

1 **Spatial patterns of species richness and nestedness in ant assemblages**
2 **along an elevational gradient in a Mediterranean mountain range**

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20 **Abstract**

21 The study of biodiversity spatial patterns along ecological gradients can serve to
22 elucidate factors shaping biological community structure and predict ecosystem
23 responses to global change. Ant assemblages are particularly interesting as study cases,
24 because ant species play a key role in many ecosystem processes and have frequently
25 been identified as useful bioindicators. Here we analyzed the response of ant species
26 richness and assemblage composition to elevational gradients in Mediterranean
27 grasslands and subsequently tested whether these responses were stable spatially and
28 temporally. We sampled ant assemblages in two years (2014, 2015) in two mountain
29 ranges (Guadarrama, Serrota) in Central Spain, along an elevational gradient ranging
30 from 685 to 2390 m a.s.l.

31 Jackknife estimates of ant species richness ranged from three to 18.5 species and
32 exhibited a hump-shaped relationship with elevation that peaked at mid range values
33 (1100 – 1400 m). This pattern was transferable temporally and spatially. Elevation was
34 significantly related to ant assemblage composition and facilitated separation of higher
35 elevation assemblages (> 1700 m) from the remaining lower elevation species groups.
36 Ant assemblages were nested; therefore species assemblages with a decreased number
37 of species were a subset of the richer assemblages, although species turnover was more
38 important than pure nestedness in all surveys. The degree of nestedness changed non-
39 linearly as a cubic polynomial with elevation. These assembly patterns were observed
40 over time but not between the two study regions.

41 We concluded double environmental stressors typical of Mediterranean mountains
42 explained species richness patterns: drought at low elevations and cold temperatures at
43 high elevations likely constrained richness at both extremes of elevational gradients.

44 The fact that species turnover showed a dominant role over pure nestedness suggested
45 current ant assemblages were context-dependent (spatio-temporal factors) and highly
46 vulnerable to global change, which threatens the conservation of present day native ant
47 communities, particularly at high elevations.

48

49 **Introduction**

50 Predicting the response of biodiversity to the main drivers of Global Change has
51 become a primary goal of modern ecology [1-3]. Consequently, the analysis of species
52 richness and assembly patterns along latitudinal and altitudinal gradients provide clues
53 to project possible effects of climate change on communities [4, 5]. The Mediterranean
54 mountains are particularly suitable for this purpose, given a characteristic combination
55 of temperature and water availability gradients in space and time, which determines a
56 progressively cooler and wetter environment at higher elevations while valleys suffer
57 more severe summer drought conditions [6, 7]. In addition, the Mediterranean Basin
58 will probable face particularly marked increases in aridity, temperature and frequency of
59 extreme climatic events [8-10]; therefore it is critical to advance our knowledge of how
60 basin communities respond to more severe abiotic factors.

61 Ants are diverse and ubiquitous, exhibit strong interspecific interactions, and perform
62 many functional processes in ecosystems [11]; therefore ants are considered a viable
63 indicator group of ecosystem change by many community ecologists. Ants are also
64 dominant terrestrial community members [12] and play an important role in plant
65 community dynamics, acting as seed harvesters [13], dispersal agents [14], and
66 influencing soil nutrient status and plant growth [15]. As predators, ants control

67 herbivore abundance, drive relevant top-down effects, and are often used as biological
68 control agents of insect pests and fungal pathogens [16]. Furthermore, ant distribution
69 and abundance patterns provide information to address specific environmental
70 management issues [17, 18]; consequently, ants are particularly useful bioindicators.

71 Previous research on ant diversity documented variable responses to altitudinal
72 gradients, which showed a certain dependency on macroclimate. For instance, studies
73 reporting monotonic decreases in species richness, were frequent in temperate
74 mountains [19-21], while monotonic increases were observed in arid environments [22,
75 23]. Longino and Colwell [24] and Nowrouzi *et al.* [25] indicated more complex
76 patterns in tropical climates, which often combined a monotonic decrease at high
77 elevations with a plateau at low elevations. Mid-elevation peaks were reported in
78 tropical areas [26, 27], although also frequent at other latitudes [28, 29]. These patterns
79 were partially attributed to geometric constraints, such as the mid-domain effect and
80 area availability [30, 31] or the Rapoport rescue effect [32]. However the role of
81 climatic factors, including temperature [19-21] and water availability [22, 29, 33, 34] as
82 direct drivers of ant diversity is also unequivocal. Moreover, several studies
83 demonstrated these climatic variables also indirectly modulated ant diversity, for
84 example, by affecting primary productivity [33, 35-37].

85 Understanding how ant diversity responds to altitudinal gradients is not sufficient,
86 however, to predict how environmental changes (e.g. rising temperatures) will affect
87 species geographic ranges, because knowledge on species composition patterns is also
88 required. Species assemblages and their distributions along ecological and geographical
89 gradients result from species tolerances to climatic (abiotic) factors and biotic
90 interactions, which interplay with niche evolution to determine community composition

91 [38-40]. Kodric-Brown and Brown [41] defined a structured community as one where
92 the organization is not due to randomness [41], and all situations in which communities
93 are not random can be explained by spatial turnover, nestedness, or combinations of
94 both [42]. Nestedness of species assemblages occurs when site biotas with smaller
95 species numbers are subsets of the biotas at richer sites [43, 44]. If environmental and
96 habitat filtering and not interspecific competition is responsible for nestedness, most
97 species can coexist. Therefore, under increasing temperatures, species could migrate or
98 expand their distribution elsewhere from the species former range, without necessarily
99 implying other resident species will be displaced by the newcomers. On the contrary,
100 spatial turnover implies the replacement of some species by others, exhibiting gains and
101 losses of species from location to location globally [45]. This is a sign that some species
102 cannot coexist, because of different climatic requirements, competitive exclusion, or
103 both. In general, global warming will extend insect species ranges to higher altitudes
104 [46], therefore with spatial turnover patterns, species will migrate up an altitudinal
105 gradient and those at higher altitudes might suffer a subsequent reduction in geographic
106 distribution range, and even disappear from the area. However, Maguire *et al.* [47]
107 acknowledged both processes and community patterns might vary with scale, and
108 exhibit spatio-temporal variation, which raises concerns on our capacity to generalize
109 the results based on local studies. Indeed, transferability of results is increasingly
110 considered in analyzing the effects of global change on species distributions, although
111 such efforts are rarer in studies of community patterns [48-50].

112 In the present study, we explored patterns of ant species diversity and community
113 composition in Mediterranean mountain grasslands, integrating spatio-temporal
114 transferability. Specifically, we addressed the following questions: (1) what is the

115 relationship between ant species richness and elevation; (2) how does elevation affect
116 ant species composition; (3) what are the relative contributions of spatial turnover and
117 nestedness in ant community composition; and (4) are our findings transferable spatially
118 and temporally?

119

120 **Methods**

121 Study areas and sampling design

122 We studied grassland ant communities in two mountains in the larger Sistema Central
123 range, Sierra de Guadarrama (reaching 2428 m a.s.l. at its highest peak) and Serrota
124 (maximum 2294 m a.s.l.). The two mountains are ~ 100 km apart with similar climatic,
125 geologic, and biotic characteristics. Mean annual temperatures range from ~ 14 °C at
126 600 m to ~ 4 °C at the summits (2300 – 2428 m); and mean annual rainfall ranges from
127 550 mm to 1500 mm, with severe summer drought [51]. Substrata are primarily
128 composed of granites, and pasturelands are distributed along the complete elevational
129 gradient, largely as the result of traditional livestock grazing.

130 Sample sites were interspersed along the elevational gradient, facing southeast to
131 southwest with gentle slopes (< 5%), and not affected by anthropogenic disturbance
132 (i.e., not close to buildings or main paths). We sampled 18 grasslands in 2014 (in
133 Guadarrama range) and 12 in 2015 (six in Guadarrama range and six in Serrota range).
134 On each grassland, we randomly placed a 4 x 3 grid of pitfall traps, 2.5 cm diameter x 5
135 cm deep, with 5 m spacing between traps, which were filled with a 3:1 ethanol/
136 monoethylene glycol mixture. Ant sampling was conducted in July, during stable
137 anticyclonic meteorological periods (Guadarrama: 17 - 23 July 2014 and 9 - 16 July

138 2015; Serrota: 1 - 8 July 2015), taking advantage of the seasonal ant activity peak
139 during summer in Central Spain [52]. Traps were collected after one week and ant
140 specimens were sorted to species, excluding winged ones.

141 Pitfall trapping is considered more objective and unbiased than other methods for
142 sampling ground ants [53, 11]. We chose pitfall traps previously tested in other studies
143 in Central Spain, which demonstrated success at capturing the complete species pool
144 and the entire ant size range variability present in the sampled area [52, 54, 55].

145

146 Statistical analyses

147 We examined the relationship between species richness, taxonomic composition, and
148 nestedness of grassland ant communities with elevation. Our analytical strategy was to
149 build descriptive models for the data gathered during the most intensive sampling in
150 Guadarrama 2014, and to validate the patterns detected with data gathered in a subset of
151 the Guadarrama grasslands during 2015 (temporal validation) and with data gathered in
152 the Serrota range during 2015 (spatial validation).

153 *Species richness*

154 First, we assessed the relationship between species richness and elevation. We estimated
155 the species pool size at each locality with the incidence-based first order jackknife
156 estimator. The relationship shape between estimates of richness and elevation was
157 explored applying a generalized additive model (GAM) with Gaussian errors and a thin
158 plate regression spline for elevation. Models were built with data from Guadarrama
159 2014 sampling and validated with data from the Guadarrama 2015 and Serrota 2015
160 samplings. Squared Pearson correlation between jackknife estimates of richness and

161 jackknife estimates predicted by the model were used to assess species richness pattern
162 constancy between years and sites.

163 *Taxonomic composition of assemblages*

164 We explored how species assemblages differed based on taxonomic composition by
165 applying non-metric multidimensional scaling (NMDS) to the hemi-matrices of binary
166 Bray-Curtis distances among grasslands derived from species occurrences in pitfall
167 traps. In addition, a model-based analysis was conducted by building separate negative
168 binomial regressions for each species abundance data (as the multivariate response
169 variable) by elevation, year, and interaction (as the explanatory variables) [56].
170 Significance of the interaction (assessed by resampling) would suggest that patterns of
171 species composition along an elevational gradient changed between years. Likewise, for
172 Guadarrama 2014 and Serrota 2015, a multivariate model was built by fitting negative
173 binomial regressions for individual species abundance, elevation, location, and
174 interaction [56]. Significance of the interaction would suggest how assemblages
175 changed with elevation were context-dependent.

176 *Nestedness patterns*

177 To assess assemblage nestedness among grasslands surveyed on each mountain and
178 year we calculated the matrix temperature (T) [57] and the NODF (Nestedness metric
179 based on Overlap and Decreasing Fill) [58]. While T has traditionally been the most
180 commonly used metric for assessing overall nestedness [59], the more recent NODF
181 index is claimed to exhibit more robust statistical properties, and separate contributions
182 to nestedness of columns (due to species incidence) and rows (due to site composition)
183 can be quantified [58, 60]. T decreases and NODF increases with nestedness.

184

185 The significance of nestedness indices was estimated by comparison with suitable
186 binary null models, which were simulated by randomizing the original matrix
187 transformed to presence/absence binary data. Two null models were built to encompass
188 the range from maximally liberal (equitable) to maximally conservative (constrained)
189 null models [61]. The first was an equiprobable model built by randomizing rows and
190 columns and therefore maintaining only the number of species presences ('r00'
191 algorithm). The second was a proportional resampling model constructed by
192 constraining randomization to maintain row and column totals (site richness and species
193 incidence, respectively), while using marginal column frequency to select species
194 ('quasiswap' algorithm). Thus, the first null model was more liberal and only accounted
195 for matrix fill (the incidence of the total species set), while the second null model was
196 more stringent, because it imposed additional structure on the data, accounting for
197 among-site differences (e.g. different carrying capacities) and among-species
198 differences (e.g. different rarities). Subsequently, significant nestedness was attributed
199 to variation in observed species richness or species incidence, if evaluated with the
200 equiprobable model, or to variation beyond that observed, if evaluated with the
201 proportional resampling model [62]. One thousand randomizations of the original
202 matrix were applied.

203 The relative degree of nestedness, i.e. how much a grassland was nested within the set
204 of sampled grasslands in the same geographic area and time period, was evaluated by a
205 nestedness rank, according to T. Poorer grasslands, i.e. those having lower species
206 diversity which were a subset of richer grasslands, were assigned higher ranks. These
207 ranks were estimated as the ordinate in nestedness plots built with the T index, which

208 were calculated as $(k - 0.5)/n$ for $k = 1 \dots, n$ rows (e.g. the bottom row in the graph,
209 where $k = 18$ was the more nested site, which for the 2014 sampling in Guadarrama had
210 a rank of $(18 - 0.5)/18 = 0.97$).

211 The shape of the relationship between nestedness and elevation during the 2014
212 sampling in Guadarrama ($n = 18$) was explored using GAM with Gaussian errors and a
213 thin plate regression spline for elevation. This model was validated using Guadarrama
214 2015 data (temporal validation). Detection of a high correlation between observed (in
215 2015) and predicted ranks would suggest the nestedness rank of plots did not vary
216 between years. Similarly, the model built with Guadarrama 2014 sampling data was
217 validated using the Serrota 2015 data (spatial validation). Detection of a high correlation
218 between observed and predicted ranks would suggest the nestedness rank of plots did
219 not vary between regions.

220 The contributions of spatial turnover and nestedness to the distribution pattern in
221 Guadarrama 2014 data were calculated using three beta diversity indices: Sørensen-
222 based multiple-site dissimilarity (β_{SOR}), Simpson-based multiple-site dissimilarity
223 (β_{SIM}), and nestedness-resultant multiple-site dissimilarity (β_{NES}). β_{SIM} accounts for
224 spatial turnover and β_{NES} integrates dissimilarity due to nestedness, while β_{SOR}
225 expresses the total dissimilarity between communities and equals the sum of β_{SIM} and
226 β_{NES} [42]. *P*-values were estimated through the equiprobable ('r00') null model (the
227 proportional resampling null model was not useful to assess this partitioning of beta
228 diversity).

229 Statistical analyses were performed using R (v 3.3.2; R Core Team 2016) and
230 specialized packages *vegan* (v. 2.4-5) [63], *mvabund* (v. 3.12-3) [56], and *betapart*
231 (1.5.0) [64].

232

233 **Results**

234 We detected 37 species, all recorded in Guadarrama (35 in 2014 and 26 in 2015, 24
235 were shared between years) and 20 species in Serrota (all species shared with
236 Guadarrama). A total of 15 species were common among the three surveys (**S1 Table**).

237 Jackknife estimates of ant species richness in Guadarrama 2014 ranged from three (SE
238 = 0) species in most of the highest grasslands to 18.5 (SE = 2.6) at intermediate
239 elevations (**Table 1**). Estimates of richness related to elevation were positive below
240 1100 m a.s.l. and negative until a lower limit was reached at ca. 2000 m a.s.l. (**Fig 1**).

241 Overall, richness exhibited a hump-shaped relationship with elevation, which we
242 described using GAM with a spline for elevation, roughly equivalent to a third-order
243 degree polynomial (equivalent $df = 3.96$, $F = 12.94$, $P < 0.0001$, $D^2 = 83.8\%$, **Fig 1**).
244 This pattern of species richness was similar between years and between mountain
245 ranges (correlations for estimates of richness and richness predicted by the model were r
246 = 0.92, $t = 4.68$, $df = 4$, $P = 0.0095$, $R^2 = 85\%$ for Guadarrama 2015 data; and $r = 0.86$, t
247 = 3.42, $df = 4$, $P = 0.0267$, $R^2 = 75\%$ for Serrota 2015 data).

248 **Table 1. Observed (S) and first-order jackknife estimator ($J \pm SE$) of ant species**
249 **richness in dry grasslands in central Spain.**

ID	Sampling	S	$J \pm SE$	N	X	Y	Elevation (m)
G1	G2014	7	7 ± 0	13	437876	4494480	685
G1	G2015	7	7.9 ± 0.9	10	437876	4494480	685

G2	G2014	8	8±0	12	434821	4496549	768
S1	S2015	14	18.5±2.4	10	351711	4474792	808
G3	G2014	14	16.7±1.6	11	440394	4503515	865
G4	G2014	14	16.8±1.6	12	435541	4506094	1012
G5	G2014	14	15.8±1.3	12	431692	4513777	1044
G5	G2015	11	11.9±0.9	12	431692	4513777	1044
S2	S2015	11	14.7±2.3	12	357653	4481333	1086
G6	G2014	13	14.8±1.3	9	414145	4507982	1171
G7	G2014	13	18.5±2.6	12	438808	4523233	1285
G8	G2014	15	15.9±0.9	11	416330	4511347	1330
G8	G2015	14	17.5±2.2	8	416330	4511347	1330
S3	S2015	13	15.8±1.6	12	340207	4476196	1374
G9	G2014	9	9±0	12	436806	4524537	1487
G10	G2014	10	12.8±1.6	12	400821	4495703	1625
S4	S2015	4	4±0	11	326465	4482790	1646
G11	G2014	3	3±0	19	400543	4496999	1675
G12	G2014	5	5.9±0.9	12	419833	4519838	1786
G12	G2015	5	5.9±0.9	12	419833	4519838	1786

G13	G2014	5	5±0	12	419076	4519012	1830
G14	G2014	4	4.9±0.9	12	418737	4519177	1920
S5	S2015	2	2±0	12	323719	4482788	2000
G15	G2014	3	3±0	12	419392	4520829	2026
G15	G2015	3	3±0	8	419392	4520829	2026
G16	G2014	3	3.9±0.9	12	417883	4521249	2139
G17	G2014	4	5.8±1.9	12	418676	4521128	2266
S6	S2015	3	3.9±0.9	12	323944	4485467	2286
G18	G2014	3	3±0	12	419420	4522544	2390
G18	G2015	3	3.9±0.9	12	419420	4522544	2390

250 Grassland plots were ordered following elevation (in m a.s.l.), identified with an ID,
 251 where G stands for Guadarrama, S stands for Serrota, and numbers represent grassland
 252 position in increasing order of elevation. Sampling: data from Guadarrama range in
 253 2014 (G2014) and 2015 (G2015) and Serrota range in 2015 (S2015). N: samples sizes
 254 (number of pitfall traps recovered from each locality). Geographic coordinates (X and
 255 Y) were provided as UTM European Datum 1950.

256 **Fig 1. Relationship between first-order jackknife estimates of ant species richness**
 257 **(see Table 1) and elevation in dry grasslands of a Mediterranean range in central**
 258 **Spain.**

259 Curve and 95% IC from GAM with Gaussian errors fit to the Guadarrama 2014 survey
260 (black circles). Richness estimates for the surveys in Guadarrama 2015 (grey circles)
261 and Serrota 2015 (open circles) were superimposed. Elevation values were slightly
262 jittered to avoid overlap among some points.

263

264 A NMDS solution was built that satisfactorily summarized the Bray-Curtis distances
265 among grasslands in both years and study regions (stress = 0.10, linear R^2 between
266 Bray-Curtis and NMDS distances = 0.95). This scaling separated grasslands roughly
267 according to elevation, but not regions or years and suggested an elevation threshold of
268 1700 m a.s.l. was a suitable elevation to distinguish the two groups (**Fig 2**). Multivariate
269 GLMs for species abundances revealed significant elevation effects ($P = 0.001$) and a
270 significant region effect ($P = 0.047$), but significant effects were not detected for year or
271 any elevation interactions (**Table 2**). These results suggested taxonomic composition
272 varied mainly with elevation, but differences between regions cannot be excluded.

273

274 **Fig 2. Non-metric multidimensional scaling (NMDS) of ant assemblages based on**
275 **binary Bray-Curtis distances among grasslands calculated with species**
276 **occurrences from pitfall traps in a Mediterranean range of central Spain.**

277 Circles represent data from Guadarrama (black: year 2014, grey: year 2015) and Serrota
278 (open circles) ranges. Symbol sizes are proportional to the elevation of sampling plots.
279 As reference, circles are superimposed to a smooth elevation surface (estimated using a
280 GAM of elevation on a bivariate spline of NMDS scores). The positions of some
281 illustrative species are given as reference.

282

283 **Table 2. Multivariate GLMs (negative binomial regressions) fitted to species abundances.**

	Deviance	P values
a)		
Elevation	192.91	0.001
Year	50.27	0.649
Elevation x Year	5.99	0.997
b)		
Elevation	178.14	0.001
Region	84.44	0.047
Elevation x Region	18.85	0.618

284 *P*-values estimated by bootstrap (n = 1000). Significant *P*-values ($P < 0.05$) are highlighted in

285 bold. a) Guadarrama 2014 vs. Guadarrama 2015. b) Guadarrama 2014 vs. Serrota 2015.

286

287 Ant species assemblages were nested, showing a pattern suggesting differences in

288 species richness among localities were more important than differences in prevalence

289 among species (nestedness among rows was higher than nestedness among columns,

290 **Table 3, S2 Table**). Nestedness ranks for Guadarrama 2014 was described with GAM

291 and curvilinear term (spline) for elevation, roughly similar to a third-degree cubic
 292 polynomial ($df = 3.89$, $F = 15.38$, $P < 0.0001$, $D^2 = 85.6\%$, **Fig 3**). The subset of these
 293 grasslands sampled in 2015 maintained their nestedness ranks and the model transferred
 294 to 2015 data (Pearson's correlation between predicted and observed ranks, $r = 0.96$, $t =$
 295 7.28 , $df = 4$, $P = 0.0018$, $R^2 = 93\%$, **S3 Fig**). The model did not transfer between study
 296 regions ($r = 0.74$, $t = 2.18$, $df = 4$, $P = 0.10$, $R^2 = 54\%$, **S4 Fig**). Largely, nestedness
 297 increased with elevation, with the exception of the lowest and highest elevation
 298 grasslands.

299 **Table 3. Nestedness indices for dry grassland ant assemblages in Guadarrama**
 300 **range 2014 surveys (18 grasslands, 35 species).**

NODF	NODFr	NODFc	T	fill
38.31: 0.001-0.015	40.62: 0.001-0.001	37.72: 0.001-0.103	25.24: 0.001-0.912	0.23

301

302 Indices were derived from the Nestedness metric based on Overlap and Decreasing Fill
 303 (NODF), NODFr for rows (i.e. localities) and NODFc for columns (i.e. species) and
 304 matrix temperature (T). Numbers under headings for indices provide the index values
 305 followed by P -values estimated by equiprobable ('r00') and proportional resampling
 306 ('quasiswap') binary null models. Significant P -values ($P < 0.05$) are in bold face. Fill:
 307 matrix fill (sum of 1s/sum of cells).

308

309 **Fig 3. Generalized additive model (GAM) of nestedness ranks (based on nestedness**
310 **temperature (T) index) for elevation in ant species assemblages in dry grasslands**
311 **of a Mediterranean range in central Spain.**

312 Curve and 95% IC from GAM with Gaussian errors fit to the Guadarrama 2014 survey
313 (black circles). Nestedness ranks for the Guadarrama 2015 (grey circles) and Serrota
314 2015 (open circles) surveys are superimposed. Low ranks indicate poorer species
315 community richness, where species are a subset of richer species communities.
316 Elevation values were slightly jittered to avoid overlap among some points.

317

318 Species turnover and nestedness were significant beta diversity components, although
319 species turnover among grasslands was more important than pure nestedness of
320 assemblages ($\beta_{\text{SOR}} = 0.88$, $\beta_{\text{SIM}} = 0.79$, $\beta_{\text{NES}} = 0.09$, all P -values = 0.001). This
321 relationship among beta diversity components did not vary among surveys (**S5 Table**).

322

323 **Discussion**

324 Ant species richness and taxonomic composition changed predictably with elevation in
325 the Mediterranean mountains we investigated, exhibiting largely consistent patterns
326 between years and among regions. These changes were more notable along mid-
327 elevations and associated more clearly with differences of species richness among sites
328 than with prevalence or abundance among species. To our knowledge, this is the first
329 study specifically designed to describe ant community species richness and taxonomic
330 composition responses to elevational changes in the Mediterranean Basin. However, we
331 restricted our study to grasslands, therefore the results might not be a suitable model

332 system for other habitat types. Notwithstanding, grasslands are among the ecosystems
333 exhibiting greater economic and ecological relevance in the Mediterranean Basin [65,
334 66].

335 Species richness showed a hump-shaped relationship with elevation, peaking at ca. 1100
336 m a.s.l. This model depiction fit to the primary dataset (Guadarrama 2014), transferred
337 adequately to the 2015 Guadarrama dataset, and also the spatial validation dataset in the
338 2015 Serrota range. Despite geometric constraints as mid-domain effects were described
339 to explain these curve types [30], more recent studies tended to downplay the
340 importance of these mechanisms [24, 29, 67]. In fact, while mid elevation peaks in
341 species diversity were reported as relatively common [28, 29], these observations are far
342 from universal, suggesting regional factors play an important role in driving elevational
343 patterns of species diversity. Interestingly, research showed monotonic increases in ant
344 species richness were common in temperate climates [19-21], where elevation was
345 correlated with temperature. In arid climates, monotonic decreases were observed [22,
346 23], where hydric stress was ameliorated with altitude. Indeed, hydric stress and
347 temperature are the two main elevational correlates in Mediterranean climates, with
348 water availability limiting communities at low elevations, while at high elevations cold
349 temperature stress is more important [6, 7]. This double constraint might drive a hump-
350 shaped spatial pattern of ant species richness in Mediterranean mountains.

351 Most studies on ant communities reported species richness positively responded to
352 temperature [19-21, 24, 26, 27, 67, 68], but a number of findings also emphasized the
353 role of water availability [22, 29, 33, 34, 69]. Cold temperatures can reduce local ant
354 species richness by direct effects that limit ant activity, such as reduced foraging time
355 [35, 70], and, at larger biogeographical scales, cold temperatures can also limit species

356 pools by lowering speciation rates [67]. Azcárate *et al.* [70] reported low humidity, in
357 turn, can limit colony activation by reducing foraging possibilities, and therefore
358 constitutes a main environmental filter. Alternatively, temperature and water availability
359 can facilitate ant species richness indirectly, these abiotic factors affecting primary
360 productivity and therefore the range and abundance of resources ant colonies exploit
361 [33, 35-37]. Diversity-productivity hypothesis states that as productivity increases, so
362 does the availability of energy and resources, so density and size of colonies also
363 increase. These relationships should increase local species richness by abundance,
364 lowering local extinction risks or activating a sampling mechanism [71, 72]. In
365 Mediterranean climates, primary productivity can be limited by cold temperatures and
366 summer drought [73], so maximum primary productivity values likely occur at
367 intermediate elevations, where summer drought is not too severe and temperatures are
368 not too cold. Therefore, if species richness increases with primary productivity, a
369 humped curve is also expected.

370 As anticipated, elevation also affected the taxonomic composition of ant communities.
371 We observed a ca. 1700 m threshold separating high mountain ant species communities
372 from those along the lower elevational gradient. This threshold was consistent among
373 regions and between years. Furthermore, although nestedness was a significant
374 component of beta diversity, most elevational shifts among communities were
375 attributable to species turnover. This result suggested the communities with lowest ant
376 species diversity (high mountain communities) were also the most unique in a regional
377 context. The singularity of high elevation ant communities was previously observed in
378 different biomes [22, 24, 34, 35], which reinforced the conservation value of the
379 Mediterranean mountains reported for other taxa [74, 75].

380 The examination of community nestedness suggested current ant assemblages are
381 context-dependent and likely highly vulnerable to global warming and other
382 anthropogenic changes. This is because, first, species turnover exhibited a dominant
383 role over pure nestedness, which indicated different and characteristic groups of ant
384 species occurred along an elevational gradient, and at the very least, ant species
385 community composition was distinct at high elevations (> 1700 m) (**Fig 2**). We want to
386 emphasize that if species distributions followed gradually changing abiotic conditions
387 (e.g. a decreasing temperature gradient with elevation), then we would expect a
388 concomitant change in the taxonomic composition of ant assemblages, rather than the
389 development of new, characteristic, species groups [42, 76]. It is also illuminating to
390 consider that nestedness arises with contributions from differences among species and
391 among sites [59]. Nestedness patterns elsewhere were explained as a simple sampling
392 mechanism, where the smaller species group in less diverse, i.e. poorer communities
393 were a subset of species in more diverse, i.e. richer communities, reportedly when the
394 studied localities differed in resource availability (or productivity) and this factor
395 determined species richness [72, 77]. However, this implied species attributes notably
396 contributed to nestedness, because rarer species with small distributional ranges (often
397 specialists or poor-dispersers) were not generally sampled by the least diverse, i.e.
398 poorest communities, while the more common taxa exhibited a wide distributional
399 range [61]. In our study, the least diverse communities were more nested than diverse
400 ant communities, but nestedness among species was less important than among sites.
401 We conclude the sampling mechanism did not fully explain the nested patterns in the
402 ant communities we identified and habitat and abiotic filtering provided more plausible
403 explanations for the patterns. However, we carefully controlled by design the habitat
404 type (arid grasslands in gentle south facing slopes), which implied those habitat filters —

405 if an integral component — should be fine grained. Nestedness patterns along the
406 elevational gradient were temporally constant, but varied between mountain ranges,
407 indicating ant community composition was spatially dependent. Finally, an historic
408 explanation of current ant species distribution patterns in a landscape context is an
409 important element to include. We studied a mountain range within the Mediterranean
410 biome where major landscape changes have not occurred over the last thirty years.
411 Extensive afforestation was conducted during 1950's and a progressive abandonment of
412 the region took place between the 1960's and 1980's. Therefore, we assume all sites are
413 equally accessible from the regional species pool. However, we cannot disregard other
414 time-related mechanisms, which might explain community composition, such as priority
415 effects favoring one or more species, depending on their relative order of arrival to a site
416 [78], or metapopulation dynamics involving local extinctions and recolonizations in
417 periods beyond this two-year study [79].

418 Overall, species taxonomic composition varied non-linearly with elevation. The
419 insufficiency of the sampling mechanism emphasizes that ant assemblages are highly
420 vulnerable to global changes on climate and anthropogenic impacts, which might affect
421 species at the habitat and/or community level. It is unlikely species' range shifts that
422 track environmental change will maintain current ant species community composition.

423

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432

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648

649 **Supporting information**

650 **S1 Table. Species presence in each survey.**

651 **S2 Table. Nestedness indices for dry grassland ant assemblages in surveys from all**

652 **study areas in central Spain.** Guadarrama range (-G2014- year 2014: 18 grasslands,

653 35 species; -G2015- year 2015: 6 grasslands, 26 species) and Serrota range (-S2015-

654 year 2015: 6 grasslands, 20 species). Indices are Nestedness metric based on Overlap

655 and Decreasing Fill (NODF), NODFr for rows (i.e., localities) and NODFc for columns

656 (i.e., species) and matrix temperature (T). Numbers under headings for indices provide

657 index values followed by *P*-values estimated by equiprobable ('r00') binary null models

658 and proportional resampling ('quasiswap'). Significant *P*-values ($P < 0.05$) are in bold

659 face. Fill: matrix fill (sum of 1s/sum of cells).

660 **S3 Fig. Temporal validation of the relationship between nestedness and elevation.**

661 Generalized additive model (GAM) of nestedness ranks (based on nestedness

662 temperature index) on elevation in ant assemblages from Guadarrama range (central

663 Spain) fit to Guadarrama 2014 data and validated with Guadarrama 2015 data.

664 **S4 Fig. Spatial validation of the relationship between nestedness and elevation.**

665 Generalized additive model (GAM) of nestedness ranks (based on nestedness
666 temperature index) on elevation in ant assemblages from Guadarrama range (central
667 Spain) fit to Guadarrama 2014 data and validated with Serrota 2015 data.

668 **S5 Table. Multiple-site dissimilarities of beta diversity.** Multiple-site dissimilarities

669 accounting for the spatial turnover (β_{SIM}) and the nestedness components (β_{NES}) of beta
670 diversity, and sum of both values (β_{SOR}) for dry grassland ant assemblages in all study
671 areas in central Spain. G2014: Guadarrama range 2014; G2015: Guadarrama range
672 2015; S2015: Serrota range 2015. *P*-values estimated by equiprobable binary null
673 models ('r00') are given between parentheses. Significant *P*-values ($P < 0.05$) are in
674 bold face.

Species richness





