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Where We're Going, We Won't Need Eyes to See: Distributional Range Size Drivers of European Subterranean Spiders

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ABSTRACT

Aim: Understanding why closely related species can have drastically different distributional range sizes is a fundamental question in biology. However, answering this question is challenging due to the multiple inter-related factors that shape species distributions, particularly in continental regions, where unclear ecological and geographic boundaries and long evolutionary histories obscure the main drivers of range size variation. Island-like subterranean ecosystems such as caves provide ideal models for studying species' biogeography and evolution due to their well-defined boundaries, reduced species pools, and often easily defined abiotic limiting factors. We aim to better understand the factors influencing distributional range size in subterranean species.

Location: Continental Europe.

Taxon: Spiders (Araneae).

Methods: We calculated the range size of all subterranean spiders in Europe. We used Variation Partitioning Analysis to determine the relative influence of phenotypic subterranean-related traits, historical factors, and potential sampling biases on various range size metrics while controlling for phylogenetic effects via different approaches.

Results: Subterranean phenotypic related traits emerged as one of the most significant determinants of range size. In addition, climatic events and conditions during the Last Glacial Maximum also played an important role in shaping the species' range sizes. Conversely, sampling biases, approximated as the density of roads and research institutions across the study area, had limited influence. We also detected that closely related species typically exhibited more similar range sizes.

Main Conclusions: While subterranean related traits emerged as the main predictor of range size variation, the processes shaping species' range sizes are complex and multifactorial. In addition to morphological specialization, historical events, phylogenetic relationships, and other unaccounted factors have also played a significant role in determining the current distributions of European subterranean spider species. Despite these uncertainties, our study represents an initial step toward understanding range size variation in subterranean spiders, with implications for cave evolution, subterranean biogeographic patterns, and conservation priorities—particularly given the close link between range size and extinction risk.

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1 | Introduction

Determining the drivers of species' range size is a fundamental question in ecology, evolutionary biology, and biogeography. Its importance lies in the fact that understanding the varying spatial extents of the species distribution may help to understand many biological aspects, such as species richness, distributions (Guo et al. 2022), or their ability to adapt to future environmental changes (Bridle and Hoffmann 2022). Not surprisingly, this knowledge has gained a crucial role in conservation evaluation strategies in the last decades (Baillie et al. 2004; Gaston and Fuller 2009).

Different factors have been proposed to explain what determines species' range size. Historically, species' distributions have been found to respond to temperature and other climatic conditions in numerous cases (G. C. Stevens 1989; Eeley and Foley 1999; Fernández and Vrba 2005; Alahuhta et al. 2020; Guo et al. 2022). The so-called Rapoport's rule (Rapoport 1982), which links species diversity and range size to their latitudinal or altitudinal distribution, has also been observed in different taxa in both marine (e.g., G. Stevens 1996; Fortes and Absalão 2010) and terrestrial ecosystems (e.g., Liu et al. 2020; Chen et al. 2022). However, factors beyond current climatic conditions have also been shown to play an important role in determining species' range size. For instance, historical events, such as glacial periods, have influenced species distributions across the globe (G. Hewitt 2003). Additionally, species' intrinsic biological traits have also been found to significantly affect their distributional range. Among these, several biological characteristics have a strong influence on species distribution, including dispersal ability (Böhning-Gaese et al. 2006), diet (Gregory and Gaston 2000) or morphological traits, such as body size (Gaston and Blackburn 1996). However, factors beyond species' intrinsic biology and their evolutionary or climatological history may also influence the observed distributional range. Previous studies have highlighted the role of human-related factors in shaping our understanding of species' true geographic distributions (see Sheth et al. 2012). For instance, the intensity and spatial uniformity of sampling efforts across a region can significantly affect our perception of a species' range (Gaston et al. 1996; Gaston 2003), resulting in underestimation of species' actual distribution due to poor or uneven sampling efforts. Altogether, these factors highlight the complexity of species' range formation and how the distributions we observe today have been shaped by multiple interacting influences (Brown et al. 1996).

Despite the well-established importance of understanding species' range size for our knowledge and the development of effective conservation strategies, vast portions of our planet's biodiversity remain undocumented. Moreover, existing knowledge is largely biased toward certain organisms that are either charismatic, useful, or harmful to humans (Mammola et al. 2023). More information is generally available on animals compared to plants (Wandersee and Schussler 1999), and among animals, research has disproportionately focused on birds and mammals compared to other groups (Bonnet et al. 2002). Within arthropods these biases are even more marked, where deeper knowledge is available only in a few cases (e.g., Van Swaay et al. 2008; Galimberti et al. 2021).

These biases are not limited to taxonomical groups. Certain environments that are difficult to access have also been underexplored, limiting our understanding of species distributions. A clear example is cave and other subterranean ecosystems, which have been systematically overlooked compared to surface habitats (Ficetola et al. 2019; Mammola et al. 2021). From our anthropocentric point of view, caves are often described as some of the most "extreme" environments on Earth (Mammola 2020). Nevertheless, this is a biased perspective, insofar as subterranean ecosystems are widespread and have been colonized by thousands of species from diverse phyla and ecological backgrounds worldwide (Barr and Holsinger 1985; Năpăruş-Aljančič et al. 2026).

Adapting to the selective conditions of caves entail the evolution of distinct traits. Some evolutionary consequences observed in subterranean-adapted species have been compared to those seen in other cases of speciation in discontinuous habitats, such as oceanic islands or mountain tops (Barr 1968; Barr and Holsinger 1985). For example, endemic species that have diversified in volcanic archipelagos tend to have lower dispersal abilities and smaller geographical ranges compared to their continental counterparts (Gillespie et al. 2008). A similar pattern can be observed in subterranean habitats, where species often exhibit limited dispersal (Trontelj 2019). Yet, dispersal ability by itself is not the only factor that may influence the variation in range size among cave-dwelling species. Subterranean organisms undergo a wide range of ecological and morphological adaptations. Subterranean fauna has been linked to traits such as loss of pigmentation, elongation of legs, and reduction of eyes (Howarth and Moldovan 2019). The degree of these morphological modifications varies depending on the extent of adaptation to cave life and the time since colonization (e.g., Desutter-Grandcolas 1997; Arnedo et al. 2007; Mammola et al. 2020; Bellvert et al. 2022). These different traits could also play an important role in determining range size differences among cave-dwelling species.

Spiders are among the most diverse animal groups on Earth (Dimitrov and Hormiga 2021), with more than 53,000 described species to date (World Spider Catalog 2025). Despite their relatively small size and the absence of morphological traits associated with long-distance dispersal, such as wings like in several insect groups, spiders have demonstrated a remarkable ability to colonize distant regions. Many species use their silk to be carried by the wind, enabling them to travel long distances—a phenomenon known as ballooning (Bell et al. 2005). This process has played a significant role in the global colonization success of spiders, which are found across nearly all terrestrial habitats worldwide, except for Antarctica (Turnbull 1973). However, the colonization success of spiders is not limited to their vast geographical distribution but also extends to their ecological diversity (Cardoso et al. 2025). Spiders inhabit a wide range of ecological niches, and notably, they have successfully colonized and diversified in cave and other subterranean environments (Figure 1A), where they often become particularly abundant (Mammola and Isaia 2017a).

Previous studies have investigated whether various factors influence spider species' range size, such as colour polymorphism

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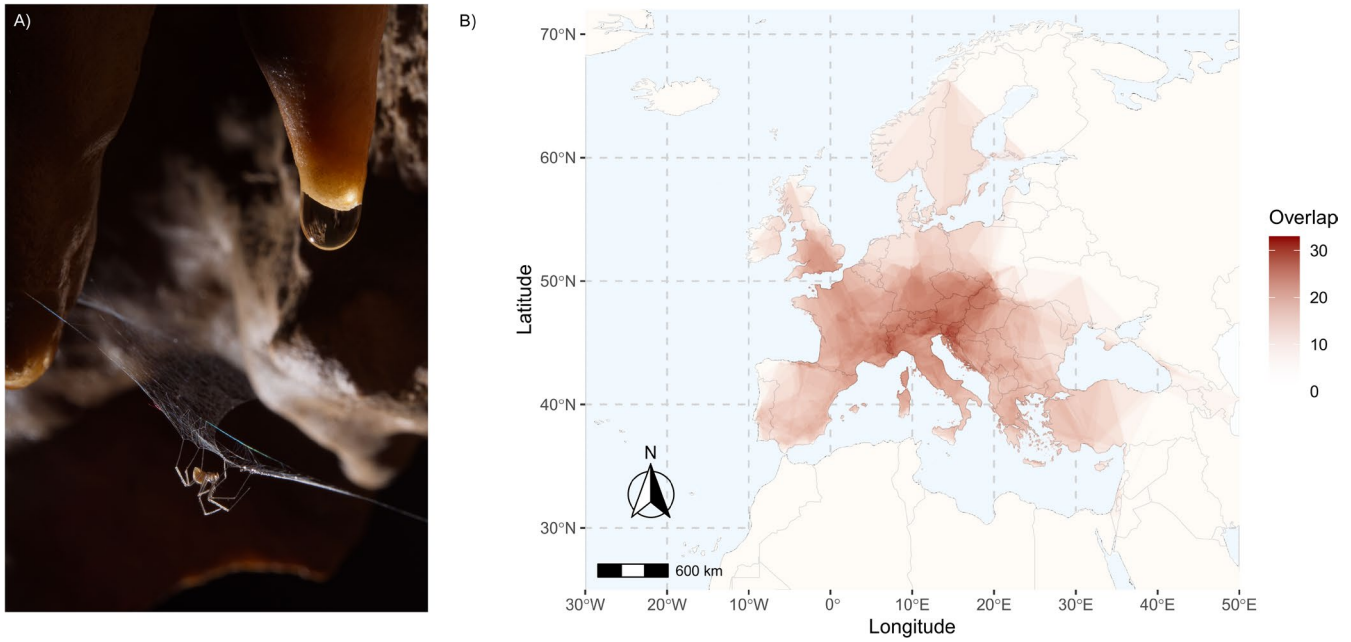

FIGURE 1 | (A) *Troglohyphantes pluto* Caporiacco, 1938 (Linyphiidae) in the cave Grotta Inferiore del Caudano (PI121, Frabosa Sottana, Cuneo, Italy), representing a spider species showing cave related traits (i.e., partial loss of pigmentations and elongation of legs). (B) Occupancy of subterranean and cave spider species at the European level. Species' range areas were calculated using convex hulls based on their known distributions. Shaded areas indicate regions where multiple species' ranges overlap, with darker shading reflecting higher degrees of overlap (double column).

(Salgado-Roa et al. 2024) and endosymbionts (Viel et al. 2024), though no significant effects were found in both cases. Other studies have explored the role of intrinsic and extrinsic biotic or abiotic interactions (Purcell and Avilés 2008). In addition, some traits have been shown to be evolutionarily preserved in spiders, such as body size (Gonçalves-Souza et al. 2014), a character also linked with the species range size (Gaston and Blackburn 1996). This would suggest that variation in species' distributions may be explained by phylogenetic relatedness. However, which factors most strongly determine the distributional range patterns observed in subterranean spiders remain unknown. Given the ongoing biodiversity decline driven by the current climate crisis (Pimm and Raven 2000; Thomas et al. 2004), addressing this knowledge gap is crucial. A deeper understanding of the differences and factors influencing the distributional occupancy of these species would not only provide valuable insights into future eco-evolutionary studies (see Urban et al. 2020 for a review on the topic), but would also be central for defining conservation priorities (e.g., Chichorro et al. 2019).

Here, we take on the challenge of gaining a deeper understanding of the factors that best explain differences in species range size among subterranean spiders across Europe—which we chose as a model system given the high availability of data compared to other regions or subterranean taxa (Mammola et al. 2022; Nicolosi et al. 2026). Specifically, we investigate which historical and biological traits might influence their current distribution, as well as whether human-related sampling biases, such as the density of road infrastructures and research institutions, affect our perception of the areas they occupy. We aimed to: (1) determine whether different spider families exhibit significant differences in species range size; (2) assess the impact of cave-related phenotypic traits (eye reduction, leg elongation, and pigmentation loss) on species distributional range; and (3) evaluate the relative contribution of phenotypic traits, past climatic and historical events, and human-induced sampling biases on the observed species range sizes.

2 | Methods

We conducted statistical analyses in R version 4.3.3 (R Core Team 2024) and spatial analyses in QGIS version 3.34 (QGIS Development Team 2024). Specific packages and functions are specified in the text.

2.1 | Focal Species

We extracted a list of subterranean spider species in Europe for which morphological and ecological data have been collected from the most recent checklist (Patiño-Sauma et al. 2026), comprising 637 species (28 families) as of 2025. Given that ecological and evolutionary dynamics can differ markedly on oceanic islands, we excluded all endemic species from Macaronesia from our analyses to prevent potential confounding factors. To estimate the range size of each species, we used the most up-to-date distributional data available (Nicolosi et al. 2026). This comprehensive dataset was compiled through a combination of field sampling, bibliographic reviews, publicly accessible online databases, and contributions from a network of researchers across Europe.

We quantified each species' range size using five metrics: (i) Extent of Occurrence (EOO), that is, the total area within the shortest continuous imaginary boundary (minimum convex polygon) encompassing all known occurrence records; (ii) the

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Area of Occupancy (AOO), which refers to the area within a species' EOO that is actually occupied by the species; (iii) maximum linear distance, that is, the maximum distance between the two most distant occurrence points; (iv) distribution dispersion, as the mean distance from all occurrence records to the distribution centroid; and (v) the total number of occurrences, included as a *proxy* measure of sampling intensity and abundance (see below). To assess the relationships among these metrics, we calculated pairwise Pearson's r correlations among them. If low correlations were observed ($|r| < 0.7$; Zuur et al. 2010), multiple range size metrics would be retained for subsequent analyses. Otherwise, a single representative metric would be selected. To minimize potential bias introduced by uneven sampling effort or highly abundant species, we prioritized the use of a range size metric that showed low correlation with the number of occurrences.

We used pairwise ANOVA comparisons to test whether range size varied significantly across spider families. We ran this analysis only on families represented by more than 10 species ($n = 282$ total species across 6 families).

2.2 | Morphological Underground Related Traits

To assess the influence of morphological traits on species' distributional range, we used phenotypic data for European cave and subterranean spider species derived from previous studies (Mammola et al. 2022; Patiño-Sauma et al. 2026). Cave adaptations are known to significantly affect morphology, with traits such as elongation of appendages, depigmentation, and eye reduction or loss being common among subterranean adapted species. To capture these key adaptations, we selected the following morphological characters: the length of the first femur and tibia (as indicators of appendage elongation), the degree of pigmentation (ordinal variable based on four levels: fully pigmented, variable, partly pigmented, depigmented), and the diameter of the anterior median eyes (AME). In cases where the AME were absent due to ontological rather than adaptive processes—particularly six-eyed families such as Dysderidae and Leptonetidae—or when AME data were unavailable, we used alternative eye measurements [e.g., anterior lateral eyes (ALE), posterior median eyes (PME), or posterior lateral eyes (PLE)].

To control for overall body size and isolate trait variation linked to cave morphologies, we calculated residuals from the regression of each morphological character against prosoma width, a widely used *proxy* for body size in spiders (Moya-Laraño et al. 2007, 2008). Finally, all different eye measurements were standardized to ensure comparability across species and eye types.

However, excluding size-related influences from the analysed traits may overlook important factors (Klingenberg 2016; Chong et al. 2024). Therefore, we repeated the analyses by incorporating allometric effects into the morphological traits. To achieve this, we included instead of the trait corrected by size the interaction between the absolute eye size and the species body size, again using the prosoma width as a proxy of this measure. We examined the relationship between the selected morphological traits and species' distributional range using Generalized Additive Models, implemented with the *mgcv* function from the "gam" R package (Hastie 2022). This analysis aimed to determine whether the degree of morphological traits, typically associated with subterranean adaptations exhibited by the different species, tends to have an effect on the distributional range sizes.

Importantly, variation in morphological traits among spider families may arise not solely from subterranean-related adaptations but also from phylogenetic constraints. Ideally, phylogenetic comparative methods would be used to disentangle the effects of evolutionary relatedness from adaptive morphological changes. However, the lack of a comprehensive and well-resolved phylogeny encompassing all subterranean-adapted spider species currently prevents such analyses. Nevertheless, we consider that an initial approach incorporating species' phylogenetic relationships is essential to better understand the relationships among factors influencing species' range size differences. To this end, we constructed a phylogenetic tree using available data from the NCBI database (Sayers et al. 2025; see Text S1 for molecular methods, Table S2.1 for the final list of used sequences, Table S2.2 for the information about the primers used, Table S2.3 for the profiles for the PCR amplifications and Figure S2.1 for the final phylogenetic tree) and our own unpublished sequences, totaling 287 species. We used a subset of our original dataset corresponding to species with available molecular information ($n = 185$) and repeated the previous analyses, correcting trait variables for phylogenetic relationships using phylogenetic independent contrasts via the *pic* function from the "ape" R package (Paradis and Schliep 2019).

Finally, to exclude morphological traits that did not play a significant role in explaining differences in species' range size from the final analyses (see below), we fitted generalized linear mixed models (GLMMs) using the *glmmTMB* function from the "glmmTMB" R package (Brooks et al. 2017) for each range size metric. We performed these analyses using both size-corrected traits and models including interactions between traits and species body size. In addition, we repeated the analyses while accounting for species' phylogenetic relationships.

For this purpose, we used the subset of species with available molecular data and controlled for phylogenetic non-independence using phylogenetic eigenvector regression (PVR). Principal coordinate eigenvectors were derived from a species-level phylogenetic distance matrix using the *pcoa* function from the "ape" R package. The two eigenvectors that best explained variation in range size were identified using GLMMs and included as covariates in all models, thereby accounting for phylogenetic autocorrelation in the residuals (Diniz-Filho et al. 2003, 2013).

2.3 | Historical Factors

In addition to the potential influence of morphological traits, other environmental factors may play a significant role in shaping species' distributional ranges. While present-day temperature is unlikely to have had a major impact, past climatic conditions or events, particularly those associated with glacial cycles, may have exerted a more substantial influence (Mammola et al. 2018, 2019; Knüsel et al. 2024). We used two proxy variables to account for these historical effects. First, we obtained mean temperature

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data from the Last Glacial Maximum (LGM) from the WorldClim 2 database (Fick and Hijmans 2017). For each species, we calculated the maximum range of mean temperatures across its known distribution during the LGM, providing a proxy for the climatic variability historically experienced within its range.

To evaluate the influence of past climatological events on species' distributional ranges, a factor previously shown to have strongly affected species distributions across Europe (G. M. Hewitt 1999), including subterranean ones (Mammola et al. 2018, 2019; Knüsel et al. 2024), we calculated the minimum distance from all currently known distributional locality for each species to the ice sheet margin that covered Europe during LGM. To do this, we created a raster layer representing Euclidean distances to the nearest point along the LGM ice sheet margin, based on the shapefile delineating its extent provided by Ehlers et al. (2011). We generated the raster with a spatial resolution of 0.0833° across the study area. To distinguish between areas covered and not covered by ice during the LGM, we applied a mask using the same shapefile. Pixels falling within the ice sheet polygons were assigned negative values, while those outside retained positive values, thereby encoding both proximity and coverage status in a single layer. The resulting raster reflects the shortest distance to the LGM ice margin, with positive values indicating ice-free areas and negative values indicating locations beneath the former ice sheet.

2.4 | Sampling Bias

Our current understanding of species distributions may also be influenced by factors unrelated to the species themselves or their biogeographic history. For example, some species may occur in regions that are more easily accessible to humans or in areas that have attracted more scientific attention due to particular ecological or biological characteristics. These factors can introduce biases into the recorded distribution data that we currently have (Hughes et al. 2021). To account for such potential sampling biases, we incorporated two proxies for human accessibility and research effort: road density and the spatial distribution of research institutions. We hypothesize that areas with higher road density and greater proximity to research institutions will exhibit increased sampling intensity and species detection rates, potentially leading to spatial biases in range size data that overrepresent species from easily accessible locations while under-sampling those from remote cave systems or logistically challenging sampling areas (Oliveira et al. 2025). We acknowledge that other human-induced impacts or factors may also alter our perception of the real species distribution. However, in the present study, we included the previously mentioned ones as a first approach to unveil if some of these biases may play any significant role in our perception of the species range size.

We obtained global road data from ArcGIS online (Esri 2025) and the geographic coordinates of universities and research institutions from the Grid Digital Science database (2021). To generate a raster layer representing the density of research institutions across Europe, we used kernel density estimation via the *Heatmap* function in QGIS. We employed the same spatial resolution as that used for the climatic variables and applied Scott's rule for bandwidth selection (Scott 1992), based on the number and variance of institution coordinates. Similarly, we calculated road density using the "Line Density" function, specifying the same pixel resolution and radius as above.

2.5 | Drivers' Impact Analyses

To assess the relative contribution of the three groups of factors (phenotypic traits, historical factors, and potential sources of sampling bias) in explaining variation in species' distributional range sizes, we conducted a variation partitioning analysis (VPA). Variation partitioning analysis decomposes the total variance in a response variable into components explained by different sets of predictor variables. Prior to this analysis, we standardized all continuous explanatory variables by subtracting the mean and dividing by the standard deviation to ensure comparable effect sizes among covariates.

We built model combinations for the VPA using generalized linear mixed models (GLMMs) implemented via the *glmmTMB* function from the "glmmTMB" R package (Brooks et al. 2017). To account for taxonomic relatedness, we included Family and Genus as in a nested random structure (1 | Family/Genus), thereby allowing us to evaluate the influence of the taxonomic relationships on species' range sizes. We carried out the VPA using the *varPart* function from the "modEvA" R package (Márcia et al. 2013), and extracted coefficients of determination (R^2) for each model using the *r.squaredGLMM* function from the "MuMIn" package (Bartoń 2024). The latter decomposes the variance explained by fixed effects alone (marginal R^2) and both fixed and random effects (conditional R^2), allowing us to also disentangle the influence of species taxonomic relatedness on range sizes. Again, we repeated these analyses incorporating species phylogenetic information including the two most relevant PVRs into the model.

3 | Results

3.1 | Subterranean Spiders Range Sizes

We included a total of 573 subterranean spider species in the analysis, representing 21 families (Agelenidae, Amaurobiidae, Anapidae, Cybaeidae, Dysderidae, Hahniidae, Leptonetidae, Linyphiidae, Liocranidae, Mysmenidae, Nesticidae, Pholcidae, Phyxelididae, Pimoidae, Segestriidae, Sicariidae, Sparassidae, Symphytognathidae, Telemidae, Tetragnathidae, and Theridiidae). The mean species area was $194{,}744.2 \pm 886{,}002.2\,km^2$ (EOO values). The species with the higher range area, *Meta menardi* (Latreille, 1804) (Tetragnathidae), occupied a total area of $9{,}210{,}512\,km^2$, whereas the most restricted species (often endemic to one or very few caves) had EOO values close to zero. The distributional records of these species encompass most of continental Europe, with some records extending into neighbouring regions such as Turkey, Georgia, and Israel (Figure 1B).

Among the range size metrics examined, the EOO showed strong positive correlations with all other metrics ($r > 0.7$; Figure S1.1). In contrast, the mean distance from the centroid exhibited the lowest correlation with the number of occurrences, making it less sensitive to abundance-related biases. Therefore, we selected both EOO and mean centroid distance for downstream analyses.

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Only six families (Agelenidae, Dysderidae, Leptonetidae, Linyphiidae, Nesticidae, and Pholcidae) contained more than 10 species and were included in the comparative analyses. These families had different mean range sizes (Figure 2) although no significant differences were observed between them. Pholcidae and Agelenidae showed the largest range sizes (Pholcidae = 461,528.3 ± 1,213,688 km^2, Agelenidae = 386,814.9 ± 1,043,180 km^2), and Leptonetidae and Dysderidae the smallest (Leptonetidae = 17,722.4 ± 71,422.3 km^2, Dysderidae = 1390.1 ± 6178.6 km^2).

3.2 | Morphological Traits and Range Size

The relationship between the morphological characters analysed and species' range size revealed that both eye reduction and pigmentation loss were associated with smaller range sizes, indicating a negative correlation between the degree of cave related traits and species distributional range (Figure 3). In contrast, this pattern was not observed for the leg-related traits, with no significant effect on the species range size for both EOO and centroid distance metric.

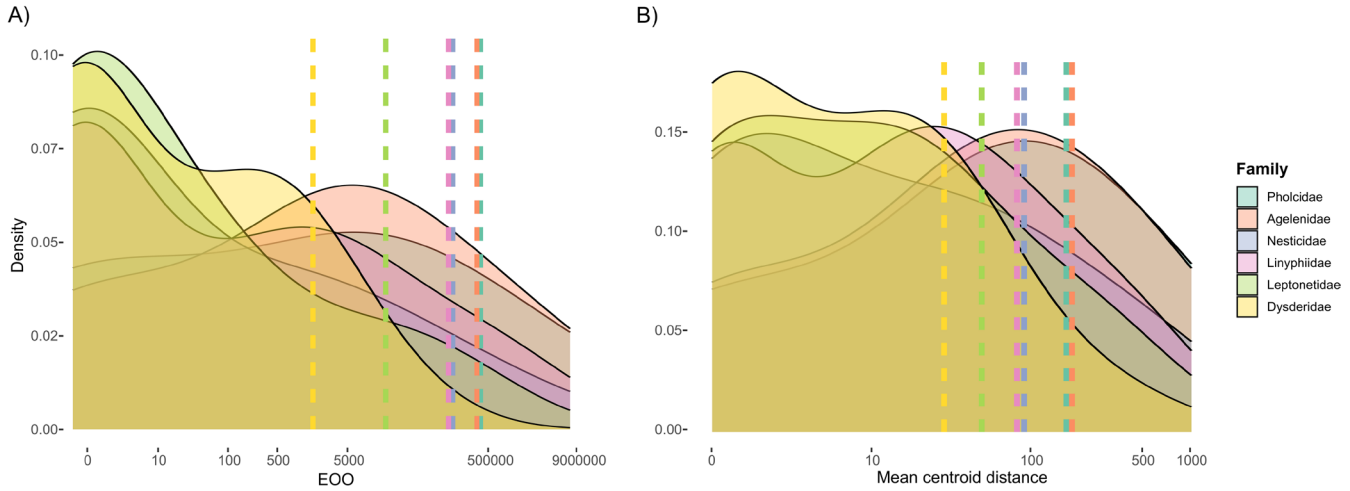

FIGURE 2 | Differences in (A) Extent of Occurrence (EOO) and (B) mean centroid distance values by family (X-axis is log-scaled to ease visualization). Some of them show significant differences between the range size values observed in different families. Dashed lines represent the mean values for each family.

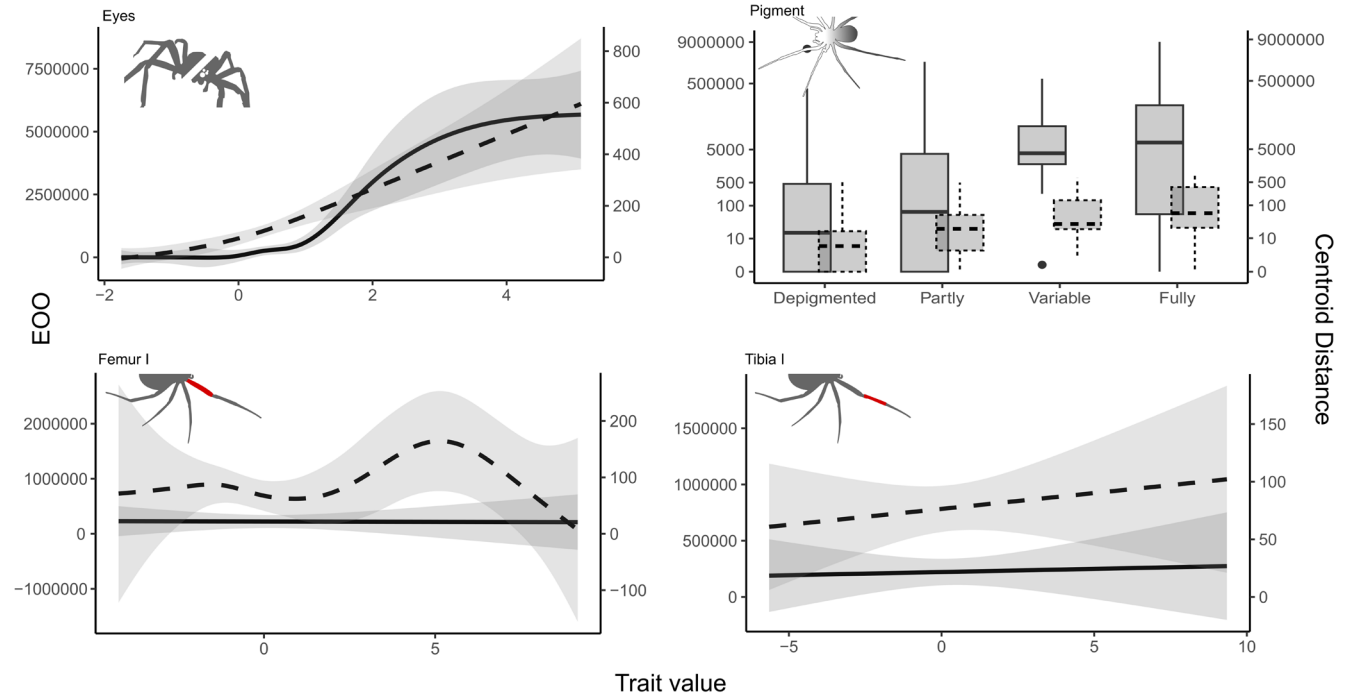

FIGURE 3 | Relationship between species' range size and the phenotypic covariates used in the present study. Solid lines/boxplots present the results obtained with the Extent of Occurrence (EOO) metric and dashed lines/boxplots are the results from the mean centroid distance metric. Y-axis in the pigmentation plot is log-scaled to ease visualization. Eye size and level of pigmentation appear to be associated with a decrease in species' range size. However, no significant pattern was observed in relation to relative leg elongation.

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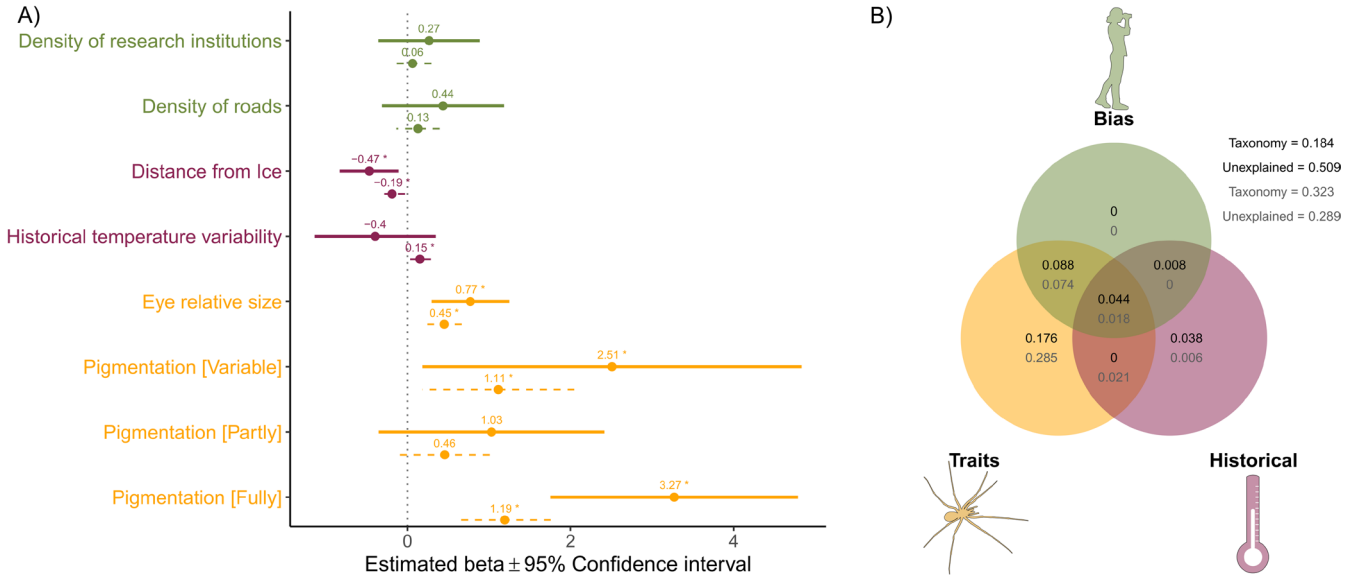

FIGURE 4 | (A) Forest plot of each species' range size covariate. Each dot and associated error bar indicate the strength and direction of the covariate effect. Asterisks (*) indicate covariates with a statistically significant effect on range size variation. Solid lines present the results obtained with the EOO metric and dashed lines are the results from the mean centroid distance metric. (B) Variation Partitioning Analysis (VPA) of the different factors used in the study. Black numbers indicate the percentage of explained variability using the Extent of Occurrence (EOO) metric, while grey numbers indicate the percentage using the mean centroid distance metric. Taxonomy is the variance explained by the random component of the model (Family/Genus).

In the analyses incorporating species' phylogenetic relationships, the morphological traits eye reduction and pigmentation showed the strongest and most consistent associations with EOO, whereas limb measurements (tibia and femur) exhibited weaker and less robust effects. For the centroid distance metric, neither femur I nor tibia I showed significant effects (femur I $z = -0.321$, $p = 0.748$, tibia I $z = -1.173$, $p = 0.241$), while for the EOO metric only femur I showed no statistical significance (femur I $z = 1.178$, $p = 0.2389$, tibia I $z = -2.156$, $p = 0.0311$). However, the corresponding z-score for tibia I was considerably lower than those of other traits (tibia I $z = -2.156$ versus the eye relative size $z = 6.158$ or the fully pigmented state with a $z = 8.826$).

For the analysis accounting for the allometric component, both femur and tibia showed no significant differences when explaining range size variation, neither for the EOO (femur I $p = 0.662186$, tibia I $p = 0.490124$) or mean centroid distance metrics (femur I $p = 0.114248$, tibia I $p = 0.822992$).

Given the potential imbalance arising from including an unequal number of variables per factor in the variation partitioning analyses and considering that leg-related morphological traits showed the weakest explanatory power for variation in species' range size, we excluded these traits to avoid inflating the variance attributed to the morphological component relative to other factors.

3.3 | Relative Contribution of Different Factors in Explaining Range Size Variation

Our models assessing the influence of different factors on species range size revealed that species with smaller relative eye size, loss of pigmentation, and distributions currently located further from areas previously covered by ice were significantly associated with smaller range sizes (Figure 4A). These results highlight the combined influence of phenotypic traits related to cave environments and historical climatic events in shaping the current distributional range of subterranean spider species.

The VPA revealed that phenotypic traits accounted for 19.4% of the total variance with the EOO metric, while historical factors explained 4.4%, and potential sources of sampling bias contributed 0.5% (Figure 4B). The joint effect of phenotypic traits and sampling bias explained 3.7%, whereas the interaction between traits and historical factors accounted for 0%. The joint contribution of all three factors explained an additional 7% of the total variance. Notably, taxonomic relationships among species accounted for a substantial 22.8% of the variance, while 47.6% variance remained unexplained, suggesting the influence of additional unmeasured factors.

When performing the same analyses using the mean distance from centroid as the range size metric, the results were largely consistent with those obtained using the EOO metric. In this case, pigmentation level, eye size, and distance from past ice sheets again had a significant effect on species' range size toward the same direction (Figure 4A). However, for the historical factors, this metric also showed a significant effect in historical temperature variability. In addition, the relative contribution of each factor category showed some variation. Phenotypic traits explained 28.5% of the total variance, historical factors accounted only 0.6%, and potential sampling biases explained 0%. Like in the previous analysis, the combinations of factor groups did not explain more variance than the individual components (Figure 4B). Taxonomic relationships had a markedly larger impact, accounting for 32.3% of

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the total variance, while 28.9% of the variance remained unexplained, possibly due to unmeasured ecological variables or stochastic processes.

When incorporating species' phylogenetic relationships into the analyses, one of the most influential PVR eigenvectors showed a significant effect on species' range size differences (PVR 5: $\beta = 2.973$, SE = 1.298, $p = 0.02$ for EOO; $\beta = 1.533$, SE = 0.486, $p < 0.01$ for centroid distance Tables S1.1 and S1.2). Overall, the results remained consistent, with the exception that eye-related traits no longer showed a significant effect on variation in species' range size (EOO: $\beta = 0.093$, SE = 0.299, $p = 0.75$; centroid distance: $\beta = 0.212$, SE = 0.109, $p > 0.05$; Table S1.1).

However, this discrepancy is likely driven by differences in sample size. The phylogenetic analyses included fewer species due to the limited availability of molecular data for many cave-dwelling spiders (304 vs. 185 species). Notably, when the non-phylogenetic corrected analyses were repeated using the same reduced dataset, the results were highly similar, with relative eye size again showing no significant effect on species' range size (EOO $p = 0.75$; centroid distance $p = 0.06$).

When incorporating the allometric component into the analyses, the interaction between eye size and species size did not show a significant effect on differences in range size (for both the EOO and centroid distance metrics, $p = 0.11$ and 0.28, respectively; Tables S1.3 and S1.4). This indicates that the effect of eye size is consistent regardless of species size. In addition, species size alone did not have a significant effect on range size variation ($p = 0.08$ and $p = 0.46$ for the EOO and centroid distance metrics, respectively), whereas eye size again showed a significant positive effect ($p = 0.05$ and $p < 0.01$ for the EOO and centroid distance metrics, respectively). These results further support the importance of eye reduction in shaping the distributional range of cave-dwelling spider species across continental Europe.

4 | Discussion

We investigated the factors shaping the distributional range sizes of cave and subterranean spider species across continental Europe. By analysing a combination of intrinsic biological traits and extrinsic factors, such as historical events, past environmental conditions, phenotypic subterranean related traits, and potential sources of sampling bias, we aimed to uncover the underlying causes of the variation in species' geographic ranges. Our findings provide insights into the ecological and historical processes that drive range size differences among European cave-dwelling spiders.

4.1 | Climatological Events Influence European Spider Distributions

Historically, the restricted distribution ranges observed in subterranean fauna have been attributed to limited dispersal capabilities, driven by both intrinsic biological constraints and extrinsic environmental factors (Crouau-Roy 1989; Holsinger 1991; Böhning-Gaese et al. 2006; Juan et al. 2010), and the biogeographic history of cave-associated fauna has been influenced by a combination of dispersal and vicariance events (Ketmaier et al. 2003). It has been proposed that during the LGM, conditions in northern Europe were unsuitable for the persistence of cave and subterranean spider species. These habitats were likely recolonized post-glaciation as climatic conditions improved, facilitating the northward dispersal of species from southern refugia (Ruzicka 1999).

Given this relatively recent recolonization, and the fact that species capable of broad colonization are typically those with higher dispersal abilities (G. M. Hewitt 1999), it is expected that the number of geographically restricted endemic species and in situ speciation events in northern Europe is lower compared to southern regions or areas that were not covered by ice during the past LGM. This would also be in line with the already seen pattern between dispersal capabilities and genetic connectivity (Gillespie et al. 2012). Consequently, species able to disperse into, or being able to adapt to, northern areas would exhibit broader distribution ranges. This is supported by our results, which indicate that current proximity to past glaciation zones significantly correlates with species' distribution. Specifically, species whose current distributional centroids lie closer to (or even inside) formerly glaciated regions tend to have bigger range sizes. This will support the previously mentioned idea of dispersal abilities in cave-related fauna shaping the biogeography of these species, and that the species with higher dispersal potential would have taken advantage of the new areas available once the ice sheet layers started to retreat in Europe (G. Hewitt 2003). However, this pattern alone does not explain why some subterranean species are able to disperse more widely than others.

Additionally, we found a slight discrepancy in the significance of the historical factors depending on the range size metric used in the present study. This may be related to how these two metrics are calculated, with the mean centroid distance being more closely associated with the degree of dispersion among species. This metric indicates that species with greater dispersion (i.e., higher centroid distances) also tend to exhibit higher temperature range variability. This pattern aligns with the interpretation above, suggesting that species with greater adaptability tend to occupy broader ranges.

4.2 | Subterranean Related Traits as a Limiting Factor

Phenotypic adaptations to subterranean ecosystems are well-documented and enable species to survive under the unique conditions of these habitats (Soares and Niemiller 2020). Among the most common convergent traits observed in subterranean species are the reduction or loss of eyes and pigmentation, as well as the elongation of appendages. The degree to which these traits are expressed is often interpreted as an indicator of how specialized or evolutionarily adapted a species is to life underground (e.g., Desutter-Grandcolas 1997; Arnedo et al. 2007; Mammola et al. 2020; Bellvert et al. 2022). Our results indicate that species exhibiting more pronounced subterranean-adapted traits, such as eye and pigment loss, tend to have smaller distributional ranges. The exception to this trend involves traits related to leg morphology. While elongation of appendages is typically considered another hallmark of subterranean adaptations, it

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is not associated exclusively with subterranean life in spiders. For instance, leg elongation may also reflect ecological strategies unrelated to cave life, such as differences in locomotion or hunting style between web-building and ground-dwelling species (Moya-Laraño et al. 2008). The subterranean spider fauna of Europe encompasses a variety of ecological guilds, including both web builders and active hunters (Mammola et al. 2022). Even among web-building species, a diversity of web types exists, which may influence morphological traits such as leg length. This ecological variation likely obscures the relationship between leg elongation and distributional range size, explaining why this trait does not follow the same pattern as other cave-adapted characteristics.

The observed negative relationship between traits associated with subterranean environments and species' distributional range, excluding leg morphology as previously discussed, suggests that the more specialized a spider species becomes for subterranean environments, the more restricted its range tends to be. These results also suggest that facultative cave-dwelling species, which typically exhibit less pronounced subterranean-related traits, tend to have broader ranges compared to more specialized species. This pattern was consistent regardless of species size, highlighting the influence of these traits on the distributional ranges of cave-dwelling spider species across Europe.

Importantly, the influence of traits on species' range size may also occur at finer scales, with different populations of the same species exhibiting distinct localized range sizes driven by local adaptations. Indeed, it is well understood that populations within a species can differ profoundly in their trait profiles, and this variation can strongly influence ecological inference (Palacio et al. 2024). Unfortunately, the lack of data on intraspecific trait variability in our dataset (Mammola et al. 2022; Patiño-Sauma et al. 2026) prevented us from exploring similar patterns.

4.3 | Potential Influence of Evolutionary History

We also found that species belonging to different spider families exhibit significant variation in their distributional range sizes. Notably, species from the families Agelenidae and Pholcidae tend to have larger ranges compared to those from other families. While these families include species with varying degrees of morphological traits related to cave environments, they generally comprise a lower proportion of obligate subterranean species and a greater number of taxa adapted to low-light or underground environments (Huber 2018; Aharon et al. 2023). Conversely, spider species from the families Leptonetidae and Dysderidae displayed the smallest range sizes among all the families analysed. Members of Leptonetidae are typically associated with subterranean habitats and often exhibit pronounced adaptations to subterranean life (Mammola and Isaia 2017a; Ledford et al. 2021), and cave-related species from the family Dysderidae have been observed to exhibit varying degrees of extreme troglomorphic adaptations when compared to their surface counterparts (Bellvert et al. 2022). These findings reinforce the pattern described earlier, with specialized subterranean species tending to have narrower distributions than their less specialized counterparts.

However, these results also suggest that, beyond ecological specialization, a shared evolutionary history is influencing species' range sizes, two processes that usually can hardly be decoupled from one another (Felsenstein 1988; Harvey and Pagel 1991; Revell et al. 2008). In the present study, we have incorporated taxonomic relationships (approximated using the Linnean ranks in the random structure of the regression models) among the factors that may explain why the studied species occupy the range that they have. This revealed that taxonomy significantly contributes to the variation in species' range sizes across both metrics used (EOO and mean centroid distance), suggesting that evolutionary conservatism, rather than solely adaptive ecological pressures, also plays an important role in shaping the distribution patterns of subterranean spider species in continental Europe. When incorporating phylogenetic information on a subset of species for which molecular data is available, we found that phylogenetic relationships play a role in explaining differences in range sizes. However, we were unable to determine whether this effect influences our overall conclusions regarding the role of morphological traits, due to differences in sample size between datasets. Future studies including more comprehensive molecular data for European cave-dwelling spider species could provide further insight into the evolutionary significance of these subterranean adaptations.

Another factor not considered in the present study is the role of interspecific interactions (e.g., competition) in explaining range size values. For example, previous research has shown that cave-dwelling spiders within the genus *Meta* (Tetragnathidae) (Brignoli 1972; Bourne 1976; Mammola and Isaia 2014, 2017b) or *Stalita* (Dysderidae) (Pavlek and Mammola 2021) display negative biotic interactions, potentially due to competitive exclusion. This indeed may also affect the range size that these species occupy. Such interactions, together with other unaccounted biotic or abiotic factors, may contribute substantially to the unexplained variability observed in our analyses, but a general scarcity of information prevented us from incorporating them in the analysis.

4.4 | Human Induced Biases

Finally, by incorporating potential human-related biases into our analysis, we aimed to determine whether the observed range sizes of the studied species reflect genuine biological and historical factors, or whether they are primarily shaped by our perception and sampling effort. We examined two proxies for sampling bias: road density, which may influence the accessibility of sites and thus the likelihood of species detection, and the density of nearby research institutions, which could lead to more intensive sampling in areas with greater scientific presence. Our results show that neither of these factors had a significant effect on species' range sizes, although they may play a minor role as seen with our VPA. These findings contrast with previous studies, which have identified these factors as playing an important role in shaping our understanding of species richness distribution (e.g., Kadmon et al. 2004; Geurts et al. 2023; Rubio-López et al. 2023). While our preliminary assessment suggests that the main drivers of the distributional patterns observed in cave-dwelling spiders across continental Europe are biological and historical in nature, we cannot exclude that other

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human-related biases may more strongly influence our findings and that future work could expand on this aspect. Specifically, it would be very interesting to include variables closely related to cave exploration in the analysis (e.g., density of speleological groups, accessibility of caves). Unfortunately, a general scarcity of similar data at a continental scale prevented us to account for more specific bias-related factors in the analysis.

5 | Conclusions

Species' dispersal abilities have long been considered a primary factor influencing range size, and in subterranean-dwelling organisms, this has often been attributed to the external limitations imposed by their habitat boundaries. Against this backdrop, we investigated the underlying drivers of variation in the distributional range sizes of subterranean spider species in continental Europe. Our results highlight the importance of taxonomic relationships, phenotypic traits associated with a subterranean life, and climatic and historical events, particularly the glaciations that affected Europe around 20,000 years ago (Clark et al. 2009), in shaping these patterns. Additionally, our findings suggest that other, as-yet unaccounted-for factors may also contribute significantly to the observed variation in range sizes. Collectively, these results underscore the complex interplay of evolutionary history, ecological specialization, and historical biogeography in determining the distributional range of cave and subterranean spider species. We see this result as an initial step toward understanding range size variation in subterranean spiders, with implications for cave evolution, subterranean biogeographic patterns, and conservation priorities—particularly given the close link between range size and extinction risk.

Author Contributions

A.B. and S.M. conceived the study and designed the methodology. A.B., G.N., M.P., and S.M. collected species-level data. A.B. and L.C. carried out analyses in GIS. M.P. resolved the species' phylogenetic relationships for the current study. A.B. carried out statistical analyses, prepared all figures, and wrote the first draft. All authors contributed to writing with critical comments and additions to the text.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in Figshare at https://figshare.com/articles/software/R_code_and_data_for_Where_we_re_going_we_won_t_need_eyes_to_see_Distributional_range_size_drivers_of_European_subterranean_spiders/30399772?file=58886605, reference number 10.6084/m9.figshare.30399772.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S2:1** Phylogenetic tree of European underground spiders based on a concatenated analysis of six markers using maximum likelihood. Numbers above branches represent ultrafast bootstrap support. **Table S1:1:** Results of a generalized linear mixed model including phylogenetic eigenvector regression using the extent of occurrence metric. **Table S1:2:** Results of a generalized linear mixed model including phylogenetic eigenvector regression using the centroid distance metric. **Table S1:3:** Results of a generalized linear mixed model including allometric component using the extent of occurrence metric. **Table S1:4:** Results of a generalized linear mixed model including allometric component using the centroid distance metric. **Figure S1:1:** Multicollinearity assessment among the different range size metrics used in the present study. On the diagonal; density plot showing variable distributions. Above the diagonal: Pairwise Pearson's r correlation values for all the different range size metrics (asterisks denote significance). Below the diagonal: scatterplots of the different observation values. AOO, area of occupancy; dst_centroid, average distance from the centroid of the distribution; EOO, extent of occurrence; max_dst, maximum distance between any two points in the distribution; n_occ, number of occurrences.

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