

15 **Highlights**

- 16 • Forest fragmentation reduces tree-to-tree competition for water
17 resources.
- 18 • Reduced competition entails enhanced acorn production at small
19 forest fragments.
- 20 • Local conditions, like fragmentation, may override climatic
21 effects on acorn crops.
- 22 • Positive effects of fragmentation need to be scaled up temporally
23 and spatially.

24

25 **Abstract**

26 The effects of fragmentation on acorn production should be mediated by their impacts
27 on the physiological status of oaks during seed development particularly in water-
28 limited systems, such as Mediterranean forests. The creation of forests edges reduces
29 tree-to-tree competition, which may in turn temper water shortage during summer and,
30 as a result, enhance acorn production. To test these two hypotheses we monitored acorn
31 production and predawn water potential during the 2012-2014 period in two holm oak
32 (*Quercus ilex*) forest archipelagos of the Iberian Peninsula.

33 Acorn production and fragmentation effects did not differ between localities despite of
34 their contrasting climatic conditions (accumulated water deficit from April to August
35 was a 60% higher in the South). In general, forest interiors showed a high proportion of
36 non-producing trees (~50%) while trees at small forest fragments showed high acorn
37 crops (acorn score ≥ 3 , ~40% of studied trees). Our results confirmed the expectation
38 that intraspecific competition in small forest fragments was reduced, which alleviated
39 summer water shortage of the trees studied. This reduced water stress entailed an
40 increased acorn production. Overall, our results show that local processes such as
41 fragmentation may counteract climatic differences among localities and could even
42 override the impacts of increased aridity on acorn crops.

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44 *Key words:* *Quercus ilex*, holm oak, acorn production, forest fragmentation,
45 competition, water stress.

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48 **1. Introduction**

49 Habitat loss, resource overexploitation and inadequate management are the main drivers
50 of forest degradation in the Mediterranean Basin, and their impacts are expected to be
51 intensified by climate change (Sala et al., 2000; Valladares et al., 2014). On one hand,
52 summer water availability is one of the main limiting factors for plant growth in
53 Mediterranean ecosystems (Flexas et al., 2014) and future scenarios of climate change
54 predict an increase in drought intensity in the coming decades (IPCC, 2013). On the
55 other hand, forest management can have pervasive effects on forest regeneration, which
56 is driven by a complex interplay between habitat availability, isolation and edge effects
57 (Valladares et al., 2014). Thus, knowledge on the combined effects of these different
58 drivers is urgently needed in order to evaluate the actual vulnerability of Mediterranean
59 forests to global environmental change (Doblas-Miranda, Martínez-Vilalta et al. 2015).

60 Holm oaks (*Quercus ilex ssp. ballota*) are an ideal study system for addressing the
61 combined effect of management and increased aridity on forest regeneration. Most holm
62 oak forests are located in anthropogenic landscapes and either an increased summer
63 drought, a given management regime or both may compromise holm oak reproduction
64 (Espelta, Riba et al. 1995; Pérez-Ramos, Ourcival et al. 2010; Misson, Degueldre et al.
65 2011). Holm oaks are considered as tolerant to severe water shortage due to their deep
66 root system (Moreno et al., 2005), to their ability to rapidly recover from tissue damage
67 caused by the summer drought, and to their resprouting capability (Tognetti et al.,
68 1998). However, when compared to other Mediterranean species, they are quite
69 vulnerable to xylem cavitation and they actually function close to their point of
70 hydraulic failure during the summer months (Martínez-Vilalta et al., 2002; Quero et al.,
71 2011). In fact, high defoliation rates and dieback episodes have been registered after
72 extreme drought events in holm oak forests (Peñuelas et al., 2000). Fruit production has

73 been also linked to water availability during spring and summer months, despite
74 complex masting processes that derive in high inter-annual variability in acorn crops. In
75 general, moister springs involve higher investment on female flowers, which entails
76 enhanced acorn production, but a very severe summer drought can lead to high abortion
77 rates and constrain final acorn production (Ogaya and Peñuelas, 2007; Espelta et al.,
78 2008; Pérez-Ramos et al., 2010; Misson et al., 2011; Rodríguez-Calcerrada et al., 2011;
79 Sánchez-Humanes and Espelta, 2011; Fernández-Martínez et al., 2012; García-Mozo et
80 al., 2012). Thus, the increased aridity expected under a climate change scenario may
81 hamper holm oak reproduction. In fact, rainfall exclusion experiments have shown that
82 a 15-30% reduction in summer rainfall, which are similar to that expected by the end of
83 the century for the Mediterranean basin (AEMET 2009), can significantly constrain
84 acorn production (Pérez-Ramos, Ourcival et al. 2010; Rodríguez-Calcerrada, Pérez-
85 Ramos et al. 2011; Sánchez-Humanes and Espelta 2011; IPCC 2013).

86 Concomitantly to climatic conditions, management practices such as tree coppicing, tree
87 thinning and shrub clearance, or fragmentation can affect water availability of
88 individual holm oak trees (Terradas, 1999; Moreno and Cubera, 2008; Campos et al.,
89 2013). In dense multi-stemmed stands, increased competition for resources limits oak
90 growth and sexual reproduction (Rodríguez-Calcerrada et al., 2011; Sánchez-Humanes
91 and Espelta, 2011). Selective thinning of the weaker stems has been proposed as a
92 management strategy for natural restocking since it stimulates tree growth (e.g. Retana
93 et al., 1992; Mayor and Roda, 1993). However, thinning effects on acorn production
94 seem minor (Rodríguez-Calcerrada et al., 2011; Sánchez-Humanes and Espelta, 2011).
95 Another way of buffering the negative effects of summer drought on holm oak water
96 status is tree clearance (Moreno and Cubera, 2008). For instance, trees in savanna-like
97 woodlands (dehesas and montados) show acorn crops one order of magnitude higher

98 than those found in forest habitats (Pulido and Díaz, 2005). Therefore, management
99 effects on holm oaks acorn production seems to be driven by local changes in
100 intraspecific competition, which modulates the negative effects of summer drought.

101 Among management regimes, fragmentation is widely spread in the Iberian Peninsula,
102 where agricultural intensification has led to the replacement of large continuous holm
103 oak forests by archipelagos of isolated fragments embedded in a cereal cropland matrix
104 (Santos and Tellería 1998). Forest fragmentation has well-known negative effects on
105 acorn dispersal and seedling recruitment (Santos and Tellería 1997; Morán-López,
106 Fernández et al. 2015). However, the creation of forest edges may entail lower
107 intraspecific competition, and thus could temper oak water stress during summer
108 (Moreno and Cubera 2008). If this was the case, forest fragmentation could have
109 positive effects on acorn production (Carevic, Fernández et al. 2010). To test this
110 hypothesis we (1) monitored acorn crops in two holm oak forest archipelagos of the
111 Iberian Peninsula during three consecutive years (2012-2014), and (2) evaluated
112 whether fragmentation effects on acorn production depended on changes in intraspecific
113 competition for water resources during summer.

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115 **2. Material and methods**

116 2.1 Study area

117 The two holm oak archipelagos studied are located in the northern and southern
118 Plateaux of the Iberian Peninsula (Fig. A1) — an extensive treeless agricultural region
119 where cereal cultivation has reduced the original forest cover to about a 7-8 % of the
120 land area (Santos and Tellería 1998). Besides, past exploitation for firewood has led to a
121 coppice structure of large forests and small fragments.

122 Fieldwork in the southern plateau was carried out in the vicinity of Quintanar de la
123 Orden (39°35'N, 02°56'W; 870 m.a.s.l.) within an area of 38,500 ha. The dominant tree
124 is the holm oak (121 stems per ha) with the understory composed by shrubby Kermes
125 oak *Q. coccifera* and shrub species typical from xeric Mesomediterranean localities (e.g.
126 *Rhamnus lycioides*, *R. alaternus*, *Cistus ladanifer*, *Asparagus acutifolius*). Average
127 canopy radius of holm oaks in Quintanar de la Orden is 3.02 m (± 0.28). Annual
128 precipitation and mean temperature are 421 mm and 14°C, respectively.

129 Fieldwork in the northern plateau was undertaken in an area of 66,500 ha around Lerma
130 (41°58'N, 03°52'W; 930m asl). The dominant tree is also holm oak (424 stems per ha),
131 with isolated Lusitanian oak *Q. faginea* and Spanish juniper *Juniperus thurifera* and
132 understory shrubs typical from wetter and cooler Supramediterranean localities (e.g.
133 *Cistus laurifolius*, *Genista scorpius*, *Thymus zygis*). Average canopy radius of holm
134 oaks in Lerma is 2.26 m (± 0.13). Annual precipitation is 567 mm and annual mean
135 temperature is 11 °C. In both localities, the dominant soils are classified as Cambisols
136 (calcics) (WRB, 2007) with 17% sand, 39% silt and 44% clay for the southern region
137 and 11% sand, 42% silt and 47% clay for the northern region (Flores-Rentería et al.
138 2015).

139 2.2 Experimental design and tree measurements

140 In each locality we selected three large forest fragments (> 100 ha), in which we defined
141 forest interiors and edges. Edges were defined as forest areas closer than 60 m from the
142 cultivated border, being interiors the remaining forest (García et al. 1998). Edge plots
143 were selected along long straight borders to avoid influences of border geometry on
144 edge effects (Fernández et al. 2002). Besides, we selected 10 and 11 small forest
145 fragments in the northern and southern locality, respectively (mean \pm SE 0.047 \pm 0.031

146 and 0.031 ± 0.024 ha in the south and north, respectively). Hence, three fragmentation
147 categories were defined — forest interior, forest edge and small fragments — in each
148 locality — northern and southern plateaus.

149 In a pilot study carried out in 2011 we observed that site-specific variability on acorn
150 production stabilized at sample sizes of about 75 (25 trees per fragmentation level).
151 Therefore, we established a sampling effort of 30 randomly selected trees per
152 fragmentation level and locality (total sample size = 180). During 2012-2013-2014 crop
153 size of focal trees was visually estimated using a semi-quantitative scale (“acorn score”)
154 with five classes- 0 (no acorns), 1 (<10% of the canopy covered by acorns), 2 (10-
155 50%), 3 (50-90%) and 4 (>90%) (Díaz et al. 2011; Koenig et al. 2013). The large
156 number of trees sampled forced the use of visual surveys, which are less time-
157 consuming than seed traps and are highly correlated with quantitative measures (Koenig
158 et al. 2013; Carevic et al., 2014b).

159 In mid-August 2012 and 2013 we measured predawn water potential (Ψ_{pd}) of focal
160 trees. In each locality, we sampled 90 focal trees (30 per fragmentation level) along six
161 days. On average, 15 trees were measured each day following a randomized factorial
162 design with respect to fragmentation category. Measurements were conducted on two
163 twigs per tree and then averaged. Excised twigs were collected into sealable plastic
164 bags, with air saturated of humidity and CO_2 , and kept refrigerated and in dark (Pérez-
165 Harguindeguy et al., 2013). All measurements were performed by means of a
166 Scholander chamber (Scholander et al., 1965).

167 In each focal tree we estimated intraspecific competition as the proportion of area
168 within a radius of 20 m from focal trees covered by other canopies (Oppie, 1968). Area
169 of influence was fixed to 20 m because it is an intermediate value between maximum

170 horizontal extension of oak roots in savanna-like woodlands (33 m, Moreno and
171 Cubera, 2005) and those found in forest stands (10 m, Rewald and Leuchner, 2009).
172 High stem density in the northern locality together with a multi-stem structure of focal
173 trees forced us to use transects as a proxy of area of influence (4 transects per tree —N,
174 S, E, W directions). We also measured canopy radius (average of four measures per
175 tree) and number of stems per stump since both variables could covary with
176 intraspecific competition and affect tree water status and acorn production of individual
177 trees (e.g. Sánchez-Humanes and Espelta, 2011; Rodríguez-Calcerrada et al. 2011).

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179 2.3 Meteorological data

180 Meteorological data for the 2012-2014 period were obtained from the closest weather
181 stations belonging to the Spanish Meteorological Agency (AEMET); Ocaña (at 57 km
182 from Quintanar de la Orden; 39°57'N, 3°29'W; 733 m a.s.l.) and Villamayor de los
183 Montes (13 km from Lerma; 42°06'N, 3°45'W; 882 m a.s.l.). To better characterize site-
184 specific climatic conditions we used longer time series from nearby meteorological
185 stations (1982-2014). Toledo weather station was used for Quintanar (89 km away; 39°
186 51'N, 4°01'W; 515 m a.s.l.) and Villafraía (39 km away; 42°21'N, 3°36'W; 891 m a.s.l.)
187 was used for Lerma. From the available meteorological data we estimated potential
188 evapotranspiration and accumulated precipitation. Two drought indexes were
189 calculated: (1) the ratio between precipitation and potential evapotranspiration on a
190 monthly basis (P/PET; UNEP, 1992) and (2) a drought index (Di), estimated as the
191 difference between accumulated precipitation and potential evapotranspiration from
192 April to August (Rigling et al., 2013). In all cases, PET was estimated following
193 Hargreaves method (Hargreaves et al., 1982).

194 2.4 Data analysis

195 To evaluate if drought severity during the studied years was within the normal ranges of
196 both localities, percentiles (5 and 95%) for monthly P/PET and yearly Di were obtained
197 for the long-term meteorological data (1982-2014). These values were compared to
198 those observed during 2012, 2013 and 2014.

199 To evaluate which local forest structure variables differed between fragmentation levels
200 in each locality we used generalized linear mixed regression models. Our response
201 variables were intraspecific competition, canopy radius and number of stem per stump
202 (binomial, gaussian and poisson models were used respectively). Since habitat quality
203 may be tightly related to fragment management history and agricultural exploitation in
204 the surroundings we introduced cluster as a random effect. Trees located within the
205 same large forest fragments were assigned to the same cluster, as well as trees located in
206 groups of nearby fragments (within areas of 35 ha). A total of 14 clusters were obtained
207 (12 focal trees per cluster on average). Lme4 R package was used (Bates et al., 2013).

208 We assessed net fragmentation effects on acorn production by means of cumulative link
209 mixed models (R package ordinal, Christensen, 2015). Such models are used for
210 analyzing ordered categorical variables like the acorn score used here (values of 0, 1, 2,
211 3 and 4), which was the response variable. Fixed effects were locality (north and south)
212 fragmentation level (interior, edge and small fragment), year (as a factor, 2012, 2013
213 and 2014) and their two-way interaction. Focal tree was introduced as a random factor,
214 as we had three measurements per tree. We did not introduce spatial correlation effects
215 due to convergence problems (condition number of hessian $> 10^4$). However, no
216 significant associations among residuals were detected in spatial autocorrelograms (ncf

217 package; Ottar, 2013). We used mosaic plots in order to visualize contingency tables
218 (Friendly, 1994).

219 To test if fragmentation effects on holm oaks water-status during summer were related
220 to changes in intraspecific competition and if such changes were consistent among
221 localities we used linear mixed models. Our response variable was predawn water
222 potential in August (Ψ_{pd}). Our explanatory variables were intraspecific competition,
223 locality (north and south) and their interaction. Cluster was introduced as a random
224 effect. Low sample size per focal tree (two measurements) precluded us from analyzing
225 all data together. Therefore, we evaluated data of 2012 and 2013 separately. R package
226 nlme was used in this analysis (Pinhero et al. 2013). The remaining forest structure
227 variables were not included in the analysis either because we did not find significant
228 differences among fragmentation categories (Table 1) or because preliminary analysis
229 showed non- significant correlations between them and tree water-status.

230 We also calculated the percentage of trees showing predawn water potentials below -3
231 or -3.5 MPa and beyond -1.5 MPa. The former values are considered thresholds of loss
232 of hydraulic conductivity and acorn production (Martínez-Vilalta et al., 2002; Alejano
233 et al., 2008; Carevic et al., 2010; Carevic et al., 2014a). The latter is an intermediate
234 value between those reported to trigger acorn production (-2.5 MPa; Carevic et al.,
235 2010) and those typically found in highly productive dehesa trees (-0.5, -1 MPa)
236 (Moreno et al., 2007).

237 Finally, we evaluated if fragmentation effects on acorn production were mediated by
238 summer water stress. In a first approximation, we used cumulative link mixed models.
239 Our response variable was acorn score (0, 1, 2, 3 and 4). Our fixed effects were predawn
240 water potential in August (Ψ_{pd}), locality (north and south) and their interaction. Like

241 before, cluster was introduced as a random effect and data of year 2012 and 2013 were
242 analyzed separately. Subsequently, we used binomial mixed models to capture
243 threshold-like responses observed in our data. In 2012, a binary response variable was
244 set to represent the probability of non-producing acorns, while in 2013 it represented the
245 probability of showing the highest acorn production. Fixed effects were predawn water
246 potential in August (Ψ_{pd}), locality (north and south) and their interaction; cluster was
247 included as a random effect.

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249 **3. Results**

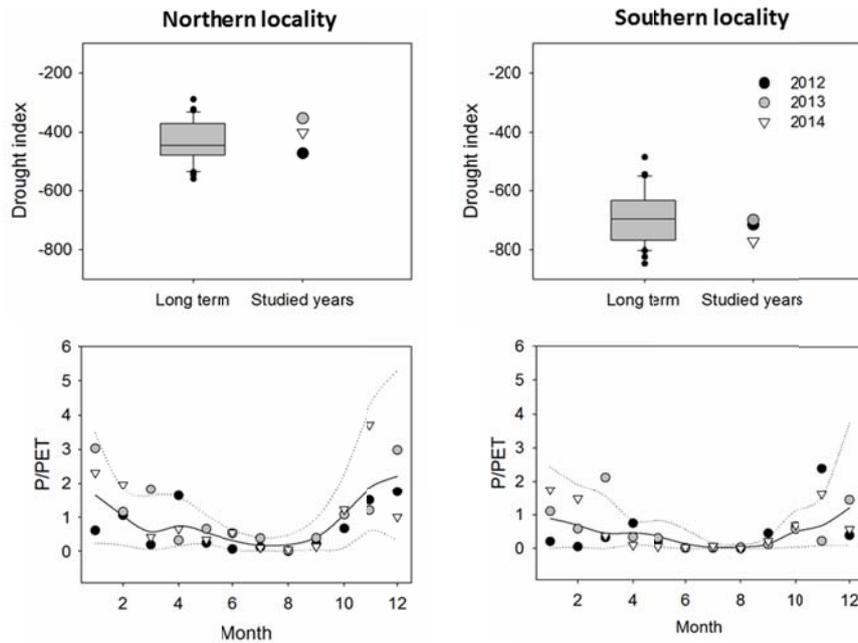
250 3.1 Meteorological variables

251 Long-term meteorological data showed that the southern locality was much drier than
252 the northern (Fig. 1). Accumulated water deficit from April to August (D_i) was 60%
253 higher on average in the south ($-431.84.2 \pm 12.64$ mm; -690.92 ± 16.88 mm; north and
254 south, respectively), and water shortage was on average 68% more severe (0.22 vs 0.07
255 average P/PET from June to August, north and south, respectively). The studied years
256 were within the site-specific normal range in both localities. In both localities, 2013 was
257 wetter than 2012 though, main differences were observed in the north (Fig. 1). There,
258 accumulated water deficit (D_i) in 2013 was 18.6% lower than the long term mean, while
259 in 2012 it was 8.9% higher. As for 2014, it was the driest year in the southern locality
260 while showed intermediate values in the north (Fig. 1)

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272 Fig.1. (Upper panels) Riglings' drought index
 273 $(\sum_{April}^{August} P - \sum_{Ap.}^{Aug.} PET; mm)$. (Lower panels) Mean long term
 274 monthly drought index (P/PET) (solid line) and confidence
 275 intervals (95%; dashed line). Mean values of studied years are also
 276 plotted. In both cases lower values indicate higher drought. Left
 277 and right panels correspond to the northern and southern locality,
 278 respectively.
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274 3.2 Differences in forest structure variables among fragmentation levels

283 In both localities the estimated intraspecific competition differed among fragmentation
 284 categories (Table 1). However, fragmentation effects varied between them. In the north,
 285 high stand densities in forest interiors (424 stems per ha on average) resulted in
 286 significant differences in intraspecific competition among all fragmentation levels. It
 287 was 20% and 52% lower in forest edges and small forest fragments with respect to
 288 forest interiors. In the south, low stand density (121 stems per ha on average) lead to
 289 much lower intraspecific competition in forest interiors (29 % lower than in the north)
 290 and less clear-cut differences among fragmentation levels. Finally, despite of
 291 differences in the stand structure of forests, trees located in small fragments from both

283 localities showed similar competition values. Regarding tree traits, only number of
 284 stems per tree was significantly larger in southern forests.

Table 1. Forest structure variables with respect to fragmentation level and locality (mean±SE). Intraspecific competition (comp.) was calculated as the proportion of area in a buffer of 20 m covered by other oak canopies. Size is given as canopy radio in m. N Stems is the number of stems per tree. Letters depict significant differences between fragmentation levels per locality (P<0.05) * Marginal significant differences (P = 0.06). Abbreviations- Loc. = locality, Frag. = fragmentation category, G = group.

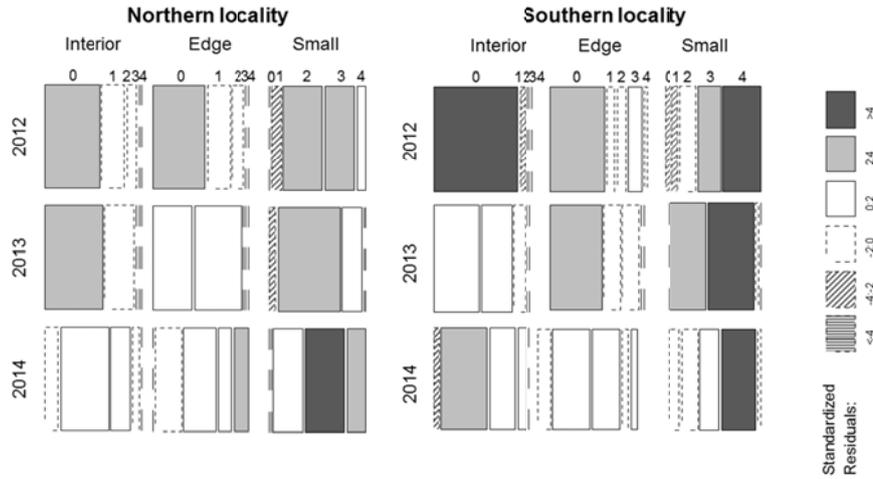
Loc.	Frag.	Competition	G (comp.)	Size	G (size)	N Stems	G(stems)
North	<i>Interior</i>	0.65±0.02	A	1.95±0.09	A	9.85±1.40	A
	<i>Edge</i>	0.52±0.02	B	2.26±0.10	A	10.41±2.05	A
	<i>Small</i>	0.31±0.08	C	2.6±0.15	A	7.70±1.28	A
South	<i>Interior</i>	0.46±0.04	a	3.73±0.42	a	10.36±2.14	a
	<i>Edge</i>	0.36±0.03	b	2.14±0.15	a*	3.58±0.44	b
	<i>Small</i>	0.27±0.14	b	3.31±0.21	a	5.57±1.26	ab

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286 3.2 General patterns of fragmentation effects on acorn production

287 Despite of high inter-annual variability, acorn production did not differ between
 288 localities and fragmentation effects were consistent among sites. In both localities,
 289 forest fragmentation enhanced acorn production (Table 2, Fig. 2). In general, forest
 290 interiors showed a significantly higher frequency of non-producing trees (49% on
 291 average) than expected at random while small forest fragments showed a significantly
 292 higher frequency of trees with intermediate and high acorn crops (37.5% on average).
 293 Trees at forest edges showed intermediate responses (Fig. 2).

294 Regarding inter-annual variability, acorn crops were largest in 2014 in both localities
 295 (2.11±0.12, 1.64±0.11 mean acorn score ± SE; north and south respectively) while 2013
 296 showed the poorest crops (0.68±0.07; 0.93±0.09; north and south respectively). Besides,
 297 differences between fragmentation categories were more pronounced in 2012, the driest
 298 year (Fig. 2, Table 2).



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Fig.2. Mosaic plot of the observed frequency of holm oak trees with different crop sizes (0,1,2,3,4) in different years and fragmentation levels. The area of each rectangle is proportional to the cell frequency of the corresponding contingency table. Solid and broken lines indicate positive and negative deviation from the expected frequencies under the null model. The shading of each rectangle is proportional to standardized residuals from the fitted model (values indicated in the legend). Grey and black rectangles indicate significant positive deviations from the expected frequencies. Striped rectangles show significant negative deviations from the expected frequencies ($P < 0.05$).

Table 2. Results of cumulative mixed model with crop size (0, 1, 2, 3 and 4) as a function of year (2012, 2013 and 2014), fragmentation (interior, edge and small fragments), locality (north and south) and their interaction. LRT = likelihood ratio test, df = degrees of freedom, P = p-value, R^2_m = marginal pseudo R^2 , R^2_c = conditional pseudo R^2 .

Effect	LRT	df	P	R^2_m	R^2_c
Fragmentation	130.11	2	<0.01		
Locality	0.145	1	0.70		
Year	107.42	2	<0.01		
Locality*Frag.	2.11	2	0.34	0.22	0.23
Locality*Year	9.69	2	<0.01		
Frag.*Year	64.44	4	<0.01		

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312 3.4 Competition effects on tree water status

315 As expected, predawn water potentials were higher in the north (20 and 15% higher on
 316 average, 2012 and 2013 respectively). Besides, in all studied years intraspecific
 317 competition for water resources negatively impacted predawn water potential of trees.

315 However, intraspecific competition effects on tree water status differed between years.
 316 In 2012, the driest year, competition effects were larger and consistent between
 317 localities while in 2013 competition effects were only significant in the north (Table 3,
 318 Fig.3).

319 In the northern locality, predawn water potentials were within -0.83 and -4.4 MPa in
 320 2012 and within -0.5 and -2.97 MPa in 2013 (Fig. 3). In 2012, 48% of measured trees
 321 showed predawn water potentials below -3 MPa. These represented 55% of measured
 322 trees in forest interiors, while 30% in small forest fragments. In 2013, 27% of measured
 323 trees showed predawn water potentials beyond -1.5 MPa. In forest interiors they
 324 represented a scarce 4% while they represented 48% of measured trees in small forest
 325 fragments.

326 In the south, predawn water potential ranged between -1.68 and -5.90 MPa in 2012 and
 327 between -0.64 and -3.46 in 2013 (Fig. 3). In 2012, 89% of trees located in forest
 328 interiors showed predawn water potentials below -3.5 MPa, while in small forest
 329 fragments only an 11% reached these values. In 2013, 19% of trees showed predawn
 330 water potentials beyond -1.5 MPa. In forest interiors they only accounted for a 7% of
 331 measured trees while in small forest fragments they represented a 36%.

Table 3. Results of linear mixed model with predawn water potential (MPa) as a function of intraspecific competition, locality and their interaction in the year 2012 and 2013. LRT = likelihood ratio test, df = degrees of freedom, P = p-value, R^2_m = marginal pseudo R^2 , R^2_c = conditional pseudo R^2 . Baseline was fixed to the northern locality and its interaction with competition.

Year	Effect	LRT	df	P	Estimate	R^2_m	R^2_c
2012	Competition	9.14	1	<0.01	-0.93±0.31	0.18	0.32
	Locality(South)	6.36	1	0.01	-0.70±0.28		
	Competition*Locality	0.81	1	0.37	0.55±0.62		
2013	Competition	4.30	1	0.04	-0.73±0.36	0.10	0.28
	Locality(South)	8.30	1	<0.01	-0.71±0.25		
	Competition*Locality	4.14	1	0.04	0.93±0.47		

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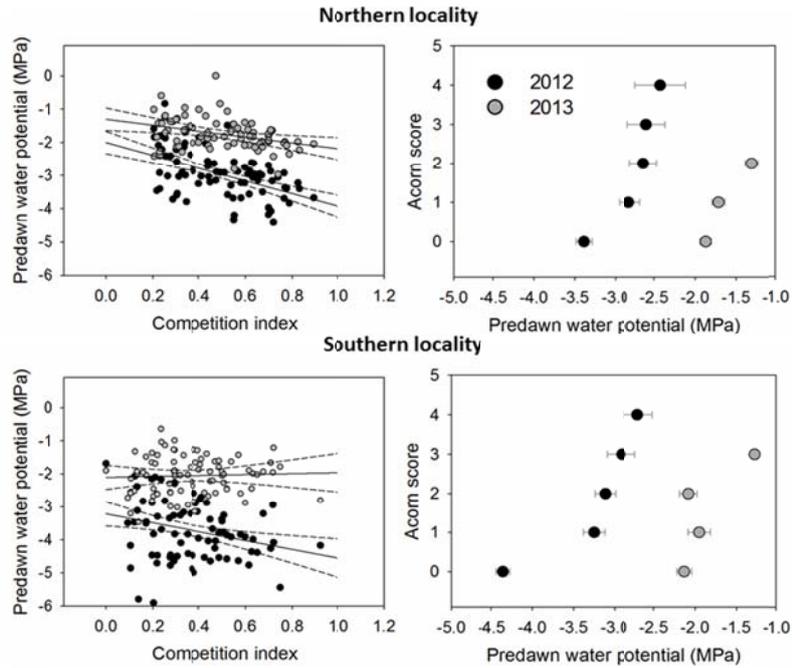
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Fig.3. (Left panels) Intraspecific competition effects on holm oaks predawn water potential in August. Solid lines correspond to model predictions per year and dashed lines to 95% confident intervals (Right panels). Predawn water potential effects on acorn production. Bars represent 95% confident intervals. Upper and lower panels correspond to the northern and southern locality respectively.

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354 3.5 Water status effects on acorn production

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Predawn water potential affected acorn production of trees in both localities. However,

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patterns differed between years (Fig 3). In 2012, trees with higher summer water stress

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were less productive and this pattern was more pronounced in the south (Table 4).

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Besides, main differences occurred between producing and non-producing trees. In the

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north, predawn water potentials below -3 MPa constrained acorn production while in

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the south this threshold dropped to -4 MPa (Fig. 3, Table 5). In 2013 we did not detect

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differences in predawn water potentials among trees with intermediate acorn scores

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(Fig. 3). In fact, effects of predawn water potential, locality or their interaction were not

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significant in cumulative mixed models (Table 4). However, the most productive trees

363 were the ones showing the highest predawn water potentials (< -1.5 MPa; Fig.3, Table
 364 5).

Table 4. Results of cumulative mixed model with crop size (0, 1, 2, 3 and 4) as a function of predawn water potential (MPa), locality (north and south) and their interaction. Ψ_{pd} = Predawn water potential, LRT = likelihood ratio test, df = degrees of freedom, P = p-value, R^2_m = marginal pseudo R^2 , R^2_c = conditional pseudo R^2 . Baseline was fixed to the northern locality and its interaction with competition.

Locality	Effect	LRT	df	P	Estimate	R^2_m	R^2_c
2012	Ψ_{pd}	36.12	1	<0.01	0.88 ± 0.39	0.14	0.28
	Locality(south)	1.56	1	0.21	-0.31 ± 1.06		
	Ψ_{pd} *Locality	15.28	1	<0.01	2.55 ± 0.69		
2013	Ψ_{pd}	0.67	1	0.12	0.84 ± 0.55	--	--
	Locality(south)	0.49	1	0.61	-0.91 ± 1.78		
	Ψ_{pd} *Locality	1.49	1	0.22	-0.91 ± 0.75		

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Table 5. Summary of binomial mixed models to test the effects of predawn water potential (MPa), locality (north and south) and their interaction on the probability of not producing acorns in the (year 2012) and of showing the highest acorn production (year 2013). Non-produc = non-producing trees, highest-prod.= trees with the highest production, LRT = likelihood ratio test, df = degrees of freedom, P = p-value, R^2_m = marginal pseudo R^2 , R^2_c = conditional pseudo R^2 . Baseline was fixed to the northern locality and its interaction with competition.

Year	Category	Effect	LRT	df	P	Estimate	R^2_m	R^2_c
2012	Non-prod.	Ψ_{pd}	6.93	1	<0.01	-1.73 ± 0.66	0.77	0.85
		Locality(South)	6.94	1	0.01	-17.74 ± 6.73		
		Ψ_{pd} *Locality	6.78	1	<0.01	-4.84 ± 1.86		
2013	Highest-prod.	Ψ_{pd}	3.53	1	0.06	3.05 ± 1.62	0.10	0.88
		Locality(South)	0.30	1	0.60	-3.46 ± 6.67		
		Ψ_{pd} *Locality	0.26	1	0.61	-1.81 ± 3.60		

366

367

368 Discussion

369 Overall, our results show a positive effect of forest fragmentation on acorn production,
 370 mediated by the mitigation of summer water stress due to relaxed intraspecific
 371 competition. Despite that the southern locality is characterized by more severe summer
 372 drought we did not find significant differences in acorn productivity between localities,
 373 and the impact of forest fragmentation was consistent among sites. In both cases, forest
 374 interiors showed a high proportion of non-producing trees while trees located at small
 375 forest fragments exhibited enhanced acorn productivity in all studied years. These

376 results support the idea that poor acorn crops in holm oak woodlands may be relatively
377 frequent since high density stands are widely spread (Espelta, Cortes et al. 2008).
378 Besides, they show that the effects of fragmentation on acorn production at a local scale
379 can override the influence of large-scale climatic differences among localities. All this
380 contrast with the most common finding of negative effects of fragmentation on plant
381 reproduction, especially in animal-pollinated plants (reviewed in Aguilar, Ashworth et
382 al. 2006). In most of these cases the impairment of plant-animal mutualistic
383 relationships due to habitat loss or edge effects decreases fruit production. Although
384 pollen availability can also constrain fruit production in fragmented populations of
385 wind-pollinated species, like oaks (Knapp et al. 2001, Sork et al. 2002, reviewed by
386 Koenig and Ashley 2003), the positive effects of fragmentation on acorn production
387 found here together with the higher number of pollen donors in small forest fragments
388 observed in previous work (Morán-López et al. 2016) suggest otherwise in our study
389 area. Instead, fragmentation effects seem to depend on other environmental factors
390 related to plant phenology and seed development.

391 As expected, fragmentation effects were driven by changes in tree-to-tree competition,
392 which exerted a strong impact on tree water-status during summer (see Moreno and
393 Cubera, 2008 for similar results in stand density gradients). Although the studied period
394 did not include extreme drought events in any of the localities, water shortage was more
395 pronounced in 2012. In that year, almost half of the trees in forest interiors of the north,
396 and more than eighty percent in the south, showed predawn water potentials below -3
397 and -3.5 MPa, respectively. This resulted in a high proportion of non-producing trees,
398 which is consistent with predawn water potential thresholds previously reported for
399 *Quercus ilex* (Alejano et al., 2008; Misson et al., 2011; Carevic et al., 2014b). When
400 water potential falls below -3.5 MPa stomatal closure and an important loss of hydraulic

401 conductivity (e.g. Tognetti et al., 1998; Martínez-Vilalta et al., 2002) constrains water
402 supply to acorns triggering an increase of abortion rates (Carevic et al., 2014a).
403 Interestingly, these thresholds seemed to be site-specific. In the north, trees
404 experiencing predawn water potentials below -3 MPa during summer 2012 failed to
405 produce acorns while this occurred at values of -4 MPa in the south. This explains the
406 lack of differences in seed crops between localities and suggests that southern
407 populations of holm oaks are more resistant to summer drought. In fact, intraspecific
408 competition only had a significant effect on tree water-status of southern holm oaks in
409 2012, the driest year.

410 In 2013, when climatic conditions were milder, predawn water potentials did not fall
411 below -3.5 MPa in any of the localities. In these conditions, main differences in summer
412 water status were found only among the trees with the largest crops. Nearly all trees in
413 small forest fragments showed moderate water stress (>-2.5 MPa; Carevic et al. 2014), a
414 condition that has been shown to enhance acorn production (Alejano et al. 2008,
415 Carevic et al. 2010). Despite of the improved water status of trees in 2013, acorn
416 production was not larger than in 2012 and forest interiors showed high proportions of
417 non-producing trees. Lower pollen availability in 2013, unsuccessful pollination
418 (García-Mozo et al. 2007) or endogenous cycles of acorn production (Siscart,1999)
419 could explain this pattern. Unfortunately, we do not have data on pollen emission rates
420 or on the fate of female flowers to evaluate the first two hypotheses. As for individual
421 resource limitation, we did not find significant correlations between current and prior
422 year crops (data not shown), and long-term studies have shown that regular patterns in
423 holm oaks acorn yields actually reflect temporal regularity of drought events (Pérez-
424 Ramos et al., 2010). Xylem anatomy adjustments boosted by climatic conditions could
425 explain the observed inter-annual variability in water potential thresholds. In holm oaks,

426 moister conditions along the growing season can result in wider and less compacted
427 xylem vessels resulting in improved hydraulic conductivity but lower resistance to
428 cavitation (Corcuera et al., 2004; Abrantes et al., 2013). Thus, a wetter summer-spring
429 in 2013 could have led to higher susceptibility to water shortage during acorn ripening.
430 Since Mediterranean climate is characterized by a high inter-annual variability (Bolle,
431 2003), future studies combining physiological monitoring with tree-ring anatomy will
432 help to draw a full picture of long-term effects of fragmentation on holm oaks acorn
433 production.

434 Though we used a broad-brush approach to estimate crops, we could detect a significant
435 effect of tree water-status on acorn production. Moreover, threshold-like responses
436 observed here are consistent with previous work (Alejano et al., 2008; Carevic et al.,
437 2010). However, we failed to detect significant differences between intermediate acorn
438 scores and the variability explained by our crop-water status models in 2013 was
439 relatively low. Probably, more quantitative estimations would have resulted in more
440 clear patterns. However, other factors related to differences in habitat quality beyond
441 changes in tree-to-tree competition cannot be ruled out (e.g. light, nutrients). For
442 instance, the soils of small forest fragments in the study area are characterized by higher
443 nutrient availability (Flores-Renteria et al., 2015) and fertilization has been shown to
444 stimulate acorn productivity in dense holm oak stands (Siscart, 1999). Changes in
445 habitat quality in small forest fragments may have acted concomitantly with
446 competition effects.

447 Contrary to the extended idea of negative effects of forest fragmentation on plant
448 populations, our results show that relaxed tree-to-tree competition in small forest
449 fragments enhance acorn production. In 2012, trees in forest interiors experienced
450 predawn water potentials close to their point of hydraulic failure, while nearby ones

451 located at small forest fragments only suffered a moderate water stress (according to
452 Carevic et al., 2010), which resulted in a much higher acorn production. These results
453 highlight the importance of local environmental conditions in modulating water
454 shortage during the summer and illustrate how fragmentation can override the impacts
455 of climate on acorn production. However, it is necessary to be cautious when
456 interpreting these positive effects of forest fragmentation. Firstly, when scaling up at the
457 population level, the scarcity of trees in extremely fragmented landscapes may
458 supersede enhanced acorn production. For instance, in the northern locality, where only
459 49% of trees in forest interiors produced acorns, in ten hectares there would be around
460 2000 producing trees. In the same locality, it would be only about 40 producing trees in
461 intensively managed agricultural areas (assuming three small forest fragments on
462 average within ten hectares of cropland). Secondly, forest fragmentation constrains
463 acorn dispersal and net positive effects on holm oak regeneration will only occur if there
464 is a higher probability of seedling recruitment in small fragments (Schupp et al., 2010).
465 Eurasian jays (*Garrulus glandarius*) - main acorn disperser in Europe— are absent in
466 small forest fragments (Brotons et al., 2004) and dispersal services provided by wood
467 mice (*Apodemus sylvaticus*) are much poorer (Santos and Telleria, 1997; Morán-López
468 et al., 2015). Besides, seedling dry out in open land microhabitats (Smit et al., 2008),
469 can act as an important post-dispersal recruitment bottleneck in surrounding croplands.
470 Therefore, to assess fragmentation effects on holm oak regeneration in a realistic way,
471 all stages of the regeneration cycle need to be integrated (see Pulido and Díaz, 2005 for
472 a similar approach in dehesas). Thanks to the wealth of studies on key processes of oaks
473 regeneration cycle, we now have the pieces in place to develop such a global approach.

474 **4 Conclusions**

475 In fragmented landscapes, the creation of forest edges reduces tree-to-tree competition
476 for water sources. As a result, trees in small forest fragments produce more acorns.
477 Thus, under a climate change scenario with more frequent and acute drought events,
478 forest fragmentation may buffer large-scale climatic effects. However, tree scarcity in
479 intensively managed agricultural areas and other key processes like acorn dispersal or
480 seedling survival need to be integrated before drawing conclusions on the impacts of
481 forest fragmentation on holm oak regeneration.

482

483 **Acknowledgements**

484 We acknowledge Javier Puy, David López Quiroga and Miguel Fernández for their
485 invaluable technical support during field work. We are also grateful to Laura Barrios for
486 her help in the statistical analysis. Teresa Morán- was beneficiary of a FPI grant (funded
487 by the Spanish Government (BES-2011-048346); Alicia Forner of a JAE-predoc
488 fellowship from the Spanish National Council (CSIC) co-funded by the European Union
489 (Fondo Social Europeo) and Dulce Florest-Rentería holds a pre-doctoral fellowship
490 awarded by the Mexican Council of Science and Technology (CONACyT). This paper
491 is a contribution to the Spanish-funded projects VULGLO (CGL2010–22180-C03–03),
492 VERONICA (CGL2013-42271-P) and REMEDINAL 2 & 3 (CM S2009 AMB 1783)
493 (S2013/MAE-2719).

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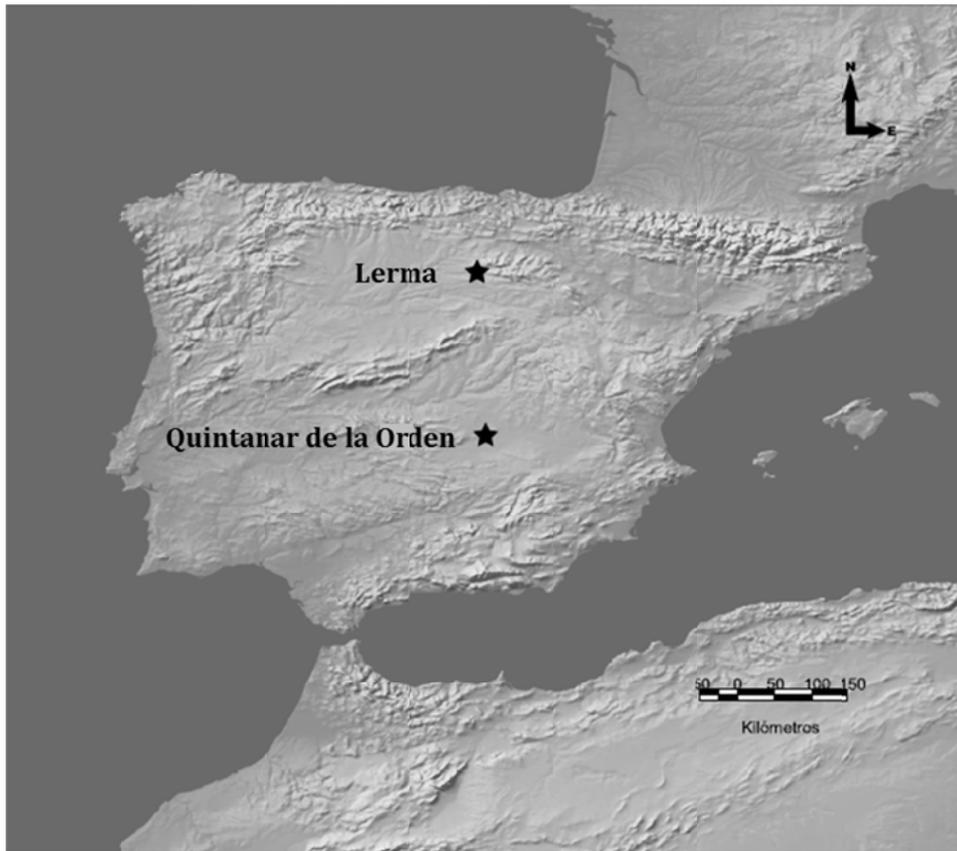
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696
697



600
701

Fig.A1 Map of the location of the study areas in the Iberian Peninsula