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## How Iberian are we? Mediterranean climate determines structure and endemism of spider communities in Iberian oak forests

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1 **How Iberian are we? Mediterranean climate determines structure and endemism of spider**  
2 **communities in Iberian oak forests**

3

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## 17 **Abstract**

18 Understanding the causes behind species richness and endemism is fundamental to explain  
19 biodiversity and assist conservation management, especially in biodiversity hotspots like the  
20 Mediterranean Basin. Here we investigate the patterns in Iberian forest spider communities and the  
21 processes behind their assembly, by testing hypotheses about the effects of climate and habitat on  
22 species richness, endemism and structure of communities at different spatial scales, and about how  
23 microhabitat and dispersal affect the level of endemism of species.

24 We studied 16 spider communities in Iberian *Quercus* forests from different climatic zones, applying  
25 a standardised sampling protocol. We examined the contribution of habitat, climate, and geography  
26 to the differences in the composition of spider communities across spatial scales using distance-based  
27 redundancy analysis models (dbRDA) and principal coordinates of neighbour matrices (PCNM). We  
28 assessed the effects of the same variables on the endemism of communities (measured by a weighted  
29 index), and tested the correlation between the microhabitat and the ballooning frequency (obtained  
30 from bibliography), and the endemism of species through generalised linear models.

31 Spider communities formed two groups — southern and one northern — based on similarity in species  
32 composition. Precipitation and temperatures were inversely related with the number of species while  
33 geography and forest type explained the compositional similarities between communities at different  
34 spatial scales. Endemism of communities increased with temperature and decreased with  
35 precipitation, whereas species endemism decreased with ballooning frequency. Our findings  
36 illustrate how niche-related processes may drive spider diversity while dispersal determines species  
37 distribution and identity and, ultimately, community composition. From a conservation viewpoint,

38 when maximising species richness is incompatible with prioritising endemism, the criteria to follow  
39 may depend on the geographic scale at which decisions are made.

40 *Keywords:* Araneae, species distributions, endemism, functional traits, white-oak forest, COBRA  
41 protocols.

42

### 43 **Introduction**

44 The study of the patterns and drivers of species communities and, more specifically, the features of  
45 species richness and endemism (here defined as how restricted the range of a species or the species  
46 of a given community are geographically), are fundamental to understand how biodiversity is formed  
47 and shaped through space and time, and provide basic indicators and/or criteria for conservation  
48 prioritisation and management (Brooks et al. 2009; Kier et al. 2009). Although certain mechanisms,  
49 such as dispersal (colonisation) and local diversification (adaptive radiation) (Givnish et al. 2009;  
50 Kier et al. 2009, Gillespie et al. 2018) may act in parallel to generate matching variations in both  
51 species diversity and community endemism (Barnard et al. 1998; Simmons et al. 1998), it is often  
52 not the case (Hughes et al. 2002; Orme et al. 2005; Irl et al. 2015).

53 The environmental conditions at different spatial scales (e.g. climate at regional scale, habitat at the  
54 local scale or microhabitat at the infra-local scale) and the geographic location of communities drive  
55 the niche and dispersal-related mechanisms (Grinnell 1917; Soberón 2007; Malumbres-Olarte et al.  
56 2013b, 2018) that, in combination with speciation (Emerson and Kolm 2005; Steinbauer et al. 2013),  
57 affect the range of a species and, ultimately, the communities that they form (Whittaker 1956; Condit  
58 et al. 2002) and their level of endemism. Likewise, the intrinsic characteristics of a species, such as  
59 its functional traits (sensu Violle et al. 2007) – such as (micro)habitat adaptations, dispersal ability or  
60 hunting strategy, which are often used to classify species into functional guilds – will limit its range,  
61 and therefore its endemism level (Rix et al. 2015). In consequence, one may expect to find  
62 communities and species with high levels of endemism in isolated areas with unique environmental

63 conditions in comparison with their surrounding matrix (Ohlemüller et al. 2008; Steinbauer et al.  
64 2012, Kaltsas et al. 2019).

65 The Mediterranean Basin has long been the focus of ecological, evolutionary and conservation  
66 research. Understanding the biological patterns of this global biodiversity hotspot (Myers 2000) and  
67 the processes behind them is paramount, more so when its biodiversity is threatened by agriculture,  
68 deforestation, construction and tourism (Morillo and Gómez-Campo 2000) and it has had a long  
69 history of interactions between natural ecosystems and human activities (Blondel et al. 2010).  
70 Compared to other temperate climatic regions, areas with Mediterranean climate show exceptionally  
71 large levels of species diversity and endemism, for which a number of hypotheses related to greater  
72 habitat availability, a warmer or more stable climate, glacial refugia or higher disturbance frequency  
73 have been invoked (Cowling et al. 1996, 2015; Keeley et al. 2003; Fattorini and Ulrich 2012; Rundel  
74 et al. 2016).

75 Because of its geographic location and mountainous topography, the Iberian Peninsula presents a  
76 variety of climatic zones that range from Mediterranean to Eurosiberian (Merino et al. 2015; Natalini  
77 et al. 2016), which, to some extent, are matched by biogeographic regions (Romo and García-Barros  
78 2010; Céréghino et al. 2012). White oak trees and relatives (genus *Quercus*, section *Quercus* and  
79 *Mesobalanus*) have adapted to many of these different climatic conditions (Sánchez de Dios et al.  
80 2009; Peguero-Pina et al. 2016). However, the once widespread Iberian oak forests have gone  
81 fragmented as a result of human activities such as agriculture, fire and grazing (Verdú et al. 2000;  
82 Acácio et al. 2009; Catry et al. 2009; Garrido-Benavent et al. 2015).

83 The Spanish National Parks form a network of protected areas that aim to preserve the most  
84 representative ecosystems of the Iberian Peninsula and educate about them. From an international  
85 perspective, this task is of major importance since the Iberian Peninsula is part of one of the main  
86 biodiversity hot spots (species richness and endemism) in Europe (Medail and Quezel 1997;  
87 Williams et al. 2000; Araújo et al. 2007). If national parks are to endure the effects of habitat and

88 climate change, their management must be based on reliable and quantitative information on their  
89 biota (Vaughan et al. 2001; Fancy et al. 2009; Val Martin et al. 2015). Furthermore, conservation  
90 policies and strategies based on sound scientific data are better suited to succeed in legal and political  
91 arenas. These data must provide knowledge on how and why the communities that inhabit the parks  
92 change in time and space (Fancy et al. 2009; Ladin et al. 2016). Most of the effort and resources  
93 invested in the research and management of the Spanish National Parks has focused on plants and  
94 vertebrates, for which there is much information on diversity and distribution. Meanwhile, the most  
95 diverse and abundant taxa – arthropods – remain poorly known, despite their potential to provide  
96 valuable information for conservation management (Kremen et al. 1993).

97 Spiders are an excellent model taxon to test ecological and evolutionary hypotheses because they are  
98 abundant and diverse both locally and worldwide (Basset et al. 2012; World Spider Catalog 2019)  
99 and they have adapted to a variety of habitats and microhabitats (Malumbres-Olarte et al. 2013a).  
100 Because of their key role as invertebrate predators in most terrestrial ecosystems (Marc et al. 1999,  
101 Michalko et al. 2018), spiders can be used as indicators of changes in other arthropods and of habitat  
102 disturbance (Wise 1993; Moretti et al. 2002; Cardoso et al. 2010; Malumbres-Olarte et al. 2013b).  
103 Furthermore, because of their different dispersal abilities – the tendency to balloon varies across  
104 species, families and used microhabitat – spiders can be used to model the effects of dispersal on  
105 community assembly (Bell et al. 2005; Malumbres-Olarte et al. 2014). In addition, spiders can be  
106 grouped into functional guilds relatively easily (Cardoso et al. 2011). Therefore, spiders can provide  
107 valuable information for conservation, both for measuring basic diversity levels and monitoring  
108 changes throughout time (Malumbres-Olarte et al. 2013b). Moreover, spiders are the only mega-  
109 diverse taxon for which we have optimised and standardised sampling protocols (Cardoso 2009;  
110 Cardoso et al. 2009, 2016; Malumbres-Olarte et al. 2017), which provide semi-quantitative and  
111 comparable data.

112 In this study we aim to answer a number of hypotheses on the diversity, composition and endemism  
113 of Iberian forest spider communities and the drivers behind them: 1) Given the past higher climatic  
114 stability, spider communities are more species-rich in Southern Iberian forests, located in areas with  
115 warmer and drier Mediterranean climates; 2) Community structure – taxonomic and functional – are  
116 mainly determined by climatic differences at large scale, by geographic distance at regional scale and  
117 by habitat structure (forest type) at the local scale; 3) Community endemism positively correlates  
118 with species richness – dry areas will show greater endemism, with the endemism of a given  
119 community represented by either the number of specimens belonging to species with the smallest  
120 known distribution or by a measure that is weighted by the number of species in the community - this  
121 hypothesis is based on the peninsular effect, according to which southern regions contain more  
122 endemic spider species because they are farther (or more disconnected) from areas that may be  
123 sources of species; and because spiders living in higher microhabitats (higher strata of the vegetation)  
124 are more exposed to the wind and, therefore, can balloon more easily, we expect that (4) endemism  
125 is greater for species that inhabit ground microhabitats and are less prone to balloon.

## 126 **Methods**

### 127 *Study areas*

128 Within our target region that was the Iberian Peninsula, we selected our sampling areas following  
129 management/historic, biogeographic and ecological (habitat) criteria. The sampling plots were: 1) in  
130 national parks distributed across the Iberian Peninsula as they host some of the best preserved oak  
131 forests; 2) distributed to cover different climatic zones (Oceanic and Mediterranean); and 3) in  
132 representative forests dominated by diverse native oak species (*Quercus* spp.) (Table 1, Figure 1).

133 The six chosen national parks contained either two or four plots, each of which was in a forest  
134 dominated by one of five *Quercus* species: Picos de Europa (*Q. petraea* and *Q. faginea*), Ordesa y  
135 Monte Perdido (*Quercus subpyrenaica* [*Q. Faginea* × *Q. pubescens*]), Aigüestortes i Estany de Sant

136 Maurici (*Q. humilis*), Monfragüe (*Q. faginea*), Cabañeros (*Q. faginea* and *Q. pyrenaica*) and Sierra  
137 Nevada (*Q. pyrenaica*) (Crespo et al. 2018) (Table 1).

### 138 *Spider sampling, identification and classification*

139 In each of the 16 plots we sampled the spider communities using the COBRA 50 sampling protocol  
140 for Mediterranean forest (Cardoso 2009). We sampled each plot once between May-June (the time  
141 when the spider communities are the most species-rich) in either 2013 or 2014. Briefly, the COBRA  
142 sampling protocols are standardised protocols composed of samples of different methods optimally  
143 combined to collect as many species as possible for a given amount of effort (Cardoso 2009). The  
144 sampling methods used were pitfall trapping, sweep-netting, aerial hand collection and foliage  
145 beating. We identified and classified all specimens to species or, when encountering undescribed  
146 species, to morphospecies following the latest taxonomic literature and the World Spider Catalogue  
147 (Natural History Museum of Bern 2019). In the cases of conflictive or difficult morphological  
148 identification we used DNA-barcoding methods to match or distinguish specimens. For a full  
149 description of the sampling sites and protocols, and morphological and molecular identification of  
150 specimens, see Crespo et al. (2018).

151 We classified species and morphospecies into: eight ecological categories following the predatory  
152 guilds of the families to which they belong (Cardoso et al. 2011); according to ballooning propensity,  
153 into rare, occasional and frequent ballooners (by family as in Carvalho et al. 2014); and into four  
154 biogeographic categories – Iberian, Mediterranean, Palearctic and Cosmopolitan – according to their  
155 known range (Crespo et al. 2018; Natural History Museum of Bern 2019). In addition, we assigned  
156 species values that represent the height of the vegetation or the microhabitat in which they are most  
157 common. To obtain these values, first we assigned each individual spider a value that corresponded  
158 to the height of the microhabitat in which it was found – 0 if it was collected on the ground using  
159 pitfall traps (ground microhabitat), 1 if it was collected by sweep-netting (herbaceous microhabitat),  
160 2 if it was collected through aerial hand collecting (very low canopy microhabitat) and 3 if we used



161 foliage beating (low canopy microhabitat) divided by the number of samples per method. Then we  
162 calculated the mean value for each species. This microhabitat index must be interpreted with caution  
163 and as an indicator of how close to the ground or to the canopy a given species is present. For instance,  
164 a species equally present in all four strata of the vegetation will have the value of 1.5.

#### 165 *Spatial, environmental and habitat data*

166 We used principal coordinates of neighbour matrices (PCNM) to identify spatial trends using the R  
167 package “spacemakeR” (Dray et al. 2006). This analysis decomposes relationships among points in  
168 space (in this case, our study plots) into orthogonal variables representing decreasing spatial scales  
169 (Borcard et al. 2004; Dray et al. 2006).

170 We extracted climatic and habitat-related data on the Iberian Peninsula from different sources. The  
171 climatic data (maximum, minimum and mean annual temperatures, mean annual precipitation, mean  
172 annual radiation) came from an Iberian database (Ninyerola et al. 2005) whereas the habitat-related  
173 information (EVI [Enhanced Vegetation Index]) originated from terrestrial MODIS (Moderate  
174 Resolution Imaging Spectroradiometer) satellite data at the spatial resolution of 250 m x 250 m  
175 (Lafage et al. 2014; Didan 2015). The EVI is a measure of plant density and compared to NDVI  
176 (Normalised Difference Vegetation Index), is corrected for the ground beneath and the air particles  
177 above the vegetation. In order to investigate the patterns within the communities, we partitioned the  
178 forest habitat into four microhabitats, according to the strata or height of the vegetation: ground,  
179 herbacious, very low canopy and low canopy microhabitats.

#### 180 *Data analyses*

##### 181 Species richness across regions

182 We assessed the efficiency of the sampling by calculating the sampling completeness based on the  
183 Chao 1 species estimator (Scharff et al. 2003; Magurran and McGill 2011), and evaluated the  
184 biodiversity of the studied spider communities calculating the total number of individuals and  
185 juveniles, the observed, estimated and rarefied (999 permutations) number of species, and the number

186 of specimens and species belonging to different predatory guilds and in different biogeographic  
187 categories.

188 After a test for autocorrelation (potentially caused by geographic proximity) resulted negative (no  
189 autocorrelation), we built generalised linear models with quasipoisson errors to determine the  
190 potential climatic and habitat-related factors behind the (rarefied and rounded) species richness of the  
191 studied communities. We tested the effects of the five climatic variables, the two habitat-related  
192 variables (forest type, represented by the dominant tree species, and EVI) and geographic distance  
193 from the southern tip of the Iberian Peninsula through forward variable selection keeping a maximum  
194 of three explanatory variables. We limited the number of variables because the total number of plots  
195 was not large enough for models with more variables – more variables may have led to over-fitting.  
196 As the three temperature variables were highly correlated with each other ( $0.99 <$ ), we only kept  
197 maximum temperature (the variable that showed the strongest effect) in the models. We chose and  
198 used only the models whose residual plots and the goodness of fit were the adequate and showed no  
199 signs of multicollinearity, and applied Tukey tests when including factorial variables.

#### 200 Taxonomic and functional changes across scales

201 To assess the similarity in the taxonomic composition and relative abundance of species between  
202 spider communities we created ordinations through non-metric multidimensional scaling (NMDS)  
203 (McCune and Grace 2002) based on dissimilarity matrices of presence/absence (Sørensen index) and  
204 relative abundance (Legendre and Legendre 1998) (Steinhaus index). Previous to this analysis (and  
205 the following matrix-based analyses) we applied the Hellinger transformation to the data to give lower  
206 weights to rare species (Legendre and Gallagher 2001).

207 We quantified the variation in the composition of spider communities explained by spatial, climatic  
208 and habitat variables, as well as their combined effects, through variation partitioning (Borcard et al.  
209 1992). To select the variables to be included in the variation partitioning, we ran a forward and  
210 backward selection in three distance-based redundancy analysis models (dbRDA) (Legendre and

211 Anderson 1999) ( $p < 0.05$ , 999 permutations), each for the spatial (the seven obtained PCNM  
212 eigenvectors), climatic (temperature, rainfall and radiation) and habitat (forest type and EVI) -related  
213 factors. The variation partitioning was based on multiple partial dbRDAs and used adjusted  $R^2$ , as  
214 unadjusted values have been suggested to be biased (Peres-Neto et al. 2006).  
215 Through a set of additive spatial scale-specific models, we assessed the separate and combined  
216 contributions of the variations in climate and habitat on community structure (species abundances) at  
217 different spatial scales (Laliberté et al. 2009). With this purpose, we constructed a set of RDAs, each  
218 of which fitted the species abundance matrix against one of the previously selected PCNM  
219 eigenvectors (four eigenvectors were selected out of the total of seven). Then, at each scale, we used  
220 the fitted values in a variation partitioning, where we included the climatic and habitat-related  
221 variables. This allowed us to know the relative importance of each variable at different spatial scales.  
222 We tested for differences in the functional structure across communities by applying a null model  
223 approach to the data on the dominance of each predatory guild. With this purpose, we computed null  
224 models (1000 simulations) varying the number of individuals per guild and per community while  
225 maintaining the total number of individuals, and calculated their percentages. We then compared the  
226 observed values with the values of the null model and considered the values above the top and below  
227 the bottom 5% percentiles as being significantly different.

#### 228 Community and species endemism

229 We assessed the level of endemism of each community by taking two approaches: one that considers  
230 species relative abundance and another that uses species presence and absence. For the former, we  
231 calculated the percentages of the specimens that belonged to the different biogeographic categories  
232 in each plot, whereas for the latter we used a diversity-corrected version of a range or inverse weighted  
233 endemism (DCWE) index (Huang et al. 2012; Linder 2014). The range-weighted endemism index  
234 is calculated by summing the endemism value of each species present in a community, where the  
235 endemism value of a species equals the inverse of its range size (Linder 2014). Since data on the

236 exact range sizes do not exist for most species, we assigned relative endemism values to the species  
237 – values of 1, 1/2, 1/3 and 1/4 to species with Iberian, Mediterranean, Palearctic and Cosmopolitan  
238 distributions, respectively. Because the number of species in each community varied, we corrected  
239 the range-weighted endemism index by dividing it by the number of species. To estimate the  
240 probability of the corrected DCWE values to occur, we created three sets of null models of each  
241 community, at the scales of: i) the Iberian Peninsula; ii) the Oceanic and Mediterranean climatic  
242 regions; and iii) geographic regions (national parks). Each of the three sets of models represented a  
243 different spatial scale, at which we expected to detect the effects of different processes behind  
244 community assembly – environmental filtering and dispersal, long-distance dispersal and short-  
245 distance dispersal, respectively. We built each set of null models using a different species pool for  
246 each community: species collected in all plots, species collected in all the plots of the same climatic  
247 region and species collected in all the plots of the same national park. We included the plots in the  
248 national parks of Picos de Europa, Ordesa and Aigüestortes in the Oceanic climatic region, and the  
249 plots in Cabañeros, Monfragüe and Sierra Nevada in the Mediterranean climatic region. These null  
250 models were based on 1000 simulated communities generated by randomising the number of species  
251 belonging to each biogeographic category while keeping the number of species. In each iteration, a  
252 corrected DCWE value was calculated from the newly generated community. We then compared the  
253 results to the observed values.

254 We ran a Pearson's Correlation test to test for the correlation between (rarefied) species richness and  
255 endemism (DCWE). To investigate the potential effects of climatic and habitat-related factors on the  
256 level of endemism of the communities, we built generalised linear models with the number of Iberian  
257 species (with Poisson error distribution as there was very little over-dispersion of residuals) and the  
258 corrected DCWE per plot as response variables, using the same approach as with the species richness  
259 models.

260 Endemism and ballooning

261 As for species-level analyses, we first calculated the level of endemism of each spider family by  
262 applying the formula of DCWE to family (instead of plot) and assigning the same values of relative  
263 endemism to the species. We then tested whether the tendency to balloon (based on family data) and  
264 the microhabitat height of each species had an effect on its level of endemism through proportional  
265 odd (cumulative) mixed-effects models family of the species as the random variable via the Laplace  
266 approximation.

267 We conducted all data manipulation and analyses using R3.6.2. (R Development Core Team 2019)  
268 and a number of packages, including “BAT” (Cardoso et al. 2015), “lme4” (Bates et al. 2015) and  
269 “vegan” (Oksanen et al. 2018).

## 270 **Results**

### 271 *Species richness across regions*

272 Our sampling yielded a total of 20,551 specimens, of which 8,533 were adults (42%) belonging to  
273 375 species or morphospecies. These results differ slightly from those of Crespo et al. (2018) because  
274 here we report only the results obtained from applying the sampling protocol COBRA (24 samples/  
275 plot, 16 plots), whereas Crespo et al. (2018) also reported species collected in additional ground  
276 sampling. Sampling completeness across plots ranged between 56-82% (Table 1), common values  
277 when applying standardised and optimised sampling protocols such as COBRA (Cardoso 2009).

278 Both the observed and rarefied values of the number of species indicated that the most species-rich  
279 spider communities were those from *Q. faginea* forests in Picos de Europa, from *Q. subpyrenaica*  
280 forests in Ordesa and from the *Q. faginea* forest communities in Cabañeros (Table 1, Fig. 2). At the  
281 lower end were the communities from Monfragüe and the *Q. petraea* forests in Picos de Europa. Our  
282 selected regression model included forest type, annual average rainfall and annual maximum  
283 temperature as explanatory variables. According to this model, the rarefied number of species  
284 changed with the forest type, with *Q. petraea*, *Q. pubescens* and *Q. pyrenaica* forests containing  
285 significantly fewer species than *Q. faginea* ( $z = 4.535, p < 0.001$ ;  $z = 5.132, p < 0.001$ ;  $z = 5.359, p <$

286 0.001, respectively) and *Q. subpyrenaica* forests ( $z = 3.078, p < 0.05$ ;  $z = 4.598, p < 0.001$ ;  $z = 3.374,$   
287  $p < 0.01$ , respectively). Although weakly, the rarefied number of species decreased with both annual  
288 average rainfall ( $b = -0.165, t = -4.3, p < 0.01$ ) and maximum temperature ( $b = -0.203, t = -5.31, p$   
289  $< 0.001$ ) (Fig. 3).

#### 290 *Taxonomic and functional changes across scales*

291 Both NMDS on the Sørensen and Steinhaus similarity indices showed similar results, according to  
292 which communities from the same park were more similar to each other than to communities  
293 elsewhere in all but one national park – Ordesa. Communities were separated along the first axis  
294 following a northern (Picos de Europa, Ordesa y Aigüestortes) vs. southern (Sierra Nevada,  
295 Cabañeros and Monfragüe) pattern (Fig. 4).

296 The variables selected through the three dbRDA were the large to medium-scale eigenvectors  
297 PCNM1, PCNM2, PCNM4 and PCNM5 as geographic variables, temperature and rainfall as climatic  
298 variables, and forest type and EVI as habitat-related variables. The variables that explained the largest  
299 portions of the variation in community composition and species relative abundance were geographic  
300 (15%) and habitat-related (12%) variables, and the combined effects of geographic and climatic  
301 variables (20%) (Fig. 5a). Climate alone only explained 4% of the community variation. As for the  
302 three partial dbRDAs, geographic variables explained similar proportions of the variation (rainfall  
303 14% and mean annual temperature 11%), and so did habitat-related variables (forest type 20% and  
304 EVI 16%). In the partial dbRDA with geographic variables, eigenvectors PCNM1, PCNM2, PCNM4  
305 and PCNM5 explained 11%, 19%, 8% and 5%, respectively.

306 The four spatial scale-specific models suggested that climate (which included temperature and mean  
307 annual rainfall), forest type and EVI have different levels of importance at different geographic scales.  
308 In the model of PCNM1 (which represented the largest spatial scale) forest type explained most of  
309 the variation in spider communities – 43% by the variable alone and 61% by its combination with  
310 climate (Fig. 5b). In the PCNM2 model the combined effects of all three variables explained 42%

311 whereas in the PCNM4 model climate alone explained 38%, EVI 21% and forest type 17%. Forest  
312 type explained, by far, the largest portion of variation (63%) in the PCNM5 model (Carvalho et al.  
313 2011b).

314 Regarding the functional or predatory guild structure, the general pattern was a similarity in  
315 percentages of species belonging to each guild across most communities (Fig. 6). Specialists,  
316 however, appeared to be more abundant in southern forests and, according to the null models, were  
317 significantly less abundant than expected by chance in the community O1 from Ordesa ( $p < 0.05$ ) and  
318 significantly more in the community M1 from Monfragüe ( $p < 0.01$ ). Likewise, there were fewer  
319 sheet web weavers in the community O1 (Ordesa,  $p < 0.05$ ) and more in the community M2  
320 (Mofragüe,  $p < 0.01$ ). Also, there were proportionally more ambush hunters in M1 (Monfragüe,  $p <$   
321  $0.05$ ) and more species classified as other hunters in O1 ( $p < 0.05$ ).

#### 322 *Community and species endemism*

323 Most of the spider communities that we studied were dominated by Palearctic species, although in  
324 the northern parks this pattern was overwhelming whereas in the communities of Cabañeros and  
325 Sierra Nevada it was less so (Fig. 7a). In the latter, Mediterranean and Iberian species had a much  
326 larger presence, the extreme being Monfragüe, where Mediterranean and Iberian species were  
327 dominant. There was a general pattern in the percentage of species of the different biogeographic  
328 categories in each microhabitat (Fig. 7b): On the ground, there were proportionally fewer Palearctic  
329 species and more Iberian species. The results of the endemism analysis followed species dominance  
330 patterns at the Iberian scale: the eight northern communities had significantly lower values of  
331 corrected DCWE than expected by chance while the two Monfragüe communities had significantly  
332 greater values (Fig. 8a). At the climatic region scale, only lower than expected endemism values  
333 surfaced, in communities from *Q. faginea* forests in Picos de Europa and Cabañeros, and from a *Q.*  
334 *pyrenaica* community in Cabañeros (Fig. 8b). At the regional scale, only the community from S2  
335 (Sierra Nevada) showed endemism values lower than expected by chance ( $p < 0.01$ ).

336 The families represented by one Iberian species – Leptonetidae, Mysmenidae, Nemesiidae,  
337 Oecobiidae and Pimoidae – and, therefore with 100% of Iberian species had the highest level of  
338 endemicity (Table 2). Among the families with more than four species, the families with the greatest  
339 level of endemicity were Oonopidae (most of which were undescribed morphospecies), Dysderidae  
340 (half of them were morphospecies), Zodariidae (half of them Iberian species), Sparassidae (half of  
341 them Iberian species) and Phrurolithidae (two Iberian, one Mediterranean and four Palearctic species).  
342 At the bottom of the list were Clubionidae, Araneidae, Miturgidae, Tetragnathidae and Hahniidae.  
343 There was no significant correlation between DCWE and the rarefied species richness (estimate = -  
344 0.09,  $t = -0.36$ ,  $df = 14$ ,  $p = 0.72$ ) but the former was positively correlated with both percentage of  
345 specialist individuals (estimate = 0.75,  $t = 4.22$ ,  $df = 14$ ,  $p < 0.01$ ) and percentage of species (estimate  
346 = 0.92,  $t = 8.8$ ,  $df = 14$ ,  $p < 0.01$ ) present in each plot. The annual average rainfall had a significant  
347 negative effect on the number of Iberian spider species ( $b = -0.002$ ,  $z = -4.98$ ,  $p < 0.001$ ) as well as  
348 on the level of community endemicity ( $b = -9.7$ ,  $t = -3.12$ ,  $p < 0.01$ ), whereas the maximum annual  
349 temperature had a significant positive effect on the community endemicity ( $b = 0.01$ ,  $t = 3.42$ ,  $p <$   
350  $0.01$ ) (Fig. 9).

### 351 *Endemicity and ballooning*

352 As for species endemicity, we found a negative effect of the tendency to ballooning on the level of  
353 species endemicity (estimate =  $-1.15$ ,  $z = -2.75$ ,  $p < 0.001$ ) with an increasing estimate of the  
354 transition from one biogeographic category to the next (Cosmopolitan | Palearctic:  $-6.376$  [ $p < 0.001$ ];  
355 Palearctic | Mediterranean:  $-1.27$  [ $p < 0.05$ ]; Mediterranean | Iberian:  $0.21$  [ $p = 0.74$ ]). However,  
356 microhabitat height did not have any effects ( $p > 0.05$ ) on endemicity.

### 357 **Discussion**

358 The processes behind spider species assembly in Iberian forests appear to be as complex as the biotic  
359 and abiotic composition of the Iberian Peninsula. Here we show that climatic, geographic and habitat-



360 related factors interact in various ways to exert differing effects on features such as species richness,  
361 taxonomic and functional structure and endemism.

### 362 *Species richness across regions*

363 The species richness of the spider communities that we studied appear to be determined by both the  
364 geographic region where the community is (and its climatic conditions) and the forest type (tree  
365 *Quercus* species) that they inhabit. In the line of other authors (Carvalho et al. 2011a), we detected  
366 signs of the effects of climate on species richness and some indication of the so-called “peninsular  
367 effect”, a hypothesis based on the idea that a decrease in the colonisation rates at the end of a peninsula  
368 leads to a decrease in the number of species (Simpson 1964). The commonly discussed and observed  
369 increase in the number of species as latitude decreases may anyway depend on the spatial scale.  
370 Indeed, this may be the case of spiders, which have been found to be affected by climate at both  
371 European and Iberian scales (Finch et al. 2008; Ysnel et al. 2008; Carvalho et al. 2012) but less so at  
372 small scales, where the relevance of climate may be substituted by factors such as the spatial  
373 distribution of microclimatic conditions or habitat structure (represented by forest type). This may be  
374 the case in our study, where the number of species can be better explained by forest type and climatic  
375 similarity between plots.

### 376 *Taxonomic and functional changes across scales*

377 The heterogeneity of climate and habitat structure vary in space, and as a consequence, so do their  
378 effects across geographic scales. Overall, the Iberian spider communities that we studied may be  
379 determined similarly by the physical and biologic characteristics of the plots that they inhabit. The  
380 idea that geography is a key driver behind the species assembly is illustrated by the large portion of  
381 variation in communities that it explained (Fig. 5a) and the ordination analysis (NMDS, Fig. 4), where  
382 the similarities in species composition between communities occurred at two scales: at the peninsular  
383 scale where communities were separated into a northern group and a southern group, and at the  
384 regional scale, where communities in the same national park (region) were clumped together.

385 Habitat structure is known to be determinant in spider community assembly (Greenstone 1984;  
386 Dennis et al. 2001; Jiménez-Valverde et al. 2007; Malumbres-Olarte et al. 2013B, 2018; Kaltsas et  
387 al. 2019), and here it is so to the point that forest type explains (alone and in combination with climate)  
388 almost all the variation in spider communities at the largest spatial scale, according to our scale-  
389 explicit spatial model. Moreover, this variable explained close to 70% of the variation at small scales  
390 (PCNM5).

391 Climate may be a key driver of the assembly of spider communities at continental and Iberian scales  
392 (Finch et al. 2008; Carvalho et al. 2011a, b) but, contrary to our expectations, it had a smaller effect  
393 on the structure of the communities that we studied. Mean annual temperature and rainfall may have  
394 a substantial influence on taxonomic community structure at the regional scale (Fig. 5b). If this scale  
395 corresponds to distances at which climate changes significantly between plots, climatic filtering may  
396 restrict the distribution and survival of the species adapted to temperate climate in the south and the  
397 competitive abilities of Mediterranean species in the cooler north of the Iberian Peninsula (Carvalho  
398 et al. 2011a).

399 Although the percentages of the species belonging to different predatory guilds are similar across  
400 communities, specialist species were more dominant in the southern communities than in the northern  
401 ones. This finding leads to interesting hypotheses on whether it is due to greater diversity of niches  
402 or niche packing (see further discussion below), available food resources – greater diversity of prey  
403 – as seen in communities of other taxa (Dalsgaard et al. 2017) or greater abundances of the prey  
404 species on which spider species are specialised (Líznarová et al. 2013).

#### 405 *Community and species endemism*

406 The biogeographic composition of spider communities (the percentage of species belonging to the  
407 four biogeographic categories) show visible geographic patterns, at both community and microhabitat  
408 levels. Northern Iberian communities are overwhelmingly dominated by species with Palearctic  
409 distribution (> 80 %) whereas in the Southern communities their percentages decrease, dropping to <

410 30 % in the two Monfragüe communities – whose low levels of endemism and sampling  
411 completeness may lead to hypotheses about the possible connections between these two measures.  
412 The north vs. south patterns in community endemism were further supported by the finding that all  
413 northern communities had lower weighted corrected endemism values than expected by chance.  
414 These patterns are likely to be the result of complex interactions between past migrations, ongoing  
415 selective pressures and speciation, all conditioned by the ecological traits of spider species.  
416 During the Quaternary glacial maxima, many warm-adapted species reduced their ranges and  
417 retreated into refugia in regions that were climatically stable during glacial periods (Stewart and Lister  
418 2001; Schmitt and Varga 2012; Abellán and Svenning 2014). These refugia could have played two  
419 roles that could explain the dominance of Palearctic species in northern regions and the abundance of  
420 endemic species in southern Iberia (García-Vázquez et al. 2017). On one side, refugia in Southern  
421 Iberia could have acted as sources of colonists after the glacial maxima, through which species  
422 previously adapted to cool temperate conditions may have expanded northward (and in some cases,  
423 re-colonised) tracking postglacial climate warming (Hewitt 2000). On the other, the confinement and  
424 isolation in Southern refugia could have promoted the speciation of certain taxa that would not be  
425 able to compete (through environmental filtering) and/or disperse as well as the colonisers in the north  
426 (Bilton et al. 1998). Indeed, the positive relationship between temperature and community  
427 endemism, and the negative relationship between the rainfall and both endemism and number of  
428 Iberian species are aligned with this idea. Again, the patterns that we found may also indicate a  
429 peninsular effect, with more endemic species in the southern regions of the Iberian Peninsula caused  
430 by the greater distances from the most likely and main source of species (i.e. rest of Western Europe).  
431 As hypothesised, we found no spatial congruence between the response of species richness and  
432 community endemism to environmental factors. Although both metrics responded negatively to  
433 rainfall, species richness decreased with temperature while community endemism increased. Our  
434 findings about the effects of rainfall do not concur with previous claims that communities (including

435 spiders) may be more species-rich under mesic conditions (those with well-balanced moisture  
436 supplies) due to greater resource availability (Bolger et al. 2008; Entling et al. 2007). If that was the  
437 case, we would have observed an increase in the number of species from dry to wet plots. As for  
438 endemism, the higher levels found in drier areas could be explained by either the peninsular effect  
439 or a greater stochasticity in water availability, caused by selective pressure for specialised adaptations  
440 (Griffin 1998; Simmons et al. 1998; Dewar and Richard 2007). One may argue that our results  
441 indicate that it is temperature, rather than humidity, what limits species ranges and, ultimately,  
442 determines how many and which species overlap in any given community. However, it is also  
443 possible that species adapted to mesic conditions – many of them of Palearctic distribution, and  
444 therefore of larger ranges and less endemic – are more likely to overlap, and therefore may form more  
445 speciose communities in the colder regions of Iberia. Phylogenetic and functional data may help  
446 identify the best explanation for the patterns found.

447 Resource availability, in interaction with climate, may also play a part in setting the endemism of  
448 spider communities. Here we define specialist species as trophic specialists, which require time to  
449 find their prey and are often of limited dispersal ability. Given that specialisation is a trait that may  
450 need time to develop, we could expect to find more specialist species in regions with climatic stability  
451 throughout time, such as those in southern Iberia. This finding opens the door to using some of the  
452 specialist spider species that we identified here as indicators of the conservation value of the natural  
453 areas or national parks where we collected them.

#### 454 *Endemism and ballooning*

455 Dispersal ability, a factor connected to colonisation, seems to play a role in the assembly and  
456 biogeographic characteristics of Iberian spider communities. Three indicators suggest the effect of  
457 dispersal ability of spiders on communities. First, the resemblance of Sierra Nevada communities to  
458 the other southern communities despite the fact that climatically they are closer to northern areas. It  
459 is likely that the inability of northern species with Palearctic distribution to reach climatically suitable

460 but remote areas is the cause of their lower numbers in this national park. Second, the larger  
461 abundance of Iberian species in southern communities, especially in forest ground communities,  
462 which generally disperse less than the species inhabiting herbaceous and canopy vegetation. Most of  
463 these species may be adapted to Mediterranean conditions and are likely to be restricted to Iberia due  
464 to their limited ability to disperse beyond the mountain ranges and the coastline that delimits the  
465 peninsula. And third, the fact that, across all families, species are more likely to be Iberian when their  
466 tendency to balloon is lower.

467 Based on our results, we cannot validate our hypothesis that species have more restricted ranges  
468 (higher endemism) if they dwell microhabitats closer to the ground. Although species ranges may be  
469 more dependent on general climatic conditions than microhabitat requirements, it is also possible that  
470 proving our hypothesis may require more detailed quantitative data about the species ranges, which  
471 is currently far from being available.

#### 472 *Conclusions*

473 The Mediterranean basin, as a biogeographic region, is indeed a hotspot of species endemism and  
474 richness, being home to the bulk of European species (Cowling et al. 1996; Blondel and Aronson  
475 1999; Myers et al. 2000; Rund et al. 2019; Underwood et al. 2009). Conservation management plans  
476 and actions often aim to maximise both species richness and endemism but the weight of each  
477 criterion to follow may vary depending on the geographic scale at which decision-making authorities  
478 act. In the case of the Spanish National Parks network, and based on our results, maximising the  
479 conservation of the Iberian biodiversity may require prioritising the protection and, when possible,  
480 expansion of areas with greater numbers and proportions of Iberian or Mediterranean species – such  
481 as Monfragüe, Cabañeros and Sierra Nevada.

482 Efficient and effective management of biodiversity will not only require more information on  
483 endemism patterns but also a greater understanding of the driving processes at different spatial  
484 scales, both of which depend on further and more extensive sampling and data collection. In the

485 Mediterranean context, this may involve using multi-scale climatic data as well as local-scale  
486 features, such as land use surrounding the parks (Bonache et al. 2016; Hewitt et al. 2016).  
487 Furthermore, these data, if combined with phylogenetic and functional information, may allow to  
488 infer past and present community dynamics and predict future changes – such as those caused by  
489 climate change (Ohlemüller et al. 2008) – on all present species in general, and endemic ones in  
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506

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788 **Figure captions**

789 Fig. 1. Map of the Iberian Peninsula with locations of National Parks (circled letters) and climatic  
790 regions according to the Koppen–Geiger climate classification (in colours). A: Parc Nacional  
791 d'Aigüestortes i Estany de Sant Maurici; C: Parque Nacional de Cabañeros; M: Parque Nacional de  
792 Monfragüe; O: Parque Nacional de Ordesa y Monte Perdido; P: Parque Nacional de Picos de Europa;  
793 S: Parque Nacional de Sierra Nevada. BWh= Hot desert climate, BWk= Cold desert climate, BSh=  
794 Hot semi-arid climate, BSk= Cold semi-arid climate, Csa= Hot-summer Mediterranean climate, Csb=  
795 Warm-summer Mediterranean climate, Cfa=Humid subtropical climate, Cfb= Temperate oceanic  
796 climate, Dsb= Warm, dry-summer continental climate, Dsc= dry-summer subarctic climate, Dfb=  
797 Warm-summer humid continental climate.

798 Fig. 2. Rarefied number of species per community (mean and 95% CI). See Table 1 for codes of plots/  
799 communities.

800 Fig. 3. Relationships between rarefied species richness and a) forest (habitat) type (with estimates of  
801 the group means and confidence intervals), b) mean annual rainfall and c) mean annual maximum  
802 temperature modelled by generalised linear models. Red circles represent partial residuals. The  
803 studied 16 plots were located in six different national parks, with each plot being dominated by one  
804 of the following five white oak (*Quercus*) species: *Q. pubescens* (Q. pub., 2 plots), *Q. pyrenaica* (Q.  
805 pyr., 4 plots), *Q. faginea* (Q. fag., 6 plots), *Q. subpyrenaica* (Q. sub., 2 plots), *Q. petraea* (Q. pet., 2  
806 plots).

807 Fig. 4. Non-Metric Multidimensional Scaling ordination plot based on species similarity and relative  
808 abundance (Steinhaus index). Colours represent the tree species that are dominant in each of the plots  
809 where spider communities were sampled.

810 Fig. 5. Percentages of taxonomic variation between communities explained by different factors  
811 obtained through variation partitioning analysis. a) Overall variation explained by geography  
812 (eigenvectors PCNM1, PCNM2, PCNM4, PCNM5), climate (mean annual rainfall and temperature)

813 and habitat structure (forest type and EVI). b) Variation explained by climatic and habitat-related  
814 variables at each of the four spatial scales obtained from additive spatial scale-specific models.  
815 Residuals represent the variation not explained by the used variables.

816 Fig. 6. Percentages of species belonging to each predatory guild per community. Species were  
817 classified according to family, following Cardoso et al 2011. See Table 1 for codes of plots/  
818 communities.

819 Fig. 7. Percentages of individuals belonging to different biogeographic categories (based on known  
820 distributions, see Methods) in each plot. a) Per entire communities and across microhabitats. b) Per  
821 community and microhabitat.

822 Fig. 8. Observed (circles) and simulated (mean and 95% CI) weighted corrected endemism of each  
823 community at the Iberian (a) and the corresponding climatic region scales (b).

824 Fig. 9. Response of the number of Iberian species (a) and weighted corrected endemism to mean  
825 annual rainfall (b) and mean annual maximum temperature (c) modelled by generalised linear models.

826

827 **Tables**

828

829 Table 1. National parks where the plots are located, dominant tree species, and corresponding diversity and collection

830 measures.

Plot	National Park	Dominant forest <i>Quercus</i> species	Juveniles (%)	Observed Species richness	Chao1 species estimation	Sampling completeness (%)
A1	Parc Nacional d'Aigüestortes i Estany de Sant Maurici	<i>Q. pubescens</i>	43	65	79.11	82
A2	Parc Nacional d'Aigüestortes i Estany de Sant Maurici	<i>Q. pubescens</i>	47	73	107.93	68
C1	Cabañeros	<i>Q. pyrenaica</i>	76	74	94.87	78
C2	Cabañeros	<i>Q. pyrenaica</i>	76	63	101.81	62
C3	Cabañeros	<i>Q. faginea</i>	68	76	132.45	57
C4	Cabañeros	<i>Q. faginea</i>	71	85	117.58	72
M1	Monfragüe	<i>Q. faginea</i>	72	54	94.56	57
M2	Monfragüe	<i>Q. faginea</i>	66	44	79.15	56
O1	Ordesa y Monte Perdido	<i>Q. subpyrenaica</i>	55	78	118.14	66
O2	Ordesa y Monte Perdido	<i>Q. subpyrenaica</i>	40	93	133.32	70
P1	Picos de Europa	<i>Q. petraea</i>	39	51	72.26	71
P2	Picos de Europa	<i>Q. faginea</i>	40	85	129.78	65
P3	Picos de Europa	<i>Q. petraea</i>	46	58	95.57	61
P4	Picos de Europa	<i>Q. faginea</i>	43	101	131.69	77
S1	Sierra Nevada	<i>Q. pyrenaica</i>	59	71	101.94	70
S2	Sierra Nevada	<i>Q. pyrenaica</i>	52	71	98.23	72

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833 **Table 2.** Number of species and endemicy of the families represented by the collected specimens. Families are in  
834 descending order according to their weighted corrected endemicy value.

Family	Predatory guild	Number of species	Weighted corrected endemicity
Leptonetidae	Space web weavers	1	1
Mysmenidae	Space web weavers	1	1
Nemesiidae	Sensing web weavers	1	1
Oecobiidae	Sensing web weavers	1	1
Pimoidae	Sheet web weavers	1	1
Oonopidae	Ground hunters	6	0.867
Dysderidae	Specialists	17	0.863
Zodariidae	Specialists	10	0.783
Sparassidae	Other hunters	4	0.708
Phrurolithidae	Ground hunters	7	0.643
Pholcidae	Space web weavers	3	0.611
Liocranidae	Ground hunters	9	0.574
Dictynidae	Ground hunters	9	0.517
Agelenidae	Sheet web weavers	9	0.5
Hersiliidae	Sensing web weavers	1	0.5
Palpimanidae	Specialists	1	0.5
Scytodidae	Other hunters	1	0.5
Sicariidae	Ambush hunters	1	0.5
Zoropsidae	Sheet web weavers	1	0.5
Gnaphosidae	Ground hunters	36	0.465
Philodromidae	Other hunters	20	0.433
Theridiidae	Space web weavers	40	0.419
Salticidae	Other hunters	23	0.417
Thomisidae	Ambush hunters	21	0.405
Eutichuridae	Other hunters	3	0.389
Mimetidae	Specialists	3	0.389
Oxyopidae	Other hunters	3	0.389
Uloboridae	Orb web weavers	3	0.389
Linyphiidae	Other hunters/ Sheet web weavers	67	0.386
Lycosidae	Ground hunters	22	0.371
Clubionidae	Other hunters	8	0.354
Araneidae	Orb web weavers	20	0.346
Anyphaenidae	Other hunters	2	0.333
Miturgidae	Other hunters	4	0.333
Pisauridae	Sheet web weavers	1	0.333
Segestriidae	Sensing web weavers	3	0.333
Tetragnathidae	Orb web weavers	6	0.333
Titanoecidae	Space web weavers	1	0.333
Hahniidae	Sheet web weavers	6	0.317

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