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A trade-off between latitude and elevation contributes to explain range segregation of broadly distributed cave-dwelling spiders

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Abstract

A fundamental goal in spatial ecology is to understand how the distribution of species varies along latitudinal and elevational gradients. This stems from the understanding that latitude and elevation are primary drivers affecting temperature variations on Earth's surface, and, in turn, that temperature plays a critical ecological role. These spatial gradients have been primarily documented using highly dispersive surface species—butterflies, birds, and plants—whereas studies on subterranean organisms remain scattered. The orb-web cave spiders *Meta bourneti* and *M. menardi* are ubiquitous inhabitants of European caves whose distributions stretches over a continental distance. They share a similar ecological niche, which should translate into competitive exclusion in co-occurring areas. Therefore, it can be predicted that there should be an effective spatial segregation between the two species along broadscale spatial gradients. Using a dataset of >3,000 georeferenced records, we show that the two species are primarily segregated along the latitudinal gradient, with *M. menardi* progressively becoming more frequent and *M. bourneti* rarer from south to north. In their overlapping range (36.5–53.4° latitude), the two species are secondarily separated along an elevational gradient, with *M. menardi* occupying, on average, sites at higher elevations than *M. bourneti*. However, in the northernmost part of its range and in the absence of its competitor, *M. menardi* inhabits caves at lower elevations. This clear pattern provides a textbook example of the trade-off between latitude and elevation in determining habitat segregation of broadly distributed competing species.

KEYWORDS

altitudinal gradient, biogeography, competitive exclusion, niche partitioning, species distribution modeling, Tetragnathidae

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1 | INTRODUCTION

Latitude and elevation are among the most conspicuous broad-scale ecological gradients used by macroecologists to explain patterns of species distributions in space and time (Hillebrand, 2004; Stevens, 1989, 1992). This stems from the understanding that these are primary drivers affecting temperature variations on Earth's surface (Aigang et al., 2009) and, in turn, that temperature plays a critical ecological role for animal life (Colinet et al., 2015; Polato et al., 2018). There is an intimate relationship between latitude and elevation in that varying these two factors in the same direction (toward higher elevations and the poles or *vice versa*) generally leads to analogous changes in thermal conditions. Ultimately, this relationship provides a convincing explanation for the disjunct arctic–alpine distributions of several animals and plants (Muster et al., 2009).

The importance of obtaining a nuanced understanding of species distributions along latitudinal and elevational gradients has gained momentum amid the current climatic emergency (Ripple et al., 2019), given that species are rapidly shifting their distribution poleward and toward higher elevations in response to a global temperature increase (Chen et al., 2011; Lenoir et al., 2020). Furthermore, there is a growing appreciation of the utility of latitude and elevation gradients for advancing ecological theory, as these gradients can be used to uncover some of the mechanisms shaping spatial biodiversity patterns (Sanders & Rahbek, 2012).

General theory predicts that segregation along spatial gradients should be particularly visible in highly dispersive species, such as birds (Auer & King, 2014; Burner et al., 2020; Graham et al., 2009), insofar as the effect of antagonistic interactions require the species to be in contact (that is, some sort of spatial proximity). Conversely, the effect of competition is often found to be of limited importance in driving the distribution of poorly dispersive species, such as subterranean ones (Mammola et al., 2020; Zakšek et al., 2019). Lacking effective dispersal, range size of subterranean organisms is often best predicted by historical factors (Zagmajster et al., 2014) and availability of habitats (Christman & Culver, 2001; Culver et al., 2006). Yet, while this reasoning applies to most specialized subterranean species, often ranging over 30 km or less (Bregović et al., 2019), there exist rare exceptions of cave-dwelling species with ranges stretching over continental distances. Often, these outliers are organisms lacking pronounced adaptations to subterranean life and able to effectively disperse through surface habitats (Mammola, 2019), meanwhile showing a high ecological plasticity in terms of habitat breadth (Ficetola et al., 2020).

An example of such widely distributed cave-dwelling organisms are orb weaver spiders in the genus *Meta* (Tetragnathidae). In general, *Meta* spiders are large-sized predators (total body length from 3.8 to 16.0 mm; Hesselberg et al., 2019) inhabiting the entrance area of caves and other habitats with similar ecological conditions such as cellars, railway tunnels, hollow trees, and crevices (Hesselberg et al., 2019; Mammola & Isaia, 2014). Two species of *Meta* occur in Europe, *M. bourneti* Simon 1922 and *M. menardi* (Latreille, 1804), both ranging over an enormous geographic expanse when compared to that of most subterranean spiders (Mammola et al., 2018; Mammola & Isaia, 2017). The explanation for this broad distribution has often been searched for in the unusual life cycle of these spiders (Mammola & Isaia, 2014: fig. 6), involving a phase of airborne dispersal (ballooning) outside caves (Smithers & Smith, 1998, Smithers, 2005a; but see Hesselberg et al., 2019 for cautionary arguments). Being ubiquitous in caves and easily identified in the field, these spiders have become "workhorses" for subterranean arachnological research (Hesselberg et al., 2019). Many aspects of their biology have been investigated in recent years including their diet (Novak et al., 2010; Smithers, 2005b), activity patterns (Mammola & Isaia, 2018), habitat preferences (Chiavazzo et al., 2015; Lunghi, 2018; Lunghi et al., 2017; Mammola & Isaia, 2014, 2017; Manenti et al., 2015; Růžička et al., 2013), the strength of interspecific competition (Novak et al., 2010; Mammola

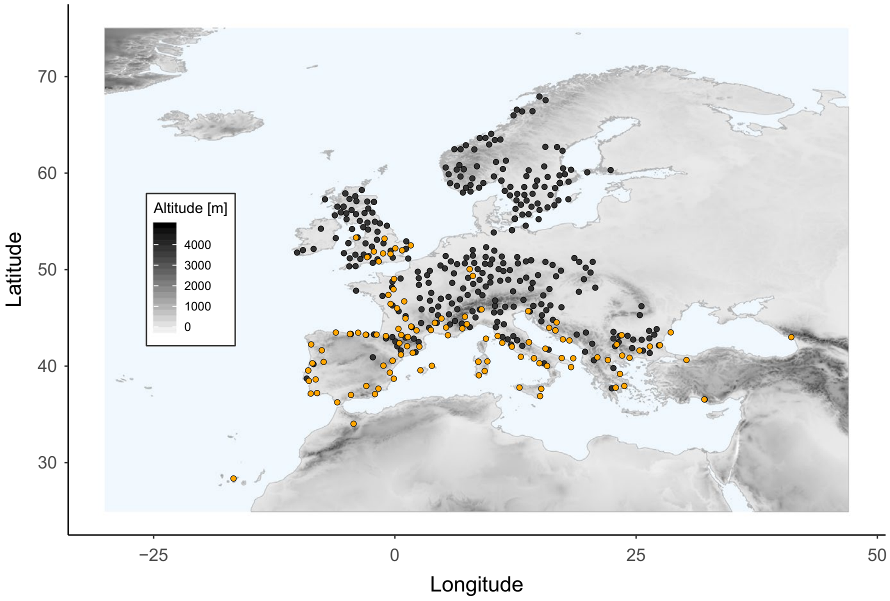

FIGURE 1 Distribution of *Meta* spiders. Occurrence localities of *M. bourneti* (orange dots; $n = 121$) and *M. menardi* (black dots; $n = 336$) used for the analysis (i.e., after spatial *thinning*)

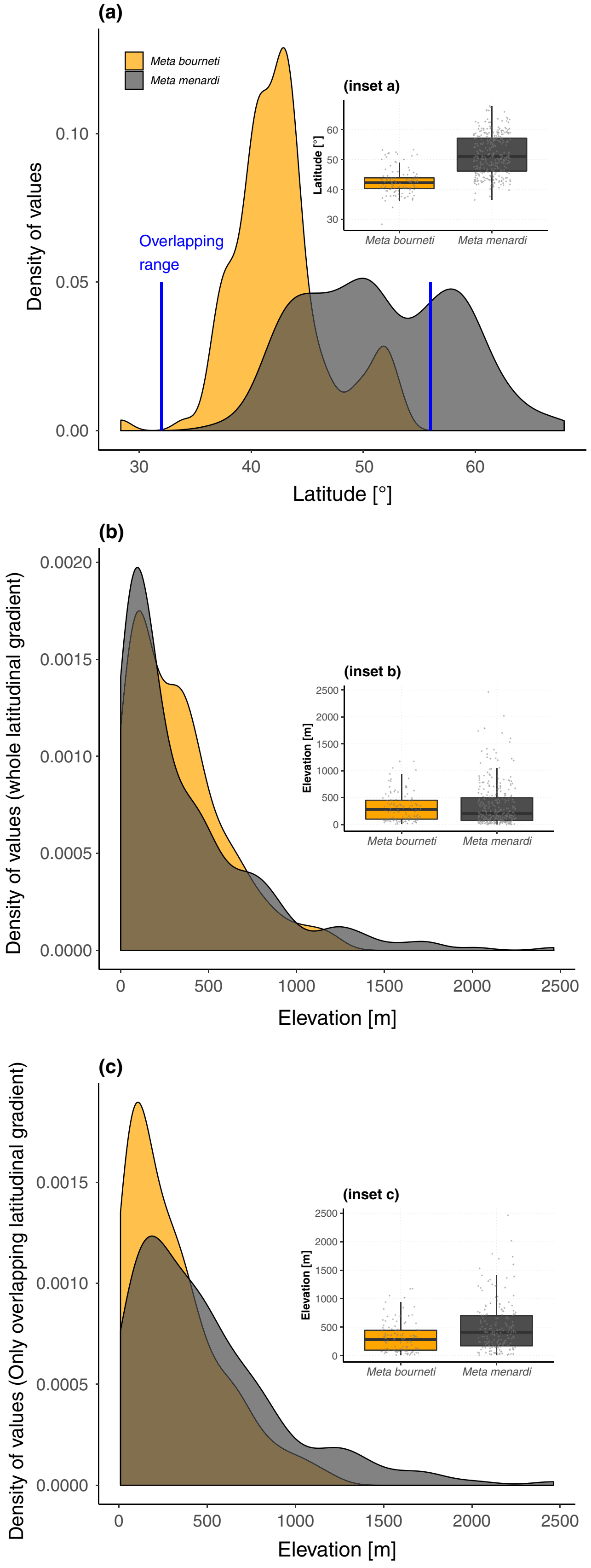

FIGURE 2 Latitudinal and elevational segregation between *Meta bourneti* and *M. menardi*. Density plots show the predicted density of values (Wickham, 2016). Inset graphs are boxplots summarizing the real distribution of values, wherein gray dots are observed values used to calculate each boxplot. A random noise (jitter) is applied to aid visualization of otherwise superimposed points. (a) Latitudinal segregation between the two species. (b) Elevational segregation considering the whole latitudinal gradients encompassed by the localities of the two species. (c) Elevational segregation between the two species in their overlapping range (i.e., the latitudinal band comprised by the two vertical blue lines in inset a)

et al., 2016), properties of their egg-case silk (Lepore et al., 2012), thermal physiology (Novak et al., 2014), and cytological adaptations (Lipovšek, 2019; Lipovšek, et al., 2018; Lipovšek, et al., 2018).

Given that the two species are of comparable size and occupy a similar niche within subterranean habitats, they should be in direct competition for space and resources (Mammola & Isaia, 2014). In fact, the coexistence between the two species within the same subterranean habitat has never been proved convincingly (see supporting information in Mammola & Isaia, 2017), suggesting that some kind of competitive exclusion dynamics may be in force. Brignoli (1971: fig. at p. 133) discussed that in the Italian peninsula, the spatial separation seemingly occurs along a south-to-north axis, with *M. bourneti* becoming more frequent moving southward and *M. menardi* northward. In northeastern Spain, Ribera (1978: figs 3–4) documented a segregation mechanism along the elevational gradient, with *M. bourneti* preferentially found in caves below 900 m and *M. menardi* at higher elevations in the Pyrenean region. While this evidence is compelling in showing potential segregation mechanisms between the two species, the lack of broad-scale data at a reasonable resolution has so far prevented us from testing the generality of these spatial patterns across the whole range of the two spiders.

We here expand on these prior observations aiming to shed light on the role of both latitudinal and elevational gradients in determining the global distribution range of *M. bourneti* and *M. menardi*. We assembled a comprehensive dataset of georeferenced occurrences of the two species by integrating Mammola and Isaia's (2017) database with recently published *Meta* records in the Global Biodiversity Information Facility (accessed on March 28, 2020) and the Spider Recording Scheme of the British Arachnological Society (accessed on February 20, 2020). Furthermore, we derived additional localities from recent literature (Covaciu-Marcov et al., 2017; Lunghi, 2018; Lunghi et al., 2017; Mammola et al., 2019).

The final database analyzed here comprises 467 unique occurrence localities for *M. bourneti* and 2,711 for *M. menardi*, for which we extracted elevation data from an elevation raster at a spatial resolution of ~1 km^2 (Fick & Hijmans, 2017). Occurrence databases of subterranean species are subjected to different types of spatial bias, which often results in artefactual gaps and areas of higher density in the distribution of occurrences (Mammola & Leroy, 2018; Zagmajster et al., 2010). This was also the case here, given that a Moran's I test (Paradis et al., 2004) revealed a significant degree of spatial autocorrelation in elevation values across

M. bourneti and *M. menardi* localities. To minimize this bias, we performed spatial thinning of the occurrences using the function *thin* in the R package "Red" (Cardoso, 2017), matching the resolution of the elevation raster. This operation reduced the database to 121 spatially independent localities for *M. bourneti* and 336 for *M. menardi* (Figure 1).

Initially, we tested for differences in latitude between sites of *M. bourneti* and *M. menardi* with a Gaussian linear model –i.e., analysis of variance (ANOVA). As expected, there was a significant segregation along the latitudinal gradient between the sites of the two species (Figure 2a; lm: 9.03 ± 0.64, $p < .001$), with *M. menardi* being more frequent between 42 and 58° latitude and *M. bourneti* between 35 and 48°. This intuitive result confirms that the latitudinal segregation observed by Brignoli (1971) in the Italian peninsula takes place at the continental scale. Yet, in contrast to the observations by Ribera (1978), apparently there was no significant difference in the elevations of sites inhabited by the two species (Figure 2b). The result is, however, an artifact: when taking into account spatial autocorrelation among sites by means of a generalized least squares model (using AIC-based model selection to identify the most appropriate correlation structure; Zuur et al., 2009), the difference in elevation turned out to be highly significant (gls: 198.24 ± 37.47, $p < .001$). The explanation for this discrepancy becomes apparent when looking at differences in elevation among sites in the part of the range where the two species overlap (Figure 2c), namely the latitudinal band between the southernmost locality of *M. menardi* (36.5° latitude) and the northernmost of *M. bourneti* (53.4°). In the overlapping range, *M. menardi* occupies sites at higher elevations than *M. bourneti*, thereby achieving an effective spatial segregation. On the other hand, in the northernmost part of its range and in the absence of its competitor, *M. menardi* selects sites at lower elevations, where climatic conditions are more suitable (Mammola & Isaia, 2017).

Given that latitudinal and elevational gradients are essentially thermal seasonality gradients, these differences between the two species are likely to reflect a shift in their climatic niches (Gasparo & Thaler, 2002). In fact, the adaptation to different climatic conditions was invoked as the main mechanism through which *M. bourneti* and *M. menardi* avoid direct competition, as empirically observed for Italian (Mammola & Isaia, 2014) and British populations (Mammola, 2017), as well as through the European range of the two species (Mammola & Isaia, 2017). However, some caution should be exercised in interpreting the pattern reported here, given that the broadscale distribution of the two species may also bear the signature of past biogeographic events and a so far undetected evolutionary component (Warren et al., 2014), and even cryptic diversity within the nominal species. Indeed, recent studies emphasized how there is often a high degree of overlooked diversity in broadly distributed subterranean species (Delić et al., 2017; Eme et al., 2018; Esposito et al., 2015; Hedin, 2015). The lack of phylogenetic data across the distribution of these two species prevented us from formally testing species hypotheses in European *Meta*, as well as to explore evolutionary hypotheses regarding both their distribution and evolution of microclimatic niche. Coupling ecological information with phylogenetic data would be an interesting future development as new DNA sequences of *Meta* become available. All in all, the segregation pattern reported can thus be taken as a neat, textbook example of the trade-off between latitude and elevation in determining habitat segregation of broadly distributed species occupying similar niches.

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AUTHOR CONTRIBUTION

EL, TH, and SM contributed data. SM performed analyses and wrote the first draft. All authors critically contributed to the writing by suggestion and additions to the text.

DATA AVAILABILITY STATEMENT

The thinned database used to generate the analysis is available in Figshare (https://doi.org/10.6084/m9.figshare.12687692). The complete database of occurrence localities of *Meta* spiders in Europe is being published and made available in an associated data paper (T. Hesselberg, E. Lunghi, F. Ballarin, B. Petcharad, & S. Mammola, unpublished data).

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REFERENCES

Aigang, L., Tianming, W., Shichang, K., & Deqian, P. (2009). On the relationship between latitude and altitude temperature effects. *International Conference on Environmental Science and Information Application Technology*, *2*, 55–58.

Auer, S. K., & King, D. I. (2014). Ecological and life-history traits explain recent boundary shifts in elevation and latitude of western North American songbirds. *Global Ecology and Biogeography*, *23*, 867–875. https://doi.org/10.1111/geb.12174

Bregović, P., Fišer, C., & Zagmajster, M. (2019). Contribution of rare and common species to subterranean species richness patterns. *Ecology and Evolution*, *9*, 11606–11618. https://doi.org/10.1002/ece3.5604

Brignoli, P. M. (1971). Note su ragni cavernicoli italiani (Araneae). *Fragmenta Entomologica*, *7*, 129–229. https://doi.org/10.21426/B67110055

Burner, R. C., Boyce, A. J., Bernasconi, D., Styring, A. R., Shakya, S. B., Boer, C., Rahman, M. A., Martin, T. E., & Sheldon, F. H. (2020). Biotic interactions help explain variation in elevational range limits of birds among Bornean mountains. *Journal of Biogeography*, *47*, 760–771. https://doi.org/10.1111/jbi.13784

Cardoso, P. (2017). red - An R package to facilitate species red list assessments according to the IUCN criteria. *Biodiversity Data Journal*, *5*, e20530. https://doi.org/10.3897/BDJ.5.e20530

Chen, I.-C., Hill, J. K., Ohlemuller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science*, *333*, 1024–1026. https://doi.org/10.1126/science.1206432

Chiavazzo, E., Isaia, M., Mammola, S., Lepore, E., Ventola, L., Asinari, P., & Pugno, N. M. (2015). Cave spiders choose optimal environmental factors with respect to the generated entropy when laying their cocoon. *Scientific Reports*, *5*(1), 7611. https://doi.org/10.1038/srep07611.

Christman, M. C., & Culver, D. C. (2001). The relationship between cave biodiversity and available habitat. *Journal of Biogeography*, *28*, 367–380. https://doi.org/10.1046/j.1365-2699.2001.00549.x

Colinet, H., Sinclair, B. J., Vernon, P., & Renault, D. (2015). Insects in fluctuating thermal environments. *Annual Review of Entomology*, *60*, 123–140. https://doi.org/10.1146/annurev-ento-010814-021017

Covaciu-Marcov, S.-D., Ferenţi, S., Urák, I., Sas-Kovács, É.-H., Cicort-Lucaciu, A.-Ş., & Sas-Kovács, I. (2017). After the last train passes: Data on the fauna from abandoned railway tunnels in Romania. *Annales Zoologici Fennici*, *54*, 335–346. https://doi.org/10.5735/086.054.0505

Culver, D. C., Deharveng, L., Bedos, A., J. Lewis, J., Madden, M., R. Reddell, J., Sket, B., Trontelj, P., & White, D. (2006). The mid-latitude biodiversity ridge in terrestrial cave fauna. *Ecography*, *29*, 120–128. https://doi.org/10.1111/j.2005.0906-7590.04435.x

Delić, T., Trontelj, P., Rendoš, M., & Fišer, C. (2017). The importance of naming cryptic species and the conservation of endemic subterranean amphipods. *Scientific Reports*, *7*, 3391. https://doi.org/10.1038/s41598-017-02938-z

Eme, D., Zagmajster, M., Delić, T., Fišer, C., Flot, J.-F., Konecny-Dupré, L., Pálsson, S., Stoch, F., Zakšek, V., Douady, C. J., & Malard, F. (2018). Do cryptic species matter in macroecology? Sequencing European groundwater crustaceans yields smaller ranges but does not challenge biodiversity determinants. *Ecography (Cop.)*, *41*, 424–436. https://doi.org/10.1111/ecog.02683

Esposito, L. A., Bloom, T., Caicedo-Quiroga, L., Alicea-Serrano, A. M., Sánchez-Ruíz, J. A., May-Collado, L. J., Binford, G. J., & Agnarsson, I. (2015). Islands within islands: Diversification of tailless whip spiders (Amblypygi, Phrynus) in Caribbean caves. *Molecular Phylogenetics and Evolution*, *93*, 107–117.

Ficetola, G. F., Lunghi, E., & Manenti, R. (2020). Microhabitat analyses support relationships between niche breadth and range size when spatial autocorrelation is strong. *Ecography*, *43*, 724–734. https://doi.org/10.1111/ecog.04798

Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, *37*, 4302–4315. https://doi.org/10.1002/joc.5086

Gasparo, F., & Thaler, K. (2002). I ragni cavernicoli del Venezia Giulia (Italia nord-orientale) (Arachnida, Araneae). *Atti e Mem. della Comm. Grotte "E. Boegan"*, *37*, 17–55.

Graham, C. H., Parra, J. L., Rahbek, C., & McGuire, J. A. (2009). Phylogenetic structure in tropical hummingbird communities. *Proceedings of the National Academy of Sciences*, *106*, 19673–19678. https://doi.org/10.1073/pnas.0901649106

Hedin, M. (2015). High-stakes species delimitation in eyeless cave spiders (Cicurina, Dictynidae, Araneae) from central Texas. *Molecular Ecology*, *24*, 346–361.

Hesselberg, T., Simonsen, D., & Juan, C. Do cave orb spiders show unique behavioural adaptations to subterranean life? A review of the evidence. *Behaviour*, *156*, 969–996.

Hillebrand, H. (2004). On the generality of the latitudinal diversity gradient. *The American Naturalist*, *163*, 192–211. https://doi.org/10.1086/381004

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

Lepore, E., Marchioro, A., Isaia, M., Buehler, M. J., & Pugno, N. M. (2012). Evidence of the most stretchable egg sac silk stalk, of the European Spider of the Year *Meta menardi*. *PLoS One*, *7*, e30500.

Lipovšek, S., Leitinger, G., Janžekovič, F., Kozel, P., Dariš, B., Perc, M., Devetak, D., Weiland, N., & Novak, T. (2019). Towards understanding partial adaptation to the subterranean habitat in the European cave spider, *Meta menardi*: An ecocytological approach. *Scientific Repors*, *9*, 9121.

Lipovšek, S., Leitinger, G., Novak, T., Janžekovič, F., Gorgoń, S., Kamińska, K., & Rost-Roszkowska, M. (2018). Changes in the midgut cells in the European cave spider, *Meta menardi*, during starvation in spring and autumn. *Histochemistry and Cell Biology*, *149*, 245–260.

Lipovšek, S., Novak, T., Janžekovič, F., Brdelak, N., & Leitinger, G. (2018). Changes in the midgut diverticula epithelial cells of the European cave spider, *Meta menardi*, under controlled winter starvation. *Scientific Reports*, *8*, 13645.

Lunghi, E. (2018). Ecology and life history of *Meta bourneti* (Araneae: Tetragnathidae) from Monte Albo (Sardinia. Italy). *PeerJ*, *6*, e6049.

Lunghi, E., Manenti, R., & Ficetola, G. F. (2017). Cave features, seasonality and subterranean distribution of non-obligate cave dwellers. *PeerJ*, *5*, e3169.

Mammola, S. (2017). Modelling the future spread of native and alien congeneric species in subterranean habitats – the case of *Meta* cave-dwelling spiders in Great Britain. *International Journal of Speleology*, *46*, 427–437. https://doi.org/10.5038/1827-806X.46.3.2134

Mammola, S. (2019). Finding answers in the dark: Caves as models in ecology fifty years after Poulson and White. *Ecography*, *42*, 1331–1351. https://doi.org/10.1111/ecog.03905

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

Mammola, S., Cardoso, P., Angyal, D., Balázs, G., Blick, T., Brustel, H., Carter, J., Ćurčić, S., Danflous, S., Dányi, L., Déjean, S., Deltshev, C., Elverici, M., Fernández, J., Gasparo, F., Komnenov, M., Komposch, C., Kováč, L'ubomír, Kunt, K., … Isaia, M. (2019). Continental data on cave-dwelling spider communities across Europe (Arachnida: Araneae). *Biodiversity Data Journal*, *7*, e38492. https://doi.org/10.3897/BDJ.7.e38492

Mammola, S., Cardoso, P., Ribera, C., Pavlek, M., & Isaia, M. (2018). A synthesis on cave-dwelling spiders in Europe. *Journal of Zoological Systematics and Evolutionary Research*, *56*, 301–316. https://doi.org/10.1111/jzs.12201

Mammola, S., & Isaia, M. (2014). Niche differentiation in *Meta bourneti* and *M. menardi* (Araneae, Tetragnathidae) with notes on the life history. *International Journal of Speleology*, *43*, 343–353.

Mammola, S., & Isaia, M. (2017). Rapid poleward distributional shifts in the European cave-dwelling *Meta* spiders under the influence of competition dynamics. *Journal of Biogeography*, *44*, 2789–2797.

Mammola, S., & Isaia, M. (2018). Day-night and seasonal variations of a subterranean invertebrate community in the twilight zone. *Subterranean Biology*, *27*, 31–51. https://doi.org/10.3897/subtbiol.27.28909

Mammola, S., & Leroy, B. (2018). Applying species distribution models to caves and other subterranean habitats. *Ecography*, *41*, 1194–1208. https://doi.org/10.1111/ecog.03464

Mammola, S., Piano, E., & Isaia, M. (2016). Step back! Niche dynamics in cave-dwelling predators. *Acta Oecologica*, *75*, 35–42. https://doi.org/10.1016/j.actao.2016.06.011

Manenti, R., Lunghi, E., & Ficetola, G. F. (2015). The distribution of cave twilight-zone spiders depends on microclimatic features and trophic supply. *Invertebrate Biology*, *134*, 242–251. https://doi.org/10.1111/ivb.12092

Muster, C., Maddison, W. P., Uhlmann, S., Berendonk, T. U., & Vogler, A. P.. (2009). Arctic-alpine distributions-metapopulations on a continental scale?. *The American Naturalist*, *173*, 313–326. https://doi.org/10.1086/596534

Novak, T., Šajna, N., Antolinc, E., Lipovšek, S., Devetak, D., & Janžekovič, F. (2014). Cold tolerance in terrestrial invertebrates inhabiting subterranean habitats. *International Journal of Speleology*, *43*, 265–272. https://doi.org/10.5038/1827-806X.43.3.3

Novak, T., Tkavc, T., Kuntner, M., Arnett, A. E., Delakorda, S. L., Perc, M., & Janžekovič, F. (2010). Niche partitioning in orbweaving spiders *Meta menardi* and *Metellina merianae* (Tetragnathidae). *Acta Oecologica*, *36*, 522–529. https://doi.org/10.1016/j.actao.2010.07.005

Paradis, E., Claude, J., & Strimmer, K. (2004). APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics*, *20*, 289–290. https://doi.org/10.1093/bioinformatics/btg412

Polato, N. R., Gill, B. A., Shah, A. A., Gray, M. M., Casner, K. L., Barthelet, A., Messer, P. W., Simmons, M. P., Guayasamin, J. M., Encalada, A. C., Kondratieff, B. C., Flecker, A. S., Thomas, S. A., Ghalambor, C. K., Poff, N. L. R., Funk, W. C., & Zamudio, K. R. (2018). Narrow thermal tolerance and low dispersal drive higher speciation in tropical mountains. *Proceedings of the National Academy of Sciences*, *115*, 12471–12476. https://doi.org/10.1073/pnas.1809326115

Ribera, C. (1978). Contribution à la Connaissance de la faune faverni-cole du nordest de 1'Espagne: le genre Meta. Proceedings of the 7th International Congress of Arachnology (Exeter, 1977), Symposium 2001 Society of London, *42*, 353–358.

Ripple, W. J., Wolf, C., Newsome, T. M., Barnard, P., & Moomaw, W. R. (2019). World scientists' warning of a climate emergency. *BioScience*, *70*, 8–12. https://doi.org/10.1093/biosci/biz088

Růžička, V., Šmilauer, P., & Mlejnek, R. (2013). Colonization of subterranean habitats by spiders in Central Europe. *International Journal of Speleology*, *42*, 133–140. https://doi.org/10.5038/1827-806X.42.2.5

Sanders, N. J., & Rahbek, C. (2012). The patterns and causes of elevational diversity gradients. *Ecography*, *35*, 1–3. https://doi.org/10.1111/j.1600-0587.2011.07338.x

Smithers, P. (2005a). The early life history and dispersal of the cave spider *Meta menardi* (Latreille, 1804) (Araneae: Tetragnathidae). *Bulletin of the British Arachnological Society*, *13*, 213–216.

Smithers, P. (2005b). The diet of the cave spider *Meta menardi* (Latreille 1804) (Araneae: Tetragnathidae). *Journal of Arachnology*, *33*, 243–246. https://doi.org/10.1636/CT-05-2.1

Smithers, P., & Smith, M. F. (1998). Observations on the behaviour of decond instars of the Cave Spider *Meta menardi* (Latreille, 1804). *Newsletter of the British Arachnological Society*, *81*, 4–5.

Stevens, G. C. (1989). The latitudinal gradient in geographical range: How so many species coexist in the tropics. *The American Naturalist*, *133*, 240–256. https://doi.org/10.1086/284913

Stevens, G. C. (1992). The elevational gradient in altitudinal range: An extension of Rapoport's latitudinal rule to altitude. *The American Naturalist*, *140*, 893–911. https://doi.org/10.1086/285447

Warren, D. L., Cardillo, M., Rosauer, D. F., & Bolnick, D. I. (2014). Mistaking geography for biology: Inferring processes from species distributions. *Trends in Ecology & Evolution*, *29*, 572–580. https://doi.org/10.1016/j.tree.2014.08.003

Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. Springer-Verlag.

Zagmajster, M., Culver, D. C., Christman, M. C., & Sket, B. (2010). Evaluating the sampling bias in pattern of subterranean species richness: Combining approaches. *Biodiversity and Conservation*, *19*, 3035–3048. https://doi.org/10.1007/s10531-010-9873-2

Zagmajster, M., Eme, D., Fišer, C., Galassi, D., Marmonier, P., Stoch, F., Cornu, J.-F., & Malard, F. (2014). Geographic variation in range size and beta diversity of groundwater crustaceans: Insights from habitats with low thermal seasonality. *Global Ecology and Biogeography*, *23*, 1135–1145. https://doi.org/10.1111/geb.12200

Zakšek, V., Delić, T., Fišer, C., Jalžić, B., & Trontelj, P. (2019). Emergence of sympatry in a radiation of subterranean amphipods. *Journal of Biogeography*, *46*, 657–669. https://doi.org/10.1111/jbi.13514

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. Springer, Ed.

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