

AperTO - Archivio Istituzionale Open Access dell'Università di Torino

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

This is the author's manuscript

Original Citation:

Availability:

This version is available <http://hdl.handle.net/2318/1647572> since 2021-03-01T16:46:05Z

Published version:

DOI:10.1111/jbi.13087

Terms of use:

Open Access

Anyone can freely access the full text of works made available as "Open Access". Works made available under a Creative Commons license can be used according to the terms and conditions of said license. Use of all other works requires consent of the right holder (author or publisher) if not exempted from copyright protection by the applicable law.

(Article begins on next page)

1 **Article type:** Original Article

2

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

5

6 Stefano Mammola^{1,2*}, Marco Isaia^{1,2}.

7

8 1. Laboratory of Terrestrial Ecosystems, Department of Life Sciences and Systems Biology, University of
9 Torino – Via Accademia Albertina 13, 10123 Torino, Italy

10 2. IUCN SSC Spider and Scorpion Specialist Group – 10123 Torino, Italy

11 * Corresponding author: stefanomammola@gmail.com

12

13

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

15 **Keywords:** Competition, Ecological Niche Modeling, Global Warming, Hutchinsonian
16 hypervolume, MaxEnt, range shift, Species Distribution Models, subterranean habitats,
17 [troglodytes](#).

18 **Word counts:** 233 (abstract); 5968 (main body of the text, inclusive of the captions and
19 references)

20 **Author contributions:** S.M. and M.I. conceived the idea and collected data. S.M.
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.

46

47

48

49

ha eliminato: Species

ha eliminato: D

ha eliminato: M

ha eliminato: to

ha eliminato: y

ha eliminato: .

Commentato [H.P.1]: Is this what you meant?

ha eliminato: ition

ha eliminato: ly

ha eliminato: ve forces

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; Deltchev, 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.

ha eliminato: Western

ha eliminato: s

111

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), 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.

ha eliminato: &

Commentato [H.P.2]: Please, for all these websites, give the date on which the data were downloaded

ha eliminato: (version

ha eliminato:)

138

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; 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

ha eliminato: Principal

ha eliminato: C

ha eliminato: A

Commentato [H.P.3]: Is this what you meant?

ha eliminato: ayed

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

Commentato [H.P.4]: Please format all R packages like this: in roman, in quotes, at at first mention with the reference. Please do this for the whole ms

ha formattato: Tipo di carattere: Non Corsivo

Commentato [H.P.5]: Is this what you mean?

ha eliminato: K

ha eliminato: D

ha eliminato: E

ha eliminato: permits to achieve a measure of

ha eliminato: s

Commentato [H.P.6]: Please format all software programs like this, in lower case, and at first mention followed by the version number and the reference

ha formattato: Maiuscoletto, Crenatura 12 pt

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

ha eliminato: Area

ha eliminato: U

ha eliminato: C

ha eliminato: Receiver

ha eliminato: O

ha eliminato: C

ha eliminato: the

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.

ha eliminato: p

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).

272

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

ha eliminato: altitude

ha eliminato: s

ha eliminato: apparition

ha eliminato: ly

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*

ha eliminato: of distribution

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).

ha eliminato: altitude

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

ha eliminato: alteration

ha eliminato: evacuation

Commentato [H.P.7]: I think you mean being dry?

ha eliminato: a

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

ha eliminato: alterations

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

368 **ACKNOWLEDGEMENTS**

369 We are grateful to all friends and colleagues who provided occurrence data of the two
370 species, namely Christo Deltchev (Balkan Peninsula), Nuria Marcias (Canary Islands),
371 Martina Pavlek (Croatia), Theo Blick and Stefan Zaenker (Germany), Maria Chatzaki
372 (Greece), Pedro Cardoso (Iberian Peninsula), Luigi Boscolo, Paolo Pantini and Fulvio
373 Gasparo (Italy), Marek Zabka (Poland), Carles Ribera (Spain), Paul Selden, Peter Harvey
374 and the UK Spider Recording Scheme team (United Kingdom). A special thanks goes to
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.

382

383

384

385

386

ha eliminato: s

388 **REFERENCES**

389 Allouche, O., Tsoar, A. & Kadmon, R. (2006) Assessing the accuracy of species distribution
390 models: prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology*,
391 **43**, 1223–1232.

392

393 Araújo, M. B. and Luoto, M. (2007) The importance of biotic interactions for modelling
394 species distributions under climate change. – *Global Ecology and Biogeography*,
395 **16**, 743–753.

396

397 Araújo, M.B. & Peterson, A.T. (2012) Uses and misuses of bioclimatic envelope modeling.
398 *Ecology*, **93**, 1527–1539.

399

400 Badino, G. (2004) Cave temperature and global climatic change. *International Journal of*
401 *Speleology*, **33**, 103–114.

402

403 Barve, N., Barve, V., Jiménez-Valverde, A., Lira-Noriega, A., Maher, S. P., Peterson, A.T.,
404 Soberón, J. & Villalobos, F. (2011) The crucial role of the accessible area in ecological
405 niche modeling and species distribution modeling. *Ecological Modelling*, **222**, 1810–1819.

406

407 Bell, J.R., Bohan, D.A., Shaw, E.M., & Weyman, G.S. (2005). Ballooning dispersal using
408 silk: world fauna, phylogenies, genetics and models. *Bulletin of Entomological Research*,
409 **95**, 69–114.

410

411 Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. & Courchamp, F. (2012) Impacts of

412 climate change on the future of biodiversity. *Ecology Letters*, **15**, 365–377.

413

414 Blonder, B. (2015) *Hypervolume: High-dimensional Kernel Density Estimation and*
415 *Geometry Operations (data analysis software system)*, R package version 1.2.2.
416 <http://CRAN.R-project.org/package=hypervolume>.

417

418 Blonder, B., Lamanna, C., Violle, C. & Enquist, B.J. (2014) The n-dimensional hyper-
419 volume. *Global Ecology and Biogeography*, **23**, 595–609.

420

421 Brignoli, P.M. (1971) Note su ragni cavernicoli italiani (Araneae). *Fragmenta Entomologica*,
422 **7**, 129–229.

423

424 Brignoli, P.M. (1972) Catalogo dei ragni cavernicoli italiani. *Quaderni di Speleologia del*
425 *Circolo Speleologico Romano*, **20**, 1–211.

426

427 Cardoso, P. (2012) Diversity and community assembly patterns of epigean vs. troglobiont
428 spiders in the Iberian Peninsula. *International Journal of Speleology*, **41**, 83–94.

429

430

431 Chen, I.C., Hill, J.K., Ohlemüller, R., Roy, D.B. & Thomas, C.D. (2011) Rapid range shifts
432 of species associated with high levels of climate warming. *Science*, **333**, 1024–1026.

433

434 Chiavazzo, E., Isaia, M., Mammola, S., Lepore, E., Ventola, L., Asinari, P. & Pugno, N.M

435 (2015) Cave spiders choose optimal environmental factors with respect to the generated
436 entropy when laying their cocoon. *Scientific Reports*, **5**, 7611.

437

438 Colinet, H., Sinclair, B.J., Vernon, P. & Renault, D. (2015) Insects in fluctuating thermal
439 environments. *Annual Review of Entomology*, **60**, 123–40.

440

441 Coudrat, C.N.Z. & Nekaris, K.-I. (2013) Modelling niche differentiation of co-existing,
442 elusive and morphologically similar species: a case study of four macaque species in
443 Nakai-Nam Theun national protected area, Laos. *Animals*, **3**, 45–62.

444

445 Davis, A.J., Jenkinson, L.S., Lawton, J.H., Shorrocks, B. & Wood, S. (1998) Making
446 mistakes when predicting shifts in species range in response to global warming. *Nature*,
447 **391**, 783–786.

448

449 Dawson, T.P., Jackson, S.T., House, J.I., Prentice, I.C. & Mace, G.M. (2011)
450 Beyond predictions: biodiversity conservation in a changing climate. *Science*, **332**,
451 53–58.

452

453 Deltchev, C. (2011) The faunistic diversity of cave-dwelling spiders (Arachnida, Araneae) of
454 Greece. *Arachnologische Mitteilungen*, **40**, 23–32.

455

456 Diniz-Filho, J.A.F., Mauricio Bini, L., Fernando Rangel, T., Loyola, R.D., Hof, C., Nogués-
457 Bravo, D. & Araújo, M.B. (2009) Partitioning and mapping uncertainties in ensembles of

458 forecasts of species turnover under climate change. *Ecography*, **32**, 897–906.

459

460 Elith, J., Phillips, S.J., Hastie, T., Dudík, M., Chee, Y.E. & Yates, C.J. (2011) A statistical
461 explanation of MaxEnt for ecologists. *Diversity and Distribution*, **17**, 43–57.

462

463 Fielding, A.H. & Bell, J.F. (1997) A review of methods for the assessment of prediction
464 errors in conservation presence/absence models. *Environmental Conservation*, **24**, 38–49.

465

466 Gasparo, F. & Thaler, K. (2000) I ragni cavernicoli del Venezia Giulia (Italia nord-orientale)
467 (Arachnida, Araneae). *Atti e Memorie della Commissione Grotte "E. Boegan"*, **37**, 17–55.

468

469 Grant, P.R. (1972) Convergent and divergent character displacement. *Biological Journal of*
470 *the Linnaean Society*, **4**, 39–68.

471

472 Guisan, A. & Thuiller, W. (2005) Predicting species distribution: offering more than simple
473 habitat models. *Ecology Letters*, **8**, 993–1009.

474

475 Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high
476 resolution interpolated climate surfaces for global land areas. *International Journal of*
477 *Climatology*, **25**, 1965–1978.

478

479 Hijmans, R.J. (2014) *raster: Geographic data analysis and modeling (data analysis*
480 *software system)*, R package version 2.3-12. <http://CRAN.R-project.org/package=raster>

481

482 Hutchinson, G. (1957) Concluding remarks. *Cold spring harbor symposium on quantitative*
483 *biology*, **22**, 415–427.

484

485 Kageyama, M., Peyron, O., Pinot, S., Tarasov, P., Guiot, J., Jousaume, S. & Ramstein, G.
486 (2001) The last glacial maximum climate over Europe and western Siberia: a PMIP
487 comparison between models and data. *Climate Dynamics*, **17**, 23–43.

488

489 Koponen, S. (1993) On the biogeography and faunistics of European spiders: latitude,
490 altitude and insularity. *Bulletin de la Société Neuchâteloise des Sciences Naturelles*, **116**,
491 141–152

492

493 Krehenwinkel, H., Rödder, D. & Tautz, D. (2015) Eco-Genomic analysis of the poleward
494 range expansion of the wasp spider *Argiope bruennichi* shows rapid adaptation and
495 genomic admixture. *Global Change Biology*, **21**, 4320–4332.

496

497 Krosby, M., Wilsey, C.B., McGuire, J.L., Duggan, J.M., Nogeire, T.M., Heinrichs, J.A.,
498 Tewksbury, J.J. & Lawler, J.J. (2015) Climate-induced range overlap among closely related
499 species. *Nature Climate Change*, **5**(9), 883–886.

500

Kuntner, M., Năpăruș, M., Li, D. & Coddington, J.A. (2014). Phylogeny predicts future
habitat shifts due to climate change. *PLoS ONE*, **9**, e98907.

501

502 Leroy, B., Bellard, C., Dubos, N., Colliot, A., Vasseur, M., Courtial, C., Bakkenes, M.,
503 Canard, A. & Ysnel, F. (2014) Forecasted climate and land use changes, and protected
504 areas: the contrasting case of spiders. *Diversity and Distributions*, **20**, 686–697.

505

506 Leroy, B., Paschetta, M., Canard, A., Bakkenes, M., Isaia, M. & Ysnel, F. (2013) First
507 assessment of effects of global change on threatened spiders: Potential impacts on
508 *Dolomedes plantarius* (Clerck) and its conservation plans. *Biological conservation*, **161**,
509 155–163.

510

511 Liu, C., Berry, P.M., Dawson, T.P. & Pearson, R.G. (2005) Selecting thresholds of
512 occurrence in the prediction of species distributions. *Ecography*, **28**, 385–393.

513

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

517

518 Mammola, S. & Isaia, M. (2017) Spiders in caves. *Proceedings of the Royal Society B:*
519 *Biological Sciences*, **284**, 20170193.

520

521 Mammola, S., Isaia, M. & Arnedo, M.A. (2015) Alpine endemic spiders shed light on the
522 origin and evolution of subterranean species. *PeerJ*, **3**, e1384.

523

524 Mammola, S., Piano, E. & Isaia, M. (2016) Step back! Niche dynamics in cave-dwelling

525 predators. *Acta Oecologica*, **75**, 35–42.

526

527 Mammola, S., Goodacre, S.L. & Isaia, M. (2017) Climate change may drive cave spiders
528 to extinction. *Ecography*, **40**, 1–10.

529

530 Manenti, R., Lunghi, E. & Ficetola, G.F. (2015) The distribution of cave twilight-zone
531 spiders depends on microclimatic features and trophic supply. *Invertebrate biology*, **134**,
532 242–251.

533

534 Merow, C., Smith, M.J. & Silander, J.A. (2013) A practical guide to MaxEnt for modeling
535 species' distributions: what it does, and why inputs and settings matter. *Ecography*, **36**,
536 1058–1069.

537

538 Meynard, C.N., Pillay, N., Perrigault, M., Caminade, P. & Ganem, G. (2012) Evidence of
539 environmental niche differentiation in the striped mouse (*Rhabdomys* sp.): inference from
540 its current distribution in southern Africa. *Ecology and Evolution*, **2**, 1008–1023.

541

542 Milner, E. (2013) Cave spiders in the London area. *Newsletter of the British Arachnological*
543 *Society*, **126**, 18–20.

544

545 Morales, N.S., Fernández, I.C., Baca-González, V. (2017) MaxEnt's parameter
546 configuration and small samples: are we paying attention to recommendations? A
547 systematic review. *PeerJ*, **5**, e3093.

548

549 Nentwig, W., Blick, T., Gloor, D., Hänggi, A. & Kropf, C. (2017) *Spiders of Europe*, Version
550 02.2017. www.araneae.unibe.ch.

551

552 Newbold, T. (2010) Applications and limitations of museum data for conservation and
553 ecology, with particular attention to species distribution models. *Progress in Physical*
554 *Geography*, **34**, 3–22.

555

556 Novak, T., Tkvac, T., Kuntner, M., Arnett, E.A., Delakorda, S.L., Perc, M. & Janžekovič, F.
557 (2010) Niche partitioning in orbweaving spider *Meta menardi* and *Metellina marianae*
558 (*Tetragnathidae*). *Acta Oecologica*, **36**, 522–529.

559

560 Novak, T., Šajna, N., Antolinc, E., Lipovšek, S., Devetak, D. & Janžekovič, F. (2014) Cold
561 tolerance in terrestrial invertebrates inhabiting subterranean habitats. *International Journal*
562 *of Speleology*, **43**, 265–272.

563

564 Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts
565 across natural systems. *Nature*, **421**, 37–42.

566

567 Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change.
568 *Annual Review of Ecology, Evolution and Systematics*, 637–669.

569

570 Peterson, A.T., Soberón, J., Pearson, R. G., Anderson, R. P., Nakamura, M., Martinez-

571 Meyer, E. & Araújo, M. B. (2011) *Ecological niches and geographical distributions*.
572 Princeton University Press, Princeton, New Jersey, USA.
573

574 Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006) Maximum entropy modeling of
575 species geographic distributions. *Ecological Modelling*, **190**, 231–259.
576

577 Phillips, S. J., Dudík, M., Elith, J., Graham, C.H., Lehmann, A., Leathwick, J. & Ferrier, S.
578 (2009) Sample selection bias and presence-only distribution models: implications for
579 background and pseudo-absence data. *Ecological Applications*, **19**, 181–197.
580

581 Quillfeldt, P., Masello, J.F., Navarro, J. & Phillips, R. (2013) Year-round distribution
582 suggests spatial segregation of two small petrel species in the South Atlantic. *Journal of*
583 *Biogeography*, **40**, 430–441.
584

585 Ribera, C. (1978) Contribution à la connaissance de la faune cavernicole du Nord-est de
586 l'Espagne: le genre *Meta*. *Proceedings of the 7th International Congress of Arachnology*
587 *(Exeter, 1977)*, **42**, 353–358.
588

589 Rizzo, V., Sánchez-Fernández, D., Fresneda, J., Cieslak, A. & Ribera, I. (2015). Lack of
590 evolutionary adjustment to ambient temperature in highly specialized cave beetles. *BMC*
591 *Evolutionary Biology*, **15**, 10.
592

593 Sánchez-Fernández, D., Rizzo, V., Cieslak, A., Faille, A., Fresneda, J. & Ribera, I. (2016)

594 Thermal niche estimators and the capability of poor dispersal species to cope with climate
595 change. *Scientific Reports*, **6**, 23381.

596

597 Saupe, E.E., Barve, V., Myers, C.E., Myers, C.E., Soberón, J., Barve, N., Hensz, C.M.,
598 Peterson, A.T., Owens, H.L. & Lira-Noriega, A. (2012) Variation in niche and distribution
599 model performance: the need for a priori assessment of key causal factors. *Ecological*
600 *Modelling*, **237**, 11–22.

601

602 Scali, S., Mangiacotti, M., Sacchi, R. & Gentili, A. (2011) A tribute to Hubert Saint Girons:
603 niche separation between *Vipera aspis* and *V. berus* on the basis of distribution models.
604 *Amphibia-Reptilia*, **32**, 223–233.

605

606 Silverman, B.W. (1992) *Density estimation for statistics and data analysis*. Chapman &
607 Hall, London.

608

609 Simon, E. (1922) Description de deux arachnides cavernicoles du midi de la France.
610 *Bulletin de la Société Entomologique de France*, 199–200.

611

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

615

616 Smithers, P. & Smith, F.M. (1998) Observations on the behaviour of second instars of the

617 cave spider *Meta menardi* (Latreille, 1804). *Newsletter of the British Arachnological*
618 *Society*, **81**, 4–5.

619

620 Snowman, C.V., Zigler, K.S. & Hedin, M. (2010) Caves as islands: mitochondrial
621 phylogeography of the cave-obligate spider species *Nesticus barri* (Araneae: Nesticidae).
622 *Journal of Arachnology*, **38**, 49–56.

623

624 Syfert, M.M., Smith, M.J. & Coomes, D.A. (2013) The effects of sampling bias and model
625 complexity on the predictive performance of MaxEnt Species Distribution Models. *PLoS*
626 *ONE*, **8**, e55158.

627

628 Szymczkowski, W. (1953) Preferendum termiczne jaskiniowego pajaka *Meta menardi* Latr.
629 (Argiopidae). *Folia Biologica Warszawa*, **1**.

630

631 Tatole, A. (2005) On the biogeography of Romanian spiders (Araneae). *Acta Zoologica*
632 *Bulgarica*, **1**, 281–285.

633

634 Travis, J., Delgado, M., Bocedi, G., Baguette, M., Barton, K., Bonte, D., Boulangeat, I.,
635 Hodgson, J.A., Kubisch, A., Penteriani, V., Saastamoinen, M., Stevens, V.M. & Bullock, J.
636 M. (2013) Dispersal and species' responses to climate change. *Oikos*, **122**, 1532–1540.

637

638 Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin,
639 J.-M., Hoegh-Guldberg, O. & Bairlein, F. (2002) Ecological responses to recent climate

640 change. *Nature*, **416**, 389–395.

641

642 Warren, R.J., Chick, L.D., DeMarco, B., McMillan, A., De Stefano, V., Gibson, R. &

643 Pinzone, P. (2016) Climate-driven range shift prompts species replacement. *Insectes*

644 *Sociaux*, **63**, 593–601.

645

646 Williams, J.W. & Jackson, S.T. (2007) Novel climates, no-analog communities, and

647 ecological surprises. *Frontiers in Ecology and Environment*, **5**, 475–482.

648

649 World Spider Catalog (2017) *World Spider Catalog*, version 18. Natural History Museum

650 Bern, online at <http://wsc.nmbe.ch>.

651

652 Yao, Z., Zheng, G., Fu, J. & Li, S. (2016) High endemism at cave entrances: a case study

653 of spiders of the genus *Uthina*. *Scientific Reports*, **6**, 35757.

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.

660

661 **Editor:** Aristeidis Parmakelis

662

663

664

665

666

667

668

669

670

671

672

673

674

675

ha eliminato: in which

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

Variable	Description	Unit	<i>Meta menardi</i>	<i>Meta bourneti</i>
			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

681

682

683

684

685

686

687

688

689

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.

703

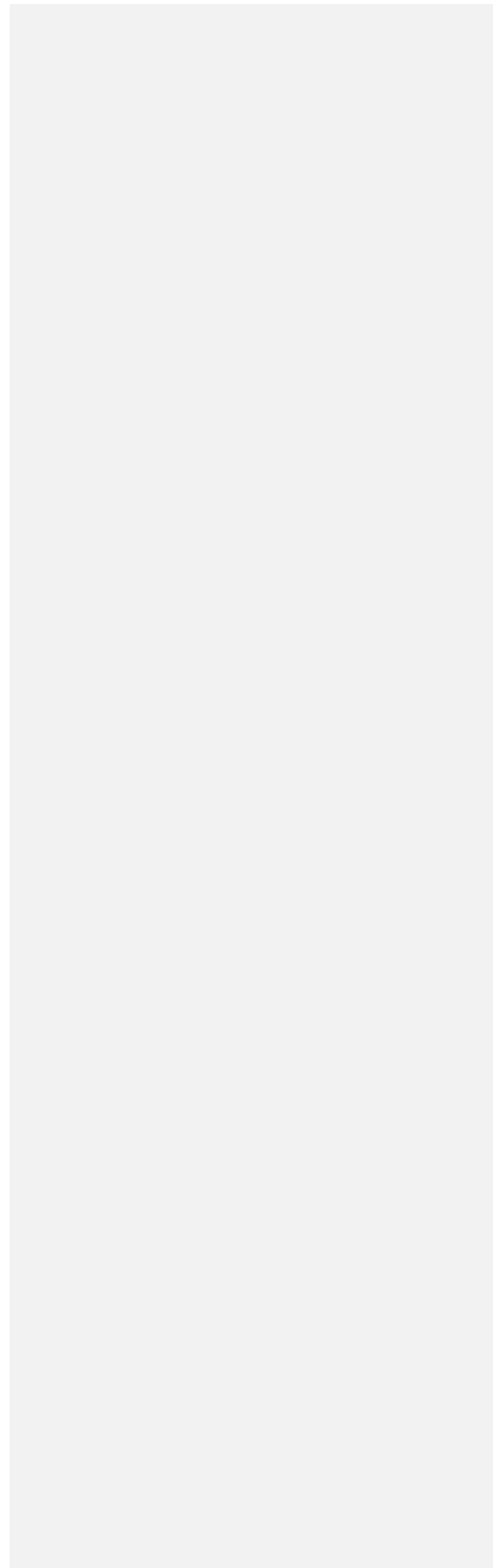
704

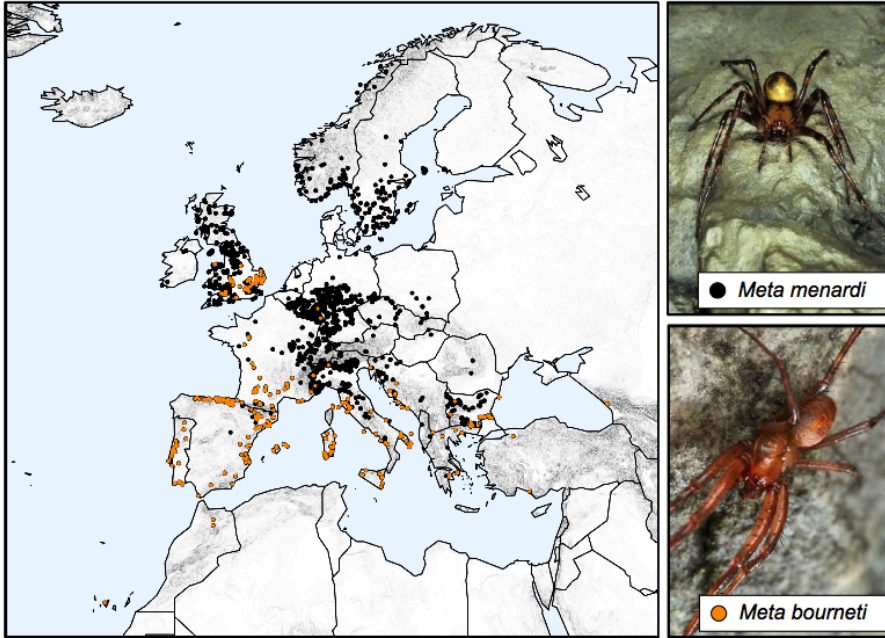
705

706

707

708





709

710 **Figure 1**

711

712

713

714

715

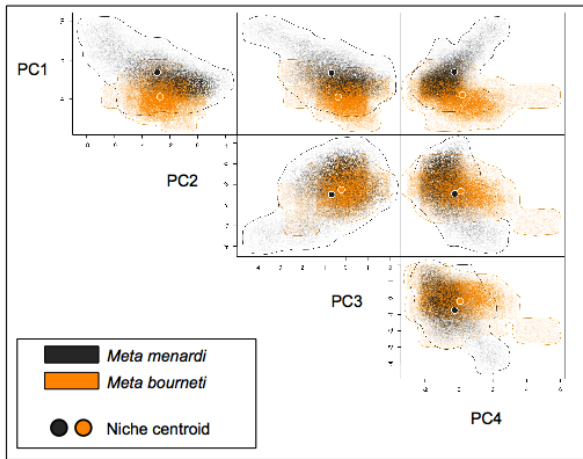
716

717

718

719

720



721

722

723 **Figure 2**

724

725

726

727

728

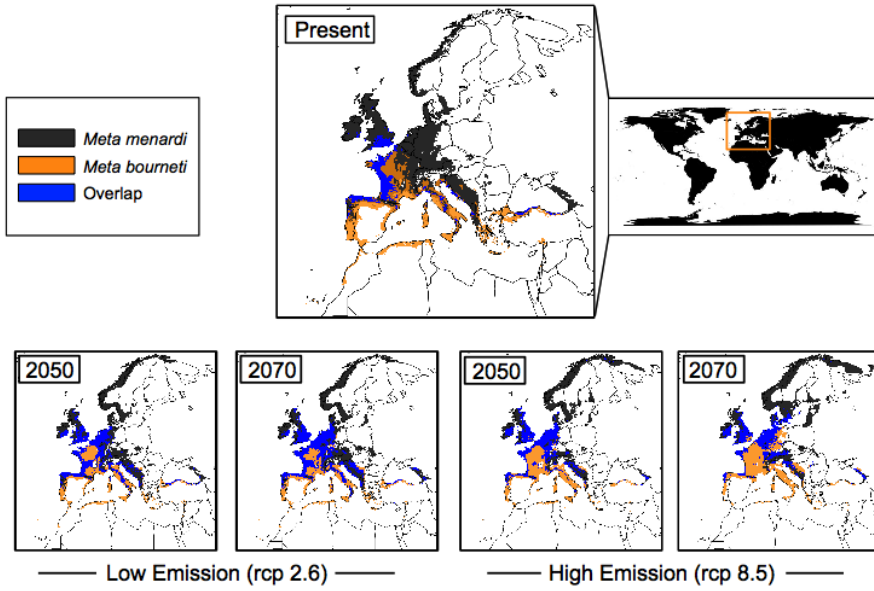
729

730

731

732

733



734

735 **Figure 3**