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**Rapid poleward distributional shifts in the European cave-dwelling Meta  
spiders under the influence of competition dynamics**

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1 **Article type:** Original Article

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3 **Rapid poleward distributional shifts in the European cave-dwelling *Meta* spiders**  
4 **under the influence of competition dynamics**

5

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7

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14 **Running heads.** Poleward shifts in cave-dwelling spiders

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21 analysed the data and led the writing. M.I. revised the paper.

22

23

24

25 **ABSTRACT**

26 Aim. To describe the distribution of two congeneric species of cave-dwelling spiders under current climatic  
27 conditions and future warming scenarios, keeping into account their bioclimatic requirements, dispersal  
28 capacity and competition dynamics.

29 Location. Europe and North Africa.

30 Methods. We gathered detailed occurrence data for *Meta menardi* and *M. bourneti* (Araneae:  
31 Tetragnathidae) and modelled their distribution across their bioclimatic range. We evaluated the breadth of  
32 the bioclimatic niche of the two species and assessed the potential overlap between their multidimensional  
33 Hutchinsonian hypervolumes. We compared these results with their current distribution maps obtained by  
34 species distribution modelling (SDMs) keeping into account dispersal and competition dynamics, and we  
35 projected future trends of distribution according to different climatic scenarios.

36 Results. The overall size of the niche hypervolumes of the two species was very similar and highly  
37 overlapping. However, when accounting for competition in the model, the predicted ranges of the two  
38 species showed only minor areas of overlap. On the base of SDM analysis, we predicted a significant  
39 poleward shift in the distribution of both species, with the appearance of a new contact area especially in  
40 Central Europe, Southern UK, France and Northern Spain.

41 Main conclusions. Interspecific competition keeps the current ranges of the two European *Meta* species  
42 apart, although their fundamental bioclimatic niches are very similar. Rapid poleward shifts of the two  
43 species are likely due to the high dispersal capacity of the two spiders. The case of *Meta* spiders exemplifies  
44 rapid shift in range of distribution associated with global warming, which are unlikely to occur in the case of  
45 most cave-dwelling arthropods.

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## 60 INTRODUCTION

61 Due to their species-specific physiological constraints, shifts in arthropod species  
62 distribution driven by climate change are expected to occur as rates of warming increase  
63 (Colinet et al., 2015). Statistical modelling of the response of a certain species to climatic  
64 variations often relies on the climate envelope methods, whereby the current distribution of  
65 a species is modelled in a present climate-space and in turn projected into future or past  
66 climatic conditions (Peterson et al., 2011). One of the common outcomes of these models  
67 is a spatial shift in distribution ranges, leading to unprecedented range contacts or  
68 overlaps and, consequently, to new potential interactions (e.g. Walther et al., 2002;  
69 Williams & Jackson, 2007; Krosby et al., 2015; Warren et al., 2016). In this regard, it is  
70 crucial to consider the dispersal ability of the different species, which poses important  
71 constraints to their current ranges (Araújo & Peterson, 2012) and determines whether or  
72 not different species will come in contact (Davis et al., 1998).

73 This issue is particularly evident in the case of low dispersal animals such as  
74 hypogean arthropods. Given their reduced physiological tolerance (e.g., Novak et al.,  
75 2014; Rizzo et al., 2015), their dispersal ability through non-subterranean habitats is  
76 indeed commonly hampered (e.g., Snowman et al., 2010; Cardoso, 2012; Mammola et al.,  
77 2015; Yao et al., 2016). However, a number of cave-dwelling invertebrates with poor  
78 subterranean adaptations have retained the ability to disperse effectively outside the caves  
79 in certain phases of their development. This is well exemplified by the troglophile cave-  
80 dwelling spiders *Meta menardi* (Latreille) and *M. bourmeti* Simon (Araneae:  
81 Tetragnathidae), ubiquitous inhabitants of the twilight zone of most hypogean sites across  
82 Europe. These species show unusual broad ranges of distribution compared to most  
83 specialized cave spiders (Koponen, 1993; Deltshv, 2011; Mammola & Isaia, 2017), which

84 can be explained in light of their life cycle (see Mammola & Isaia, 2014: 351, f. 6).

85 Females of *Meta* lay their cocoons in the vicinity of the cave entrance (Smithers,  
86 2005; Novak et al., 2010; Mammola & Isaia, 2014; Chiavazzo et al., 2015; Mammola et al.,  
87 2016). After hatching, spiderlings leave the cocoon, migrate towards the cave entrance  
88 and disperse outside passively, via ballooning (Smithers & Smith, 1998; Smithers, 2005).  
89 Thanks to this airborne dispersal, *Meta* spiders can travel over long distances, thus  
90 colonizing hypogean sites that are far apart from each other and extending their  
91 distribution at a continental scale.

92 Due to their high dispersal abilities, the two species of European *Meta* would easily  
93 come into contact. However, they have never been observed to coexist within the same  
94 hypogean site (Brignoli, 1971, 1972; Ribera, 1978; Gasparo & Thaler, 2000; Milner, 2013),  
95 at least over long period of time (but see Appendix S1 in Supporting Information about  
96 doubtful records of co-occurrence). In a previous work set at a local scale in the western  
97 Italian Alps, we demonstrated that the two species do not come into contact because of  
98 niche segregation dynamics. Although the ecological requirements of *M. menardi* and *M.*  
99 *bourneti* are very similar, when the microclimatic conditions in a cave are favorable for *M.*  
100 *menardi*—narrow ranges of low temperature and high humidity—*M. bourneti* is excluded  
101 by competition (Mammola & Isaia, 2014).

102 In this study we aim to predict the future rearrangement in the species distribution  
103 in future warming scenarios and whether the competition that we observed at a local scale  
104 is reflected by large scale distribution patterns at the continental scale. Specifically, we  
105 hypothesize that i) the bioclimatic range of the two species overlaps at the continental  
106 scale; ii) competition plays an important role in determining the range of distribution of the  
107 two species; and iii) under the assumption of no dispersal limitation, *Meta* spiders will shift  
108 their distribution in future climate change.

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## 112 **MATERIALS AND METHODS**

### 113 **Distributional data**

114 Geo-referenced occurrences of *M. bourneti* and *M. menardi* were obtained from the  
115 Global Biodiversity Information Facility ([www.gbif.org](http://www.gbif.org)), the Spider Recording Scheme of  
116 the British Arachnological Society (<http://srs.britishspiders.org.uk>), the Record Maps for  
117 Arachnids in Germany (<http://www.spiderling.de.vu>) and the Benelux spider distribution  
118 maps (<http://www.tuite.nl/iwg/Araneae/SpiBenelux>). Additional data were provided to us  
119 directly by colleagues (see Acknowledgments). We integrated missing countries by  
120 obtaining occurrences from the literature—i.e., for France, Italy and Switzerland. As for  
121 early published records, we derived the geo-coordinate of each locality from online  
122 speleological archives and/or from Google Earth 7.1.2.2041. **To increase the accuracy of**  
123 **the analysis, we excluded the following records:** i) localities for which we were not able to  
124 obtain precise coordinates; ii) records before 1922 (the year of the description of *M.*  
125 *bourneti*); iii) unverified records of the coexistence of the two species (see "unverified"  
126 records in the Appendix S1 in Supporting Information); iv) record of *M. bourneti* in the  
127 Canary Islands, due to taxonomical issues currently unresolved (C. Ribera, pers. comm.  
128 2016).

129 In order to take into account the potential bias of haphazard sampling, we  
130 designated a sampling bias grid (Phillips et al., 2009; Syfert et al., 2013). Within each cell  
131 in the grid—which had a width equal to the grain of the bioclimatic rasters—all the points  
132 but one were randomly removed (see Newbold, 2010). By doing so, we minimized spatial  
133 autocorrelation, given that proximate localities likely comprised similar environmental  
134 variables.

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### 139 Climatic variables

140 We employed 19 bioclimatic variables and elevation data at a resolution of 2.5' (nearly 4.5  
141 km at the equator) to represent current climatic conditions (1950–2000; Hijmans et al.,  
142 2005; available at: [www.worldclim.org](http://www.worldclim.org); Tab. 1). Bioclimatic variables are a set of variables  
143 derived from monthly mean temperature and rainfall regime, including annual trends,  
144 seasonality and extreme or limiting environmental factors. They are considered to be  
145 'biologically meaningful variables', thus reflecting a more realistic relationship with species-  
146 specific physiological constraints than simple monthly averages (Hijmans et al., 2005).  
147 Analogous data layers at the same spatial resolution were obtained for the future  
148 scenarios. Future data represent downscaled and calibrated climate projections for 2050  
149 and 2070 from three different general circulation models (GCMs; namely: CCSM4, BCC-  
150 CSM1-1, MIROC5) and two representative concentration pathways (RCPs), namely a low-  
151 emission (RCP 2.6) and a high-emission (RCP 8.5) scenarios. Multiple GCMs were  
152 employed to take into account variation and uncertainty between mathematical simulations  
153 (Kageyama et al., 2001; Diniz-Filho et al. 2009).

154 Prior to model fitting, we reduced collinearity among bioclimatic layers by  
155 performing a principal components analysis (PCA) on the 20 variables, generating new  
156 axes that summarized variation in fewer dimensions. We retained the first four axes of the  
157 PCA, which cumulatively explained over 99% of the overall variance in our dataset.

158

### 159 Niche overlap

160 We relied on Hutchinson's (1957) criteria to quantify a reliable *proxy* of the fundamental  
161 bioclimatic niche of *Meta menardi* and *M. bourmeti* as a n-dimensional hypervolume, as

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166 implemented in the `hypervolume` R package (Blonder, 2015). The hypervolume  
167 construction relies on a kernel density estimation (KDE) procedure, that quantifies the  
168 geometry of the multidimensional Hutchinsonian hypervolume and to assess the  
169 intersection between the hypervolumes of two or more species; mathematical details are in  
170 Blonder et al. (2014). We computed the n-dimensional hypervolume for both *Meta bourneti*  
171 and *M. menardi* based on the occurrences of the two species corrected for the spatial  
172 autocorrelation, and the PCA space spanned for the first four PCs which represent the  
173 bioclimatic conditions. In accordance with Blonder et al. (2014), we standardized the  
174 choice of bandwidth for each variable through a Silverman estimator (Silverman, 1992)  
175 and we set a threshold that included 100% of the total probability density. Two measures of  
176 niche overlap (Intersection and Sørensen-Dice index) were obtained using the relevant  
177 functions of the *hypervolume* R package (Blonder, 2015).

178

### 179 **Species distribution modelling (SDM)**

180 As it is widely recommended in literature (e.g. Peterson et al., 2011; Saupe et al., 2012;  
181 Merow et al. 2013), SDMs were calibrated within the accessible area—often referred to as  
182 **M** area (Barve et al., 2011). **M** represents the geographic extent hypothesized to fall within  
183 the long-term dispersal and colonization potential for a certain species over its evolutionary  
184 history. In our case, **M** was approximated by buffering the occurrence records by a radius  
185 of 500 km via the `circle r` command (Hijmans, 2014), and combining all circles in a final  
186 shape representing a *proxy* of the accessible area. A linear distance of 500 km represents  
187 a good approximation of the distance potentially covered by the ballooning dispersal of  
188 *Meta* spiders—at least over several generations (see, e.g., Bell et al., 2005).

189 SDMs for both species were constructed with `MAXENT` (Phillips et al., 2006), a  
190 machine-learning technique which relies on the principle of maximum entropy, that permits

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196 the estimation of the potential distribution of a species by fitting the probability distribution  
197 of maximum entropy for presences-only points constrained in a set of environmental  
198 explanatory variables (Phillips et al. 2006; Elith et al., 2011). We accounted for the  
199 potential competition dynamics between the two species which we previously documented  
200 at the local scale, following the approach of Araújo & Luoto (2007). Specifically, we initially  
201 constructed a SDM model for *M. menardi* and, in-turn, we used the probability surface  
202 predicted by the model as an additional predictor for constructing the model of *M. bourmeti*.  
203 We decided to use a distribution map as a predictor in the model of *M. bourmeti* because of  
204 the strong support for the existence of a negative interaction between the two species  
205 (Mammola & Isaia, 2014). Indeed, in lack of *a priori* information on the species biology,  
206 there is the risk that the inclusion of species distribution as a predictor in the model of  
207 another species will not represent a biotic interaction, but simply the lack of important  
208 environmental predictors (see Guisan & Thuiller, 2005).

209 SDMs were fitted in the *dismo* R package (Hijmans et al. 2011). We used a default  
210 configuration of the feature classes and regularization multiplier parameters considering  
211 the large sample size of our dataset (Morales et al., 2017). To generate the present-day  
212 prediction, we ran 50 bootstrap replicates of the model, and the median output was used in  
213 the analyses. For each bootstrap replicate, we used a random partition of 20% of the  
214 occurrence points for model validation. Model performance was evaluated for each  
215 random partition of occurrence points, via the area under the curve (AUC) of the receiver  
216 operating characteristic (ROC) plot (Fielding & Bell, 1997) and the true skill statistics (TSS;  
217 Allouche et al., 2006). We generated a final model for each species using the same  
218 parameters and calibrated the resulting model with the complete occurrence data set for  
219 each species. We later transferred the model into each future GCMs and we calculated the  
220 median values for each GCM combination. Results were projected into a geographic

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228 space representing the entire European range, with a bounding rectangle within 25° to 75°  
229 latitude and from -30° to 50° longitude. Modelled species probabilities of occurrence were  
230 transformed into presence and absence maps using a cut-off of 0.42 for *M. bourmeti* and of  
231 0.45 for *M. menardi*, which was defined by the species prevalence in the studied area (Liu  
232 et al. 2005).

233

## 234 RESULTS

### 235 Distribution

236 *Meta menardi* has been found in most European countries, reaching the northern latitudes  
237 in the Scandinavian Peninsula and the eastern longitudes in Ukraine and Turkey. The  
238 distribution range of *M. bourmeti* is centred on the Iberian, Balkan and Italian peninsulas  
239 and the northern shore of Africa. The species has also been found in a few caves in  
240 France, the United Kingdom, Germany and Romania (Nentwig et al., 2017; World Spider  
241 Catalog—WSC, 2017). Overall, we included occurrence records on the entire known range  
242 of distribution of the two species (Fig. 1). We assembled 381 unique occurrences for *Meta*  
243 *bourmeti* and 2,222 for *M. menardi*. These occurrences were filtered down to 364 and  
244 1,935 reliable and geo-referenced records, which were further corrected for spatial  
245 correlation. The overall pattern of occurrences suggested a geographically broad  
246 distribution, with more intense sampling efforts conducted in Central and Western Europe,  
247 the Scandinavian Peninsula and the United Kingdom. Occurrence data were much more  
248 sparse in Eastern Europe (Fig. 1).

249

### 250 Fundamental bioclimatic niche

251 The overall size of the 4-dimensional hypervolumes of the two species was fairly similar.

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253 The niche volume of *Meta bournetii* was slightly larger (514.08) compared to that of *M.*  
254 *menardi* (418.29), with an intersection of 248.60 and a high overlap (Sørensen-Dice index:  
255 0.53). Overall, these results suggest the occurrence of a significant overlap in the  
256 fundamental bioclimatic niches of the two species. We report a graphical representation of  
257 the two hypervolumes in Fig. 2.

258

### 259 **Current distribution and future projections**

260 The predictive performance of the SDMs was high both for *Meta bournetii* (mean AUC  $\pm$   
261 SD= 0.9521  $\pm$  0.022; TSS = 0.629 $\pm$ 0.025) and *M. menardi* (AUC= 0.9346  $\pm$  0.0217; TSS=  
262 0.579 $\pm$ 0.082). The suitable areas predicted by the model are congruent with the known  
263 distribution of the two species (Fig. 3). Current predictions identified suitable areas for *M.*  
264 *bournetii* across the Mediterranean countries, whereas the most suitable areas for *M.*  
265 *menardi* were found at higher latitude and elevation. Range overlaps were predicted in  
266 Western France, Italy, Southern UK and in the Pyrenees, which represent the current  
267 contact zones between the two species. For each considered emission scenario,  
268 projections indicated a northward shift in the range of distribution of the two species, with  
269 greater variation for the higher emission scenario (rcp 8.5). A northward shift in the contact  
270 area between the two species was also observed, with the appearance of new contact  
271 area especially in Central Europe, Southern UK, France and Northern Spain (Fig. 3).

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### 273 **DISCUSSION**

274 In this study, we assembled a comprehensive dataset summarizing the occurrences of  
275 *Meta bournetii* and *M. menardi* in Europe, and we provided a detailed analysis of their  
276 bioclimatic ranges and their potential distribution under current and future climatic

281 conditions. In accordance with different authors (Davis et al., 1998; Araújo & Luoto, 2007;  
282 Araújo & Peterson, 2012; Travis et al., 2012), when modelling the distribution ranges, we  
283 took into account the dispersal ability (by means of the M area) and the potential effect of  
284 competition between the two species (by including the probability of presence of *M.*  
285 *menardi* into the model of *M. bourneti*).

286 In recent years, a series of papers have relied on spatial modelling to describe  
287 niche segregation in epigeal taxa, including vipers (Scali et al., 2011), sea birds (Quillfeldt  
288 et al., 2013), mice (Meynard et al., 2012) and macaques (Coudrat & Nekaris, 2013).  
289 However, although it examines a similar issues, this work represents the first attempt to  
290 model the bioclimatic niche of subterranean animals at a continental scale, implementing  
291 the potential effect of dispersal and competition. Our analysis of the niche hypervolume of  
292 the two species points toward a significant overlap in their fundamental bioclimatic niches  
293 (Fig. 2). Indeed, these spiders are able to exploit similar micro-habitats in the twilight zone  
294 of caves and other subterranean habitats (Smithers, 2005; Mammola & Isaia, 2014;  
295 Nentwig et al., 2017).

296 The hypervolume of *M. bourneti* was found to be slightly wider than that of *M.*  
297 *menardi*, as the former species exhibits higher ecological plasticity (Tatole, 2005)—  
298 especially in terms of microclimatic requirements (Mammola & Isaia, 2014). On the other  
299 hand, the smaller hypervolume of *M. menardi* suggests that this species is more  
300 stenoecious, in accordance with its documented preference for sheltered habitats  
301 characterized by narrow microclimatic conditions (e.g. Szymczkowsky, 1953; Novak et al.,  
302 2010; Mammola & Isaia, 2014; Manenti et al., 2015; Mammola et al., 2016; Table 1).

303 SDM projections showed that the realized distribution range of the two species only  
304 partially overlaps. Specifically, we observed how, at increasing latitude, the habitat  
305 suitability of *M. menardi* gradually increases whereas the suitability of *M. bourneti*

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307 decreases. At a smaller scale, a similar trend has already been suggested by Brignoli  
308 (1971) in the attempt to explain empirically the distribution of these two species in the  
309 Italian Peninsula. Areas of partial overlap in the distribution ranges of the two species have  
310 been predicted in southern UK [where *M. bourneti* was probably introduced (Browning &  
311 Tams, 1944; Gasparo & Thaler, 2000)], France, Italy and Spain. In this regard, it is worth  
312 noticing that even in these areas, the two species were never found in syntopy, with a  
313 clear segregation in respect to elevation (Ribera, 1978), exposure (Mammola & Isaia,  
314 2014) or other natural and artificial barriers (Milner, 2013).

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315 In spite of its narrower ecological requirements, the projected distribution range of  
316 *M. menardi* in Europe is wider than that of *M. bourneti*, as a cool temperate climate  
317 dominates across the investigated area. These results confirm a bioclimatic segregation  
318 between the two species, which takes place at a continental scale. More precisely, in a  
319 previous work (Mammola & Isaia, 2014), we pointed out the fact that *M. menardi* has an  
320 optimal preference for caves with high relative humidity (>97%) and temperatures ranging  
321 from 8 to 12 °C, and the fact that *M. bourneti* has a preference for caves with relative  
322 humidity >90% and temperatures ranging from 10 to 17 °C. Whenever suitable for both  
323 species (temperature 10–12 °C and relative humidity 97–100%), *M. bourneti* is apparently  
324 excluded. The competitive exclusion potentially implies that competition plays a role in  
325 determining future distribution ranges in these two species.

326 Our model projections suggest that the distribution of *Meta* spiders will be affected  
327 by climate changes, with a significant loss of suitable areas in both cases and the  
328 appearance of new suitable areas, north of their current range. According to our models,  
329 the climatic change would potentially lead to the abandonment of southern caves by *M.*  
330 *menardi* due to its low tolerance to drought and higher temperatures. In parallel, a  
331 retraction of the southern range margin of *M. bourneti* is also projected, as this species will

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336 experience unsuitable climate in some of the southern caves that are currently occupied.  
337 Since the excluding competitive force will be released, our model predicts the cave  
338 occupation by the more tolerant *M. bourmeti* (Fig. 3) and the consequent expansion of its  
339 range in the absence of the competitor—competitive release *sensu* Grant (1972).  
340 According to our model projection, area of distribution overlaps will also increase in the  
341 future, leading to new potential interactions between the two species. In light of the high  
342 dispersal capacity of the two species, we expect that these distribution shifts will occur in a  
343 relatively short time-scale.

344 In the few works modelling the potential fate of subterranean organisms in global  
345 change scenarios (e.g. Sánchez-Fernández et al., 2016; Mammola et al., 2017), either a  
346 range contraction or the persistence of species *in situ* were observed. However, these  
347 works focused on true troglobionts displaying a general stenothermal profile and a reduced  
348 dispersal potential. On the other hand, *Meta* spiders represent peculiar cases of cave  
349 dwelling organisms, given their high extra-cave mobility and wide ecological plasticity  
350 which may promote a fast colonization of new areas. The predicted northward shifts in the  
351 distribution range seem to indicate that *Meta* will react to climatic ~~change more like an~~  
352 epigean, rather than a hypogean animal. Indeed, poleward range expansions have been  
353 documented for a broad range of epigean organisms (e.g., Walther et al., 2002; Parmesan  
354 & Yohe, 2003; Parmesan, 2006; Walther, 2010; Chen et al., 2011; Dawson et al., 2011;  
355 Bellard et al., 2012), including spiders (e.g. Leroy et al., 2013, 2014; Kuntner et al., 2014).

356 The case of *Meta* spiders in Europe therefore exemplifies rapid biological changes  
357 associated with global warming, which are unlikely to occur in the case of most  
358 troglobionts. It is also worth noting that, according to theoretical models (Badino, 2004),  
359 the increased energy flux due to global warming is expected to be deposited primarily in  
360 the superficial sectors of caves—where *Meta* spiders live—whereas the warming of deep

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362 hypogean systems is expected to occur within a certain time-lag (see discussion in  
363 Mammola et al., 2017). It is thus expected that the shift in the projected range of  
364 distribution will occur almost synchronously with the external climatic alterations. However,  
365 it is clear that the potential northward expansion in the range of distribution in *Meta* spiders  
366 will also depend upon the presence of suitable subterranean habitats to colonize.

367

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375 Alexandra Jones for proofreading our English.

376

### 377 **SUPPORTING INFORMATION**

378 Additional Supporting Information may be found in the online version of this article:

379

380 **Appendix S1** Cases of coexistence of *Meta bourneti* and *M. menardi* documented in  
381 literature.

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654 **BIOSKETCHES**

655 Stefano Mammola is an ecologist whose scientific activity focuses primarily on statistical  
656 modeling. He recently finished his PhD at the University of Torino, where he studied the  
657 ecology, biogeography and the taxonomy of subterranean spiders in the Alps.

658 Marco Isaia is an ecologist and taxonomist, with an interest on the use of spiders as  
659 models for the study of ecological dynamics in terrestrial ecosystems, especially caves.

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661 **Editor:** Aristeidis Parmakelis

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677 **Table 1.** Bioclimatic variables used in this study and their extracted values (mean and  
678 standard deviation) for the occurrences of *Meta menardi* (n= 1935) and *M. bourneti* (n=  
679 364).

680

			<i>Meta menardi</i>	<i>Meta bourneti</i>
Variable	Description	Unit	Extracted values (mean±SD)	Extracted values (mean±SD)
Bio01	Annual Mean Temperature	°C	8,31 ± 1,78	13,06 ± 2,48
Bio02	Mean Diurnal Range	°C	7,73 ± 1,10	8,31 ± 1,32
Bio03	Isothermality (BIO2/BIO7) (* 100)	°C	31,31 ± 3,31	35,63 ± 3,82
Bio04	Temperature Seasonality (standard deviation *100)	°C	6024,35 ± 939,78	5279,47 ± 1041,74
Bio05	Max Temperature of Warmest Month	°C	21,62 ± 2,62	25,93 ± 3,22
Bio06	Min Temperature of Coldest Month	°C	-2,85 ± 2,47	2,71 ± 3,25
Bio07	Temperature Annual Range (BIO5-BIO6)	°C	24,47 ± 3,57	23,21 ± 3,91
Bio08	Mean Temperature of Wettest Quarter	°C	11,40 ± 5,30	10,42 ± 3,61
Bio09	Mean Temperature of Driest Quarter	°C	5,38 ± 5,65	16,61 ± 6,99
Bio10	Mean Temperature of Warmest Quarter	°C	16,03 ± 2,02	19,99 ± 2,68
Bio11	Mean Temperature of Coldest Quarter	°C	0,64 ± 2,25	6,58 ± 3,11
Bio12	Annual Precipitation	mm	863,16 ± 251,59	723,06 ± 203,19
Bio13	Precipitation of Wettest Month	mm	96,47 ± 31,12	93,78 ± 27,67
Bio14	Precipitation of Driest Month	mm	50,00 ± 14,37	27,62 ± 19,01
Bio15	Precipitation Seasonality (Coefficient of Variation)	mm	20,33 ± 6,58	34,79 ± 19,63
Bio16	Precipitation of Wettest Quarter	mm	271,94 ± 87,79	256,05 ± 75,33
Bio17	Precipitation of Driest Quarter	mm	163,50 ± 45,96	105,16 ± 60,45
Bio18	Precipitation of Warmest Quarter	mm	229,41 ± 56,44	124,05 ± 65,13
Bio19	Precipitation of Coldest Quarter	mm	203,46 ± 81,94	219,69 ± 80,53
Alt	Altitude a.s.l	m	432,08 ± 386,77	319,86 ± 297,69

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690 **Figure 1** - Occurrences of *Meta menardi* and *M. bournetii*. Photo credits: Francesco  
691 Tomasinelli (top-right) and Emanuele Biggi (bottom-right).

692

693 **Figure 2** - Pair plots showing the estimated four-dimensional hypervolumes for *Meta*  
694 *menardi* (black points) and *M. bournetii* (orange points). The coloured points reflect the  
695 stochastic points sampled from the inferred hypervolume rather than original observations,  
696 and represent the real hypervolume boundaries (10,000 random points for each species  
697 are shown). Contour lines are calculated through the *MASS:kde2d* R function, and drawn  
698 only for visual presentation.

699

700 **Figure 3** - Current and future potential distribution map for *M. menardi* and *M. bournetii*  
701 based on present-day and projected climatic conditions for 2050 and 2070. Shaded areas  
702 are modeled suitable conditions, and white areas are unsuitable conditions.

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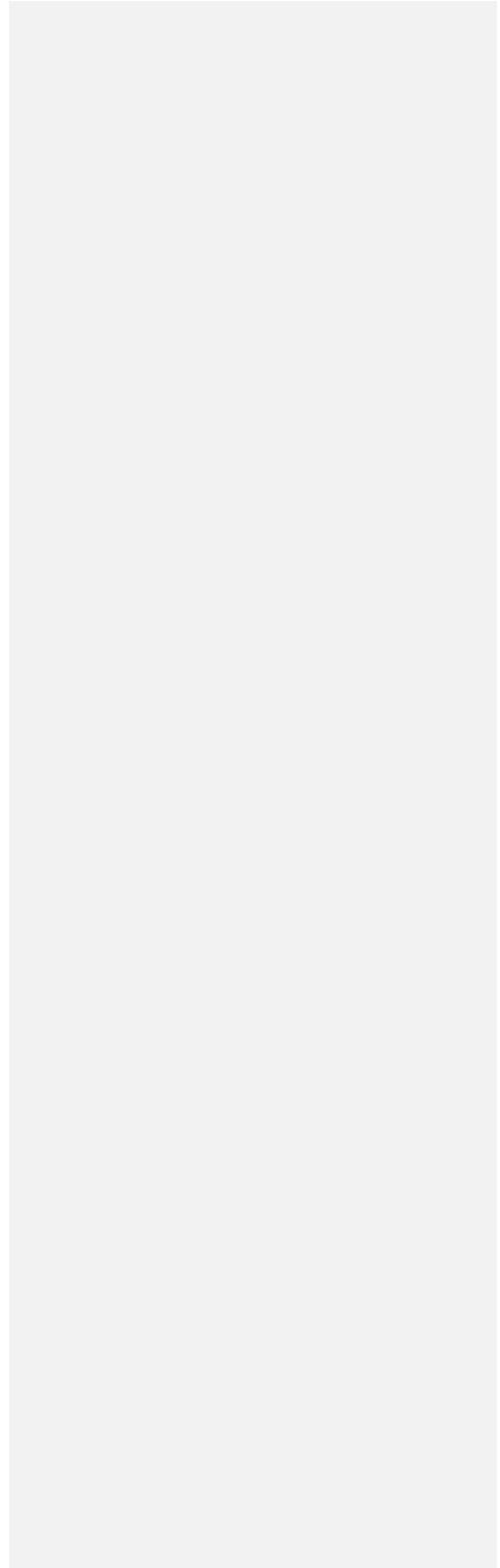
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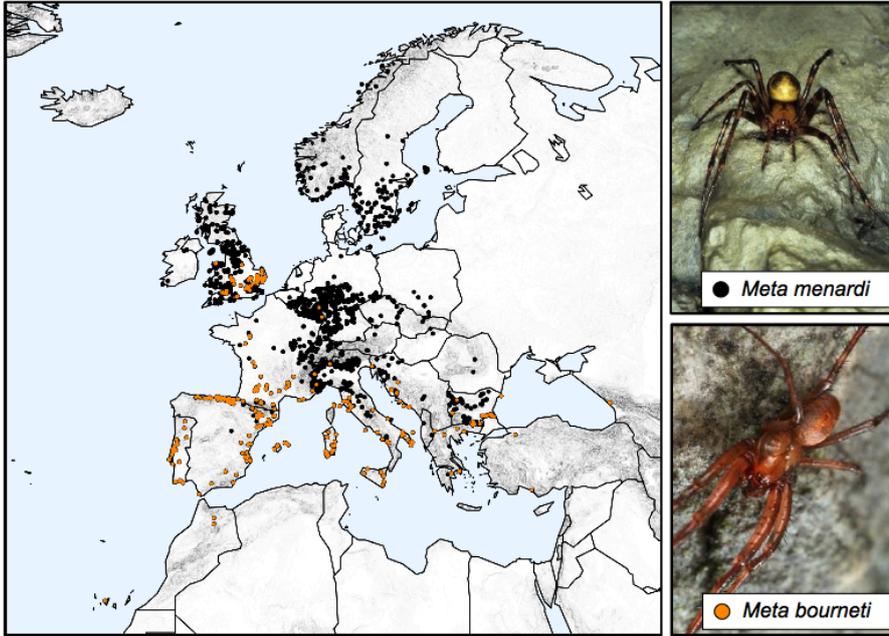
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710 **Figure 1**

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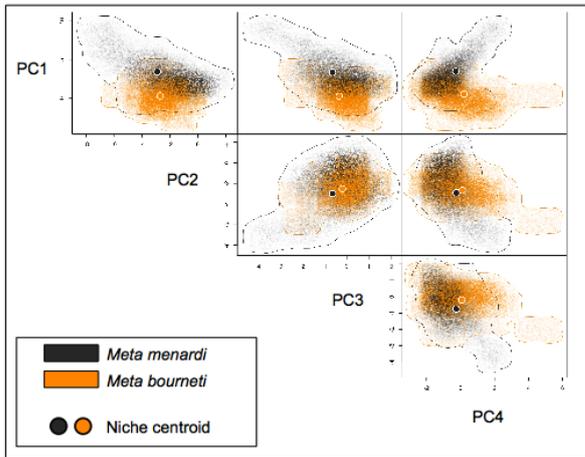
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723 **Figure 2**

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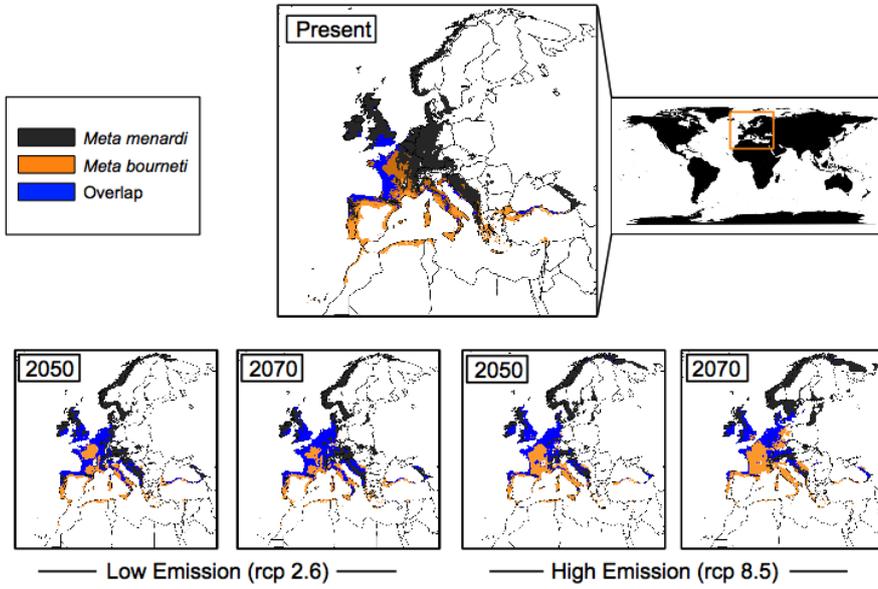
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735 **Figure 3**