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1 **Multiscale assessment of woody species recruitment in Mediterranean shrublands:**
2 **facilitation and beyond**

3

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35 **ABSTRACT**

36 **Questions:** Forest recovery in Mediterranean environments is influenced by factors such as
37 aridity, herbivory and facilitation by shrubs, as well as by seed limitation in the case of highly
38 fragmented forests. How these various factors interact can determine the direction of secondary
39 succession, yet these interactions are poorly understood. We assessed the relative importance
40 of several factors in forest species recruitment in *Retama sphaerocarpa* (L.) Boiss (*Retama*)
41 shrublands at different spatial scales.

42 **Location:** Centre of the Iberian Peninsula.

43 **Methods:** We surveyed mid- and late-successional woody species common in Holm oak forests
44 in 29 *Retama* shrublands that are distributed along an environmental gradient of increasing
45 aridity and herbivory (regional scale) and are located at various distances from forest patches
46 of different sizes (landscape and local scale). In each *Retama* shrubland, we analysed the effects
47 of microhabitat (under *Retama* canopy vs. open gaps); aridity; presence of nurse shrubs;
48 herbivory, based on the density of pellet droppings; and propagule pressure, measured as the
49 ratio between the size of forest patches acting as seed sources and their distance to *Retama*
50 shrubs.

51 **Results:** *Quercus ilex*, *Asparagus acutifolius* and *Juniperus oxycedrus* were the mid- and late-
52 successional woody species most recruited in *Retama* shrublands. Their frequency, which
53 increased with precipitation, was greater under *Retama* canopy than in gaps. Differences in *Q.*
54 *ilex* recruitment between *Retama* canopy or gaps increased with rainfall, suggesting a decrease
55 in *Retama* facilitation effectivity with increasing aridity. Frequency of recruited oaks increased
56 with the total area of woodland remnants located <0.5 km, yet propagule pressure did not
57 modulate the positive effect of *Retama* and rainfall on recruitment. Forest patches at distances
58 >0.5 km did not contribute to recruitment.

59 **Conclusions:** Presence of the shrub *Retama sphaerocarpa* and dispersal related processes at
60 local scale are main determinants of the colonisation of shrublands by late successional woody
61 species. Preserving *Retama* shrublands and *Q. ilex* woodland remnants is therefore crucial for
62 extensive passive restoration of Mediterranean oak forests. However, facilitation by *Retama* is
63 much weaker when both aridity and herbivory are high, regardless of seed source availability.

64

65 **Keywords:** facilitation, herbivory, aridity, oak, *Retama sphaerocarpa*, restoration, seed
66 availability, seed dispersal, woodland regeneration

67 INTRODUCTION

68 Plant recruitment depends on multiple ecological processes such as seed production and
69 dispersion as well as seedling survival, and these processes are modulated by environmental
70 factors (García & Houle 2005; Cuesta et al. 2010). Ecological processes affecting plant
71 recruitment are especially vulnerable to drought, meaning that plant regeneration progresses
72 slowly in semi-arid ecosystems, such as in most Mediterranean forests (Puerta-Piñero et al.
73 2007; Rey Benayas et al. 2015). Several biotic factors may also affect Mediterranean forest
74 regeneration. Wild and domestic herbivores can deter performance of juveniles (MacDougall
75 et al. 2015), and annual herbs frequently outcompete tree seedlings when colonising old fields
76 or large forest gaps (Cuesta et al. 2010; Benavides et al. 2016). Other biotic interactions may
77 promote plant recruitment. Many plant species concentrate juveniles and adults of other plant
78 species under their canopy to a greater extent than gaps. Often this occurs because of facilitative
79 interactions, in which the nurse plant mitigates the abiotic and biotic stresses that other plants
80 experience outside the nurse canopy (Aerts et al. 2006; Gómez-Aparicio et al. 2008). Shrubs
81 are important nurse plants globally (Gómez-Aparicio et al. 2009); they trigger the ability of
82 mid- and late-successional forest trees and shrubs to colonise large gaps in woodlands or
83 abandoned fields in Mediterranean ecosystems (Gómez-Aparicio et al. 2004; Rolo et al. 2013).

84 Whether plant interactions tend to be facilitative or competitive depends on the
85 environmental context. Bertness & Callaway (1994) proposed the *Stress Gradient Hypothesis*
86 (SGH), which predicts that facilitative interactions become more important than competitive
87 ones as abiotic stress and herbivory increase. While the SGH has substantial empirical support
88 (Callaway et al. 2002; Gómez-Aparicio et al. 2009; He et al. 2013 and references therein), some
89 studies suggest that facilitative interactions do not necessarily increase monotonically with
90 environmental stress. Instead, competition can become the dominant plant interaction under
91 very stressful conditions (Maestre & Cortina 2004; Maestre et al. 2005; Koyama & Tsuyuzaki
92 2013). Furthermore, herbivore pressure might shift the direction of plant-plant interactions
93 along environmental gradients (Soliveres et al. 2011b; Louthan et al. 2014). It seems likely that
94 facilitative interactions also depend on functional characteristics of the nurse and beneficiary
95 plants (Padilla & Pugnaire 2009; Schöb et al. 2013). For example, Maestre et al. (2009)
96 proposed that facilitation would be more likely when the nurse plant is competitive, the
97 beneficiary plant is stress-tolerant, and the stressors are drought or extreme temperature. Since
98 the suite of nurse and beneficiary plants usually shifts as one moves along the environmental
99 gradient (Callaway et al. 2002; Holzapfel et al. 2006; Armas et al. 2011), it becomes difficult
100 to disentangle effects of environment from effects of functional plant characteristics.

101 Plant recruitment is tightly linked to seed availability and dispersal. Low seed input can
102 be a major bottleneck slowing forest recovery after intense forest fragmentation: this is the case,
103 for example, in the Mediterranean region following centuries of intensive land use (Rey
104 Benayas et al. 2008). Many areas in the Mediterranean basin are a mosaic of different crops
105 with interspersed shrublands, pasturelands and small, if any, forest remnants. Fast-growing
106 pioneer shrubs has colonised much crop- and pastureland because of rural abandonment over
107 the last 70 years, while colonisation by mid- and late-successional forest species has progressed
108 very slowly (Rey Benayas et al. 2015). As a result of the sparse, small forest patches, dispersible
109 seeds are not in abundance and seed dispersion by animals is ineffective (Jordano & Schupp
110 2000; McConkey & Farril 2016); these propagule limitations are probably exacerbated by the
111 harsh Mediterranean climate. Seed availability and dispersal are likely to be such strong factors
112 in plant recruitment that can influence nucleation regardless nurse plants effectively mitigate
113 stresses (Pausas et al. 2006). This occurs when seed rain is higher under the nurse canopy than
114 in the gaps because animal dispersers disperse the seeds to nurse plants (Jordano & Schupp
115 2000; Verdú & García-Fayos 1996).

116 While most studies of forest colonisation have focused on climate, herbivory and
117 facilitation as factors of plant recruitment (García & Houle 2005; Benavides et al. 2016), less
118 is known about features of forest remnants in the landscape as potential factors affecting the
119 colonisation by forest species. These features include the size of forest remnants and their
120 distance to suitable regeneration sites (Pueyo & Alados 2007; Gómez-Aparicio et al. 2009;
121 Sheffer et al. 2013), which together are the primary determinants of propagule pressure (García
122 et al. 2005). How these factors interact with climate, herbivory and facilitation by shrubs to
123 influence forest species recruitment is also unclear (Pueyo & Alados 2007; Lara-Romero et al.
124 2016).

125 In this study, we analysed the relative importance of several factors on the colonisation
126 of Mediterranean shrublands by mid- and late-successional woody species. These factors
127 included the presence of nurse shrubs, herbivory, rainfall, size of forest remnants and their
128 distance to regeneration sites. Since they operate at different spatial scales, we analysed their
129 importance on the regional, landscape, local and microsite levels. We selected shrublands
130 dominated by *Retama sphaerocarpa* (L.) Boiss (hereafter *Retama*) along an environmental
131 gradient varying in aridity and herbivory. *Retama* is a leguminous shrub native to the Iberian
132 Peninsula and northwest Africa that facilitates both annual herbs and woody species such as
133 oaks (Cuesta et al. 2010; Armas et al. 2011; Rolo et al. 2013), which are the main structural
134 species in many Mediterranean forests. In our study, nurse and beneficiary plant species were

135 the same across the surveyed shrublands. This meant that we could attribute any observed
136 changes in facilitation to changes in stress factors rather than to changes in the functional
137 characteristics of interacting species.

138 We addressed the following questions: (1) Does the recruitment of woody forest species
139 under *Retama* shrubs increase with environmental stress, as predicted by the SGH? (2) Does
140 the size of forest remnants and their distance to *Retama* shrublands affect colonisation by forest
141 species? (3) Does an increase in seed propagule pressure outweigh the negative effect of aridity
142 on the colonisation of *Retama* shrublands by woody species? We hypothesised that: (i) the
143 relative importance of facilitation by *Retama* shrubs increases with environmental stress; (ii)
144 recruitment is enhanced by seed propagule pressure on a local scale (within shrubland), and this
145 recruitment is related to the size of forest remnants and their distance to vegetation remnants
146 that act as seed sources; and (iii) the positive effect of seed availability on recruitment increases
147 with decreasing environmental stress.

148

149 **MATERIAL AND METHODS**

150 *Natural history of study area*

151 The study area lies in the centre of the Iberian Peninsula (40°12′-40°49′N, 3°20′-4°18′W) and
152 covers a surface area of *ca.* 6,000 km². Altitude decreases southwards from 900 to 600 m a.s.l.
153 The climate is Mediterranean continental, with hot and dry summers and cold winters. Annual
154 rainfall increases northwards from 400 to 700 mm, while mean annual temperature decreases
155 from 15.5 to 12.5 °C. Most soils are acid and developed on granites, quartzite, and arkose
156 bedrock, although some sites in the southern part of the study area were on limestone and
157 gypsum soils. The landscape is dominated by rainfed cereal cropland, pastureland and
158 shrubland. Some olive and almond groves occur in the southern part of the study area. Most
159 shrublands are dominated by *R. sphaerocarpa*, *Cistus ladanifer* L., *Lavandula stoechas* Lam.,
160 *Genista hirsute* Vahl and *Rosmarinus officinalis* L. The shrublands are used mainly for hunting
161 and less frequently for extensive livestock grazing. Woodland occupies a small surface and
162 consists of oak woodland remnants and monospecific pine plantations of variable size. Oak
163 woodland remnants are dominated by *Quercus ilex* subsp. *ballota* (Desf.) Samp. (hereafter *Q.*
164 *ilex*), *Quercus coccifera* L. and, less frequently, by *Quercus faginea* Lam, while pine plantations
165 are mainly of *Pinus halepensis* Mill. and *Pinus pinea* L. The primary wild herbivores in the
166 area are rabbits, hares, roe deer and wild boars. Abundance of rabbits increases southwards
167 concomitant with decreasing rainfall and increasing temperature (Saldaña et al. 2007).

168 *Recruitment sampling and explanatory factors*

169 We randomly selected 29 patches of *Retama* shrubland (see Appendix S1 for detailed
170 characteristics) using vegetation maps of the Regional Government of Madrid, the Geographic
171 Information System for Agricultural Plots (SIGPAC®, available at
172 <http://sigpac.mapa.es/fega/visor/>) and the Climatic Atlas of the Iberian Peninsula (Ninyerola et
173 al. 2005). For each *Retama* shrubland we recorded annual rainfall based on Ninyerola et al.
174 (2005). *Retama* shrublands were considered eligible when they met the following criteria: (1)
175 large enough to fit a 200 m x 5 m transect; 2) a high proportion of healthy adult *Retama* shrubs,
176 *i.e.* individuals with a minimum height of 1.6 and minimum width of 1.5 m; and (3) <1,000
177 adult *Retama* shrubs ha⁻¹, ensuring the presence of relatively large gaps among individual
178 shrubs. Mean area and density of *Retama* shrublands were, respectively, 19.0 ± 4.8 ha and 422
179 ± 28 shrubs ha⁻¹ (Appendix S1). We discarded patches dominated by decaying *Retama* adults,
180 which may have lower facilitation capacity (Schöb et al. 2013). We also avoided small *Retama*
181 shrubs, since a minimum shrub size is needed for seedling facilitation (Allegrezza et al 2016).

182 In each *Retama* shrubland, we randomly established a 200 × 5 m belt transect and used a
183 hand-held GPS receiver (Garmin 12XL, Olathe, USA) to map all *Retama* shrubs with heights
184 > 1.6 m and width > 1.5 m. We sampled a total of 1,263 *Retama* shrubs. The numbers of
185 established woody plants were counted in the area under each *Retama* shrub and in a paired
186 control gap of similar size as the *Retama* shrub. Sampled gaps were located on the north side
187 of the *Retama* shrubs, 1-2 m apart from the canopy. In this study, we refer to each pair of
188 counting plots as a “*Retama* site” ($n = 1,263$), and to the counting plots under the *Retama*
189 canopy and gaps as a “microhabitat” ($n = 2,526$). In each microhabitat, we recorded the number
190 of seedlings and saplings of vines, shrubs and tree species characteristic of mid- and late-
191 successional stages in oak woodlands. Early successional chamaephytes and shrubs such as
192 *Thymus* sp., *Genista hirsuta* or *Lavandula stoechas* were not considered. To avoid counting
193 plants that had established prior to the establishment of the *Retama* shrub, we discarded saplings
194 taller than one third of the *Retama* height. We also estimated herbivore relative abundance by
195 counting the number of pellet droppings of rabbits, hares and ungulates present on a 50 × 50
196 cm quadrat randomly placed within each counting plot. Counting faecal accumulation has been
197 used to estimate herbivore relative abundance (Marques et al. 2001).

198 We accounted for the effects of surrounding vegetation on recruitment of mid- and late-
199 successional woody species at two scales. At the local scale (within shrublands) we identified
200 every patch of shrubland, olive grove, oak and pine woodland (including isolated trees) within
201 a circular area (radius, 0.5 km) around each *Retama* site. Then we measured the area of each
202 vegetation patch and its distance to the sampled *Retama* site using ArcView 3.2 GIS software

203 (ESRI, New York, USA). We chose the 0.5-km radius based on (1) the distance of acorn
204 dispersal by the Eurasian jay (*Garrulus glandarius*), the major disperser of *Quercus* seeds in
205 Mediterranean woodlands, which is usually <0.5 km (Gómez 2003; Pons & Pausas 2007); and
206 (2) the dispersal distance for small and medium-size frugivorous birds (Jordano et al. 2007).
207 For each *Retama* site, we calculated an index of seed pressure potential (*SPP*) as:

$$208 \quad SPP = \sum \frac{S_i}{d_{ij}^{1.65}} \quad (\text{ha km}^{-1})$$

209 where S_i is the area (ha) of each vegetation patch (i) within the circular area (radius, 0.5 km)
210 around the *Retama* site j , and d_{ij} is the distance (km) from patch i to *Retama* site j . As seed
211 dispersal frequently declines exponentially with distance, we raised d_{ij} to the power of 1.65
212 based on previous studies on *Q. ilex* acorn dispersal by European jays in the Sierra Nevada
213 (Spain) (Gómez 2003). We calculated *SPP* for either all vegetation patches or only for oak-
214 dominated forest patches (including isolated trees). At the landscape scale we measured the
215 distance of the closest oak woodland stand with a size of >2.5 ha and located >0.5 km from the
216 middle of each *Retama* transect. This allowed us to analyse the effect of distant oak forest
217 patches on the recruitment of woody species to *Retama* shrublands. We established this
218 minimum size based on Santos et al. (2002), which concluded that patches <2 ha are not
219 effective in harboring forest frugivorous bird populations.

220 ***Data analysis***

221 The presence or absence of woody species was analysed using generalised linear mixed models
222 (GLMMs) with a logit-link function, because our response variable followed a binomial
223 distribution. We applied a mixed model because our experimental approach involved
224 structuring the data hierarchically, resulting in non-independency among observations within
225 the same *Retama* site and within each *Retama* shrubland patch. Thus, we considered a *Retama*
226 site nested within *Retama* shrubland as a random effect factor. The explanatory variables were
227 microhabitat (under *Retama* or in gaps), annual rainfall, *SPP*, and the distance to oak woodland
228 stand > 2.5 ha and located > 0.5 km from each *Retama* shrubland.. GLMMs were fitted
229 separately for the presence of saplings of all mid- and late-successional woody species or for
230 the presence of only *Q. ilex* saplings. Continuous variables (*i.e.* rainfall, *SPP* and distance to
231 closest oak woodland) were standardised by subtracting the mean from each value and dividing
232 by the standard deviation. Standardisation of variables allows comparisons across model-
233 estimated parameters and testing interactions (Zuur et al. 2009).

234 Model selection was performed according to a backward, stepwise procedure and the
235 principle of parsimony, in which Akaike's Information Criterion (AIC) and the Bayesian
236 Information Criterion (BIC) served as indicators of both parsimony and likelihood (Burnham
237 & Anderson 2002). First, we fitted a saturated model including all fixed effects and the triple
238 interaction to be tested (microhabitat \times rainfall \times *SPP*), and we compared the saturated model
239 with a reduced model in which the triple interaction term was dropped (Round 1, Appendix
240 S2). Second, we compared the model selected after Round 1 to models in which each pair-wise
241 interaction was ignored (Rounds 2-3, Appendix S2). Then, we compared the selected model
242 after previous rounds with models that ignored main effects (Rounds 4-6, Appendix S2). If the
243 difference in AIC or BIC between the reduced and full models was ≤ 2 , then the simpler model
244 was selected and the model was considered to have substantial support (Burnham & Anderson
245 2002). Parameter estimates and confidence intervals of the best-supported model were obtained,
246 and the pseudo- R^2 was used to estimate the variance explained by fixed and random factors
247 (Nakagawa & Schielzeth 2013). All statistical analyses were performed using the packages
248 '*lme4*', '*stats*' and '*piecewiseSEM*' in R version 3.2 (R Core Development Team, Vienna,
249 Austria).

250 Herbivore relative abundance was not included in the GLMMs due to convergence
251 problems probably because it was strongly correlated with microhabitat at the *Retama* site scale,
252 and with rainfall at the *Retama* shrubland scale (see Results). Differences in herbivory between
253 microhabitats were assessed using a Wilcoxon's signed-rank test for two related samples
254 (microhabitat within *Retama* site). We used Spearman rank correlation analysis to explore the
255 relationships between oak juvenile frequency and the two components of the *SPP* index, *i.e.*
256 total area and mean distance of *Q. ilex* forest patches from the surveyed *Retama* shrubs.

257 258 **RESULTS**

259 ***Recruitment survey***

260 The selected *Retama* shrublands ranged in annual rainfall from 429 to 690 mm (Appendix S1),
261 and in the number of pellet droppings from 7.5 to 37.1. Rainfall and herbivory were negatively
262 correlated ($r = -0.63$, $p < 0.01$), with drier *Retama* shrublands showing greater herbivore
263 abundance. Mean distance (\pm SD) was 2.8 ± 3.4 km to oak woodland stands > 2.5 ha located $>$
264 0.5 km from each *Retama* shrubland.

265 We recorded a total of 211 juveniles of four mid- and late-successional woody species
266 and a crop tree in the *Retama* shrublands, namely *Asparagus acutifolius* L. (96), *Q. ilex* (84
267 individuals), *Juniperus oxycedrus* L. (27), *Rosa canina* L. (2), and *Prunus dulcis* (Mill) D.A.

268 (2). Five *Retama* patches, corresponding to 17% of shrublands studied, lacked saplings of any
269 woody species; *Q. ilex* saplings were not recorded in 12 *Retama* patches.

270 ***Factors influencing recruitment***

271 The model selected to analyse all woody species included microhabitat and rainfall as main
272 terms (Appendix S2a, $R^2 = 0.18$). The most parsimonious model for recruitment of *Q. ilex*
273 included the main terms microhabitat, rainfall and *SPP*, as well as the interaction between
274 microhabitat and rainfall (Appendix S2b, $R^2 = 0.40$). Thus, microhabitat was the most important
275 factor explaining the recruitment of woody species in the *Retama* shrublands (Figure 1).
276 Recruited plants occurred more frequently under *Retama* canopy than in gaps: 87% of all
277 recruited woody plants and 84% of *Q. ilex* juveniles were recorded under *Retama* canopy. The
278 frequency of recruited woody species in *Retama* shrublands, especially of *Q. ilex*, increased
279 with rainfall (see model coefficients in Table 1). Interestingly, for *Q.ilex* we detected a
280 significant interaction between microhabitat and rainfall: rainfall increased the relative
281 difference in *Q. ilex* frequency between *Retama* canopy and gap microhabitats (Figure 2).

282 Frequency of *Q. ilex* juveniles correlated positively with rainfall and the *SPP* of oak
283 woodlands (Table 1, Figure 3). *SPP* positively correlated with rainfall for all woodland types
284 ($r = 0.49$, $p < 0.01$) and oak patches ($r = 0.53$, $p < 0.01$). However, the lack of significance of
285 the interaction microhabitat \times rainfall \times *SPP* showed that the increasing differences in recruited
286 plants between both microhabitat types (gaps vs. under *Retama* canopy) was not confounded
287 by greater potential seed pressure in the *Retama* shrublands located in the wettest sites of the
288 study area. In other words, *SPP* may determine the extent of recruitment, but not the direction
289 of the interaction between microhabitat and rainfall. When the two components of oak *SPP*,
290 oak forest patches area and distance, were analysed separately, frequency of *Q. ilex* juveniles
291 correlated positively with total area of oak woodland patches located < 0.5 km from *Retama*
292 sites (Figure 4a). In contrast, no significant relationship was found between *Q. ilex* juvenile
293 frequency and mean distance to the oak forest patches located < 0.5 km from *Retama* site
294 (Figure 4b).

295 At the landscape scale, the distance to the closest oak stand > 2.5 ha located > 0.5 km away
296 from the *Retama* shrublands did not affect the frequency of woody species recruits (Table 1).
297 The number of pellet droppings of rabbits, hares and ungulates was greater in gaps (mean \pm SE,
298 15.6 ± 0.33) than under *Retama* canopy (11.1 ± 0.24 ; $Z = 13.28$, $p < 0.001$).

299

300 **DISCUSSION**

301 Our results highlight the positive effect of *R. sphaerocarpa* shrubs on colonisation of
302 Mediterranean shrublands by mid- and late-successional trees and shrubs. They also highlight
303 the importance of propagule limitations (based on the extent of forest remnants) on this
304 colonisation.

305 ***Facilitation of plant recruitment in Retama shrublands***

306 Recruitment of mid- and late-successional woody species in shrublands was approximately
307 three times higher under *Retama* canopy than in gaps, confirming the facilitative capacity of
308 this shrub (Pugnaire et al. 1996; Cuesta et al. 2010; Rolo et al. 2013). Plant recruitment by nurse
309 shrub species in Mediterranean areas has often been linked to the nurse species' ability to
310 mitigate abiotic stresses (Gómez-Aparicio et al. 2008; Padilla & Pugnaire 2009). For example,
311 the *Retama* canopy reduces radiation and temperature, resulting in lower seedling mortality
312 than in gaps (Cuesta et al. 2010). In addition, the canopy may help increase soil fertility, reduce
313 soil compaction and prevent seed desiccation (Verdú & García-Fayos 1996; Gómez-Aparicio
314 et al. 2005). In addition to these direct facilitative mechanisms, the *Retama* canopy can recruit
315 oak seedlings through indirect mechanisms such as reducing herb competition (Cuesta et al.
316 2010). Our observation of different numbers of pellet droppings between microhabitat types
317 suggest that the *Retama* canopy might also protect against herbivores (Gómez-Sánchez 2016).

318 *Retama* can also recruit mid- and late-successional woody species by attracting seed-
319 dispersing animals (Verdú & García-Fayos 1996). All recruited woody species found in this
320 study were zoochorous (Pemán et al. 2012). For the endozoochorous species, frugivorous birds
321 may use *Retama* shrubs as perches, which leads to seed rain beneath *Retama* (Verdú & García-
322 Fayos 1996; Aerts et al. 2006). For oaks and other nut-producing species, rodents and some
323 corvids such as the Eurosiberian jay and magpies are major dispersers (Gómez 2003; Pons &
324 Pausas 2007; Castro et al. 2017). Rodents prefer to disperse acorns to shrubs, but they consume
325 most cached acorns before seedling emergence (Perea et al. 2011). European jays (Gómez 2003,
326 Pons & Pausas 2007) and likely magpies (Castro et al. 2017) cache acorns not only in
327 woodlands but also in open areas in heterogeneous landscapes. We hypothesise that *Retama*
328 shrubs can act as singular landscape elements for acorn dispersal by corvids. Large shrubs such
329 as *Retama* may be safe landmarks (*sensu* Vander Wall 1990) for acorn caching and recovery
330 (Gómez 2003). Future studies are needed to corroborate the role of corvids and rodents in *Q.*
331 *ilex* colonisation of Mediterranean shrublands.

332 A major finding of our study is that differences in the recruitment of *Q. ilex* between
333 microhabitat types increased with decreasing environmental severity, which does not support
334 our first hypothesis related to the SGH (Bertness & Callaway 1994). Our results also contrast

335 with those reported by Armas et al. (2011) in which facilitation of herbs by *Retama* shrubs
336 increased with aridity. These differences might be explained by functional differences between
337 beneficiary species (Maestre et al. 2009). Consistent with our finding, Maestre & Cortina (2004)
338 reported that as aridity increases, facilitative interactions decrease between the nurse grass *Stipa*
339 *tenacissima* and the beneficiary shrub *Pistacia lentiscus*. Similarly, positive plant-plant
340 interactions have been predicted to be more intense and frequent at moderate rather than
341 extreme stress levels (Holmgren & Scheffer 2010). At the same time, our failure to observe the
342 facilitation-stress relationship predicted by the SGH may reflect the action of multiple stress
343 factors acting in different directions, or of changes in the competitive network of the beneficiary
344 plant species (Cuesta et al. 2010; Soliveres et al. 2011a, 2015).

345 ***The role of vegetation remnants as seed sources in Mediterranean shrublands***

346 Establishment of new plants depends not only on climate and the availability of suitable
347 microsites for seedling recruitment, but also on seed disperser activity, seed source abundance
348 and distance to seed sources (Schupp et al. 2010). Consistent with our second hypothesis, an
349 increase in *Q.ilex* recruitment in *Retama* shrublands was positively affected by potential acorn
350 availability (*i.e.* oak *SPP*). However, in contrast to our third hypothesis, we did not detect a
351 synergistic interaction between *SPP* and rainfall, even though both separately did enhance oak
352 recruitment. These results indicate that woodland patch preservation or creation should be
353 considered a key restoration measure for fostering colonisation of Mediterranean areas by oaks
354 (Rey-Benayas et al. 2008). Our observation of minimal recruitment in the driest shrublands
355 suggests as well that preserving vegetation remnants is especially critical in arid areas, where
356 recruitment is strongly limited by harsh conditions.

357 At the shrubland scale, recruitment of *Q. ilex* seedlings correlated with the total area of
358 oak remnant patches but not with their distance to *Retama* shrubs (Fig. 4). This indicates that,
359 on a local scale, *Q. ilex* recruitment to Mediterranean shrublands is limited more by the amount
360 of seeds and, probably, seed dispersal (McConkey & O'Farill, 2016) than by the distance to
361 seed sources. In contrast, Verdú & García-Fayos (1998) found that recruitment of the
362 endozoochorous shrub *Daphne gnidium* in an abandoned olive grove decreased with distance to
363 the seed source, although the proposed model failed to explain dispersion at distances >250 m.
364 The discrepancy between this study and our work may reflect differences in the disperser:
365 European jays disperse *Q. ilex* acorns at distances of 250-500 m (Gómez 2003; Sheffer et al.
366 2013), consistent with the mean distance between *Retama* shrubs and patches of oak remnants.

367 In contrast to our results for *Q. ilex*, we did not find any relationship between recruitment
368 frequency and *SPP* when we analysed all woody species together. This suggests different

369 dispersal constraints acting on different woody species colonising *Retama* shrublands.
370 *Juniperus oxycedrus*, *A. acutifolius* and *Q. ilex* were the three most abundant woody species
371 recruited in *Retama* shrublands. The fruits of *J. oxycedrus* and *A. acutifolius* are dispersed by
372 endozoochory (birds and small to medium size mammals) at distances longer than those
373 reported for *Q. ilex* (Alonso et al. 2004), suggesting a more complex dispersal pattern, perhaps
374 operating on coarser spatial scales (Spiegel & Nathan 2007; Escribano-Ávila et al. 2014). At
375 the landscape scale, woody species recruitment in *Retama* shrublands was not related to the
376 distance to large oak woodland remnants. This suggests that dispersal activity in *Retama*
377 shrublands occurs at local spatial scales (*i.e.* within the shrubland patch), highlighting the role
378 of nearby vegetation remnants in the colonisation of these areas. Long distance to woodland
379 remnants can limit the activity of dispersers (García et al. 2010), which may explain why we
380 found no recruitment in four shrublands located >3 km to the closest oak woodland remnant.

381

382 **CONCLUSIONS**

383 Recruitment of mid- and late-successional plant species in Mediterranean shrublands is a
384 challenging process, which outcome depends on the interaction among multiple factors, such
385 as the availability of suitable recruiting microsites and seed sources, abiotic constraints, and
386 interactions with herbivores, animal dispersers and other plant species. We show that *R.*
387 *sphaerocarpa* catalyses secondary succession in Mediterranean shrublands (Maestre et al.
388 2001; Gómez-Aparicio et al. 2004) by facilitating the recruitment of mid- and late-successional
389 forest woody species under its canopy. Contrary to our expectations and the SGH predictions,
390 the facilitative efficacy of *Retama* was lower at the harshest part of our environmental gradient,
391 likely reflecting the simultaneous increase in aridity and herbivory. We also highlight the
392 importance of oak woodland remnants as seed sources within or close to shrublands. On a local
393 scale, oak recruitment is limited more by the extent of forest remnants than by the distance
394 separating these remnants from *Retama* shrubs.

395 The results of this study have practical implications for restoring Mediterranean
396 shrublands and abandoned cropland. They suggest that using pre-existing pioneer shrubs as
397 nurse plants (Gómez-Aparicio 2009; Cuesta et al. 2010) may enhance the success of active
398 restoration measures, such as direct seeding or planting of seedlings of mid- and late-
399 successional trees and shrubs. In addition, our results suggest that preserving woodland
400 remnants or creating islets of late successional forest species may accelerate secondary
401 succession in these areas (passive restoration) by acting as seed sources and providing habitat
402 for dispersers (Rey Benayas et al. 2008).

403

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588

589 **Additional Supporting Information**

590 Appendix S1. Additional information on the 29 surveyed *Retama* shrubland patches.

591 Appendix S2. Comparison of models to assess the effect of explanatory variables on the
592 recruitment of woody species in *Retama* shrublands

593

594

595 **TABLES**

596 **Table 1.** Mean value and 95% confident intervals for each estimated parameter in the selected
 597 models for the recruitment of all woody species or only of *Quercus ilex* in *Retama* shrublands.
 598 For both models, “under *Retama*” is the reference level for the microhabitat factor.

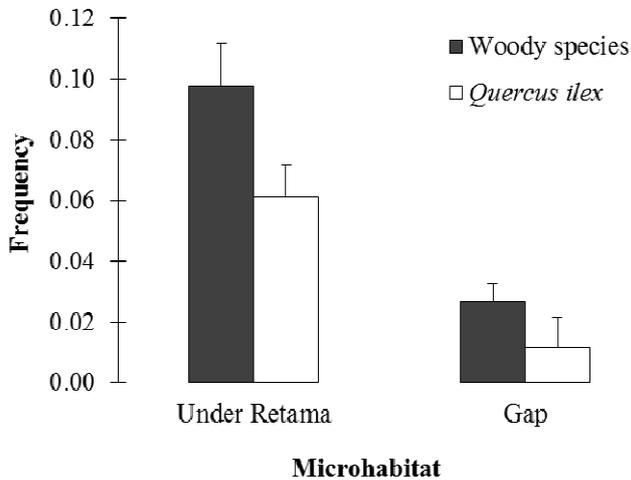
Selected model	All woody species		<i>Quercus ilex</i>	
	Microhabitat × rainfall + <i>SPP</i> _{oak}		Microhabitat + rainfall	
<i>Parameter</i>	<i>Mean value</i>	<i>Confidence interval</i>	<i>Mean value</i>	<i>Confidence interval</i>
Intercept [“under <i>Retama</i> ”]	-2.79	[-3.04, -2.54]	-11.97	[-13.8, -10.14]
Microhabitat [“gap”]	-1.59	[-1.92, -1.36]	-5.95	[-7.27, -4.63]
Rainfall	0.59	[0.34, 0.84]	2.13	[1.14, 3.12]
<i>SPP</i>	-	-	0.64	[0.23, 1.05]
Rainfall × Microhabitat [“gap”]	-	-	0.57	[0.17, 0.97]

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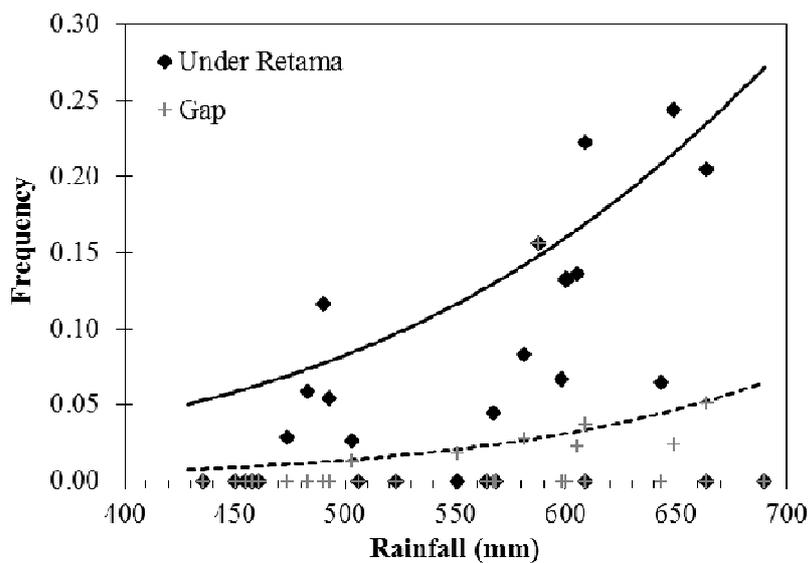
600

601 **FIGURES**

602 **Figure 1.** Frequency of occurrence (recruitment) of all four woody species or of *Q. ilex* under
603 the *Retama* canopy and in gaps in shrublands of the central part of the Iberian Peninsula. Bars
604 indicate standard errors.

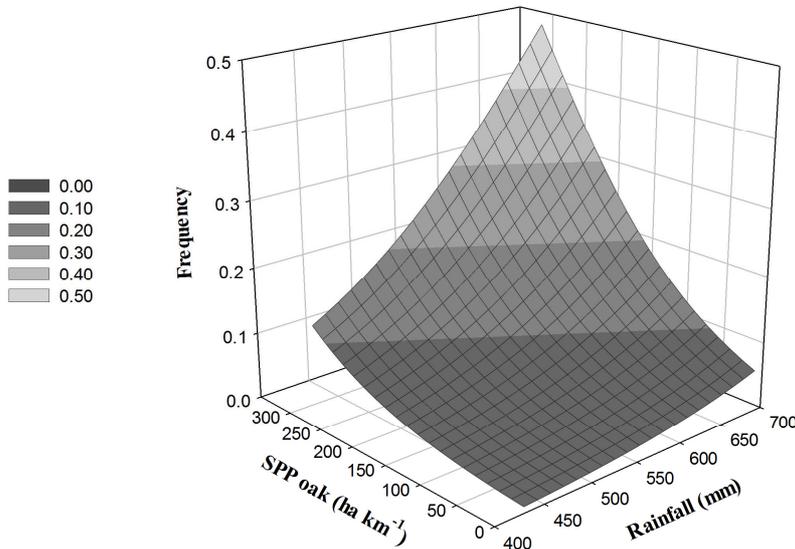


605 **Figure 2.** Relationship between recruitment of *Q. ilex* under the *Retama* canopy and in gaps in
606 the central part of the Iberian Peninsula and rainfall. The black solid and dashed lines depict
607 predicted recruitment under *Retama* canopy and in gaps, respectively. Recruitment was
608 predicted by the best model parameters using a fixing mean *Q. ilex* seed pressure potential
609 ($SPP_{oak} = 29.84 \text{ ha km}^{-1}$). Points show observed recruitment under *Retama* canopy (black
610 diamond) and in gaps (grey cross) for each surveyed shrubland.
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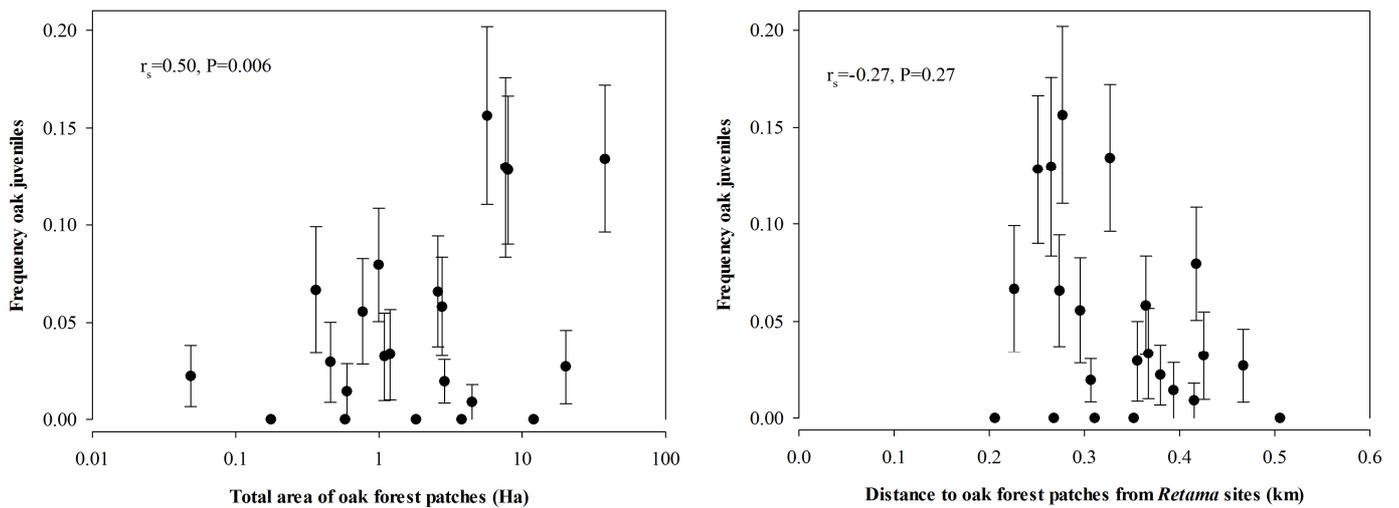
615 **Figure 3.** Predicted *Q. ilex* recruitment under the *Retama* canopy as a function of rainfall and
 616 oak seed pressure potential in surveyed *Retama* shrublands in the central part of the Iberian
 617 Peninsula.



618
 619

620 **Figure 4.** Frequency of *Q. ilex* seedlings in relation to the two components of *Q. ilex* seed
 621 pressure potential (SPP_{oak}): (a) total area of oak forest patches at distances < 0.5 km from
 622 *Retama* sites, and (b) mean distance of *Retama* sites to oak forest patches located within an area
 623 of a 0.5-km radius.

624



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