($\beta_{ratio} > 0.5$) (Table 2). The amount of nestedness-resultant dissimilarity between southern and northern Europe was well explained by dispersal traits of spider families. The best model included ballooning tendency (more nestedness in infrequent balloners), maximum female body size (positive effect) and vegetation strata (less nestedness in higher strata) of spider families ($R^2 = 0.68$, $F_{4,10} = 5.28$, $p = 0.01$) (Tables S6 and S11). In turn, the best

model of the relationship between dispersal traits and North–South species turnover only included female size and was not significant ($R^2 = 0.14$, $F_{1,13} = 2.19$, $p = 0.16$) (Tables S6 and S12). Equally plausible models ($\Delta AIC < 2$) are reported in Table S6.

4 | DISCUSSION

Our results show that dispersal limitation is the main factor shaping present-day beta diversity patterns of European spiders at the continental scale. We can draw this conclusion because, in southern Europe, (i) spatial and climatic distances are not correlated, (ii) community similarity is well explained by spatial distance but not by climatic distance and (iii) slopes are much steeper in spatial than climatic distance-decays. In turn, in northern Europe, the explanatory power of spatial and climatic distances is similar, as expected from the high correlation of spatial and climatic distances. Therefore, in northern Europe, we cannot easily infer the causal processes behind the observed distance-decay patterns. We could speculate that either (i) climatic constraints are more relevant in northern Europe due to the prevalence of harsher climatic conditions or, alternatively, (ii) that the same dispersal limitation observed in southern Europe is behind the observed distance-decay patterns in the North, and climatic distance explains the pattern just because it is correlated to spatial distance. Finally, dispersal-related traits of spider families explain (i) the North–South difference between slopes of spatial
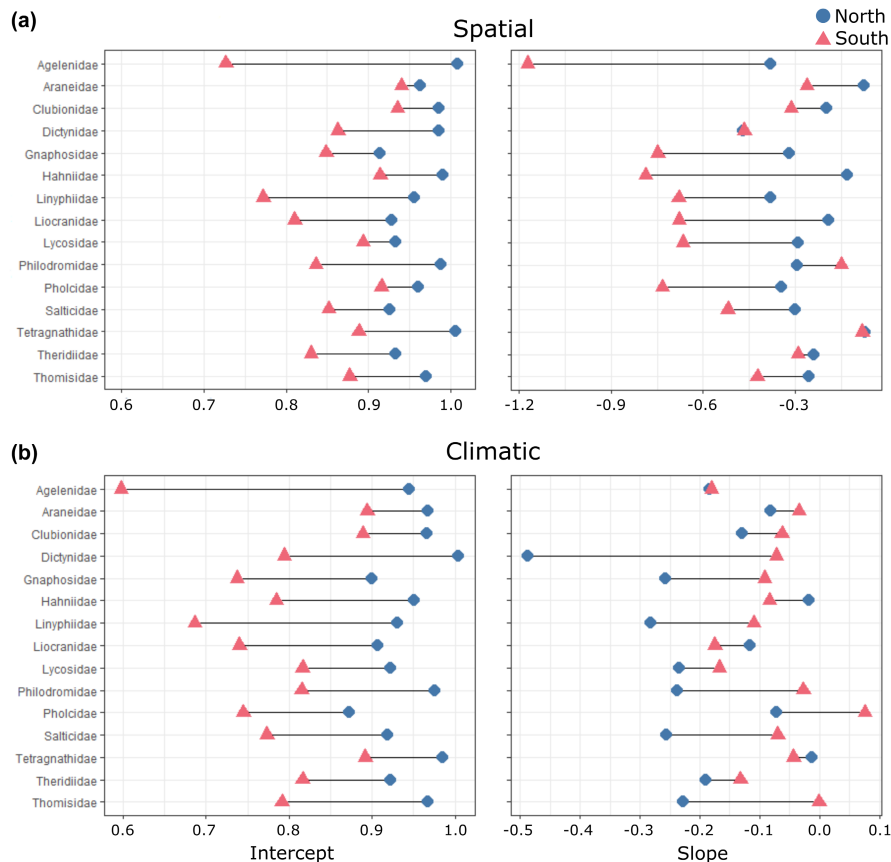
FIGURE 3 Difference between northern (blue dots) and southern Europe (red triangles) in intercepts and slopes of (a) spatial and (b) climatic distance-decay models.

distance-decay curves, and (ii) the amount of nestedness-resultant dissimilarity between northern and southern faunas. Moreover, the relationships between differences in slope and the morphological and ecological traits of spiders were in agreement with the predictions derived from their hypothesized link with dispersal. Taking all together, our results point to a major role of dispersal limitation and postglacial recolonization lags in biogeographic patterns of spiders at a continental scale, as previously found for beetles (Gómez-Rodríguez & Baselga, 2018).

Previous studies have revealed that community composition in spiders generally depends on the combination of dispersal and environmental (climate and vegetation structure) constraints (Ávila et al., 2020; Barton et al., 2017; Carvalho et al., 2011; Mammola et al., 2019; Rodriguez-Artigas et al., 2016; Tonkin et al., 2016; Zhang et al., 2018), but the importance of each process seems to change with scale. At small spatial scales, species sorting has been frequently suggested as the most important process driving spider community composition due to the strong relationship between environmental variables and spider communities (Bowden & Buddle, 2010; Finch et al., 2008; Jiménez-Valverde et al., 2010; Jiménez-Valverde & Lobo, 2007). Dispersal limitation has also been shown to affect the spatial structure of spider communities, for example, in dune and cave systems (Bonte et al., 2004; Carvalho et al., 2011; Mammola et al., 2019). At the continental scale, the preponderance of dispersal limitation as a driver of differences in

species composition is here revealed by multiple results, as argued above. These lines of evidence not only include macroecological patterns based purely on the distribution of species (as the contrast between climatic and spatial distance-decay models) but also clear relationships between these distributional patterns and organismal traits related to dispersal (ballooning, vegetation stratum or body size). For example, ballooning was negatively associated with North–South differences in distance-decay slopes, suggesting that smaller differences in slope were linked to families with higher dispersal ability. Marked North–South differences in the slopes of spatial distance-decay curves have been previously interpreted as the result of dispersal limitation in a previous paper on European beetles (Gómez-Rodríguez & Baselga, 2018). The rationale behind Gómez-Rodríguez and Baselga (2018) study is that, under strong dispersal limitation, most species have not been able to recolonize the North of Europe, so these species are restricted to southern territories. This leads to steeper distance-decay curves in southern Europe. In contrast, the few species able to colonize the northern regions are good dispersers which tend to occupy larger regions, leading to flatter distance-decay slopes in northern Europe. For European spiders, here we show the same contrast between northern and southern slopes and, as for beetles, the difference between slopes is well explained by dispersal-related traits. The relationship between these traits and the North–South difference in climatic distance-decay intercepts might just
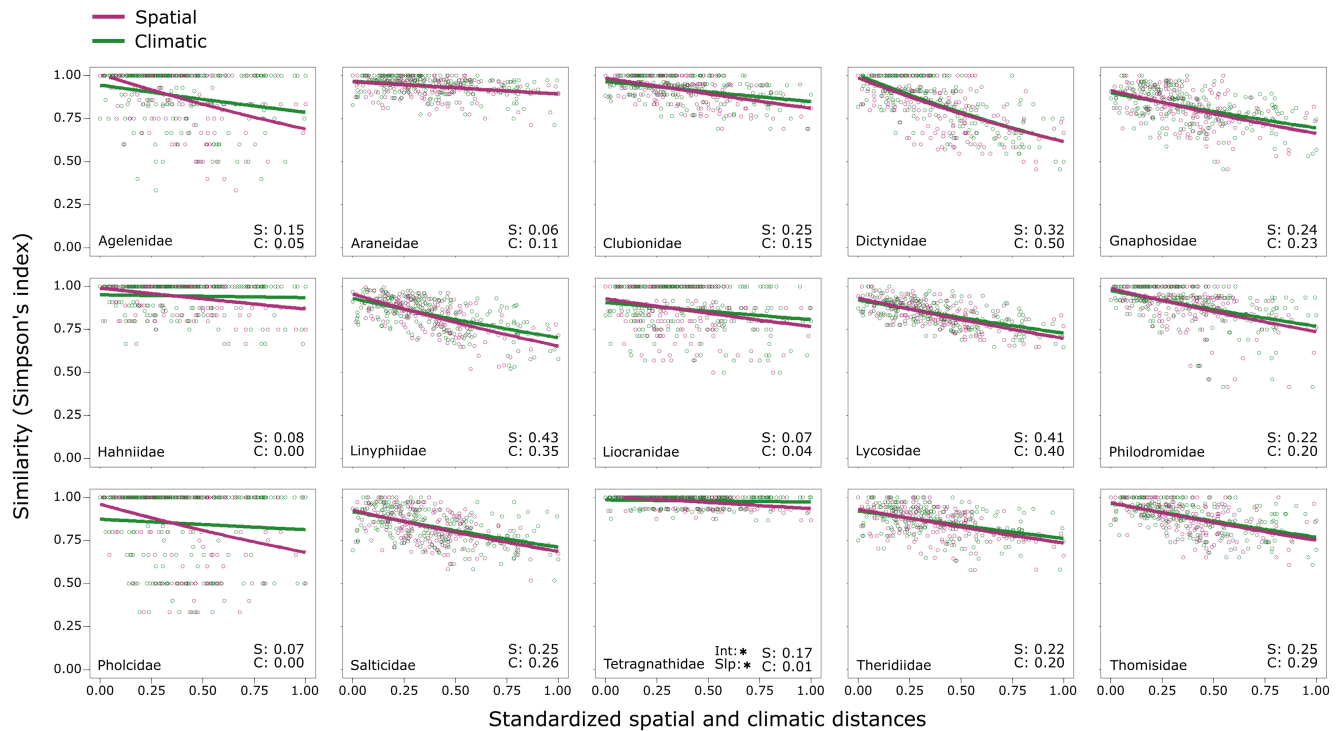
FIGURE 4 Distance-decay models (fitted with a negative exponential function) using standardized spatial and climatic distances for 15 spider families in northern Europe. Spatial and climatic distances were scaled to [0, 1] range to allow a direct comparison of model parameters. S and C indicate the pseudo-R^2 of the spatial and climatic distance-decay models, respectively. Int: * indicates significant differences between intercepts and Slp:* indicates significant differences between slopes.

TABLE 2 Dissimilarity between northern and southern spider faunas derived from species turnover (β_{sim}), derived from nestedness-resultant dissimilarity (β_{sne}) and proportion of total observed dissimilarity (β_{sor}) derived from turnover (the ratio between β_{sim} and β_{sor}, β_{ratio}) for each spider family.

	β_{sim}	β_{sne}	β_{ratio}
Agelenidae	0.118	0.571	0.171
Araneidae	0.063	0.132	0.321
Clubionidae	0.114	0.080	0.587
Dictynidae	0.214	0.105	0.670
Gnaphosidae	0.143	0.345	0.292
Hahniidae	0.063	0.223	0.219
Linyphiidae	0.294	0.152	0.659
Liocranidae	0.100	0.329	0.233
Lycosidae	0.220	0.142	0.607
Philodromidae	0.111	0.233	0.323
Pholcidae	0.083	0.393	0.175
Saliticidae	0.114	0.292	0.281
Tetragnathidae	0.053	0.197	0.208
Theridiidae	0.093	0.268	0.258
Thomisidae	0.207	0.190	0.521

Note: The higher the β_{ratio}, the higher the relative importance of turnover over nestedness.

reflect the tendency to smaller biotic similarities in southern than in northern Europe. This inference can be reached because, in southern Europe, similarity depends on spatial distance but is unrelated to climatic distance, and spatial and climatic distances are mostly decoupled. This suggests that smaller intercepts in climatic distance-decay models in the South are just the result of spatially distant pairs of countries (with low similarity) that are climatically similar (small climatic distances). These results do not rule out the relevance of species sorting and biotic processes (e.g. priority or competitive exclusion) at smaller spatial scales, but suggest that dispersal limitation is the major process behind compositional differences at large spatial scales.

Besides leading to marked North–South differences in distance-decay patterns, dispersal limitation and incomplete postglacial colonization also resulted in northern faunas being a subset of southern ones, as has also been observed in a variety of taxa (e.g. Fattorini & Ulrich, 2012; Griffiths, 2017; Hortal et al., 2011), including spiders in northern Canada (Loboda & Buddle, 2018) and subterranean spiders in Europe (Mammola et al., 2019). It could be argued that environmental tolerances in a climatic gradient may also produce a nested structure if only organisms with high tolerance could colonize the extreme climates of northern Europe (Ulrich et al., 2009). Previous work has already pointed out that temperature is an important variable driving spider alpha and beta diversity (Finch

et al., 2008; Jiménez-Valverde et al., 2010), especially at large scales (Carvalho et al., 2011). However, the relationship between spider dispersal traits and the nestedness-resultant dissimilarity between North and South points to nestedness being primarily caused by differences in dispersal ability among families. However, it should be stressed that the dominant role of dispersal limitation is here being discussed for the spider faunas as a whole, but species sorting, including environmental filtering and biotic interactions, could still be especially relevant for some specific spider families. For example, several families such as the sheet weaver spiders (Linyphiidae), wolf spiders (Lycosidae) and crab spiders (Thomisidae) present relatively high North–South species turnover (high β_{ratio}), suggesting that they are better dispersers and closer to equilibrium with climatic conditions. These families, particularly Linyphiidae, tend to be dominant in northern territories (Koponen, 1991), especially in boreal and arctic areas (Dahl et al., 2018; Marusik & Koponen, 2002), so a deep study of the processes underlying the high North–South species turnover in these particular families still deserves future work, as previously suggested by Koponen (1991).

Our study is subject to several limitations. First, our findings must be considered at the spatial scale at which we have analysed the patterns of variation in species composition. The coarse grain of our data is appropriate to assess the relative relevance of dispersal limitation and species sorting along climatic gradients, but cannot be used to investigate the role of biotic interactions in local communities because its signal is lost at large spatial scales (Araújo & Rozenfeld, 2014). Even if previous works suggest a limited role of competitive exclusion in spider communities (Burger et al., 2001; Mammola et al., 2020; Villanueva-Bonilla et al., 2019), its relative relevance compared to species sorting and dispersal limitation should be investigated at much smaller grains in future studies. Second, using countries as units of analysis is not ideal because their sizes differ. This might introduce noise in the patterns, but we can assume a small effect of it because we used the Simpson's index of similarity, which accounts only for differences due to species replacement, and it is not affected by differences in species richness (Baselga, 2010; Baselga & Leprieur, 2015; Koleff et al., 2003). Therefore, differences in species richness caused by differences in country size should not have any effect in our results. Thus, although not perfect, this type of data allows us to assess the large-scale patterns of beta diversity at continental scale and to infer their major drivers, as previously done in Gómez-Rodríguez et al. (2015) and Gómez-Rodríguez and Baselga (2018).

In conclusion, our results show that although spiders are usually considered to have good dispersal ability, dispersal limitation appears to be the main process behind the variation in species composition between European territories. This does not negate the fact that some spider species have outstanding dispersal abilities and can use ballooning to travel large distances (as shown in Bell et al., 2005). Those species are probably the ones that have been able to colonize northern Europe since the LGM. However, a large proportion of species seem to have limited dispersal ability, and hence, their distribution is still restricted to southern Europe. This

emerges as contrasting beta diversity patterns between the northern and southern regions, a legacy of the incomplete recolonization of northern Europe, as also shown for other biological groups (Baselga et al., 2012; Gómez-Rodríguez & Baselga, 2018; Pinkert et al., 2018; Svenning et al., 2015; Svenning & Skov, 2007; Willner et al., 2009). An incomplete recolonization of northern regions implies that species distributions are far from equilibrium with climatic conditions, which poses further important challenges for biodiversity in the context of climate change (Lenoir et al., 2020).

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All data used in this work were obtained from araneae.nmbe.ch (spiders presence by territory) Worldclim (climatic data) and existing literature (spiders families traits), cited in the text. Presence/absence tables, climatic and spatial variables table, spider family-level traits table and the script used to perform this study are available as supplementary material.

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REFERENCES

Agnarsson, I., Gotelli, N. J., Agostini, D., & Kuntner, M. (2016). Limited role of character displacement in the coexistence of congeneric *Anelosimus* spiders in a Madagascan montane forest. *Ecography*, *39*(8), 743–753. https://doi.org/10.1111/ecog.01930

Araújo, M. B., & Rozenfeld, A. (2014). The geographic scaling of biotic interactions. *Ecography*, *37*(5), 406–415. https://doi.org/10.1111/j.1600-0587.2013.00643.x

Astorga, A., Oksanen, J., Luoto, M., Soininen, J., Virtanen, R., & Muotka, T. (2012). Distance decay of similarity in freshwater communities: Do macro- and microorganisms follow the same rules? *Global Ecology and Biogeography*, *21*(3), 365–375. https://doi.org/10.1111/j.1466-8238.2011.00681.x

Ávila, A. C., Pires, M. M., Rodrigues, E. N. L., Costi, J. A. R., Stenert, C., & Maltchik, L. (2020). Drivers of the beta diversity of spider assemblages in southern Brazilian temporary wetlands. *Ecological Entomology*, *45*(3), 466–475. https://doi.org/10.1111/een.12816

Ayinde, K., Lukman, A. F., & Arowolo, O. (2015). Robust regression diagnostics of influential observations in linear regression model. *Open Journal of Statistics*, *05*(04), 273–283. https://doi.org/10.4236/ojs.2015.54029

Baldissera, R., Rodrigues, E. N. L., & Hartz, S. M. (2012). Metacommunity composition of web-spiders in a fragmented neotropical Forest:

Relative importance of environmental and spatial effects. *PLoS ONE*, *7*(10), e48099. https://doi.org/10.1371/journal.pone.0048099

Barton, P. S., Evans, M. J., Foster, C. N., Cunningham, S. A., & Manning, A. D. (2017). Environmental and spatial drivers of spider diversity at contrasting microhabitats. *Austral Ecology*, *42*(6), 700–710. https://doi.org/10.1111/aec.12488

Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, *19*(1), 134–143. https://doi.org/10.1111/j.1466-8238.2009.00490.x

Baselga, A., & Leprieur, F. (2015). Comparing methods to separate components of beta diversity. *Methods in Ecology and Evolution*, *6*(9), 1069–1079. https://doi.org/10.1111/2041-210X.12388

Baselga, A., Lobo, J. M., Svenning, J.-C., Aragón, P., & Araújo, M. B. (2012). Dispersal ability modulates the strength of the latitudinal richness gradient in European beetles. *Global Ecology and Biogeography*, *21*(11), 1106–1113. https://doi.org/10.1111/j.1466-8238.2011.00753.x

Baselga, A., & Orme, C. D. L. (2012). Betapart: An R package for the study of beta diversity. *Methods in Ecology and Evolution*, *3*(5), 808–812. https://doi.org/10.1111/j.2041-210X.2012.00224.x

Baselga, A., Orme, D., Villeger, S., De Bortoli, J., Leprieur, F., Logez, M., Martínez-Santalla, S., Martín-Devasa, R., Gómez-Rodríguez, C., & Crujeiras, R. M. (2023). *betapart: Partitioning beta diversity into turnover and nestedness* (1.6) [computer software]. http://CRAN.R-project.org/package=betapart

Bell, J. R., Bohan, D. A., Shaw, E. M., & Weyman, G. S. (2005). Ballooning dispersal using silk: World fauna, phylogenies, genetics and models. *Bulletin of Entomological Research*, *95*(2), 69–114. https://doi.org/10.1079/BER2004350

Bishop, L., & Riechert, S. E. (1990). Spider colonization of agroecosystems: Mode and source. *Environmental Entomology*, *19*(6), 1738–1745.

Blandenier, G. (2009). Ballooning of spiders (Araneae) in Switzerland: General results from an eleven-year survey. *Arachnology*, *14*(7), 308–316. https://doi.org/10.13156/arac.2009.14.7.308

Blandenier, G., & Fürst, P. A. (1998). Ballooning spiders caught by a suction trap in agricultural landscape in Switzerland. In *Proceedings of the 17th European Colloquium of Arachnology* (pp. 177–186). British Arachnological Society.

Bonte, D., Baert, L., Lens, L., & Maelfait, J.-P. (2004). Effects of aerial dispersal, habitat specialisation, and landscape structure on spider distribution across fragmented grey dunes. *Ecography*, *27*, 343–349.

Borcard, D., Legendre, P., & Drapeau, P. (1992). Partialling out the spatial component of ecological variation. *Ecology*, *73*(3), 1045–1055.

Bowden, J. J., & Buddle, C. M. (2010). Spider assemblages across elevational and latitudinal gradients in the Yukon territory, Canada. *Arctic*, *63*(3), 261–272.

Burger, J. C., Patten, M. A., Prentice, T. R., & Redak, R. A. (2001). Evidence for spider community resilience to invasion by non-native spiders. *Biological Conservation*, *98*(2), 241–249. https://doi.org/10.1016/S0006-3207(00)00159-2

Cardoso, P., Pekár, S., Jocqué, R., & Coddington, J. A. (2011). Global patterns of guild composition and functional diversity of spiders. *PLoS ONE*, *6*(6), e21710. https://doi.org/10.1371/journal.pone.0021710

Carvalho, J. C., & Cardoso, P. (2014). Drivers of beta diversity in Macaronesian spiders in relation to dispersal ability. *Journal of Biogeography*, *41*(10), 1859–1870. https://doi.org/10.1111/jbi.12348

Carvalho, J. C., Cardoso, P., Crespo, L. C., Henriques, S., Carvalho, R., & Gomes, P. (2011). Determinants of beta diversity of spiders in coastal dunes along a gradient of mediterraneity. *Diversity and Distributions*, *17*(2), 225–234. https://doi.org/10.1111/j.1472-4642.2010.00731.x

Dahl, M. T., Yoccoz, N. G., Aakra, K., & Coulson, S. J. (2018). The Araneae of Svalbard: The relationships between specific environmental factors and spider assemblages in the High Arctic. *Polar Biology*, *41*(5), 839–853. https://doi.org/10.1007/s00300-017-2247-4

Dean, D. A., & Sterling, W. L. (1985). Size and phenology of ballooning spiders at two locations in Eastern Texas. *Journal of Arachnology*, *13*, 111–120.

Dobrovolski, R., Melo, A. S., Cassemiro, F. A. S., & Diniz-Filho, J. A. F. (2012). Climatic history and dispersal ability explain the relative importance of turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, *21*(2), 191–197. https://doi.org/10.1111/j.1466-8238.2011.00671.x

Duffey, E. (1998). Aerial dispersal in spiders. In *Proceedings of the 17th European Colloquium of Arachnology* (pp. 187–191). British Arachnological Society.

Edwards, J., & Thornton, I. W. B. (2001). Colonization of an islan volcano, Long Island, Papua New Guinea, and an emergent Island, Motmot, in its caldera lake. VI. The pioneer artropod community of Motmot. *Journal of Biogeography*, *28*, 1379–1388.

Esyunin, S. L., & Sozontov, A. N. (2016). On a new Eurasian species of *Dictyna Sundevall*, 1833 (Aranei: Dictynidae), with taxonomic notes on poorly known Palaearctic Dictyna species. *Arthropoda Selecta*, *25*(2), 199–206.

Fattorini, S., & Ulrich, W. (2012). Spatial distributions of European Tenebrionidae point to multiple postglacial colonization trajectories: Tenebrionid distribution in Europe. *Biological Journal of the Linnean Society*, *105*(2), 318–329. https://doi.org/10.1111/j.1095-8312.2011.01797.x

Fernandez-Fournier, P., & Avilés, L. (2018). Environmental filtering and dispersal as drivers of metacommunity composition: Complex spider webs as habitat patches. *Ecosphere*, *9*(2), e02101. https://doi.org/10.1002/ecs2.2101

Finch, O.-D., Blick, T., & Schuldt, A. (2008). Macroecological patterns of spider species richness across Europe. *Biodiversity and Conservation*, *17*(12), 2849–2868. https://doi.org/10.1007/s10531-008-9400-x

Foelix, R. F. (2011). *Biology of spiders* (3rd ed.). Oxford University Press.

Freeman, J. A. (1946). The distribution of spiders and mites up to 300 ft. in the air. *Journal of Animal Ecology*, *15*(1), 69–74.

Gittleman, J. L., & Kot, M. (1990). Adaptation: Statistics and null model for estimating phylogenetic effects. *Systematic Zoology*, *39*(3), 227–241.

Glick, P. A. (1939). *The distribution of insects, spiders and mites in the air* (673). Technical Bulletin, United States Department of Agriculture.

Gómez-Rodríguez, C., & Baselga, A. (2018). Variation among European beetle taxa in patterns of distance decay of similarity suggests a major role of dispersal processes. *Ecography*, *41*(11), 1825–1834. https://doi.org/10.1111/ecog.03693

Gómez-Rodríguez, C., Freijeiro, A., & Baselga, A. (2015). Dispersal and ecological traits explain differences in beta diversity patterns of European beetles. *Journal of Biogeography*, *42*(8), 1526–1537. https://doi.org/10.1111/jbi.12523

Graco-Roza, C., Aarnio, S., Abrego, N., Acosta, A. T. R., Alahuhta, J., Altman, J., Angiolini, C., Aroviita, J., Attorre, F., Baastrup-Spohr, L., Barrera-Alba, J. J., Belmaker, J., Biurrun, I., Bonari, G., Bruelheide, H., Burrascano, S., Carboni, M., Cardoso, P., Carvalho, J. C., … Soininen, J. (2022). Distance decay 2.0–A global synthesis of taxonomic and functional turnover in ecological communities. *Global Ecology and Biogeography*, *31*(7), 1399–1421. https://doi.org/10.1111/geb.13513

Gravel, D., Canham, C. D., Beaudet, M., & Messier, C. (2006). Reconciling niche and neutrality: The continuum hypothesis. *Ecology Letters*, *9*(4), 399–409. https://doi.org/10.1111/j.1461-0248.2006.00884.x

Greenstone, M. H., Morgan, C. E., & Hultsch, A.-L. (1987). Ballooning spiders in Missouri, USA, and New South Wales, Australia: Family and mass distributions. *Journal of Arachnology*, *15*, 163–170.

Griffiths, D. (2017). Connectivity and vagility determine beta diversity and nestedness in North American and European freshwater fish.

Journal of Biogeography, *44*(8), 1723–1733. https://doi.org/10.1111/jbi.12964

Hewitt, G. M. (1996). Some genetic consequences of ice ages, and their role in divergence and speciation. *Biological Journal of the Linnean Society*, *58*, 247–276.

Hewitt, G. M. (1999). Post-glacial re-colonization of European biota. *Biological Journal of the Linnean Society*, *68*, 87–112.

Hewitt, G. M. (2000). The genetic legacy of the quaternary ice ages. *Nature*, *405*, 907–913.

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, *25*(15), 1965–1978. https://doi.org/10.1002/joc.1276

Hortal, J., Diniz-Filho, J. A. F., Bini, L. M., Rodríguez, M. Á., Baselga, A., Nogués-Bravo, D., Rangel, T. F., Hawkins, B. A., & Lobo, J. M. (2011). Ice age climate, evolutionary constraints and diversity patterns of European dung beetles: Ice age determines European scarab diversity. *Ecology Letters*, *14*(8), 741–748. https://doi.org/10.1111/j.1461-0248.2011.01634.x

Hubbell, S. P. (2001). *The unified neutral theory of biodiversity and biogeography* (1st ed.). Princeton University Press. https://doi.org/10.1515/9781400837526

Hughes, A. L. C., Gyllencreutz, R., Lohne, Ø. S., Mangerud, J., & Svendsen, J. I. (2016). The last Eurasian ice sheets—A chronological database and time-slice reconstruction. *Boreas*, *45*(1), 1–45. https://doi.org/10.1111/bor.12142

Jiménez-Valverde, A., Baselga, A., Melic, A., & Txasko, N. (2010). Climate and regional beta-diversity gradients in spiders: Dispersal capacity has nothing to say? *Insect Conservation and Diversity*, *3*(1), 51–60. https://doi.org/10.1111/j.1752-4598.2009.00067.x

Jiménez-Valverde, A., & Lobo, J. M. (2007). Determinants of local spider (Araneidae and Thomisidae) species richness on a regional scale: Climate and altitude vs habitat structure. *Ecological Entomology*, *32*, 113–122.

Koch, L. (1879). Arachniden aus Sibirien und Novaja Semlja, eingesammelt von der schwedischen expedition im Jahre 1875. *Kongliga Svenska Vetenskaps-Akademiens Handlingar*, *16*(5), 1–136.

Koleff, P., Gaston, K. J., & Lennon, J. J. (2003). Measuring beta diversity for presence-absence data. *Journal of Animal Ecology*, *72*(3), 367–382. https://doi.org/10.1046/j.1365-2656.2003.00710.x

Koponen, S. (1991). On the biogeography and faunistics of European spiders: Latitude, altitude and insularity. *XIIIe Colloque Européen d'Arachnologie. Bulletin de La Societe Neuchateloise des Sciences Naturelles.*, *116*, 141–152.

Larrivée, M., & Buddle, C. M. (2011). Ballooning propensity of canopy and understorey spiders in a mature temperate hardwood forest. *Ecological Entomology*, *36*(2), 144–151. https://doi.org/10.1111/j.1365-2311.2010.01255.x

Ledoux, J.-C. (2014). Les Hahniidae de la faune française (Araneae). *Revue Arachnologique*, *1*, 29–40.

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., Holt, R. D., Shurin, J. B., Law, R., Tilman, D., Loreau, M., & Gonzalez, A. (2004). The metacommunity concept: A framework for multi-scale community ecology: The metacommunity concept. *Ecology Letters*, *7*(7), 601–613. https://doi.org/10.1111/j.1461-0248.2004.00608.x

Lenoir, J., Bertrand, R., Comte, L., Bourgeaud, L., Hattab, T., Murienne, J., & Grenouillet, G. (2020). Species better track climate warming in the oceans than on land. *Nature Ecology & Evolution*, *4*(8), 1044–1059. https://doi.org/10.1038/s41559-020-1198-2

Leprieur, F., Olden, J. D., Lek, S., & Brosse, S. (2009). Contrasting patterns and mechanisms of spatial turnover for native and exotic freshwater fish in Europe. *Journal of Biogeography*, *36*(10), 1899–1912. https://doi.org/10.1111/j.1365-2699.2009.02107.x

Loboda, S., & Buddle, C. M. (2018). Small to large-scale patterns of ground-dwelling spider (Araneae) diversity across northern Canada. *Facets*, *3*(1), 880–895. https://doi.org/10.1139/facets-2018-0007

Macías-Hernández, N., Domènech, M., Cardoso, P., Emerson, B. C., Borges, P. A. V., Lozano-Fernandez, J., Paulo, O. S., Vieira, A., Enguídanos, A., Rigal, F., Amorim, I. R., & Arnedo, M. A. (2020). Building a robust, densely-sampled spider tree of life for ecosystem research. *Diversity*, *12*(8), 288. https://doi.org/10.3390/d12080288

Macías-Hernández, N., Ramos, C., Domènech, M., Febles, S., Santos, I., Arnedo, M., Borges, P., Emerson, B., & Cardoso, P. (2020). A database of functional traits for spiders from native forests of the Iberian Peninsula and Macaronesia. *Biodiversity Data Journal*, *8*, e49159. https://doi.org/10.3897/BDJ.8.e49159

Mammola, S., Arnedo, M. A., Fišer, C., Cardoso, P., Dejanaz, A. J., & Isaia, M. (2020). Environmental filtering and convergent evolution determine the ecological specialization of subterranean spiders. *Functional Ecology*, *34*(5), 1064–1077. https://doi.org/10.1111/1365-2435.13527

Mammola, S., Cardoso, P., Angyal, D., Balázs, G., Blick, T., Brustel, H., Carter, J., Ćurčić, S., Danflous, S., Dányi, L., Déjean, S., Deltshev, C., Elverici, M., Fernández, J., Gasparo, F., Komnenov, M., Komposch, C., Kováč, L., Kunt, K. B., … Isaia, M. (2019). Local- versus broad-scale environmental drivers of continental β-diversity patterns in subterranean spider communities across Europe. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1914), 20191579. https://doi.org/10.1098/rspb.2019.1579

Martín-Devasa, R., Martínez-Santalla, S., Gómez-Rodríguez, C., Crujeiras, R. M., & Baselga, A. (2022a). Comparing distance-decay parameters: A novel test under pairwise dependence. *Ecological Informatics*, *72*, 101894. https://doi.org/10.1016/j.ecoinf.2022.101894

Martín-Devasa, R., Martínez-Santalla, S., Gómez-Rodríguez, C., Crujeiras, R. M., & Baselga, A. (2022b). Species range size shapes distance-decay in community similarity. *Diversity and Distributions*, *28*(7), 1348–1357. https://doi.org/10.1111/ddi.13550

Marusik, Y. M., & Koponen, S. (1998). New and little known spiders of the subfamily Dictyninae (Araneae: Dictynidae) from South Siberia. *Entomological Problems*, *29*(2), 79–86.

Marusik, Y. M., & Koponen, S. (2002). Diversity of spiders in boreal and arctic zones. *The Journal of Arachnology*, *30*, 205–210.

Nekola, J. C., & McGill, B. J. (2014). Scale dependency in the functional form of the distance decay relationship. *Ecography*, *37*(4), 309–320. https://doi.org/10.1111/j.1600-0587.2013.00407.x

Nekola, J. C., & White, P. S. (1999). The distance decay of similarity in biogeography and ecology. *Journal of Biogeography*, *26*(4), 867–878. https://doi.org/10.1046/j.1365-2699.1999.00305.x

Nentwig, W., Blick, T., Bosmans, R., Gloor, D., Hänggi, A., & Kropf, C. (2022). Spiders of Europe. https://doi.org/10.24436/1

New, T. R., & Thornton, I. W. B. (1988). A pre-vegetation population of crickets subsisting on allochthonous aeolian debris on Anak Krakatau. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*, *322*(1211), 481–485. https://doi.org/10.1098/rstb.1988.0140

Orme, D., Freckleton, R., Thomas, G., Petzoldt, T., Fritz, S., Isaac, N., & Pearse, W. (2018). Caper: Comparative analyses of phylogenetics and evolution in R. https://CRAN.R-project.org/package=caper

Padgham, M., & Sumner, M. D. (2021). geodist: Fast. *Dependency-Free Geodesic Distance Calculations. Version*, *7*. https://CRAN.R-project.org/package=geodist

Pavlek, M., & Mammola, S. (2020). Niche-based processes explaining the distributions of closely related subterranean spiders. *Journal of Biogeography*, *48*(1), 118–133. https://doi.org/10.1111/jbi.13987

Pearce, S., Zalucki, M. P., & Hassan, E. (2005). Spider ballooning in soybean and non-crop areas of southeast Queensland. *Agriculture, Ecosystems & Environment*, 105(1–2), 273–281. https://doi.org/10.1016/j.agee.2004.02.010

Pinkert, S., Dijkstra, K.-D. B., Zeuss, D., Reudenbach, C., Brandl, R., & Hof, C. (2018). Evolutionary processes, dispersal limitation and climatic history shape current diversity patterns of European dragonflies. *Ecography*, 41(5), 795–804. https://doi.org/10.1111/ecog.03137

Platnick, N. I. (1976). Concepts of dispersal in historical biogeography. *Systematic Zoology*, 25(3), 294. https://doi.org/10.2307/2412499

Ponomarev, A. V. (2009). New species and finds of spiders (Aranei) from the south of Russia and Western Kazakhstan. *Caucasian Entomological Bulletin*, 5(2), 143–146.

Qian, H., Ricklefs, R. E., & White, P. S. (2005). Beta diversity of angiosperms in temperate floras of eastern Asia and eastern North America. *Ecology Letters*, 8(1), 15–22. https://doi.org/10.1111/j.1461-0248.2004.00682.x

Revell, L. J. (2012). Phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, 3(2), 217–223. https://doi.org/10.1111/j.2041-210X.2011.00169.x

Rodriguez-Artigas, S. M., Ballester, R., & Corronca, J. A. (2016). Factors that influence the beta-diversity of spider communities in northwestern Argentinean grasslands. *PeerJ*, 4, e1946. https://doi.org/10.7717/peerj.1946

Saito, V. S., Soininen, J., Fonseca-Gessner, A. A., & Siqueira, T. (2015). Dispersal traits drive the phylogenetic distance decay of similarity in Neotropical stream metacommunities. *Journal of Biogeography*, 42(11), 2101–2111. https://doi.org/10.1111/jbi.12577

Simpson, G. G. (1943). Mammals and the nature of continents. *American Journal of Science*, 241(1), 1–31.

Smith, T. W., & Lundholm, J. T. (2010). Variation partitioning as a tool to distinguish between niche and neutral processes. *Ecography*, 33(4), 648–655. https://doi.org/10.1111/j.1600-0587.2009.06105.x

Soininen, J., McDonald, R., & Hillebrand, H. (2007). The distance decay of similarity in ecological communities. *Ecography*, 30(1), 3–12. https://doi.org/10.1111/j.0906-7590.2007.04817.x

Steinbauer, M. J., Dolos, K., Reineking, B., & Beierkuhnlein, C. (2012). Current measures for distance decay in similarity of species composition are influenced by study extent and grain size. *Global Ecology and Biogeography*, 21(12), 1203–1212. https://doi.org/10.1111/j.1466-8238.2012.00772.x

Suárez, D., Arribas, P., Macías-Hernández, N., & Emerson, B. C. (2023). Dispersal ability and niche breadth influence interspecific variation in spider abundance and occupancy. *Royal Society Open Science*, 10(5), 230051. https://doi.org/10.1098/rsos.230051

Svenning, J.-C., Eiserhardt, W. L., Normand, S., Ordonez, A., & Sandel, B. (2015). The influence of paleoclimate on present-day patterns in biodiversity and ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, 46(1), 551–572. https://doi.org/10.1146/annurev-ecolsys-112414-054314

Svenning, J.-C., Fløjgaard, C., & Baselga, A. (2011). Climate, history and neutrality as drivers of mammal beta diversity in Europe: Insights from multiscale deconstruction: Deconstructing mammal beta diversity. *Journal of Animal Ecology*, 80(2), 393–402. https://doi.org/10.1111/j.1365-2656.2010.01771.x

Svenning, J.-C., & Skov, F. (2007). Could the tree diversity pattern in Europe be generated by postglacial dispersal limitation? *Ecology Letters*, 10(6), 453–460. https://doi.org/10.1111/j.1461-0248.2007.01038.x

Szymkowiak, P., Górski, G., & Bajerlein, D. (2007). Passive dispersal in arachnids. *Biological Letters*, 44(2), 75–101.

Tonkin, J. D., Stoll, S., Jähnig, S. C., & Haase, P. (2016). Contrasting metacommunity structure and beta diversity in an aquatic-floodplain system. *Oikos*, 125(5), 686–697. https://doi.org/10.1111/oik.02717

Tyschchenko, B. (1965). A new genus and ten new species of spiders (Arachnida, Araneae) from Iran. *ZooKeys*, 44(3), 696–704.

Ulrich, W., Almeida-Neto, M., & Gotelli, N. J. (2009). A consumer's guide to nestedness analysis. *Oikos*, 118(1), 3–17. https://doi.org/10.1111/j.1600-0706.2008.17053.x

Villanueva-Bonilla, G. A., Safuan-Naide, S., Pires, M. M., & Vasconcellos-Neto, J. (2019). Niche partitioning and coexistence of two spiders of the genus Peucetia (Araneae, Oxyopidae) inhabiting Trichogoniopsis adenantha plants (Asterales, Asteraceae). *PLoS ONE*, 14(10), e0213887. https://doi.org/10.1371/journal.pone.0213887

Willner, W., Di Pietro, R., & Bergmeier, E. (2009). Phytogeographical evidence for post-glacial dispersal limitation of European beech forest species. *Ecography*, 32(6), 1011–1018. https://doi.org/10.1111/j.1600-0587.2009.05957.x

Wise, D. H. (1993). *Spiders in ecological webs*. Cambridge University Press.

World Spider Catalog. (2023). *World Spider Catalog*. https://doi.org/10.24436/2

Wu, L., Si, X., Didham, R. K., Ge, D., & Ding, P. (2017). Dispersal modality determines the relative partitioning of beta diversity in spider assemblages on subtropical land-bridge islands. *Journal of Biogeography*, 44(9), 2121–2131. https://doi.org/10.1111/jbi.13007

Zhang, Q., He, D., Wu, H., Shi, W., & Chen, C. (2018). Local-scale determinants of arboreal spider beta diversity in a temperate forest: Roles of tree architecture, spatial distance, and dispersal capacity. *PeerJ*, 6, e5596. https://doi.org/10.7717/peerj.5596

BIOSKETCH

Ramiro Martín-Devasa is a researcher in community ecology interested in the development of new techniques and methodologies for the study of biodiversity patterns, in particular those of European invertebrates, with special interest in their biogeographical and macroecological drivers.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.