

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

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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 herbaceous, 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 endemism
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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