Universidad de Alcalá
BIBLIOTECA

Document downloaded from the institutional repository of the University of Alcala: http://dspace.uah.es/dspace/

This is a peer reviewed version of the following article:

Andivia, E. et al., 2017. Multiscale assessment of woody species recruitment in Mediterranean shrublands: facilitation and beyond. *Journal of Vegetation Science*, 28(3), pp.639–648.

Which has been published in final form at http://dx.doi.org/10.1111/jvs.12520

(Article begins on next page)

1   **Multiscale assessment of woody species recruitment in Mediterranean shrublands:**

2   **facilitation and beyond**

3

4   Enrique Andivia, Pedro Villar-Salvador, Liliana Tovar, Sonia Rabasa & José M. Rey Benayas

5

6   **List of authors**

7   Andivia, E. (Corresponding author, e.andivia@gmail.com)[1]

8   Villar-Salvador, P. (pedro.villar@uah.es)[1]

9   Tovar, L. (lilotovar@hotmail.com)[1]

10   Rabasa, S. (sonia.rabasa@gmail.com)[2]

11   Rey Benayas, J.M. (josem.rey@uah.es)[1]

12

13   [1] Forest Ecology and Restoration Group, Departamento de Ciencias de la Vida, Edificio de

14   Ciencias, Universidad de Alcalá, 28805 Alcalá de Henares, Spain

15   [2] Museo Nacional de Ciencias Naturales-CSIC, C/Serrano 115 bis, 28006 Madrid, Spain

16

17   **Printed journal page estimate:** 10 pages: 6,597 words (8.2 pages) + Tables (0.3 pages) +

18   Figures (1.5 pages)

19

20   **Nomenclature:** Castroviejo et al. (1986–2010)

21

22   **Running head:** Multiscale assessment of plant recruitment

23

24

25

26

27

28

29

30

31

32

33

34

ABSTRACT

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

Location: Centre of the Iberian Peninsula.

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

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

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

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

INTRODUCTION

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

Whether plant interactions tend to be facilitative or competitive depends on the environmental context. Bertness & Callaway (1994) proposed the *Stress Gradient Hypothesis* (SGH), which predicts that facilitative interactions become more important than competitive ones as abiotic stress and herbivory increase. While the SGH has substantial empirical support (Callaway et al. 2002; Gómez-Aparicio et al. 2009; He et al. 2013 and references therein), some studies suggest that facilitative interactions do not necessarily increase monotonically with environmental stress. Instead, competition can become the dominant plant interaction under very stressful conditions (Maestre & Cortina 2004; Maestre et al. 2005; Koyama & Tsuyuzaki 2013). Furthermore, herbivore pressure might shift the direction of plant-plant interactions along environmental gradients (Soliveres et al. 2011b; Louthan et al. 2014). It seems likely that facilitative interactions also depend on functional characteristics of the nurse and beneficiary plants (Padilla & Pugnaire 2009; Schöb et al. 2013). For example, Maestre et al. (2009) proposed that facilitation would be more likely when the nurse plant is competitive, the beneficiary plant is stress-tolerant, and the stressors are drought or extreme temperature. Since the suite of nurse and beneficiary plants usually shifts as one moves along the environmental gradient (Callaway et al. 2002; Holzapfel et al. 2006; Armas et al. 2011), it becomes difficult 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 (40º12´-40º49´N, 3º20´-4º18´W) and

152 covers a surface area of *ca.* 6,000 km^2. 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 ºC. 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

6

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

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 × rainfall × *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 (± 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 × rainfall × *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 ± SE,

298   15.6 ± 0.33) than under *Retama* canopy (11.1 ± 0.24; Z = 13.28, p < 0.001).

299

300   **DISCUSSION**

9

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 zoochorus (Pemán et al. 2012). For the endozoochorus 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   endozoochorus 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

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

CONCLUSIONS

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

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

414 **REFERENCES**

415 Aerts, R., November, E., Van der Borght, I., Behailu, M., Hermy, M. & Muys, B. 2006. Effects
416   of pioneer shrubs on the recruitment of the fleshy-fruited tree *Olea europea* ssp.
417   *cuspidata* in Afromontane savana. *Applied Vegetation Science* 9: 117-126.

418 Allegrezza, M., Corti, G., Cocco, S., Pesaresi, S., Chirico, G.B., Saracino, A. & Bonanomi, G.
419   2016. Microclimate buffering and fertility island formation during *Juniperus communis*
420   ontogenesis modulate competition–facilitation balance. *Journal of Vegetation Science*
421   27: 616-627.

422 Alonso, C., Garrido, J.L. & Herrera, C.M. 2004. Investigaciones sobre plantas y animales en
423   las sierras de Cazorla, Segura y Las Villas: 25 años de estudios por el Consejo Superior
424   de Investigaciones Científicas (CSIC), Junta de Andalucía, Sevilla, ES.

425 Armas, C., Rodríguez-Echeverría, S. & Pugnaire, F.I. 2011. A field test of the stress-gradient
426   hypothesis along an aridity gradient. *Journal of Vegetation Science* 22: 818–827.

427 Benavides, R., Escudero, A., Coll, L., Ferrandis, P., Ogaya, R., Gouriveau, F., Peñuelas, P. &
428   Valladares, F. 2016. Recruitment patterns of four tree species along elevation gradients
429   in Mediterranean mountains: Not only climate matters. *Forest Ecology and*
430   *Management* 360: 287–296.

431 Bertness, M.D. & Callaway, R. 1994. Positive interactions in communities. *Trends in Ecology*
432   *and Evolution* 9: 192-194.

433 Burnham, K.P. & Anderson, D.R. 2002. Model Selection and Multimodel Inference: A
434   Practical Information-Theoretic Approach. Springer-Verlag, New York, USA.

435 Callaway, R.M., Brooker, R.W., Choler, P., Kikvidze, Z., Lortie, C.J., Michalet, R., Paolini, L.,
436   Pugnaire, F.I., Newingham, B., Aschehoug, E.T., Armas, C., Kikodze, D. & Cook, B.J.
437   2002. Positive interactions among alpine plants increase with stress. *Nature* 417: 844–
438   848.

439 Castro, J., Molina-Morales, M., Leverkus, A.B., Martínez-Baroja, L., Pérez-Camacho,
440   L., Villar-Salvador, P., Rebollo, S. & Rey-Benayas, J.M. 2017. Effective nut dispersal
441   by magpies (Pica pica L.) in a Mediterranean agroecosystem. Oecologia *under review*.

442 Cuesta, B., Villar-Salvador, P., Puértolas, J., Rey Benayas, J.M. & Michalet, R. 2010.
443   Facilitation of *Quercus ilex* in Mediterranean shrubland is explained by both direct and
444   indirect interactions mediated by herbs. *Journal of Ecology* 98: 687-696.

445 Escribano-Ávila, G., Calviño-Cancela, M., Pías, B., Virgós, E., Valladares, F. & Escudero, A.
446   2014. Diverse guilds provide complementary dispersal services in a woodland
447   expansion process after land abandonment. *Journal of Applied Ecology* 51: 1701-1711.

García, D. & Houle, G. 2005. Fine-scale spatial patterns of recruitment in red oak (*Quercus rubra*): What matters most, abiotic or biotic factors? *Ecoscience* 12: 223-235.

García, D., Zamora, R. & Amico, G.C. 2010. Birds as suppliers of seed dispersal in temperate ecosystems: conservation guidelines from real-world landscapes. *Conservation Biology* 24: 1070-1079.

Gómez, J.M. 2003. Spatial patterns in long-distance dispersal of *Quercus ilex* acorns by jays in a heterogeneous landscape. *Ecography* 26: 573-584.

Gómez-Aparicio, L., Zamora, R., Gómez, J., Castro, J. & Baraza, E. 2004. Applying plant facilitation to forest restoration: a meta-analysis of the use of shrubs as nurse plants. *Ecological Applications* 14: 1128–1138.

Gómez-Aparicio, L., Gómez, J.M., Zamora, R. & Boettingerm, J. 2005. Canopy vs. soil effects of shrubs facilitating tree seedlings in Mediterranean montane ecosystems. *Journal of Vegetation Science* 16: 191–198.

Gómez-Aparicio, L., Zamora, R., Castro, J. & Hódar, J.A. 2008. Facilitation of tree saplings by nurse plants: microhabitat amelioration or protection against herbivores. *Journal of Vegetation Science* 19: 161-172.

Gómez-Aparicio, L. 2009. The role of plant interaction in the restoration of degraded ecosystems: a meta-analysis across lifeforms and ecosystems. *Journal of Ecology* 97: 1202–1214.

Gómez-Aparicio, L., Zavala, M.A., Bonet, F.J. & Zamora, R. 2009. Are pine plantations valid tools for restoring Mediterranean forests? An assessment along abiotic and biotic gradients. *Ecological Applications* 19: 2124–2141.

Gómez-Sánchez, D. 2016. La capacidad de colonización de matorrales de retama (*Retama sphaerocarpa*) y los factores que lo regulan difieren en dos *Quercus* mediterráneos. MSc Thesis. Universidad de Alcalá.

He, Q., Bertness, M.D. & Altieri, A.H. 2013. Global shifts towards positive species interactions with increasing environmental stress. *Ecology letters* 16:695–706.

Holmgren, M. & Scheffer, M. 2010. Strong facilitation in mild environments: the stress gradient hypothesis revisited. *Journal of Ecology* 98: 1269-1275.

Holzapfel, C., Tielbörger, K., Parag, H.A., Kigel, J. & Stemberg, M. 2006. Annual plant-shrub interactions along an aridity gradient. *Basic and Applied Ecology* 7: 268–279.

Jordano, P., García, C., Godoy, J.A. & García-Castaño, J.L. 2007. Differential contribution of frugivores to complex seed dispersal patterns. *Proceedings of the National Academy of Sciences* 104: 3278–3282.

482   Koyama, A. & Tsuyuzaki, S. 2013. Facilitation by tussock-forming species on seedling
483   establishment collapses in an extreme drought year in a post-mined Sphagnum peatland.
484   *Journal of Vegetation Science* 24: 473–483.

485

486   Lara-Romero, C., de la Cruz, M., Escribano-Ávila, G., García-Fernández, A. & Iriondo, J.M.
487   2016. What causes conspecific plant aggregation? Disentangling the role of dispersal,
488   habitat heterogeneity and plant – plant interactions. *Oikos* 125: 1304-1313.

489   Louthan, A.M., Doak, D.F., Doheen, J.R., Palmer, T.M. & Pringle, R.M. 2014. Mechanisms of
490   plant–plant interactions: concealment from herbivores is more important than abiotic-
491   stress mediation in an African savannah. *Proceedings of the Royal Society B* 281:
492   20132647.

493   MacDougall, A.S., Duwyn, A. & Jones, N.T. 2015. Consumer-based limitations drive oak
494   recruitment failure. *Ecology* 91: 2092–2099.

495   Maestre, F.T. & Cortina, J. 2004. Do positive interactions increase with abiotic stress? A test
496   from a semi-arid steppe. *Proceedings of the Royal Society of London. Series B* 271: 331–
497   333.

498   Maestre, F.T., Bautista, S., Cortina, J. & Bellot, J. 2001. Potential for using facilitation by
499   grasses to establish shrubs on a semiarid degraded steppe. *Ecological Applications* 11:
500   1641–1655.

501   Maestre, F.T., Valladares, F. & Reynolds, J.F. 2005. Is the change of plant-plant interactions
502   with abiotic stress predictable? A meta-analysis of field results in arid environments.
503   *Journal of Ecology* 93: 748–757.

504   Maestre, F.T., Callaway, R.M., Valladares, F. & Lortie, C.J. 2009. Refining the stress gradient
505   hypothesis for competition and facilitation in plant communities. *Journal of Ecology*
506   97: 199-205.

507   Marques, F.F.C., Buckland, S.T., Goffin, D., Dixon, C.E., Borchers, D.L., Mayle, B.A. &
508   Peace, A.J. 2001. Estimating deer abundance from line transect surveys of dung: sika
509   deer in southern Scotland. *Journal of Applied Ecology* 38: 349–363.

510   McConkey, K.R. & O'Farrill, G. 2016. Loss of seed dispersal before the loss of seed dispersers.
511   *Biological Conservation* 201: 38–49.

512

513   Nakagawa, S. & Schielzeth, H. 2013. A general and simple method for obtaining R^2 from
514   generalized linear mixed-effects models. *Methods in Ecology and Evolution* 4: 132-142.

515   Ninyerola, M., Pons, X. & Roure, J.M. 2005. Atlas Climático Digital de la Península Ibérica.
516   Metodología y aplicaciones en bioclimatología y geobotánica. Universidad Autónoma
517   de Barcelona, Bellaterra, ES.

518   Padilla, F.M. & Pugnaire, F.I. 2009. Species identity and water availability determine
519   establishment success under the canopy of *Retama sphaerocarpa* shrubs in a dry
520   environment. *Restoration Ecology* 17: 900-907.

521   Pausas, J.G., Bonet, A., Maestre, F.T. & Climent, A. 2006. The role of the perch effect on the
522   nucleation process in Mediterranean semi-arid old fields. *Acta Oecologica* 29: 346-352.

523   Pemán, J., Navarro-Cerrillo, R.M., Nicolás, J.L., Prada, M.A. & Serrada, R. 2012. Producción
524   y Manejo de Semillas y Plantas Forestales. Vol. 1 and 2. Organismo Autónomo Parques
525   Nacionales. Serie Forestal. Madrid (Spain)

526   Perea, R., San Miguel, A., Gil, L. 2011. Acorn dispersal by rodents: The importance of re-
527   dispersal and distance to shelter. *Basic and Applied Ecology* 12: 432-439.

528   Pons, J. & Pausas, J.G. 2007. Acorn dispersal estimated by radio-tracking. *Oecologia* 153: 903-
529   911.

530   Puerta-Piñero, C., Gómez, J.M. & Valladares F. 2007. Irradiance and oak seedling survival
531   and growth in a heterogeneous environment. *Forest Ecology and Management* 242:
532   462-469.

533   Pueyo, Y. & Alados, C.L. 2007. Effects of fragmentation, abiotic factors and land use on
534   vegetation recovery in a semi-arid Mediterranean area. *Basic and Applied Ecology* 8:
535   158–170.

536   Pugnaire, F., Haase, P. & Puigdefábregas, J. 1996. Facilitation between higher plant species in
537   a semi-arid environment. *Ecology* 77: 1420–1426.

538

539   Rey Benayas, J.M., Navarro, J., Espigares, T., Nicolau, J.M. & Zavala, M.A. 2005. Effects of
540   artificial shading and weed mowing in reforestation of Mediterranean abandoned
541   cropland with contrasting *Quercus* species. *Forest Ecology and Management* 212: 302–
542   314.

543   Rey Benayas, J.M., Bullock, J.M. & Newton, A.C. 2008. Creating woodland islets to reconcile
544   ecological restoration, conservation, and agricultural land use. *Frontiers in Ecology and
545   the Environment* 6: 329–336.

546   Rey Benayas, J.M., Martínez, L., Pérez-Camacho, L., Villar-Salvador, P. & Holl, K. 2015.
547   Predation and aridity slow down the spread of 21 year old planted woodland islets in
548   restored Mediterranean farmland. *New Forests* 46: 841-853.

549   Rolo, V., Plieninger, T. & Moreno, G. 2013. Facilitation of holm oak recruitment through two

550   contrasted shrubs species in Mediterranean grazed woodlands. *Journal of Vegetation*

551   *Science* 24: 344-355.

552   Saldaña, A., García-Salgado, G. & Rebollo, S. 2007. European rabbit (*Oryctolagus cuniculus*

553   L.) abundance at a regional scale: controlling factors. In Bunce, R. G. H. et al. 25 years

554   Landscape Ecology: Scientific Principles in Practice. *Proceedings of the 7th IALE*

555   *World Congress*. Wageningen, The Netherlands: IALE Publication series 4: 375–376.

556   Santos, T., Tellería. J.L. & Carbonell, R. 2002. Bird conservation in fragmented Mediterranean

557   forests of Spain: Effects of geographical location, habitat and landscape degradation.

558   *Biological Conservation* 105:113–125.

559   Schöb, C., Armas, C., Guler, M., Prieto, I. & Pugnaire, F.I. 2013. Variability in functional traits

560   mediates plant interactions along stress gradients. *Journal of Ecology* 101: 753–762.

561   Schupp, E.W., Jordano, P. & Gómez, J.M. 2010. Seed dispersal effectiveness revisited: a

562   conceptual review. *New Phytologist* 188: 333-353.

563   Sheffer, E., Canham, C.D., Kigel, J. & Perevolotsky, P. 2013. Landscape-scale density-

564   dependent recruitment of oaks in planted forests: more is not always better. *Ecology* 94:

565   1718-1728.

566   Soliveres, S., Eldridge, D.J., Maestre, F.T., Bowker, M.A., Tighe, M. & Escudero, A. 2011a.

567   Microhabitat amelioration and reduced competition among understorey plants as drivers

568   of facilitation across environmental gradients: towards a unifying framework.

569   *Perspectives in Plant Ecology, Evolution and Systematics* 13: 247–258.

570   Soliveres, S., García-Palacios, P., Castillo-Monroy, A.P., Maestre, F.T., Escudero, A. &

571   Valladares, F. 2011b. Temporal dynamics of herbivory and water availability

572   interactively modulate the outcome of a grass–shrub interaction in a semi-arid

573   ecosystem. *Oikos* 120: 710-719.

574   Soliveres, S., Smit, C. & Maestre, F.T. 2015. Moving forward on facilitation research: response

575   to changing environments and effects on the diversity, functioning and evolution of

576   plant communities. *Biological Reviews* 90: 297-313.

577   Spiegel, O. & Nathan, R. 2007. Incorporating dispersal distance into the disperser effectiveness

578   framework: frugivorous birds provide complementary dispersal to plants in a patchy

579   environment. *Ecology Letters* 10: 718–728.

580   Vander Wall, S.B. 1990. Food hoarding by animals. Chicago University Press, Chicago, USA.

581   Verdú, M. & García-Fayos, P. 1996. Nucleation processes in a Mediterranean bird dispersed

582   plant. *Functional Ecology* 10: 275-280.

583   Verdú, M. & García-Fayos, P. 1998. Old-field colonization by *Daphne gnidium* seedling
584   distribution and spatial dependence at different scales. *Journal of Vegetation Science* 9:
585   713-718.
586   Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. 2009. Mixed effects models
587   and extensions in ecology with R. Springer, Heidelberg, DE.
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

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.

|	**All woody species**		***Quercus ilex***	
Selected model	Microhabitat × rainfall + *SPP*$_{oak}$		Microhabitat + rainfall	
Parameter	*Mean value*	*Confidence interval*	*Mean value*	*Confidence interval*
Intercept ["under *Retama*"]	-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]
SPP	-	-	0.64	[0.23, 1.05]
Rainfall × Microhabitat ["gap"]	-	-	0.57	[0.17, 0.97]

599

600

FIGURES

Figure 1. Frequency of occurrence (recruitment) of all four woody species or of *Q. ilex* under

the *Retama* canopy and in gaps in shrublands of the central part of the Iberian Peninsula. Bars

indicate standard errors.
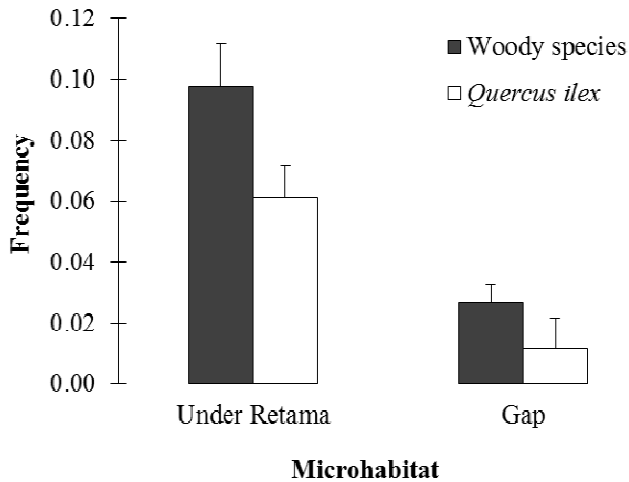
Figure 2. Relationship between recruitment of *Q. ilex* under the *Retama* canopy and in gaps in

the central part of the Iberian Peninsula and rainfall. The black solid and dashed lines depict

predicted recruitment under *Retama* canopy and in gaps, respectively. Recruitment was

predicted by the best model parameters using a fixing mean *Q. ilex* seed pressure potential

(SPP_{oak} = 29.84 ha km^{-1}). Points show observed recruitment under *Retama* canopy (black

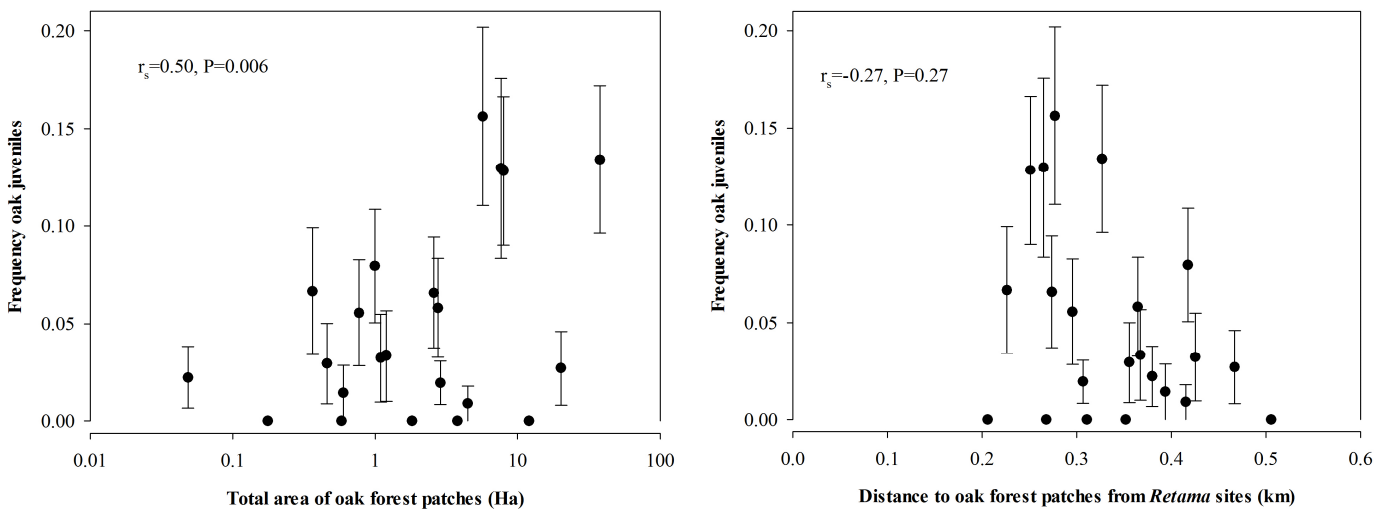diamond) and in gaps (grey cross) for each surveyed shrubland.
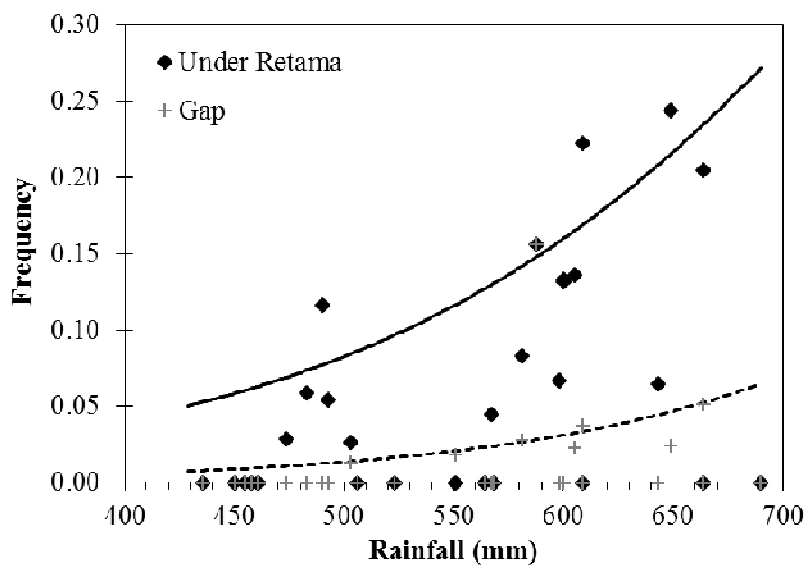
615 **Figure 3.** Predicted *Q. ilex* recruitment under the *Retama* canopy as a function of rainfall and
616 oak seed pressure potential in surveyed *Retama* shrublands in the central part of the Iberian
617 Peninsula.
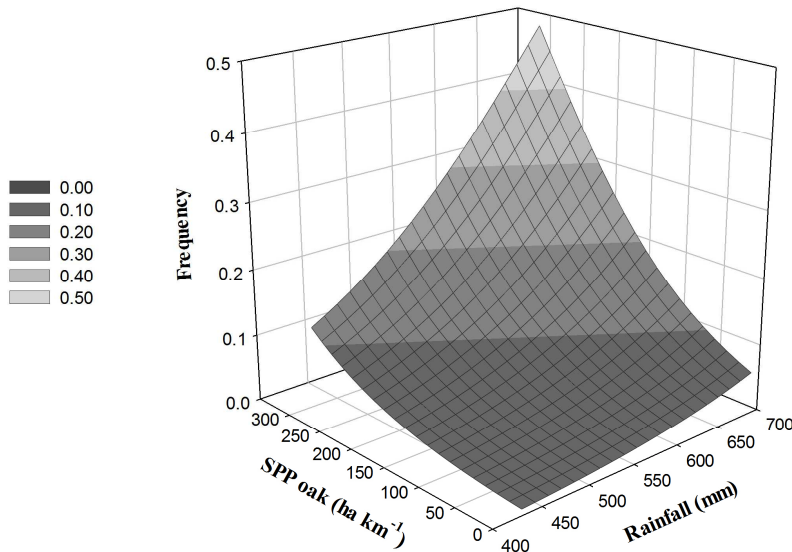
618
619
620 **Figure 4.** Frequency of *Q. ilex* seedlings in relation to the two components of *Q. ilex* seed
621 pressure potential (SPP_{oak}): (a) total area of oak forest patches at distances < 0.5 km from
622 *Retama* sites, and (b) mean distance of *Retama* sites to oak forest patches located within an area
623 of a 0.5-km radius.

624

625