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## RESEARCH ARTICLE

# Functional convergence underground? The scale-dependency of community assembly processes in European cave spiders

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## Abstract

**Aim:** Quantifying the relative contribution of environmental filtering versus limiting similarity in shaping communities is challenging because these processes often act simultaneously and their effect is scale-dependent. Focusing on caves, island-like natural laboratories with limited environmental variability and species diversity, we tested: (i) the relative contribution of environmental filtering and limiting similarity in determining community assembly in caves; (ii) how the relative contribution of these driving forces changes along environmental gradients.

**Location:** Europe.

**Time period:** Present.

**Major taxa studied:** Subterranean spiders.

**Methods:** We used data on distribution and traits for European cave spiders ( $n=475$  communities). We estimated the trait space of each community using probabilistic

Stefano Mammola and Caio Graco-Roza contributed equally to this study.

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hypervolumes, and obtained estimations of functional richness independent of the species richness of each community via null modelling. We model functional diversity change along environmental gradients using generalized dissimilarity modelling.

**Results:** Sixty-three percent of subterranean spider communities exhibited a prevalence of trait underdispersion. However, most communities displayed trait dispersion that did not depart significantly from random, suggesting that environmental filtering and limiting similarity were both exerting equally weak or strong, yet opposing influences. Overdispersed communities were primarily concentrated in southern latitudes, particularly in the Dinaric karst, where there is greater subterranean habitat availability. Pairwise comparisons of functional richness across caves revealed these effects to be strongly scale-dependent, largely varying across gradients of cave development, elevation, precipitation, entrance size and annual temperature range. Conversely, geographical distance weakly affected trait composition, suggesting convergence in traits among communities that are far apart.

**Main conclusions:** Even systems with stringent environmental conditions maintain the potential for trait differentiation, especially in areas of greater habitat availability. Yet, the relative influence of environmental filtering and limiting similarity change with scale, along clear environmental gradients. The interplay of these processes may explain the assembly of species-poor subterranean communities displaying high functional specialization.

**KEYWORDS**

Araneae, beta diversity, cave, functional diversity, functional guild, morphology, trait space, troglobiont

## 1 | INTRODUCTION

An omnipresent scheme in introductory textbooks of ecology illustrates the numerous filters selecting which species end up assembling into local communities from a regional pool. An elusive problem concerning this ‘filtering’ metaphor is quantifying the relative contribution of abiotic and biotic factors in shaping communities (Chalmandrier et al., 2022; Kraft et al., 2015; Lamanna et al., 2014). In a nutshell, environmental filtering is the process whereby abiotic constraints prevent species from establishing in a community, selecting for a narrow set of traits suitable to cope with the local conditions, leading to lower differences in trait composition than expected by chance (‘trait underdispersion’). Conversely, limiting similarity drives functionally similar species to diverge in key phenotypic traits to reduce niche overlap, leading to higher differences in trait composition than expected by chance (‘trait overdispersion’). It follows that looking at biological communities through the lens of functional ecology (i.e. the traits expressed in each community) is one of the most effective ways to quantify the interplay between these two assembly processes (McGill et al., 2006). The use of traits in lieu of species identities allows an explicit focus on the mechanisms generating biodiversity patterns, often facilitating the conceptualization of general principles that are valid across species pools or distantly related taxa (Luza et al., 2023).

Even with trait-based approaches, however, it remains difficult to separate the main mechanisms filtering the species pool of potential resident species to the subset that occurs within a given community ( $\alpha$ -diversity) and in driving variations across communities ( $\beta$ -diversity) (Vellend, 2010). The distinction between environmental filtering and limiting similarity is too often conceptualized as a ‘black or white’ dichotomy, whereby communities are described to be dominated by one or the other process. The ecological reality is instead more nuanced, with the two processes acting simultaneously in shaping communities, although with different intensities given the local environmental conditions (Germain et al., 2018; Loughnan & Gilbert, 2017). Furthermore, like any dimension of biodiversity, functional diversity change is scale-dependent (Graco-Roza et al., 2022; Jarzyna & Jetz, 2018), forcing us to account for the pervasive effect that scale has on emerging patterns (McGill, 2010). Since biotic interactions require spatial proximity, the effect of limiting similarity should often decrease with increasing scale and, vice versa, the filtering effect posed by the abiotic environment should increase with spatial scale—generally resulting in a predominance of trait overdispersion at local scales and trait underdispersion at broader scales (Belmaker et al., 2013; Lhotsky et al., 2016).

Mounting evidence demonstrates that the relative influence of environmental filtering and limiting similarity broadly changes along spatial and temporal gradients—for example, for vertebrates

(Belmaker et al., 2013; Jarzyna & Jetz, 2018; McLean et al., 2021; Mouillot et al., 2014; Toussaint et al., 2021) and plants (Kraft et al., 2008; Lamanna et al., 2014; Lhotsky et al., 2016). However, there is still discussion on the direction of these changes and their causes (Germain et al., 2018; Kraft et al., 2015; Loughnan & Gilbert, 2017). To minimize confounding factors and achieve a better understanding of community assembly rules, scientists are therefore increasingly turning their attention to island-like model systems (e.g. oceanic islands, lakes, tank-bromeliads, floating plant-island, mountain summits; Itescu, 2019; Srivastava et al., 2004) and specific biological communities within them (e.g. plants [Ottaviani et al., 2020; Schrader et al., 2021]; birds [Ross et al., 2019; Sato et al., 2020; Triantis et al., 2022]). The use of island-like systems, that is, mostly closed, with known histories, and with a relatively low richness of species, allows ecologists to more easily disentangle community assembly processes while controlling for immigration, extinction and dispersal dynamics (Itescu, 2019; Mammola, 2019; Whittaker et al., 2017).

Under this framework, caves and other subterranean ecosystems stand out as ideal model systems for the study of community assembly processes through a functional lens. Foremost, caves are semi-closed systems extensively replicated across the Earth (Culver & Pipan, 2019), where stringent environmental conditions promote trait convergence among successful colonizers (Cardoso, 2012; Lunghi et al., 2015; Trontelj et al., 2012). Second, subterranean communities generally exhibit lower species richness and functional diversity than neighbouring surface communities (Cardoso, 2012; Gibert & Deharveng, 2002; Hose et al., 2022; but see Fernandes et al., 2016), making it easier to disentangle the relative effect of environmental conditions in selecting species possessing specialized traits within the community (Mammola, Arnedo, et al., 2020). Third, caves have clear surface-subterranean environmental gradients (Kozel et al., 2019; Lunghi et al., 2015; Tobin et al., 2013) and display a reduced variability in their abiotic conditions (Badino, 2010), two factors that avoid many of the confounding factors typical of other systems (Mammola, 2019).

To study community assembly rules, we leveraged the unprecedented amount of data available for subterranean spiders in Europe (Mammola et al., 2018), namely community composition data for selected caves across the continent (Mammola et al., 2019a) and standardized traits for all species (Mammola et al., 2022). A previous analysis of the taxonomic component of this dataset demonstrated a quick turnover in the taxonomic diversity of subterranean spiders across Europe, mediated primarily by geographical distance among caves, and secondarily by the climatic conditions and availability of karst. Conversely, local-scale characteristics of caves exerted a negligible effect on species turnover (Mammola et al., 2019b). Here, we explore the functional dimension of these patterns, testing: (i) the relative contribution of environmental filtering and limiting similarity in determining community assembly in caves, and (ii) how the contribution of these driving forces changes along environmental gradients.

At the  $\alpha$ -diversity level, we expect ( $H_{1\alpha}$ ) communities to be predominantly functionally underdispersed because the stringent

environmental conditions of caves should filter a narrow set of trait combinations, resulting in lower functional richness than what would be expected for a given species richness. Concurrently, we predict that ( $H_{1b}$ ) limiting similarity plays a stronger role in cases where more niches are available and where local conditions allow for smaller niche overlap (e.g. larger caves, larger karst areas, regions with higher diversity of climates), leading to character displacement.

At the  $\beta$ -diversity level, we hypothesize that ( $H_2$ ) environmental factors have a stronger effect than geographical distance on functional turnover. This is because we expect that functional composition is strongly influenced by local environmental conditions, which modulate the availability of niches and the potential for species interactions.

## 2 | MATERIALS AND METHODS

### 2.1 | Community-level data

We obtained data for subterranean spider communities across Europe from Mammola et al. (2019a). The dataset comprises data from 475 subterranean sites (limestone, volcanic, talus and salt caves, as well as artificial sites including mines, blockhouses and cellars; the general term 'cave' is used hereafter) across 27 European countries, covering a latitudinal range from 35° to 70°. The dataset only includes subterranean sites for which the spider fauna is exhaustively known. For each site, the spider composition is represented as incidence data—presence/absence of each species. The database includes 326 species (average [ $\pm$ SD] number of species per cave of 4.3 [ $\pm$ 2.35]; range: 0–15). Note that we focused solely on 'subterranean spiders' (Mammola et al., 2018, 2022), excluding 'accidental' surface species (sensu Trajano & de Carvalho, 2017) occasionally found underground.

### 2.2 | Environmental and geographical gradients

We collated a site-by-environment matrix including local-scale environmental characteristics of each cave and broad-scale variables extracted from raster layers using the coordinates of the cave entrance. Furthermore, from the coordinates of each cave we calculated pairwise geographical distances among caves (expressed in decimal degrees), useful for  $\beta$ -diversity analyses (see subsection 'Calculation of  $\alpha$ - and  $\beta$ -diversity').

As local-scale predictors, we used the altitude of the cave entrance (in metres a.s.l.), the main entrance size (estimated area of the main entrance in square metres), cave development (total planimetric development of the cave in metres) and cave depth (total drop in metres). These are frequently used variables in macroecological analyses focused on caves (Jiménez-Valverde et al., 2017), which we here interpreted as proxies for local-scale conditions and niche space availability. For example, caves with a

vertical drop and a large entrance tend to accumulate more external food resources (detritus) than horizontal caves with a narrow entrance.

As broad-scale predictors, we included three climatic variables (mean annual temperature, annual temperature range, cumulative precipitation), one variable reflecting availability of carbonatic rocks (karst) and one biogeographical factor (the distance of each cave to the margin of the glacier in Last Glacial Maximum; ca. 21,000 years ago). We extracted climatic data from WordClim 2 rasters (Fick & Hijmans, 2017) at a resolution of 2.5 min. Although broad-scale variables may fall short in capturing microclimatic variability within caves (Ficetola et al., 2020), they are good surrogates for general subterranean climatic conditions (Christman et al., 2016; Mammola & Leroy, 2018; Sánchez-Fernández et al., 2018; Zigmajster et al., 2014). We extracted the size of the karst patch in which a cave occurs using the World Map of Carbonate Rock Outcrops (version 3.0). Given that most locations in our database were karst caves, we interpreted this variable as a *proxy* of habitat availability in the surrounding of each cave, and an indirect measure of habitat connectivity (Bregović & Zigmajster, 2016; Curl, 1986). Finally, we derived the distance of each cave from the Last Glacial Maximum glacier from reconstructions by Ehlers et al. (2011). We interpreted this as a *proxy* for the influence of past glacial cycles on the current distribution of subterranean species (Assmann et al., 2010; Mammola, Schönhofer, et al., 2019).

## 2.3 | Functional traits

For each spider species included in the database, we derived functional traits from Mammola et al. (2022). This trait database contains 64 traits, with some redundancy across traits, and many traits riddled with a high proportion of missing data (>50% observations). For this analysis, we selected a subset of 20 traits (8 continuous, 9 binary and 3 fuzzy coded) from the whole trait matrix. This subset of traits maximizes the information contained in the trait database (Mammola et al., 2022), while minimizing the number of missing data and hence the need for trait imputation (the full list of traits and their distributions is available in Figure 1). The selected traits represent: (i) general morphology and size of species (average body size, prosoma shape, sexual size dimorphism). Body size and shape are meant to be related to habitat (pore) size (Pipan & Culver, 2017) and metabolic processes (Mammola & Isaia, 2017). Sexual size dimorphism is meant to provide information on sexual selection mechanisms operating in subterranean environments (Mammola et al., 2022); (ii) morphological adaptation to subterranean conditions (eye measures [AME, ALE, PME, PLE], eye reduction, degree of pigmentation, leg elongation). This combination of traits captures the degree to which each species is morphologically adapted to the permanent darkness of subterranean ecosystems (Culver & Pipan, 2015; Mammola & Isaia, 2017) and (iii) webs and hunting strategies, including numerous traits capturing important differences in the modes of life of spiders

(Cardoso et al., 2011). To ensure exact matching between the spider species names in the community and trait matrices, we standardized and updated taxonomy using the function *checknames* in the R package 'arakno' version 1.1.1. (Cardoso & Pekar, 2022).

## 2.4 | Data analysis

We analysed data in R version 4.1.2 (R Core Team, 2021), using the suite 'tidyverse' (Wickham et al., 2019) for data manipulation and visualization. In all functional diversity analyses, we followed the general analytical pipeline described in Mammola et al. (2021), and the protocol for transparent reporting by Palacio et al. (2022). A reproducibility checklist for the study is available in Table S1. Since functional analyses were computationally demanding, we ran all analyses in high-performance computing services (see 'Acknowledgments').

### 2.4.1 | Data exploration

We carried out data exploration following Palacio et al. (2022), checking variable distribution, multicollinearity and the presence of missing data (Figure 1). As a result of data exploration, we standardized all continuous traits (mean = 0 and standard deviation = 1) to ensure comparable ranges among different traits. In the environmental matrix, we checked variable distributions and log-transformed all numerical variables (except coordinates, annual temperature range and mean temperature) to homogenize distribution and reduce the effect of outliers. None of the predictors showed correlation values higher than Pearson's  $r > \pm 0.7$  (Zuur et al., 2009).

### 2.4.2 | Functional space estimation

We estimated the trait space of each cave using probabilistic hypervolumes (Blonder, 2019; Blonder et al., 2014; Mammola & Cardoso, 2020). Probabilistic hypervolumes have a key advantage over other commonly used trait-space characterizations (e.g. dendrograms [Petchey & Gaston, 2002] or convex hulls [Cornwell et al., 2006]), in that they allow the detection of areas of higher or lower density in the trait space, thus representing uneven probabilities of finding a species with a given trait combination throughout the boundaries of the trait space (Blonder, 2016; Mammola & Cardoso, 2020).

Prior to analyses, we excluded caves with less than three species because these might lead to uninformative trait spaces, resulting in a total sample size of 367 caves. Since the trait matrix was a mixture of continuous, binary and fuzzy-coded traits, and contained missing data for certain traits, we used a Gower distance to estimate trait dissimilarity among species (Gower, 1971). In calculating Gower distance, we used the optimization method by de Bello et al. (2021) to attribute weight to traits within the three groups of variables (column 'grouping' in Figure 1). This method addresses the issue of uneven contributions from different traits,

FUNCTIONAL TRAIT	MEAN ± SD	RANGE	N (%)	DISTRIBUTION	GROUP
AVERAGE BODY LENGTH	4.30 ± 3.02	0.52 – 25.00			Morphology
PROSOMA SHAPE	1.25 ± 0.25	0.29 – 2.62			Morphology
SEXUAL SIZE DIMORPHISM	0.94 ± 0.12	0.62 – 1.72			Morphology
ANTERIOR LATERAL EYES (ALE)	0.08 ± 0.07	0.00 – 0.27			Adaptation
ANTERIOR MEDIAN EYES (AME)	0.05 ± 0.06	0.00 – 0.30			Adaptation
POSTERIOR LATERAL EYES (PLE)	0.09 ± 0.14	0.00 – 1.00			Adaptation
POSTERIOR MEDIAN EYES (PME)	0.09 ± 0.14	0.00 – 1.00			Adaptation
FEMUR ELONGATION	0.80 ± 0.40	0.18 – 2.67			Adaptation
ABSENCE OF EYES		Yes/No	48 (18.11%)		Adaptation
EYE REGRESSION		Yes/No	68 (25.66%)		Adaptation
<b>EYE ONTOLOGY</b>					
PRESENT		Yes/No	189 (71.05%)		Adaptation
ABSENT DUE TO ADAPTATION		Yes/No	24 (9.02%)		Adaptation
ABSENT DUE TO ONTOLOGY		Yes/No	53 (19.92%)		Adaptation
<b>PIGMENTATION</b>					
PIGMENTED		Yes/No	67 (25.19%)		Adaptation
PARTLY PIGMENTED		Yes/No	44 (16.54%)		Adaptation
VARIABLE		Yes/No	11 (4.14%)		Adaptation
DEPIGMENTED		Yes/No	144 (54.14%)		Adaptation
<b>GUILD</b>					
ACTIVE HUNTER		Yes/No	39 (14.66%)		Ecology
AMBUSH HUNTER		Yes/No	1 (0.38%)		Ecology
ORB WEB		Yes/No	6 (2.26%)		Ecology
SHEET WEB		Yes/No	165 (62.03%)		Ecology
SPACE WEB		Yes/No	188 (70.68%)		Ecology
TUBE WEB		Yes/No	28 (10.53%)		Ecology
<b>HUNTING STRATEGY</b>					
CAPTURE WEB		Yes/No	228 (85.71%)		Ecology
SENSING WEB		Yes/No	1 (0.38%)		Ecology
NO WEB		Yes/No	37 (13.91%)		Ecology
SPECIALIZED DIET (STENOPHAGOUS)		Yes/No	2 (0.75%)		Ecology

**FIGURE 1** Summary of the traits used in the analysis. We refer to Mammola et al. (2022) for a full description of traits and their hypothesized functional meaning. Column 'Group' refers to the grouping used in the estimation of weights for the Gower distance sensu de Bello et al. (2021), whereby: 'Adaptation' are traits related to morphological adaptation to subterranean conditions (especially darkness); 'Morphology' are traits describing general morphology of species and 'Ecology' refers to traits describing webs and hunting strategies.

especially fuzzy-coded ones, in calculating multi-trait dissimilarities. The solution involves determining weights that minimize variations in the correlation between the dissimilarity of individual traits and the multi-trait dissimilarity. This ensures that each set of traits exerts a comparable influence on the overall multi-trait dissimilarity (de Bello et al., 2021).

We analysed the resulting distance matrix through Principal Coordinate Analysis with the R package 'ape' version 5.5.0 (Paradis

& Schliep, 2019), extracting three orthogonal axes that we used to delineate the probabilistic hypervolumes for each cave. Using three trait axes ensures a good trade-off between accuracy and computation time (Graco-Roza et al., 2022; Mouillot et al., 2021). We constructed hypervolumes with a Gaussian kernel density estimator and a default bandwidth for each axis (Blonder et al., 2018), as implemented in the function *hypervolume\_gaussian* in the package 'hypervolume' version 3.0.1 (Blonder, 2022).

### 2.4.3 | Calculation of $\alpha$ - and $\beta$ -diversity

We measured the properties of the estimated trait spaces using hypervolume-based functions (Mammola & Cardoso, 2020) from the R package 'BAT' version 2.7.1 (Cardoso et al., 2015, 2021). We calculated the functional richness of each community ( $\alpha$ -diversity) as the total volume of each hypervolume (*kernel.alpha* function). We estimated pairwise functional  $\beta$ -diversity among communities as a Sørensen dissimilarity index, calculated through a modified version of the *kernel.beta* function that enables parallel estimation of pairwise comparisons (Graco-Roza et al., 2022). This estimation of  $\beta$ -diversity further decomposes the two processes underlying overall dissimilarity ( $\beta_{\text{total}}$ ) among hypervolumes following Carvalho and Cardoso (2020), namely: the replacement of trait space between communities ( $\beta_{\text{replacement}}$ ), and the net differences between the amounts of trait space enclosed by the two communities ( $\beta_{\text{richness}}$ ).  $\beta$ -diversity ranges from 0 (identical trait spaces) to 1 (fully dissimilar trait spaces).

### 2.4.4 | Null modelling

Estimations of functional diversity are mathematically dependent on the taxonomic diversity, particularly the species richness feature for  $\alpha$ -diversity and species composition for the  $\beta$ -diversity. Statistically controlling for this association may reveal the actual degree of importance of trait composition to community patterns (Götzenberger et al., 2016; Mammola et al., 2021). To this end, we randomly permuted without replication the rows of the initial trait matrix 999 times to generate a null distribution of each hypervolume-based trait space. For each random iteration, we calculated all  $\alpha$ - and  $\beta$ -diversity measures. We estimated significant deviation of observed values from the null distribution as the proportion of instances where the estimated values were less than the observed values, plus half of the instances where the estimated values were equal to the observed values, divided by the total number of estimated values. Specifically, we determined significance by a threshold of rank  $<0.025$  or  $>0.975$ . We estimated standard effect sizes (SES) using probit-transformed  $p$ -values (Lhotsky et al., 2016). Probit transformation is used as an alternative to logit transformation in generalized linear models to transform probabilities into the minus-infinity-to-infinity range (Dobson, 2002). We chose this approach because it is known to be less sensitive to skewed distribution of null values (Lhotsky et al., 2016). This approach is known to partially underestimate the effect size when the observed value is completely outside the null distribution; however, this problem was trivial in our case, as none of our observed values fell outside the null distribution (that is,  $p$ -value of 0 or 1).

### 2.4.5 | Hypothesis testing

To test our first set of hypotheses on alpha diversity patterns ( $H_1$ ), we modelled the relationship between SES values for functional richness ( $\alpha$ -diversity), and all local and broad-scale environmental

characteristics of each cave using a generalized least squares fitted with the package 'nlme' version 3.1-157 (Pinheiro et al., 2019). To account for spatial autocorrelation, we introduced an exponential correlation structure on the longitude and latitude coordinates of each cave. Prior to model fitting, we standardized all predictors (mean=0 and standard deviation=1) to ease model convergence. We validated the model by inspecting the normality of residuals, heteroscedasticity and degree of collinearity (Zuur et al., 2009).

To test our hypothesis on beta diversity pattern ( $H_2$ ), we used a Bayesian bootstrap extension of generalized dissimilarity modelling (BBGDM), as implemented in the R package 'bbgdm' version 1.0.1 (Woolley et al., 2017). Generalized dissimilarity modelling is a matrix regression technique that incorporates variation in the rate of compositional turnover along an environmental or spatial gradient (non-stationarity) in a monotonic nonlinear fashion (Ferrier et al., 2007; Mokany et al., 2022). Because the elements of a dissimilarity matrix are not fully independent, BBGDM uses a Bayesian bootstrap procedure to correct the uncertainty of model parameters (Woolley et al., 2017). We used as input the predictors and the functional  $\beta$ -diversity matrices. We fitted individual BBGDMs for the three functional  $\beta$ -diversity matrices ( $\beta_{\text{total}}$ ,  $\beta_{\text{replacement}}$  and  $\beta_{\text{richness}}$ ) with default parameters of three I-splines for each predictor and default knot values.

Because we ran BBGDM for both the actual  $\beta$ -diversity matrices and also the  $\beta$ -diversity matrices resulting from null trait matrices (see section 'Null modelling'), several metrics of SES could be derived to address different questions. Here, we tested whether a given variable had a stronger or weaker effect on  $\beta$ -diversity than what would be expected for a given change in species composition by extracting the sum of splines coefficients for each variable in the 999 BBGDMs. This way, we generated a null distribution of model coefficients which could further be tested using non-parametric SES. The sum of spline coefficients of each variable describes the total change in  $\beta$ -diversity promoted by a single predictor holding all other predictors constant. Furthermore, we tested whether SES values change along the environmental or geographical gradient. This is relevant to evaluate if changes in trait composition are disproportionately stronger (positive SES) than changes in species composition when caves are in close geographical proximity, and disproportionately weaker (negative SES) than changes in species composition when caves are far apart. To this end, we extracted the prediction values for all the sites in each of the null BBGDMs and used these to generate a null distribution of prediction values which was further compared against the observed predictions and converted into SES values.

## 3 | RESULTS

### 3.1 | Cave spider's trait space

A representation of the trait space in which the species included in the analysis are positioned is shown in Figure 2. Most traits included in the analysis contributed to the three synthetic PCoA axes, except

for sensing web, ambush hunters and food specialist (Table S2). Adaptations to subterranean conditions mostly correlate with both PCoA 1 and 2, encompassing traits related to eye diameter and leg elongation. Body length correlates predominantly with PCoA 1, creating a gradient from large to small-sized species. Hunting strategy is mainly correlated with PCoA 2, resulting in a gradient due to spiders employing different types of webs and active hunters that do not rely on webs for prey capture. The functional composition of the species included in our dataset clustered in three major groups. The first cluster (Figure 2, top left) includes large web-weaver spiders (e.g. *Meta* spp., *Pimoa* spp., various genera of Agelenidae), typically inhabiting cave entrances and thus exhibiting a lower degree of morphological adaptation to subterranean conditions. The second cluster (Figure 2, bottom left) consists primarily of large-sized active hunters, such as Segestridae and Dyseridae. The latter includes some of the most specialized subterranean species in the database

(several eyeless and fully depigmented species), which are primarily found in the Dinaric karst. The third cluster (Figure 3) on the right is the most dense, encompassing most Linyphiidae, Nesticidae and Leptonetidae, with numerous species of smaller size showing varying degrees of subterranean adaptations and mostly hunting with webs.

### 3.2 | $\alpha$ -Diversity

SES values for the functional richness of each community were left-skewed, with 63% of caves displaying a prevalence of functional underdispersion over functional overdispersion (Figure 3a,b). Still, most of these caves clustered towards SES values close to zero (Figure 3b), with only seven communities completely underdispersed and one completely overdispersed ( $p < 0.05$ ). In general, caves with a prevalence of

TABLE 1 Estimated regression coefficients for the generalized least square model.

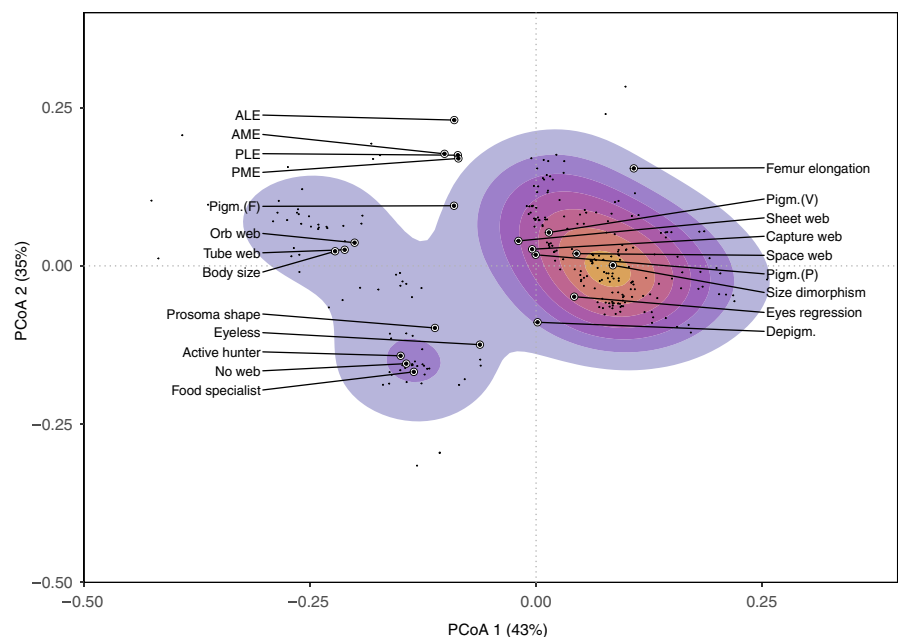
Term	Estimate	Standard error	t-Statistic	p-Value	VIF <sup>a</sup>
Intercept	-0.23	0.05	-5.02	>0.001	
Entrance size (m <sup>2</sup> )	-0.01	0.05	-0.16	0.870	1.17
Development (m)	-0.02	0.05	-0.38	0.707	1.27
Negative drop (m)	0.11	0.05	2.16	0.031	1.21
Elevation (m)	0.1	0.05	1.77	0.077	1.35
LGM ice distance (km)	0	0.06	0.01	0.994	1.3
Karst area (km <sup>2</sup> )	0.12	0.05	2.33	0.020	1.22
Temperature (°C)	0.06	0.06	0.91	0.364	1.86
Annual range (°C)	0.26	0.06	4.22	>0.001	1.66
Precipitation (mm)	0.01	0.06	0.14	0.889	1.7

Note: Significant values are highlighted in bold.

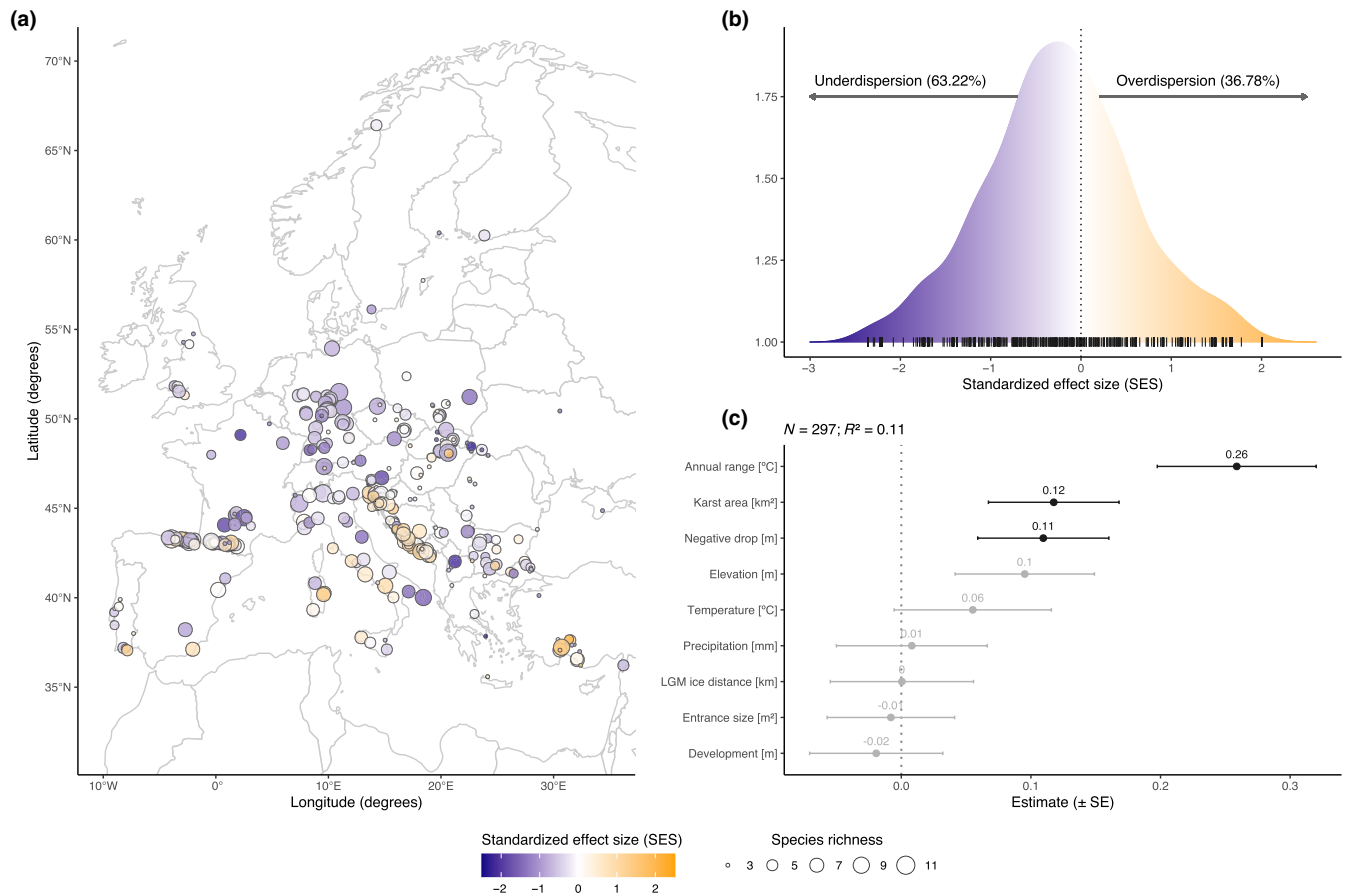
Abbreviation: LGM, last glacial maximum.

<sup>a</sup>Variance Inflation Factor.

FIGURE 2 Distribution of European subterranean spiders along the first two axes of a principal coordinate analysis describing the trait similarity among species. Gradient of colour denote density of species—higher density in darker areas. The small dots in the figure represent the position of each species in the trait space while the larger circles indicate the centroid position of each trait value.







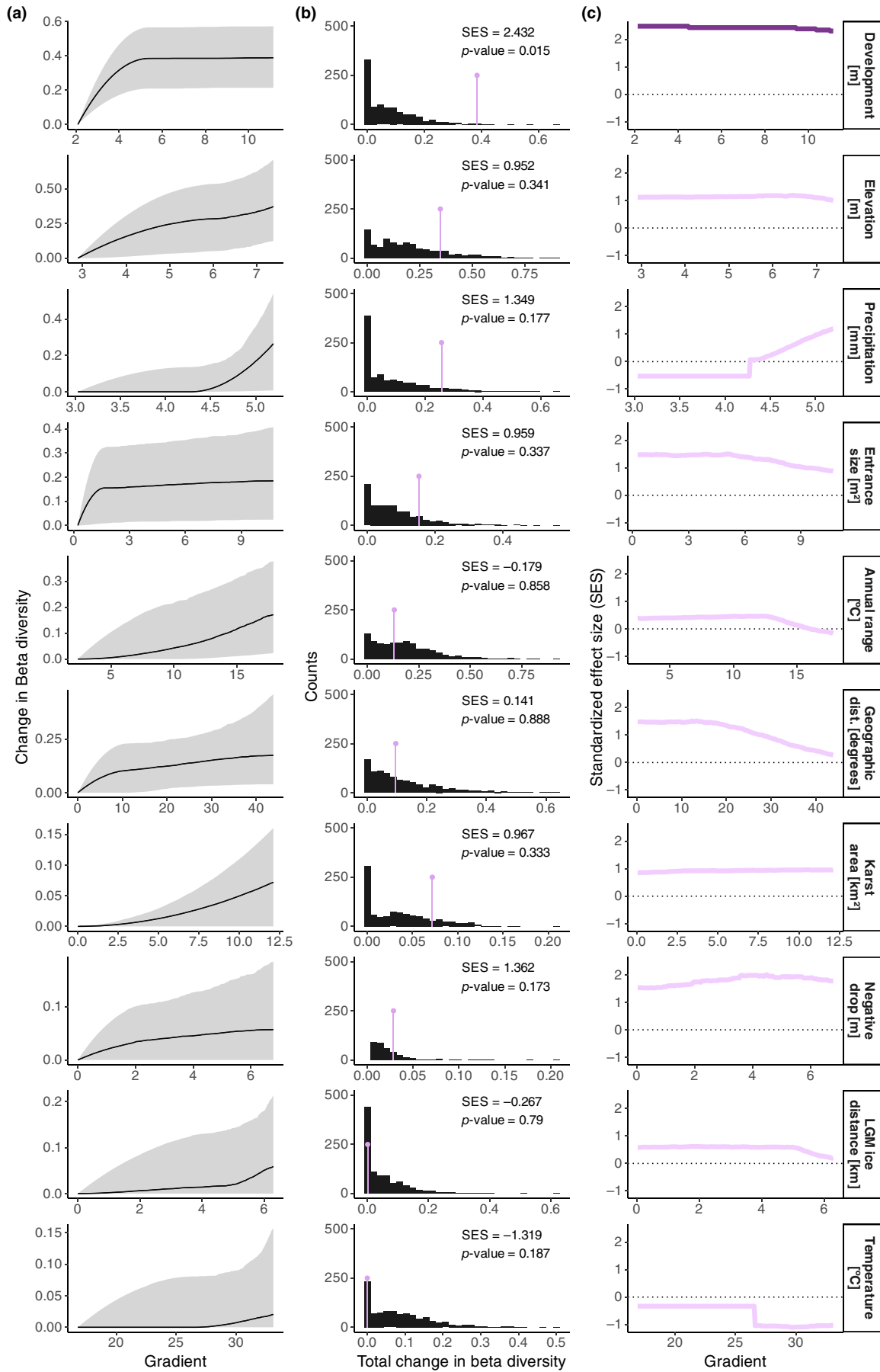
**FIGURE 3** Functional diversity at the  $\alpha$ -diversity level for subterranean spider communities in Europe. (a) Distribution of the studied caves ( $N=367$  caves). The size of each dot represents species richness. Dots are coloured according to their standard effect size (SES) value for functional richness, where functional richness is estimated as the volume of the hypervolume representing each cave's trait space. (b) Density of SES for functional richness across the studied caves. Percentage of caves with negative or positive SES values are indicated. Dark lines at the bottom of the density curve show the frequency of observed values. (c) Environmental factors driving variation of SES values for functional richness. Estimated parameters are based on a generalized least square model (significant effect in a darker colour). Error bars indicate standard errors. The exact estimated regression parameters and  $p$ -values for the model are in Table 1. Note that the sample size of this model is 297 (not 367) because of missing data in the environmental data for some caves. LGM, last glacial maximum.

overdispersion were concentrated at southern latitudes, especially in the Dinaric karst (western Balkans) (Figure 3a). A generalized least squares model fitted through the data suggested that communities in caves with a greater depth (negative drop), occurring within larger karst areas, and in areas with a broader annual temperature range were more likely to be functionally overdispersed (Figure 3c). The addition of spatial component did not improve our model significantly, suggesting the absence of spatial correlation in our data.

### 3.3 | $\beta$ -Diversity

Patterns of functional  $\beta$ -diversity were primarily driven, based on effect sizes, by cave development, elevation, precipitation, entrance size and annual range of temperature. The contribution of additional predictors was negligible (Figure 4). The rate of turnover along the cave development gradient was monotonically asymptotic, with rates of turnover steeply increasing in the first portion of the gradient

**FIGURE 4** Results of Bayesian bootstrap generalized dissimilarity modelling for change in total functional  $\beta$ -diversity ( $\beta_{\text{total}}$ ) of subterranean spider communities across Europe (i.e. unit increase in mean  $\beta$  along a given gradient). Variables are sorted by their contribution (on top: highest contribution). (a) Fitted I-splines (partial regression fits) for the considered environmental and geographical gradients. The maximum height reached by each curve indicates the total amount of compositional turnover explained by that variable (holding all other variables constant), whereas the shape of each spline indicates how the rate of compositional turnover varies along the gradient. (b) Distribution of expected values (histogram) versus the observed value (coloured line) of each gradient, based on null modelling (999 iterations). In other words, these panels provide information as to whether the effect of a given variable is higher or smaller than expected given species composition. (c) Variation in the magnitude of the standard effect size (SES) values along the observed gradient. In other words, these panels provide information as to whether the effect of a given variable in determining trait dispersion changes along the gradient. In (b) and (c), significant effects (Rank  $<0.025|>0.975$ ) are highlighted with a darker purple.



before reaching a plateau (Figure 4a). This effect was significant along the whole gradient (Figure 4c). We also observed some degree of turnover along the gradients of elevation, precipitation and temperature range. That is, communities in caves with different elevations, temperatures and precipitation regimes tend to express different functions. For precipitation, SES values indicated that there is underdispersion along the first half of the gradient and an increasing predominance of functional overdispersion in the second half of the gradient. The pattern was reversed for the annual range of temperature.

The effect of geographical distance on functional  $\beta$ -diversity followed a power-law curve (linearly asymptotic), and was rather weak—that is to say, at increasing distance between two caves, there was only a limited turnover in functional richness (Figure 4a). Interestingly, when looking at variation in the effect over the geographical gradient (Figure 4c), we observed a prevalence of trait overdispersion at a smaller spatial scale which progressively decreased towards zero when caves were >2000 km apart.

Most of the variation in  $\beta$ -diversity was due to replacement of trait space among communities ( $\beta_{\text{replacement}}$ ; Figure S1), with patterns largely mimicking the variation in total  $\beta$ -diversity ( $\beta_{\text{total}}$ ). Conversely, the contribution of  $\beta_{\text{richness}}$  was negligible in all cases except for cave drop (Figure S2).

## 4 | DISCUSSION

Focusing on the natural laboratory offered by caves, we studied functional diversity patterns in subterranean spider communities across Europe, testing general hypotheses ruling community assembly. Two important points, largely generalizable across systems and species pools, emerge from our analysis.

The first point is that environmental filtering and limiting similarity are not mutually exclusive processes (Pillar et al., 2009). Even in caves, where environmental filtering is meant to be particularly strong (Gibert & Deharveng, 2002), the relative influence of these two processes varied substantially given the local habitat conditions. Whereas the direction of SES for functional richness was predominantly towards underdispersion (Figure 2b), the majority of values were close to zero. This result may be an outcome of environmental filtering and limiting similarity both acting in equally weak or strong, but opposing, directions—although other scenarios cannot be ruled out. Environmental filtering is indeed a demonstrably strong factor in caves, with many traits and portions of the potential functional space being absent. Yet, our results add quantitative evidence to a growing body of literature (Culver & Pipan, 2015; Fernandes et al., 2016; Mammola et al., 2016; Trontelj et al., 2012) emphasizing the importance of reconsidering the role of niche-based processes as an important force driving the evolution of cave communities.

Subterranean communities with local trait overdispersion were more frequently associated with large karst patches, areas with broader temperature ranges and deeper caves (Figure 2c),

all conditions that provide more niche space to be exploited. This was particularly evident in the Dinaric karst (western Balkans), the most important global hotspot of subterranean biodiversity (Culver et al., 2006; Sket, 2011), where virtually all cave trait spaces were predominantly overdispersed. Large patches of karst, such as in the Dinarides, imply greater habitat availability (Bregović & Zagmajster, 2016) and, possibly, connectivity (Curl, 1986), hence a broader niche space. In contrast, in smaller regions the limited habitat availability (i.e. more stringent conditions) constrained the functional space and the number of co-existing functional forms hence leading to fewer overdispersed communities compared to larger Karstic regions. However, the size and resolution of our dataset may not be sufficient to confirm the relevance of limiting similarity to our patterns, as they could also emerge from weaker environmental filtering or stronger niche complementarity. Likewise, the positive association between trait overdispersion and temperature range can be interpreted in the light of the influence of temperature variability on species range size and dispersal (Ghalambor et al., 2006; Janzen, 1967; Polato et al., 2018), including subterranean spiders (Mammola, Piano, et al., 2019). Finally, communities in caves with a greater drop tend to be, on average, predominantly overdispersed. Deeper caves tend to express more areas with differing availability of resources, offering higher trait differentiation.

The second point emerging from our study is the importance of scale in the perception of community assembly patterns. Accounting for scale in trait analyses has been achieved, for example, by looking at variations in individual trait values along ecological gradients (e.g. elevation; Swenson et al., 2011), or by contrasting taxonomic and functional diversity change in highly dispersive organisms (e.g. birds; Jarzyna & Jetz, 2018). Here, we devised a novel approach to account for the magnitude of trait dispersion change along the studied ecological gradients, combining gradients and traits in a single model. We observed how functional  $\beta$ -diversity patterns varied along multiple ecological gradients. The most important one was the difference in the development among the studied caves, whereby the largest replacement of functions occurred between pairs of caves with divergent development (i.e. large vs. small caves; with an inflection point with cave >5 m in development). A plausible explanation is that cave development is a proxy for the availability of spatial niches. In particular, small caves will be primarily colonized by spiders adapted to the cave entrance conditions, and large caves will often sustain a greater number of specialized species, accounting, overall, for drastically different functions. Other important gradients of variations were elevation and precipitation, reflecting the influence of climatic conditions and habitat heterogeneity in the local structuring of functions.

In terms of distance decay in functional diversity, trait composition changed randomly with respect to species composition, with a slightly higher likelihood of a more pronounced replacement of traits that decreased along the gradient (Figure 4c). This means that, although some replacement of traits does occur, overall turnover happens by substitution of species pursuing similar functions. Still, when decoupling functional patterns from taxonomic diversity, the functional responses varied along the geographical gradient according to

theoretical expectations, showing stronger overdispersion at smaller distances, and progressive moving towards SES values of zero at larger distances. This highlights the scale dependency of regional trait dispersion, with nearby caves more likely to have interacting communities and such effect becoming weaker with increasing spatial distance.

## 5 | CONCLUSIONS

The use of caves as model systems for investigating (macro-)ecological patterns in space and time is still underexploited (Mammola, Amorim, et al., 2020). This is partly a problem related to the objective difficulties of working in caves (resulting in a general lack of data at the right resolution) and partly a methodological problem. Nonetheless, thanks to the recent development in databases of species distributions and traits, and the emergence of novel analytical tools, there is a vast potential to leverage these systems as ideal settings in which to model across space. Using an explicit functional diversity approach, we showed that (i) even systems with stringent environmental conditions maintain the potential for trait differentiation, especially in areas of greater habitat connectivity and (ii) the relative influence of environmental filtering and limiting similarity changes with scale, along ecological gradients of cave development, elevation, precipitation, entrance size and annual temperature range. Overall, our findings reconcile contrasted views about the relative importance of the two main mechanisms shaping patterns of biodiversity and provide a conceptual foundation to account for scaling effects in the study of community assembly. This information is key amidst escalating global anthropogenic threats affecting surface (Bowler et al., 2020) and subterranean ecosystems (Nanni et al., 2023; Vaccarelli et al., 2023), insofar as realistic predictions of biodiversity change require explicitly accounting for community assembly processes (Ovaskainen et al., 2019).

### AUTHOR CONTRIBUTIONS

SMA, CG-R and PC conceived the idea. SMA and CG-R designed methodology. All authors except SMA, PC and CG-R collected trait data. CG-R led the analysis, with support by SMA. SMA wrote the first draft, with support by CG-R. All authors contributed to the writing with suggestions and critical comments.

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### CONFLICT OF INTEREST STATEMENT

None declared.

### DATA AVAILABILITY STATEMENT

Data used in the study are available in Figshare (Community data: <https://doi.org/10.6084/m9.figshare.8224025.v1>; Trait data: <https://doi.org/10.6084/m9.figshare.16574255>). Metadata and data collection methods are described in Mammola et al. (2019a); Mammola et al. (2022). Climatic rasters are available from WordClim 2 (Fick & Hijmans, 2017), last glacial maximum reconstruction from Ehlers et al. (2011) and carbonate rocks maps from the World Map of Carbonate Rock Outcrops version 3.0. Annotated R codes to generate the analysis are available on GitHub ([https://github.com/StefanoMammola/Mammola\\_et\\_al\\_Macroecology\\_spider\\_traits.git](https://github.com/StefanoMammola/Mammola_et_al_Macroecology_spider_traits.git)).

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## SUPPORTING INFORMATION

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

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