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**Associations between habitat quality, body size, and reproductive fitness in the alpine endemic spider *Vesubia jugorum***

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(Article begins on next page)

1 **Assessing species distribution model performance via functional traits:**  
2 **habitat suitability predicts body size and reproductive fitness in terrestrial**  
3 **invertebrates**

4

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28 **ABSTRACT**

29 *Aim.*

30 In theory, the most suitable habitat across a species range should support individuals  
31 displaying the highest fitness, making it possible to provide a biological verification of the  
32 reliability of species distribution models by exploring the relationships between habitat  
33 suitability and functional traits. However, relationships between habitat suitability and  
34 functional traits have been tested almost exclusively in plants, resulting in a general lack of  
35 consensus. We investigated the degree to which morphological and reproductive traits of  
36 an alpine habitat-specialist spider vary along a gradient of habitat suitability projected via  
37 species distribution models (SDMs), testing whether we could provide a biological  
38 verification of the model performance grounded in field-collected data.

39

40 *Location.*

41 South-western Alps (France and Italy)

42

43 *Time period.*

44 2007–2018

45

46 *Major taxa studied.*

47 *Vesubia jugorum* (Simon 1881) (Arachnida: Araneae: Lycosidae)

48

49 *Methods.*

50 We used a combination of climatic, topographical and geomorphological variables at a  
51 resolution of 250 m to model the habitat suitability of *V. jugorum*, using multiple SDM  
52 algorithms (Generalized Additive Models, Boosted Regression Trees, Maximum Entropy  
53 Models). In parallel, we carried out field samplings aimed at obtaining fresh specimens for  
54 measuring functional traits related to size and reproductive success. We tested the  
55 relationship between functional traits and habitat suitability using Linear Mixed Models  
56 (LMM).

57

### 58 *Results.*

59 We found that the species distribution could be adequately approximated via a  
60 combination of habitat and climatic variables. We further demonstrated that optimal habitat  
61 conditions maximized both body and egg clutch size.

62

### 63 *Main conclusions.*

64 Bridging biogeography and functional ecology is a promising avenue for obtaining a  
65 realistic construction of species niches, achieving a better understanding of the interplay  
66 between climate, functional traits, species distribution and individual fitness. We  
67 emphasize the importance of using field-collected data for obtaining objective evaluations  
68 of SDM performance.

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## 73 INTRODUCTION

74 Species distribution models (SDMs) are a family of statistical methods that permit the  
75 investigation of the relationship between occurrence data and environmental variables,  
76 with the general goal of projecting a probability surface onto a geographical space to  
77 represent the potential distribution or the ecological niche of a certain species (Peterson et  
78 al., 2011). Over the last three decades, development of correlative SDMs has been rapid  
79 (Booth, 2018; Lobo, Jiménez- Valverde, & Hortal, 2010; Zimmermann, Edwards, Graham,  
80 Pearman, & Svenning, 2010). These kinds of models are particularly appreciated because  
81 they offer the possibility of transferring current distribution models in space and time  
82 (Yates et al., 2018), with important applications in global change biology (Dormann, 2007;  
83 Hijmans & Graham, 2006; Pearson & Dawson, 2003), invasion biology (Peterson, 2003;  
84 Peterson & Vieglais, 2001), and conservation studies (Guisan et al., 2013).

85 Whilst the usefulness of SDMs in ecology and biogeography has been widely  
86 acknowledged (Guisan & Zimmermann, 2000; Pearson & Dawson, 2003; Peterson et al.,  
87 2011), different authors have argued that the potential of these statistical tools is still not  
88 fully expressed (e.g., Araujo & Guisan, 2006; Hällfors et al., 2016; Sinclair, White, &  
89 Newell, 2010). More than ten years ago, Guisan & Thuiller (2005) foresaw that SDMs may  
90 offer "*more than simple habitat models*", for instance by incorporating or addressing biotic  
91 interactions, migration processes, dispersal limitations and population dynamics (Araujo &  
92 Luoto, 2007; Boulangeat, Gravel, & Thuiller, 2012; Franklin, 2010; Thuiller, Albert, Dubuis,  
93 Randin, & Guisan, 2010; Violle, Reich, Pacala, Enquist, & Kattge, 2014; Zimmermann et  
94 al., 2010). One additional possibility, that has received little attention so far, is to  
95 investigate the relationship between the habitat suitability predicted by the model for a  
96 certain species, and the variation in the species functional traits. In other words, under the  
97 assumption that the habitat of higher suitability should support the best performing

98 individuals (Nagaraju et al., 2013; Thuiller et al. 2010; Wittmann, Barnes, Jerde, Jones, &  
99 Lodge, 2016), SDMs can potentially be validated by checking whether the most suitable  
100 areas predicted by the model actually support subpopulations displaying higher fitness  
101 compared to the average. For instance, in one of the latest attempts to address this issue,  
102 Wittmann et al. (2016) found a positive correlation ( $r= 0.5$ ) between the growth rate of a  
103 wild Grass Carp and the species' habitat suitability projected by a maximum entropy  
104 model.

105 Up to now, few studies have explicitly tested the relationship between habitat  
106 suitability and species traits, using mainly plants as model organisms (Elmendorf & Moore,  
107 2008; Nagaraju et al., 2013; Pollock, Morris, & Vesk, 2012; Smith, Alsdurf, Knapp, Baer, &  
108 Johnson, 2017; Thompson & McCarthy, 2008; Thuiller, Lavorel, Midgley, Lavergne, &  
109 Rebelo, 2004; Thuiller et al., 2009; Wright, Davies, Lau, McCall, & McKay, 2006) and more  
110 sporadically vertebrates (fishes: Larson, Olden, & Usio, 2010; Michel, Chien, Beachum,  
111 Bennett, & Knouft, 2017; Wittmann et al., 2016; salamanders: Lunghi et al., 2018). Results  
112 of these studies are heterogeneous: a positive relationship between habitat suitability and  
113 species fitness—measured using different proxies—has not been confirmed in all species  
114 (Elmendorf & Moore, 2008; Larson et al., 2010; Thuiller et al., 2009) or ecotypes tested  
115 (Wittmann et al., 2016; Wright et al., 2006).

116 Stemming from these considerations, and taking into account the lack of similar  
117 tests for terrestrial invertebrates, we provide the first such analysis using an arthropod as a  
118 model species. Under the assumptions that a habitat-specialist displays more effective  
119 functional traits for thriving in specific environmental conditions (Devictor et al., 2010), and  
120 should be more sensitive to climatic variations than a generalist (Clavel, Julliard, &  
121 Devictor, 2011), we focused on a mountaintop specialist species. In a first step, we used  
122 SDM to investigate species-to-environment relation and predict habitat suitability across its

123 distribution range and secondly, we investigated the degree to which functional traits  
124 measured in individuals collected from across the whole range, vary along a gradient of  
125 projected habitat suitability. We hypothesized that there is a positive, significant  
126 relationship between the habitat suitability predicted by SDM and the functional traits of the  
127 species. If proven correct, such relation provides an appropriate biological verification of  
128 the SDM results, grounded in field-collected data.

129

## 130 **MATERIAL AND METHODS**

### 131 **Model organism and study area**

132 We focused on the alpine endemic spider *Vesubia jugorum* (Simon, 1881), one of the  
133 largest wolf spider (Lycosidae) occurring in Europe (Isaia, Paschetta, & Chiarle, 2015). *V.*  
134 *jugorum* is a mountaintop habitat-specialist that resides exclusively in rocky lands such as  
135 boulder fields and alpine screes at high elevation (subnival and nival zones, from 2000 to  
136 3000 m a.s.l.; Mammola, Milano, Cardoso, & Isaia, 2016; Tongiorgi, 1968, 1969; see  
137 Appendix S1 in Supporting Information). This endangered species (Isaia & Mammola,  
138 2018) has a small distribution range, encompassing the Ligurian and Maritime Alps, the  
139 southern part of the Cottian Alps and the Provence Alps. Most of the species range falls  
140 within the boundaries of national parks, sites of community importance and special  
141 protection areas, namely Parco Naturale Alpi Marittime and Parco Naturale del Marguareis  
142 in Italy and Parc National du Mercantour in France (Mammola et al., 2016). In these areas,  
143 elevation ranges from ca. 300 to 3297 m a.s.l. (Mount Argentera, the highest peak). The  
144 general climate is Mediterranean in the south and more Continental in the north (climatic  
145 details in Patsiou, Conti, Zimmermann, Theodoridis, & Randin, 2014).

146

## 147 **Species distribution modelling**

### 148 *Occurrence data*

149 We assembled a dataset consisting of 101 occurrence localities of *Vesubia jugorum* (Fig.  
150 1), based on original data gathered during recent fieldwork surveys (2010–2018) and  
151 additional data available from literature published between 2007 and 2018 (Isaia, Pantini,  
152 Beikes, & Badino, 2007; Isaia et al., 2015; Mammola et al., 2016; Milano, Mammola,  
153 Rollard, Leccia, & Isaia, 2018). The few available old literature records published before  
154 2007 (Maurer & Thaler, 1988; Simon, 1881, 1937; Tongiorgi, 1968, 1969) were included in  
155 the analyses only after their further corroboration during recent field surveys – note that  
156 most of the older records were reconfirmed, possibly hinting that the distribution of the  
157 species did not varied in recent time. Full details about the assemblage of the dataset and  
158 field methods are given in Appendix [S2](#).

159 In order to minimize spatial sampling heterogeneity in the localities, we aggregated  
160 data within cells at the resolution of the environmental predictors to avoid inflation of the  
161 numbers of presences.

162

### 163 *Environmental predictors*

164 We used a combination of climatic, topographical and geomorphological variables as  
165 predictors (Table 1), at a resolution of 250 m. In line with recent literature (Brandt et al.,  
166 2017; Fourcade, Besnard, & Secondi, 2018; Mammola & Leroy, 2018; Saupe et al., 2012),  
167 the initial set of predictors was selected based on our knowledge on the species biology  
168 (i.e. variables likely to be associated with habitat quality for the species), and only then  
169 sub-selected using statistical inference.

170 In order to represent the peculiar climate of the Maritime Alps in which the species  
171 occurs (Patsiou et al., 2014), we selected three climatic variables reflecting continentality,  
172 namely mean annual temperature, annual temperature range and annual precipitations.  
173 Temperature variables were produced by statistical downscaling data from the ALADIN-  
174 Climat general circulation model provided by the French National Meteorological Research  
175 Center (1976–2005; Herrmann, Somot, Calmanti, Dubois, & Sevault, 2011). ALADIN-  
176 Climat model provides regionalized climate projections at a resolution of 12 km, based on  
177 Euro-CORDEX 2014 data, European part of international project CORDEX for  
178 Coordinated Regional Climate Downscaling Experiment (Jacob et al., 2014). We increased  
179 climate data resolution from 12 kilometers to 250 meters, using multiple linear regression  
180 calculations performed between topographic variables and data from the ALADIN-Climat  
181 model (Martin, Carrega & Adnes, 2013). Sum of annual precipitation was obtained by a  
182 geostatistical interpolation of ALADIN-Climat grid centroids.

183 Considering the importance of snow cover for modelling the distribution of high-  
184 altitude species (Niittynen & Luoto, 2018), and the expected influence of snow cover  
185 duration on the developmental season of *Vesubia jugorum* (Mammola et al. 2016), we  
186 further generated a variable representing the snow coverage. We downloaded the MODIS  
187 Terra “MOD10A2.006” time series from the National Snow & Ice Data center, covering a  
188 period from January 2002 to December 2017. This dataset represents a snow index  
189 database at a resolution of 500 m (Masuoka, Fleig, Wolfe, & Patt, 1998). We extracted the  
190 “Eight Days Snow Cover” dataset, and realized a conversion between the snow  
191 occurrence chronobyte toward a number of days (0 to 8). Then, we computed the addition  
192 of number of days of snow occurrence, and calculated the mean over a 16-year period.

193 Given that the model species is a habitat-specialist dwelling almost exclusively in  
194 rocky lands (Tongiorgi, 1968, 1969; Mammola et al., 2016), we further generated a raster

195 representing the availability of this habitat in the study area. To generate this variable, we  
196 downloaded Landsat ETM+ (27 Jul 2000) and OLI (27 Aug 2014) multispectral rasters  
197 from the United States Geological Survey (USGS) interface, at a resolution of 30 m. We  
198 realized the remote sensing of rocky surfaces by using a Normalized Difference  
199 Vegetation Index (NDVI) threshold ( $<0$ ) for both dates and selection of pixels with negative  
200 values of NDVI on both dates (Fretwell, Convey, Fleming, Peat, & Hughes, 2011).

201         Considering that the species inhabits topographically complex high alpine habitats  
202 (Patsiou et al., 2014; Mammola et al., 2016), we further generated two variables reflecting  
203 roughness and slope exposure (aspect). Indeed, it has been suggested that topographic  
204 variables distinct from elevation may be useful in representing non-climatic aspects of a  
205 species' niche (Title & Bemmels, 2017). We used SRTM Digital Elevation Model's (DEM)  
206 raster layer at a resolution of 90 m, derived from the Shuttle Radar Topography Mission  
207 (SRTM) digital elevation data from United States Geological Survey (USGS) database  
208 (Reuter, Nelson & Jarvis, 2007). Roughness was generated by calculating, for each pixel,  
209 the difference between highest and lowest elevation data value in a square of  $7 \times 7$  pixels  
210 (e.g. approximately 650 meters of resolution). For slope exposure, only a north-south  
211 exposure index was retained because 0 to  $360^\circ$  raw aspect data is not a quantitative data.

212         To avoid collinearity in the initial set of predictors (Braunisch et al., 2013), we  
213 calculated pairwise Pearson correlations (Table 2), using a standard  $r > |0.70|$  threshold  
214 (Dormann et al., 2013).

215

#### 216 *Calibration area*

217 We calibrated and projected SDMs within the accessible area (Anderson & Raza, 2010;  
218 Barve et al., 2011; Owens et al., 2013), i.e. the geographical extent hypothesized to fall

219 within the long-term dispersal and colonization potential for a certain species over its  
220 evolutionary history. Lacking data on the gene flow and field observations on dispersal, we  
221 assumed a low dispersal potential considering the restricted distribution of the species. We  
222 masked the environmental predictors with a bounding rectangle within 6° to 8° latitude and  
223 from 43.5° to 44.5° longitude. Given that the species is a high altitude specialist, we further  
224 excluded lowlands (areas below 1500 m a.s.l.) from the accessible area (Fig. 1).

225

### 226 *Modelling procedure and projection*

227 A wide suite of algorithms for modelling the distribution of species exists (Peterson et al.,  
228 2011). Qiao, Soberón, & Peterson (2015) recently suggested that a diligent modelling  
229 protocol would be to assess the performance of potentially competing SDM algorithms,  
230 and selecting the best performing one given the specific occurrence dataset at hand. We  
231 tested the relative performance of three well-acknowledged statistical techniques  
232 belonging to the three main categories of algorithms for SDMs: regression [Generalized  
233 Additive Models (GAM); Hastie & Tabshirani, 1990], regression trees [Generalized  
234 Boosted Regression Models (GBM); Ridgeway, 2017] and machine-learning [maximum  
235 entropy model (MaxEnt); Phillips, Anderson, & Schapire, 2006].

236 We fitted GAM using the *gam* R function (Hastie, 2017). We used 1,000  
237 pseudoabsence points for contrasting the presences, which we randomly extracted from  
238 across the accessible area. We fitted an initial model including all the uncollinear variables  
239 of interest (Pearson  $r < |0.70|$ ), estimating the optimum amount of smoothing for each  
240 variable through generalized cross-validation. Whenever the effect of a variable was linear  
241 (estimated degrees of freedom,  $edf \approx 1$ ), we dropped the smoothed term and introduced  
242 the parametric terms, thus adopting a linear approach. Model reduction was carried out on  
243 the full model by sequentially deleting non-significant terms according to the Akaike's

244 information criterion (AIC) values, until a minimum adequate model of significant terms  
245 remained (Zuur, Ieno, Walker, Saveliev, & Smith, 2009).

246 We constructed Generalized Boosted Regression Models (GBM) using the *gbm* R  
247 function (Ridgeway, 2017) and following the general protocol by Elith, Leathwick, & Hastie  
248 (2008). For contrasting the occurrences, we extracted a number of absence points equal  
249 to the number of presence points, using the '2°far' method (Barbet-Massin, Jiguet, Albert,  
250 & Thuiller, 2012). A Gaussian distribution was specified, and the optimal number of trees  
251 was estimated by means of cross-validation, using the *gbm.perf* R function (Ridgeway,  
252 2017). We evaluated variable contribution to the final model by examining the variable  
253 relative influence (%).

254 We constructed Maximum entropy model (MaxEnt) using the *maxent* function in the  
255 'dismo' R package (Hijmans, Phillips, Leathwick, & Elith, 2014). For calibrating the model,  
256 we used 1,000 background points (Phillips & Dudik, 2008). Considering the sample size of  
257 our dataset (<100 occurrences), we specified MaxEnt's feature classes and regularization  
258 multiplier manually rather than using default settings (Morales, Fernández, & Baca-  
259 González, 2017). We estimated the most suitable configuration of these two parameters  
260 *via* the *ENMevaluate* function in the 'ENMeval' R Package (Muscarella et al., 2014). We  
261 evaluated variable contribution to the final model using the permutation importance  
262 (Phillips, 2017).

263 For each algorithm, we ran 50 bootstrap replicates of models, keeping a random  
264 partition of 20% of the points for each run to assess the predictive ability. Predictive ability  
265 of the three models was obtained by calculating two standard predictive metrics—Area  
266 Under the Curve (AUC) and True Skill Statistics (TSS)—using the 'ROCR' R package  
267 (Sing, Sander, Beerenwinkel, & Lengauer, 2005). Although we acknowledge that the ability  
268 of available evaluation statistics to correctly assess the performance of SDMs has been

269 recently questioned (Fourcade et al., 2018), we calculated these two metrics anyway in  
270 order to compare the performance of the three algorithms relative to each other (Qiao et  
271 al., 2015)—rather than their absolute predictive ability. We generated a final model using  
272 the complete dataset and the most performing modelling technique(s). We projected the  
273 model into the accessible area to obtain a graphical representation of the current  
274 distribution of *V. jugorum*.

275

## 276 **Analysis of functional traits**

### 277 *General considerations*

278 We investigated the degree to which functional traits of *Vesubia jugorum* measured in  
279 individuals collected from across the distribution range varies along the gradient of habitat  
280 suitability predicted via SDMs. Following the definition by Violle et al. (2007), we  
281 considered a functional trait as a morphological feature measurable at the individual level  
282 which reflects its individual performance. In predatory arthropods, body size represents  
283 one of the main properties of an organism, determining its ability to thrive in a specific  
284 habitat and the amount of resources that an individual can allocate to reproduction—and  
285 thus a direct *proxy* of its fitness (Jakob, Marshall, & Uetz, 1996; Sokolovska, Rowe, &  
286 Johansson, 2000). As far as spiders are concerned, a direct relationship between body  
287 size and reproductive success has been demonstrated in a number of species (Marshall &  
288 Gittleman, 1994), including wolf spiders (Ameline et al., 2018; Anderson, 1974, 1990;  
289 Uetz, Papke, & Kilinc, 2002; Workman, 1979).

290

### 291 *Data acquisition*

292 For forty localities scattered across the whole range of distribution, we obtained fresh  
293 specimens for morphological analyses. Given the wide variability in size of juveniles  
294 (variation of an order of magnitude in all traits considered; n= 29), and the paucity of males  
295 (n=9), only adult female specimens were considered for the analysis.

296 In total, we examined 102 female specimens for five morphological traits related to  
297 body size, namely femur, tibia and metatarsus length and carapace length and width  
298 (details in Appendix S3). We used both leg and carapace measures as they offer good  
299 estimations for the overall spider body size (Elgar, Ghaffar, & Read, 1990; Hagstrum,  
300 1971; Persons & Uetz, 2005; Wilder & Rypstra, 2008)—in fact, these structures are fixed  
301 in size at maturity. We acquired measurements using a Leica M80 stereoscopic  
302 microscope (up to 60x magnification). To standardize data acquisition, measurements  
303 were taken from digital pictures made with a Leica EC3 digital camera and calculated with  
304 the Leica LAS EZ 3.0 software (Leica Microsystems, Switzerland).

305 In wolf spiders, females actively carry around the egg sac (hereinafter cocoon)  
306 attached to the spinnerets at the rear of their body. A few females observed during field  
307 work were carrying their cocoon. For these specimens (n= 14), we estimated the cocoon  
308 diameter directly in the field, using a digital caliper. Cocoon size was expressed in class  
309 sizes, thus obtaining an indirect measure of reproductive fitness (Bowden, Høye & Buddle,  
310 2013; Marshall & Gittleman, 1994). After measurements, females with cocoon were  
311 released.

312

### 313 *Relationship between habitat suitability and morphological traits*

314 Using the coordinates of the collection localities of each measured specimen (females), we  
315 extracted the value of habitat suitability derived from the SDM projection. We assessed

316 multicollinearity among morphological traits using pairwise Pearson  $r$  correlation, setting  
317 the threshold for collinearity at  $r > |0.7|$  (Dormann et al., 2013). We tested the relationship  
318 between morphological traits and habitat suitability using Linear Mixed Models (LMM) fitted  
319 in the 'nlme' R package (Pinheiro, Bates, DebRoy, Sarkar & R Core Team, 2017). Rather  
320 than calculating a correlation between the estimated habitat suitability and the species  
321 traits as in previous studies (e.g. Wittmann et al., 2016), we adopted a regression  
322 framework aiming at estimating the significance of the trends and making potential  
323 predictions (Zuur & Ieno, 2016). This mixed procedure allowed us to deal with the violation  
324 of spatial independence derived from the fact that we measured multiple individuals from  
325 the same populations. We thus included the sampling locality as a random factor in order  
326 to account for the variation it introduced in our samples and thus to correctly estimate the  
327 regression coefficients. Variance explained by the regression models was expressed as  
328 marginal  $R^2$ , i.e. the variance expressed only by the fixed terms. We validated the model  
329 by constructing standard validation plots using model's residuals and fitted values (Zuur &  
330 Ieno, 2016; Zuur et al., 2009), and investigated the existence of possible non-linear  
331 patterns in the residuals with the *gam* R command (Hastie, 2017).

332         In order to visualize the spatial pattern of variation in functional traits, we further  
333 tested the linear relationship between the trait itself and the longitude and latitude of the  
334 localities. For this analysis, we used the same mixed structure and modelling procedure  
335 explained above. In the longitudinal model, the quadratic term (Longitude<sup>2</sup>) was introduced  
336 in order to capture a non-linear parabolic pattern in the residuals which we detected during  
337 model validation.

338         Given the reduced number of cocoons measured ( $n = 14$ ), it was not possible to fit a  
339 stable LMM to estimate the relationship between cocoon size and habitat suitability.  
340 Instead, we used a Pearson's  $r$  correlation test to assess this relationship, under the null

341 hypothesis of no correlation between cocoon size and habitat suitability ( $r= 0$ ). We  
342 reported hypothesis testing using both 95% confidence intervals of the coefficient of  
343 correlation and p-value based on t-test.

344

## 345 **RESULTS**

### 346 **Species distribution model and projected distribution**

347 After the removal of occurrence duplicates and invalid records (see Appendix S2), we  
348 ended up with 89 occurrences to generate the SDMs. Analysis of multicollinearity among  
349 environmental variables revealed some degree of correlation amongst predictors (Table  
350 2). As a result, we selected six uncollinear variables for constructing the models, namely  
351 snow coverage, percentage of rock, sum of precipitation, annual temperature range,  
352 roughness, and aspect. The three SDM algorithms gave similar outputs, although there  
353 were some differences between the most important variables identified by MaxEnt and  
354 GBM algorithms (Table 1). All models revealed a positive relationship between the  
355 probability of presence of the model species and sum of precipitation, the species being  
356 preferentially found in areas with a higher rainfall regime. The probability of presence of *V.*  
357 *jugorum* also increased with the percentages of rocky habitats. The distribution of the  
358 species was further explained by the snow coverage: the probability of presence of the  
359 species increased rapidly in those areas where the mean numbers days/year with snow  
360 was higher than 40 days/year, reaching an optimum around 80 days/years (Appendix S4).  
361 Instead, the contribution of temperature range and the topographical variables in  
362 explaining the distribution of *Vesubia* was negligible (all MaxEnt permutation importance <  
363 1; all GBM relative influence <5; not significant according to the GAM).

364 Standard validation metrics (AUC, TSS) revealed that all SDM algorithms tested  
365 had a high fit, with none clearly outperforming the others in terms of predictive ability (all  
366 AUC > 0.90; TSS > 0.70; median of the 50 bootstraps). Therefore, as is recommended in  
367 the literature (Araujo & New, 2007; Guisan & Thuiller, 2005), we used an ensemble of the  
368 three model projections to represent the species distribution (Fig. 2a)—median value of  
369 the three individual projections weighted by the TSS. Overall, suitable areas predicted by  
370 the model were congruent with the known distribution of *V. jugorum* (Mammola et al.,  
371 2016), with most suitable areas corresponding to the Mercantour-Argentera massif at the  
372 Italian-French border. This core area presented a roughly continuous suitable habitat with  
373 high predicted habitat suitability, ensuring connectivity between local populations. Two  
374 additional suitable areas, more fragmented, were predicted at the eastern and north-  
375 western corners of the range, corresponding to the Ligurian and Cottian Alps.

376

### 377 **Relationship between habitat suitability and morphological traits**

378 Females of *Vesubia jugorum* (n= 102) revealed variability in all morphological traits  
379 considered (summary of measures in Appendix S3). There was a high degree of  
380 correlation among all leg articles (all Pearson  $r > 0.90$ ) and between leg and carapace  
381 length and width (all Pearson  $r > 0.70$ ; Appendix S3). Therefore, we arbitrarily selected  
382 femur length as a representative measure for body size (Fig. 2a). We found a positive,  
383 significant relationship between femur length and habitat suitability predicted by the model  
384 (estimated  $\beta \pm \text{s.d.} = 1.19 \pm 0.24$ ;  $p < 0.001$ ; marginal  $R^2 = 0.31$ ), with more suitable areas  
385 supporting the individuals of a larger size (Fig. 2b). As far as femur length and carapace  
386 size are positively correlated, it was possible to obtain the same positive linear relationship  
387 by constructing a LMM with carapace width as a dependent variable (estimated  $\beta \pm \text{s.d.} =$

388 0.73±0.20,  $p < 0.001$ ). The cocoon size was also positively correlated with habitat suitability  
389 [ $r = 0.62$ , 95% CI (0.20–0.85);  $t = 3.07$ ,  $p = 0.007$ ;  $n = 14$ ] (Fig. 2c).

390 There was a significant increase in femur length at increasing longitudes (estimated  
391  $\beta \pm \text{s.d.} = 23.55 \pm 8.05$ ;  $p = 0.004$ ) and a decrease with longitude quadratic function (estimated  
392  $\beta \pm \text{s.d.} = -1.64 \pm 0.56$ ;  $p = 0.005$ ), resulting in a parabolic trend with highest femur values at  
393 intermediate longitudes within the range of distribution (conditional  $R^2 = 0.15$ ; Fig. 3a).  
394 There was also significant increase in femur length at increasing latitudes (estimated  
395  $\beta \pm \text{s.d.} = 741.98 \pm 317.04$ ;  $p = 0.022$ ) and a decrease with latitude quadratic function  
396 (estimated  $\beta \pm \text{s.d.} = -8.39 \pm 3.58$ ;  $p = 0.022$ ), resulting in a parabolic trend with lowest femur  
397 values at decreasing latitudes within the range of distribution (conditional  $R^2 = 0.22$ ; Fig.  
398 3b).

399

## 400 **DISCUSSION**

401 In this study we reconciled two lines of evidence deriving from species distribution  
402 modelling and functional morphology analyses, with the aim of achieving a better  
403 understanding of the potential relationships between the probability of occurrence and the  
404 optimal distribution of morphological traits. We highlight implications for the SDM  
405 evaluation and provide future directions.

406

### 407 **Interpretation of the SDM**

408 Overall, SDMs fits were very good, suggesting that the species distribution is adequately  
409 predicted by a combination of habitat and climatic variables—while the topographic  
410 variables had negligible effects (Table 1). Interestingly, the projected habitat suitability  
411 revealed a close match with the predicted distribution of other relict habitat specialists

412 occurring in the same area, such as the plant *Saxifraga florulenta* Moretti (Saxifragaceae)  
413 (Patsiou et al., 2014). From a climatic perspective, the areas of higher habitat suitability  
414 are characterized by higher precipitations within a Mediterranean setting. As expected  
415 when modeling the distribution of habitat specialists (e.g. Sardà-Palomera & Vieites, 2011;  
416 Warren et al., 2001; Williams et al., 2009), availability of habitats—here modeled as the  
417 percentage of rocky lands—played an important, additional role in constructing the SDMs.  
418 It is worth noting that the percentage of rocky lands is positively correlated with altitude.  
419 Rocky habitats are indeed preferentially found at higher altitudes, whereas pastures and  
420 scrubs occurring at lower altitudes naturally limit the spread of the species downward. The  
421 high level of direct solar radiation in rocky habitats may represent an additional key factor,  
422 especially for thermoregulation during the day. The melanic coloration of *V. jugorum*  
423 indirectly confirms this relationship: black-colored arthropods are frequent in cold mountain  
424 environment with high levels of solar radiation, as a dark pigmentation helps to raise body  
425 temperature more rapidly, but also gives protection against the injurious effects of the  
426 intense ultra-violet radiation (Mani, 2013; Nentwig, 2013).

427         The third important factor in determining the predicted distribution was the snow  
428 coverage (Appendix S4). Intuitively, snow has a direct influence on the duration of the  
429 developmental season of *V. jugorum*, taking place in a relatively short snow-free period in  
430 summer-early autumn (Mammola et al., 2016)—during the rest of the year, the individuals  
431 most likely survive in the superficial layers of the alpine screes, which are buffered from  
432 the external conditions under a deep blanket of snow (see, e.g., Zhang, 2005). A  
433 significant decline in the habitat suitability was also observed where the mean numbers  
434 days/year covered by snow was too low (<40 days), a condition found at lower altitudes,  
435 not very suitable for the species. A slight decline in the habitat suitability was also  
436 observed those areas where the mean numbers of days/year with snow coverage exceeds

437 100. Such conditions are found either at very high altitudes (above 2800–3000 m a.s.l.)  
438 within the core of the distribution range or at northern latitudes within the calibration area.  
439 Tentatively, a late summer snow melting determines a significant shortening of the  
440 developmental season.

441

#### 442 **Relationship between functional traits and habitat suitability**

443 Few studies have investigated the relationship between habitat suitability and species  
444 functional traits at the scale of geographic distribution, using primarily plants as model  
445 organism (studies are reviewed in Wittmann et al., 2016). As far as we are aware, this is  
446 the first time in which a similar relationship has been demonstrated in a terrestrial  
447 invertebrate. Specifically, we found that the body size and reproductive success of  
448 *Vesubia jugorum* were positively related with the habitat suitability predicted via an  
449 ensemble of three SDM projections. We were able to predict that the populations  
450 displaying the greatest size and the largest cocoons preferentially occur in the core of the  
451 distribution (Pulliam, 2000), namely areas of higher habitat suitability which result from a  
452 combination of key environmental conditions.

453 Using an elevation gradient along mountain clines or latitudinal gradients, an  
454 intimate relationship between climatic conditions and body size has been extensively  
455 demonstrated in ectotherm invertebrates (Atkinson, 1994; Mousseau, 1997), including  
456 spiders (Ameline et al., 2018; Entling, Schmidt-Entling, Bacher, Brandl, & Nentwig, 2010).  
457 The peculiar climatic condition occurring in the rocky land inhabited by *Vesubia* is likely to  
458 be the underlying factor at the base of the positive relationship we observed (Fig. 2).  
459 Moreover, the relationship we found between traits and suitable habitats corroborates the  
460 observed general pattern of reduction in body size in spiders occurring in marginal habitats

461 (Joqué, 1981). Smaller individuals of *V. jugorum* were indeed observed at the margin of  
462 the distribution (Fig. 3) in sub-optimal climatic conditions.

463 In adult female spiders, carapace size is also correlated with the dimension of the  
464 egg clutch (Marshall & Gittleman, 1994). Thus, body size is an indirect measure of the  
465 expected number of offspring. This relation possibly indicates an increasing reproductive  
466 performance in areas with higher habitat suitability for our model species. Although based  
467 on a limited number of egg sacs (n= 14), this is further confirmed using a direct measure of  
468 reproductive fitness (Fig. 2c).

469 In light of the IUCN conservation status of *V. jugorum* (Endangered category, Isaia  
470 & Mammola, 2018) and the consequent need of monitoring future population trends in a  
471 climate change perspective (Mammola et al., 2016), the relation between traits and climate  
472 herein demonstrated may represent a promising approach for setting up monitoring  
473 programs. Indeed, measuring the variation of morphological traits offers a practical, non-  
474 invasive mean for assessing population health through time.

475

#### 476 **Biological realism of SDM and implications for model evaluation**

477 Despite our study focused on an endemic species occurring in a limited sector of the Alps,  
478 our results offer insightful evidence contributing to the recent debate about the biological  
479 realism of SDM projections and the possibility of evaluating model accuracy and fit using  
480 field collected data.

481 The use of SDM to predict species distribution has several merits, but also evident  
482 limits. Even if these models may provide satisfactory predictions for species distribution,  
483 the link between model predictions and real-life biological process is often difficult to  
484 demonstrate (Guisan & Thuiller, 2005). This is mostly due to the fact that species

485 distribution models are most often constructed from a set of distribution data downloaded  
486 from online repositories (e.g. GBIF) and a standard set of variables (e.g. the Bioclimatic  
487 dataset; Hijmans et al., 2005; Fick & Hijmans, 2017), lacking a biological verification based  
488 upon field-collected data (but see Wright et al., 2006). Our study suggests that, being  
489 diligent in constructing a model based both on a carefully constructed distribution dataset  
490 and meaningful and high-resolution environmental variables (Brandt et al., 2017; Fourcade  
491 et al., 2018; Mammola & Leroy, 2018; Saupe et al., 2012), it is possible to obtain a  
492 projection of presence/absence that can be correlated to functional traits acting as *proxies*  
493 of species performance in its habitat.

494         Therefore, this approach can potentially be used as an experimental verification of  
495 SDM projections, as it offers a simple way for assessing model performance—a good-  
496 performing model may theoretically be used to predict variation in species traits (Wittmann  
497 et al., 2016)—and its ability to represent true ecological processes—more suitable areas  
498 should theoretically maximise species performance (Pulliam, 2000). This is of crucial  
499 important because the ability of the conventional statistical metrics to evaluate SDM  
500 predictive ability has been repeatedly questioned (e.g. Bahn & McGill, 2013; Fourcade et  
501 al., 2018; Wenger & Olden, 2012;), highlighting a general paucity of objective criteria for  
502 discriminating between competing SDMs. Although we acknowledged that similar datasets  
503 of functional traits across species distributions are often lacking, especially for widespread  
504 species, and that similar analyses are time-consuming, we strongly encourage SDM users  
505 to increasingly incorporate functional data—either morphological, physiological or  
506 genetic—into their modelling fitting exercises.

507

## 508 **CONCLUSIONS AND PERSPECTIVES**

509 Latest advances in methodological and statistical approaches are revolutionizing the way  
510 in which we study and perceive an array of ecological patterns and processes. On one  
511 hand, there has been gigantic leaps forward in the utilization of trait-based approaches in  
512 ecological and evolutionary research (Blonder, 2018; Violle et al., 2007). On the other,  
513 novel tools for modeling the distribution of species are becoming widely accessible, thus  
514 being routinely used to tackle different biogeographical and macroecological questions  
515 (Lobo et al., 2010; Peterson et al., 2011; Zimmermann et al., 2010). In order to obtain  
516 more robust supports to ecological patterns and predictions, many authors have stressed  
517 out the importance of combining multiple lines of evidence (Carstens & Richards, 2007;  
518 Guillot, Renaud, Ledevin, Michaux, & Claude, 2012; Metcalf et al., 2014; Peterson, 2009).  
519 From this perspective, the integration of correlative distribution analyses and functional  
520 approaches has been recently advocated (Michel et al., 2017; Thuiller et al., 2010;  
521 Wittmann et al., 2016), enhancing the possibility of bridging biogeography and functional  
522 ecology towards the novel field of '*functional biogeography*' (Violle et al., 2014). In spite of  
523 these premises, attempts to relate SDM predictions and functional traits have been few,  
524 and so far only focused on a limited number of plant and vertebrate *taxa*. There is little  
525 doubt that integrating approaches at the crossroads between biogeography and functional  
526 ecology would greatly benefit both disciplines, helping to further increase their applicability  
527 in ecological research and to achieve a better way to assess the accuracy of our modelling  
528 fitting exercises.

529

530 **Data accessibility statement:** If the paper will be accepted, the data supporting the  
531 results will be archived in an appropriate public repository and the data DOI will be  
532 included at the end of the article.

533

534 **Conflict of interest statement:** None declared.

535

536 **SUPPLEMENTARY MATERIALS**

537 **Appendix S1** – Habitat details

538 **Appendix S2** – Notes on sampling procedure

539 **Appendix S3** – Morphological measures

540 **Appendix S4** – Relationship with snow coverage

541

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950 **TABLES**

951 **Table 1.** Initial set of variables selected for constructing the species distribution models,  
 952 their description and their relative importance according to the three algorithms  
 953 considered. Estimated parameters and variable contributions are only given for uncollinear  
 954 variables introduced in the models (Table 2). For the Generalize Additive Model (GAM),  
 955 estimated  $\beta$  and p-values are given for the linear terms (n.s.= not significant variable  
 956 dropped during model selection), whereas estimated degrees of freedoms (edf) and p-  
 957 values based on  $\chi^2$  test for the smoothed term Snow. For the Generalized Boosted  
 958 Regression Models (GBM) and the maximum entropy model (MaxEnt) the variable' relative  
 959 influence and permutation importance are reported, respectively.

960

Variable	Description	GAM	GBM	MaxEnt
Snow	Snow coverage—mean N° days/year with snow	edf= 2.21, $\chi^2$ = 12.90, p< 0.001	18.7	40.7
Rock	Percentage of scree habitats in the raster pixel	$\beta \pm SE = 0.01 \pm 0.01$ , p< 0.001	49.6	23.8
Prec	Sum of annual precipitation (mm)	$\beta \pm SE = 2.70 \pm 0.61$ , p< 0.001	21.3	34.9
T_range	Temperature annual range (°C)	n.s	6.5	0.4
T_mean	Mean annual temperature (°C)	–	–	–
Elev	Elevation a.s.l. (m)	–	–	–
Roug	Roughness	n.s	1.7	0.2
Asp	Slope exposure (°)	n.s	2.5	0.0

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965 **Table 2.** Pairwise Pearson *r* correlations among the environmental predictors—all Pearson  
 966 coefficients values are rounded to the first decimal. Uncollinear introduced in the model  
 967 are highlighted in bold.

	<b>Snow</b>	<b>Rock</b>	<b>Prec</b>	<b>T_Range</b>	T_Mean	Elev	<b>Rough</b>	<b>Asp</b>
<b>Snow</b>	-							
<b>Rock</b>	0.6	-						
<b>Prec</b>	-0.1	-0.1	-					
<b>T_Range</b>	-0.3	-0.1	-0.4	-				
T_Mean	-0.7	-0.6	0.3	-0.1	-			
Elev	0.7	0.6	-0.2	-0.1	-1.0	-		
<b>Rough</b>	-0.1	0.3	-0.1	0.5	-0.2	0.1	-	
<b>Asp</b>	-0.1	0.1	0.1	0.1	0.1	0.1	0.1	-

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981 **FIGURE CAPTIONS**

982 **Figure 1.** Occurrences of *Vesubia jugorum* across the accessible area.

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984 **Figure 2.** Species distribution and relationship between habitat suitability and functional  
985 traits. (a) Projected habitat suitability (average model projection) of *Vesubia jugorum*  
986 across its accessible area. (b) Predicted linear relationship (filled line) and 95% confidence  
987 interval (dotted lines) between habitat suitability and femur length, derived from the linear  
988 mixed model. Only fixed effects are shown. (c) Scatter plot of cocoon size and habitat  
989 suitability. The black line represents the positive linear trend according to the Pearson  
990 correlation.

991

992 **Figure 3.** Predicted variation in femur length across the range of distribution. Predicted  
993 relationship (filled line) and 95% confidence interval (dotted lines) between femur length  
994 and latitude (a) and longitude (b), derived from the linear mixed models. Only fixed effects  
995 are shown.

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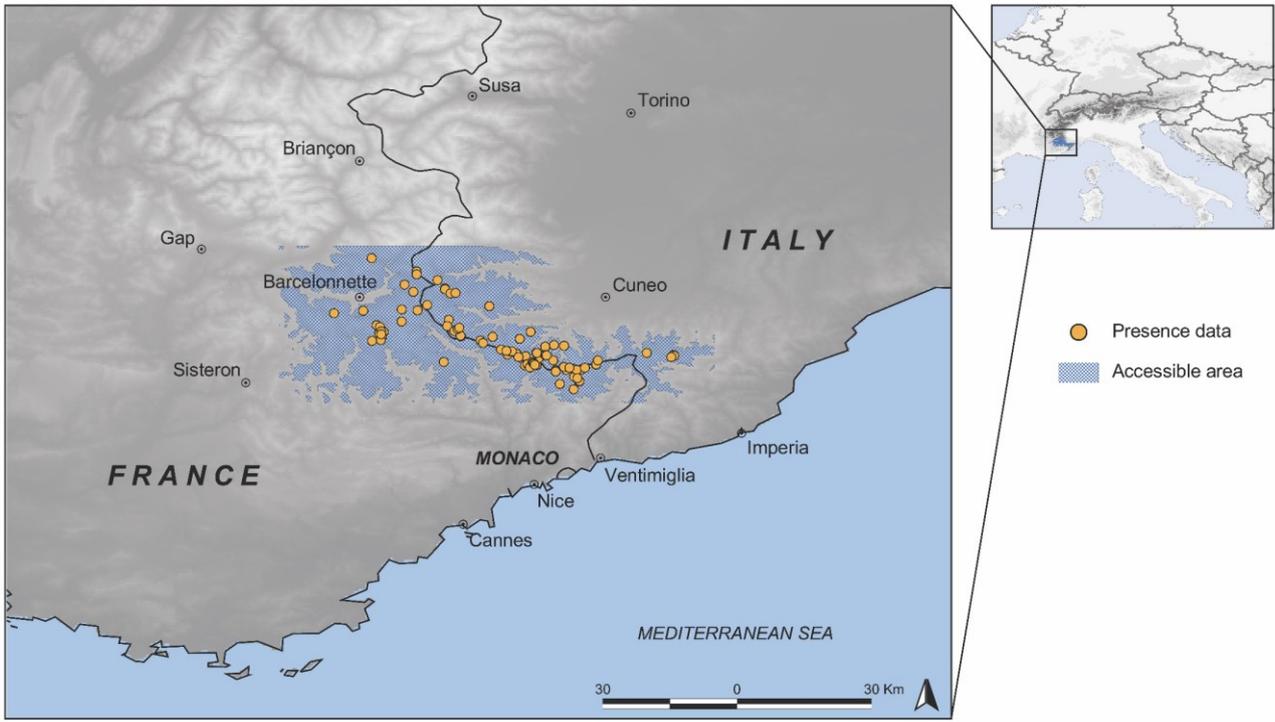
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1006 **Figure 1**

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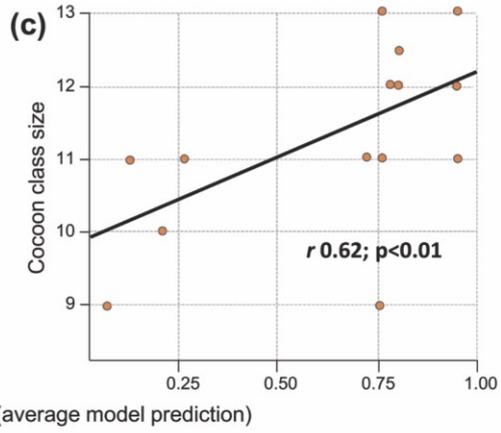
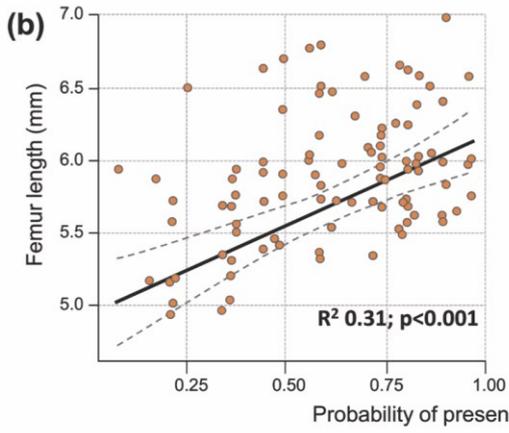
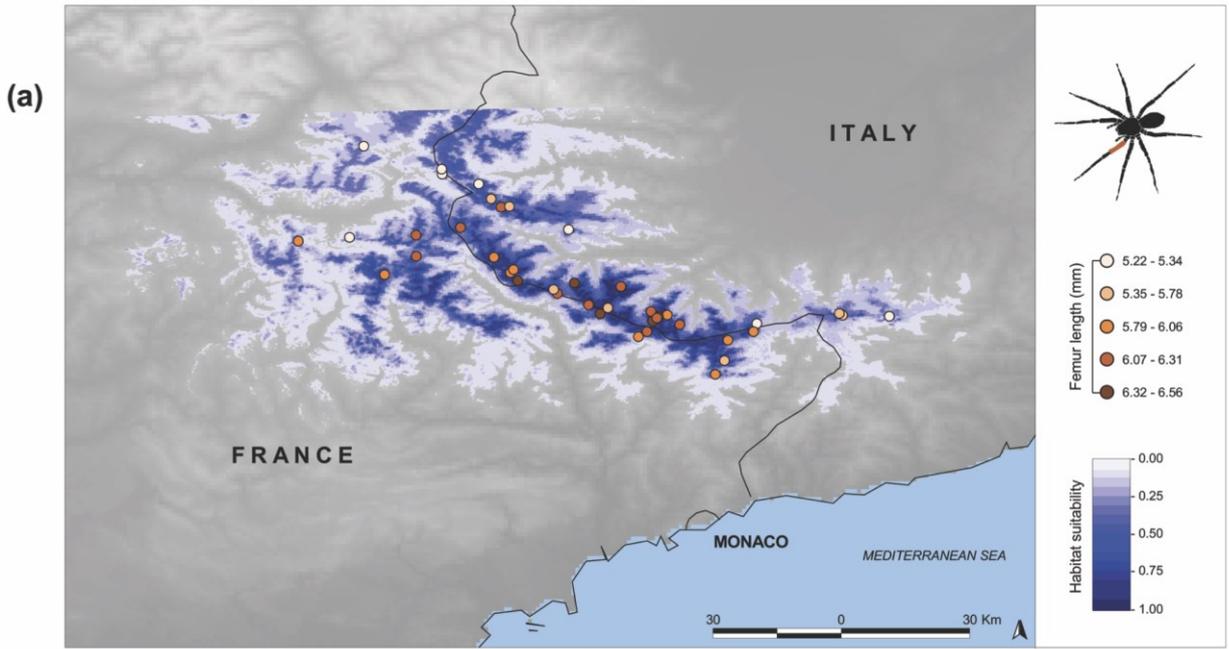
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1019 **Figure 2**

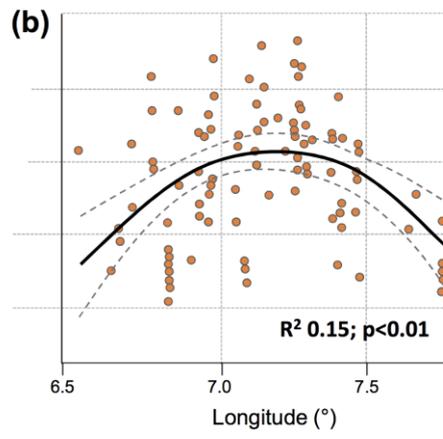
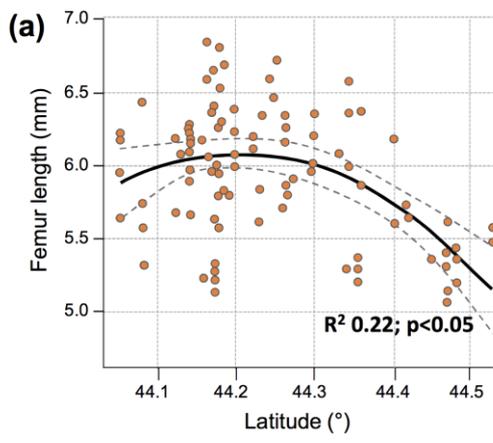
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1027 **Figure 3**