



## Some positive effects of the fragmentation of holm oak forests: Attenuation of water stress and enhancement of acorn production



Teresa Morán-López <sup>\*,1</sup>, Alicia Forner <sup>1</sup>, Dulce Flores-Rentería, Mario Díaz, Fernando Valladares

Department of Biogeography and Global Change (BGC-MNCN), National Museum of Natural Science CSIC, C/Serrano 115 bis, E-28006 Madrid, Spain

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### ABSTRACT

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

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

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### 1. Introduction

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

Holm oaks (*Quercus ilex* ssp. *ballota*) are an ideal study system for addressing the combined effect of management and increased aridity on forest regeneration. Most holm oak forests are located

in anthropogenic landscapes and either an increased summer drought, a given management regime or both may compromise holm oak reproduction (Espelta et al., 1995; Pérez-Ramos et al., 2010; Misson et al., 2011). Holm oaks are considered as tolerant to severe water shortage due to their deep root system (Moreno et al., 2005), to their ability to rapidly recover from tissue damage caused by the summer drought, and to their resprouting capability (Tognetti et al., 1998). However, when compared to other Mediterranean species, they are quite vulnerable to xylem cavitation and they actually function close to their point of hydraulic failure during the summer months (Martínez-Vilalta et al., 2002; Quero et al., 2011). In fact, high defoliation rates and dieback episodes have been registered after extreme drought events in holm oak forests (Peñuelas et al., 2000). Fruit production has been also linked to water availability during spring and summer months, despite complex masting processes that derive in high inter-annual variability in acorn crops. In general, moister springs involve higher investment on female flowers, which entails enhanced acorn production, but a very severe summer drought can lead to high abortion rates and constrain final acorn production (Ogaya and Peñuelas, 2007; Espelta et al., 2008; Pérez-Ramos et al., 2010; Misson et al., 2011; Rodríguez-Calcerrada et al., 2011; Sánchez-Humanes and Espelta, 2011; Fernández-Martínez et al., 2012; García-Mozo et al., 2012). Thus, the increased aridity expected under a climate

\* Corresponding author.

E-mail address: [tmoranlopez@gmail.com](mailto:tmoranlopez@gmail.com) (T. Morán-López).

<sup>1</sup> First and second authors equally contributed to this work.

change scenario may hamper holm oak reproduction. In fact, rain-fall exclusion experiments have shown that a 15–30% reduction in summer rainfall, which are similar to that expected by the end of the century for the Mediterranean basin (AEMET, 2009), can significantly constrain acorn production (Pérez-Ramos et al., 2010; Rodríguez-Calcerrada et al., 2011; Sánchez-Humanes and Espelta, 2011; IPCC, 2013).

Concomitantly to climatic conditions, management practices such as tree coppicing, tree thinning and shrub clearance, or fragmentation can affect water availability of individual holm oak trees (Terradas, 1999; Moreno and Cubera, 2008; Campos et al., 2013). In dense multi-stemmed stands, increased competition for resources limits oak growth and sexual reproduction (Rodríguez-Calcerrada et al., 2011; Sánchez-Humanes and Espelta, 2011). Selective thinning of the weaker stems has been proposed as a management strategy for natural restocking since it stimulates tree growth (e.g. Retana et al., 1992; Mayor and Roda, 1993). However, thinning effects on acorn production seem minor (Rodríguez-Calcerrada et al., 2011; Sánchez-Humanes and Espelta, 2011). Another way of buffering the negative effects of summer drought on holm oak water status is tree clearance (Moreno and Cubera, 2008). For instance, trees in savanna-like woodlands (dehesas and montados) show acorn crops one order of magnitude higher than those found in forest habitats (Pulido and Díaz, 2005; Díaz, 2014). Therefore, management effects on holm oaks acorn production seems to be driven by local changes in intraspecific competition, which modulates the negative effects of summer drought.

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

## 2. Material and methods

### 2.1. Study area

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

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

Fieldwork in the northern plateau was undertaken in an area of 66,500 ha around Lerma (41°58'N, 03°52'W; 930 m asl). The

dominant tree is also holm oak (424 stems per ha), with isolated Lusitanian oak *Quercus faginea* and Spanish juniper *Juniperus thurifera* and understory shrubs typical from wetter and cooler Supramediterranean localities (e.g. *Cistus laurifolius*, *Genista scorpius*, *Thymus zygis*). Average canopy radius of holm oaks in Lerma is 2.26 m ( $\pm 0.13$ ). Annual precipitation is 567 mm and annual mean temperature is 11 °C. In both localities, the dominant soils are classified as Cambisols (calcics) (WRB, 2007) with 17% sand, 39% silt and 44% clay for the southern region and 11% sand, 42% silt and 47% clay for the northern region (Flores-Rentería et al., 2015).

### 2.2. Experimental design and tree measurements

In each locality we selected three large forest fragments (>100 ha), in which we defined forest interiors and edges. Edges were defined as forest areas closer than 60 m from the cultivated border, being interiors the remaining forest (García et al., 1998). Edge plots were selected along long straight borders to avoid influences of border geometry on edge effects (Fernández et al., 2002). Besides, we selected 10 and 11 small forest fragments in the northern and southern locality, respectively (mean  $\pm$  SE 0.047  $\pm$  0.031 and 0.031  $\pm$  0.024 ha in the south and north, respectively). Hence, three fragmentation categories were defined – forest interior, forest edge and small fragments – in each locality – northern and southern plateaus.

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

In mid-August 2012 and 2013 we measured predawn water potential ( $\Psi_{pd}$ ) of focal trees. In each locality, we sampled 90 focal trees (30 per fragmentation level) along six days. On average, 15 trees were measured each day following a randomized factorial design with respect to fragmentation category. Measurements were conducted on two twigs per tree and then averaged. Excised twigs were collected into sealable plastic bags, with air saturated of humidity and CO<sub>2</sub>, and kept refrigerated and in dark (Pérez-Harguindeguy et al., 2013). All measurements were performed by means of a Scholander chamber (Scholander et al., 1965).

In each focal tree we estimated intraspecific competition as the proportion of area within a radius of 20 m from focal trees covered by other canopies (Oppie, 1968). Area of influence was fixed to 20 m because it is an intermediate value between maximum horizontal extension of oak roots in savanna-like woodlands (33 m, Moreno et al., 2005) and those found in forest stands (10 m, Rewald and Leuchner, 2009). High stem density in the northern locality together with a multi-stem structure of focal trees forced us to use transects as a proxy of area of influence (4 transects per tree –N, S, E, W directions). We also measured canopy radius (average of four measures per tree) and number of stems per stump since both variables could covary with intraspecific competition and affect tree water status and acorn production of individual trees (e.g. Sánchez-Humanes and Espelta, 2011; Rodríguez-Calcerrada et al., 2011).

### 2.3. Meteorological data

Meteorological data for the 2012–2014 period were obtained from the closest weather stations belonging to the Spanish

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

#### 2.4. Data analysis

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

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

We assessed net fragmentation effects on acorn production by means of cumulative link mixed models (R package ordinal, Christensen, 2015). Such models are used for analyzing ordered categorical variables like the acorn score used here (values of 0, 1, 2, 3 and 4), which was the response variable. Fixed effects were locality (north and south) fragmentation level (interior, edge and small fragment), year (as a factor, 2012, 2013 and 2014) and their two-way interaction. Focal tree was introduced as a random factor, as we had three measurements per tree. We did not introduce spatial correlation effects due to convergence problems (condition number of hessian  $>10^4$ ). However, no significant associations among residuals were detected in spatial autocorrelograms (ncf package; Ottar, 2013). We used mosaic plots in order to visualize contingency tables (Friendly, 1994).

To test if fragmentation effects on holm oaks water-status during summer were related to changes in intraspecific competition and if such changes were consistent among localities we used

linear mixed models. Our response variable was predawn water potential in August ( $\Psi_{pd}$ ). Our explanatory variables were intraspecific competition, locality (north and south) and their interaction. Cluster was introduced as a random effect. Low sample size per focal tree (two measurements) precluded us from analyzing all data together. Therefore, we evaluated data of 2012 and 2013 separately. R package nlme was used in this analysis (Pinhero et al., 2013). The remaining forest structure variables were not included in the analysis either because we did not find significant differences among fragmentation categories (Table 1) or because preliminary analysis showed non-significant correlations between them and tree water-status.

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

Finally, we evaluated if fragmentation effects on acorn production were mediated by summer water stress. In a first approximation, we used cumulative link mixed models. Our response variable was acorn score (0, 1, 2, 3 and 4). Our fixed effects were predawn water potential in August ( $\Psi_{pd}$ ), locality (north and south) and their interaction. Like before, cluster was introduced as a random effect and data of year 2012 and 2013 were analyzed separately. Subsequently, we used binomial mixed models to capture threshold-like responses observed in our data. In 2012, a binary response variable was set to represent the probability of non-producing acorns, while in 2013 it represented the probability of showing the highest acorn production. Fixed effects were predawn water potential in August ( $\Psi_{pd}$ ), locality (north and south) and their interaction; cluster was included as a random effect.

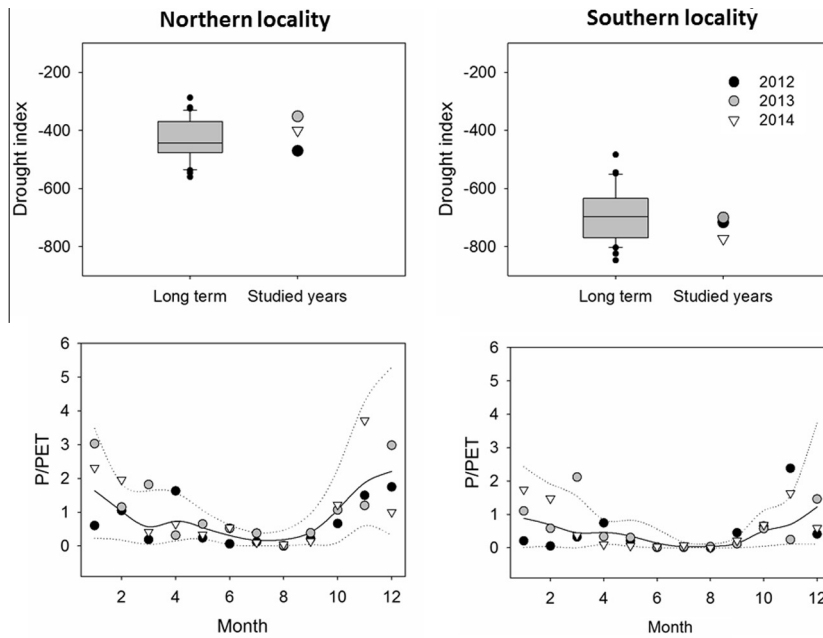
### 3. Results

#### 3.1. Meteorological variables

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

**Table 1**  
Forest structure variables with respect to fragmentation level and locality (mean  $\pm$  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	Interior	0.65 $\pm$ 0.02	A	1.95 $\pm$ 0.09	A	9.85 $\pm$ 1.40	A
	Edge	0.52 $\pm$ 0.02	B	2.26 $\pm$ 0.10	A	10.41 $\pm$ 2.05	A
	Small	0.31 $\pm$ 0.08	C	2.60 $\pm$ 0.15	A	7.70 $\pm$ 1.28	A
South	Interior	0.46 $\pm$ 0.04	a	3.73 $\pm$ 0.42	a	10.36 $\pm$ 2.14	a
	Edge	0.36 $\pm$ 0.03	b	2.14 $\pm$ 0.15	a*	3.58 $\pm$ 0.44	b
	Small	0.27 $\pm$ 0.14	b	3.31 $\pm$ 0.21	a	5.57 $\pm$ 1.26	ab



**Fig. 1.** (Upper panels) Riglings' drought index ( $\sum_{April}^{August} P - \sum_{April}^{August} PET; mm$ ). (Lower panels) Mean long term monthly drought index (P/PET) (solid line) and confidence intervals (95%; dashed line). Mean values of studied years are also plotted. In both cases lower values indicate higher drought. Left and right panels correspond to the northern and southern locality, respectively.

### 3.2. Differences in forest structure variables among fragmentation levels

In both localities the estimated intraspecific competition differed among fragmentation categories (Table 1). However, fragmentation effects varied between them. In the north, high stand densities in forest interiors (424 stems per ha on average) resulted in significant differences in intraspecific competition among all fragmentation levels. It was 20% and 52% lower in forest edges and small forest fragments with respect to forest interiors. In the south, low stand density (121 stems per ha on average) lead to much lower intraspecific competition in forest interiors (29% lower than in the north) and less clear-cut differences among fragmentation levels. Finally, despite of differences in the stand structure of forests, trees located in small fragments from both localities showed similar competition values. Regarding tree traits, only number of stems per tree was significantly larger in southern forests.

### 3.3. General patterns of fragmentation effects on acorn production

Despite of high inter-annual variability, acorn production did not differ between localities and fragmentation effects were consistent among sites. In both localities, forest fragmentation enhanced acorn production (Table 2, Fig. 2). In general, forest

**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*<sub>m</sub><sup>2</sup> = marginal pseudoR<sup>2</sup>, *R*<sub>c</sub><sup>2</sup> = conditional pseudoR<sup>2</sup>.

Effect	LRT	<i>df</i>	<i>P</i>	<i>R</i> <sub>m</sub> <sup>2</sup>	<i>R</i> <sub>c</sub> <sup>2</sup>
Fragmentation	130.11	2	<0.01	0.22	0.23
Locality	0.145	1	0.70		
Year	107.42	2	<0.01		
Locality * Frag.	2.11	2	0.34		
Locality * Year	9.69	2	<0.01		
Frag. * Year	64.44	4	<0.01		

interiors showed a significantly higher frequency of non-producing trees (49% on average) than expected at random while small forest fragments showed a significantly higher frequency of trees with intermediate and high acorn crops (37.5% on average). Trees at forest edges showed intermediate responses (Fig. 2).

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

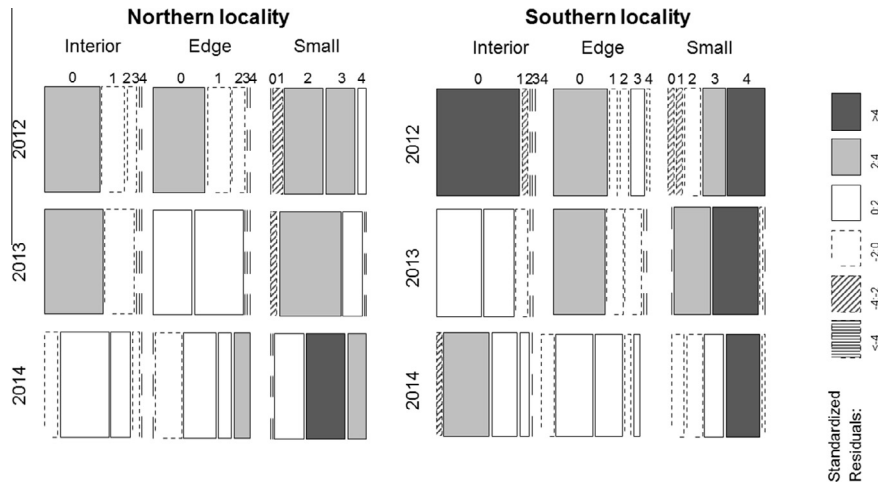
### 3.4. Competition effects on tree water status

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

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

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

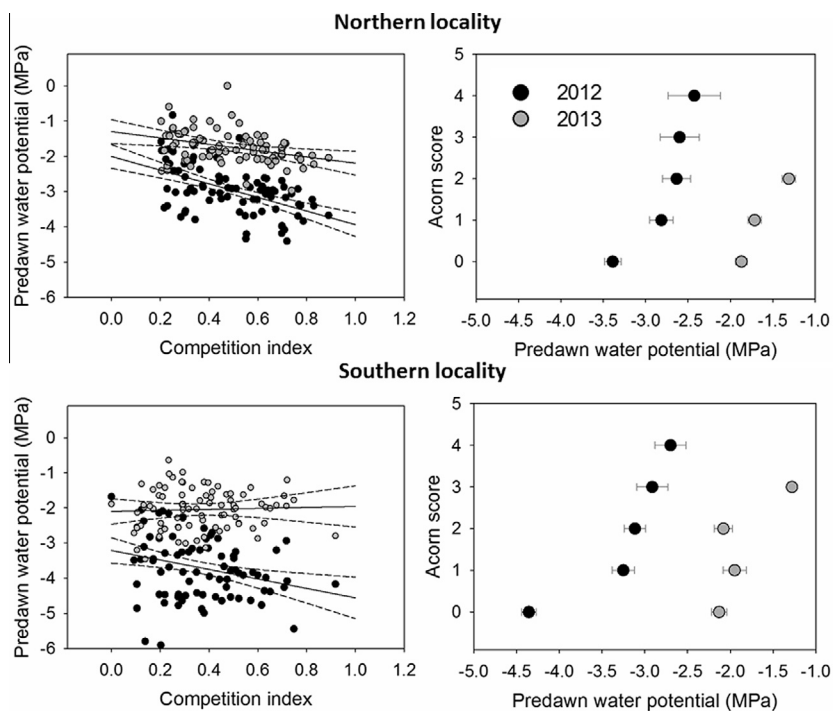
In the south, predawn water potential ranged between  $-1.68$  and  $-5.90$  MPa in 2012 and between  $-0.64$  and  $-3.46$  in 2013 (Fig. 3). In 2012, 89% of trees located in forest interiors showed predawn water potentials below  $-3.5$  MPa, while in small forest fragments only an 11% reached these values. In 2013, 19% of trees showed predawn water potentials beyond  $-1.5$  MPa. In forest



**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 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,  $R_m^2$  = marginal pseudo $R^2$ ,  $R_c^2$  = conditional pseudo $R^2$ . Baseline was fixed to the northern locality and its interaction with competition.

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



**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.



interiors they only accounted for a 7% of measured trees while in small forest fragments they represented a 36%.

### 3.5. Water status effects on acorn production

Predawn water potential affected acorn production of trees in both localities. However, patterns differed between years (Fig 3). In 2012, trees with higher summer water stress were less productive and this pattern was more pronounced in the south (Table 4). Besides, main differences occurred between producing and non-producing trees. In the north, predawn water potentials below  $-3$  MPa constrained acorn production while in the south this threshold dropped to  $-4$  MPa (Fig. 3, Table 5). In 2013 we did not detect differences in predawn water potentials among trees with intermediate acorn scores (Fig. 3). In fact, effects of predawn water potential, locality or their interaction were not significant in cumulative mixed models (Table 4). However, the most productive trees were the ones showing the highest predawn water potentials ( $> -1.5$  MPa; Fig. 3, Table 5).

## 4. Discussion

Overall, our results show a positive effect of forest fragmentation on acorn production, mediated by the mitigation of summer water stress due to relaxed intraspecific competition. Despite that the southern locality is characterized by more severe summer drought we did not find significant differences in acorn productivity between localities, and the impact of forest fragmentation was consistent among sites. In both cases, forest interiors showed a high proportion of non-producing trees while trees located at small forest fragments exhibited enhanced acorn productivity in all studied years. These results support the idea that poor acorn crops in holm oak woodlands may be relatively frequent since high density stands are widely spread (Espelta et al., 2008). Besides, they show that the effects of fragmentation on acorn production at a local scale can override the influence of large-scale climatic differences among localities. All this contrast with the most common finding of negative effects of fragmentation on plant reproduction, especially in animal-pollinated plants (reviewed in Aguilar et al., 2006). In most of these cases the impairment of plant-animal mutualistic relationships due to habitat loss or edge effects decreases fruit production. Although pollen availability can also constrain fruit production in fragmented populations of wind-pollinated species, like oaks (Knapp et al., 2001; Sork et al., 2002, reviewed by Koenig and Ashley, 2003), the positive effects of fragmentation on acorn production found here together with the higher number of pollen donors in small forest fragments observed in previous work (Morán-López et al., 2016) suggest otherwise in our study area. Instead, fragmentation effects seem to depend on other environmental factors related to plant phenology and seed development.

As expected, fragmentation effects were driven by changes in tree-to-tree competition, which exerted a strong impact on tree water-status during summer (see Moreno and Cubera, 2008 for similar results in stand density gradients). Although the studied period did not include extreme drought events in any of the localities, water shortage was more pronounced in 2012. In that year, almost half of the trees in forest interiors of the north, and more than eighty percent in the south, showed predawn water potentials below  $-3$  and  $-3.5$  MPa, respectively. This resulted in a high proportion of non-producing trees, which is consistent with predawn water potential thresholds previously reported for *Q. ilex* (Alejano et al., 2008; Misson et al., 2011; Carevic et al., 2014b). When water potential falls below  $-3.5$  MPa stomatal closure and an important loss of hydraulic conductivity (e.g. Tognetti et al., 1998;

**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.  $\Psi_{pd}$  = Predawn water potential, LRT = likelihood ratio test,  $df$  = degrees of freedom,  $P$  =  $p$ -value,  $R_m^2$  = marginal pseudo $R^2$ ,  $R_c^2$  = conditional pseudo $R^2$ . Baseline was fixed to the northern locality and its interaction with competition.

Locality	Effect	LRT	df	P	Estimate	$R_m^2$	$R_c^2$
2012	$\Psi_{pd}$	36.12	1	<0.01	$0.88 \pm 0.39$	0.14	0.28
	Locality (South)	1.56	1	0.21	$-0.31 \pm 1.06$		
	$\Psi_{pd} * \text{Locality}$	15.28	1	<0.01	$2.55 \pm 0.69$		
2013	$\Psi_{pd}$	0.67	1	0.12	$0.84 \pm 0.55$	-	-
	Locality (South)	0.49	1	0.61	$-0.91 \pm 1.78$		
	$\Psi_{pd} * \text{Locality}$	1.49	1	0.22	$-0.91 \pm 0.75$		

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

In 2013, when climatic conditions were milder, predawn water potentials did not fall below  $-3.5$  MPa in any of the localities. In these conditions, main differences in summer water status were found only among the trees with the largest crops. Nearly all trees in small forest fragments showed moderate water stress ( $> -2.5$  MPa; Carevic et al., 2014), a condition that has been shown to enhance acorn production (Alejano et al., 2008; Carevic et al., 2010). Despite of the improved water status of trees in 2013, acorn production was not larger than in 2012 and forest interiors showed high proportions of non-producing trees. Lower pollen availability in 2013, unsuccessful pollination (García-Mozo et al., 2007) or endogenous cycles of acorn production (Siscart, 1999) could explain this pattern. Unfortunately, we do not have data on pollen emission rates or on the fate of female flowers to evaluate the first two hypotheses. As for individual resource limitation, we did not find significant correlations between current and prior year crops (data not shown), and long-term studies have shown that regular patterns in holm oaks acorn yields actually reflect temporal regularity of drought events (Pérez-Ramos et al., 2010). Xylem anatomy adjustments boosted by climatic conditions could explain the observed inter-annual variability in water potential thresholds. In holm oaks, moister conditions along the growing season can result in wider and less compacted xylem vessels resulting in improved hydraulic conductivity but lower resistance to cavitation (Corcuera et al., 2004; Abrantes et al., 2013). Thus, a wetter summer-spring in 2013 could have led to higher susceptibility to water shortage during acorn ripening. Since Mediterranean climate is characterized by a high inter-annual variability (Bolte, 2003), future studies combining physiological monitoring with tree-ring anatomy will help to draw a full picture of long-term effects of fragmentation on holm oaks acorn production.

Though we used a broad-brush approach to estimate crops, we could detect a significant effect of tree water-status on acorn production. Moreover, threshold-like responses observed here are consistent with previous work (Alejano et al., 2008; Carevic et al., 2010). However, we failed to detect significant differences between intermediate acorn scores and the variability explained by our crop-water status models in 2013 was relatively low. Probably, more quantitative estimations would have resulted in more clear patterns. However, other factors related to differences in habitat quality beyond changes in tree-to-tree competition cannot be ruled out (e.g. light, nutrients). For instance, the soils of small

**Table 5**

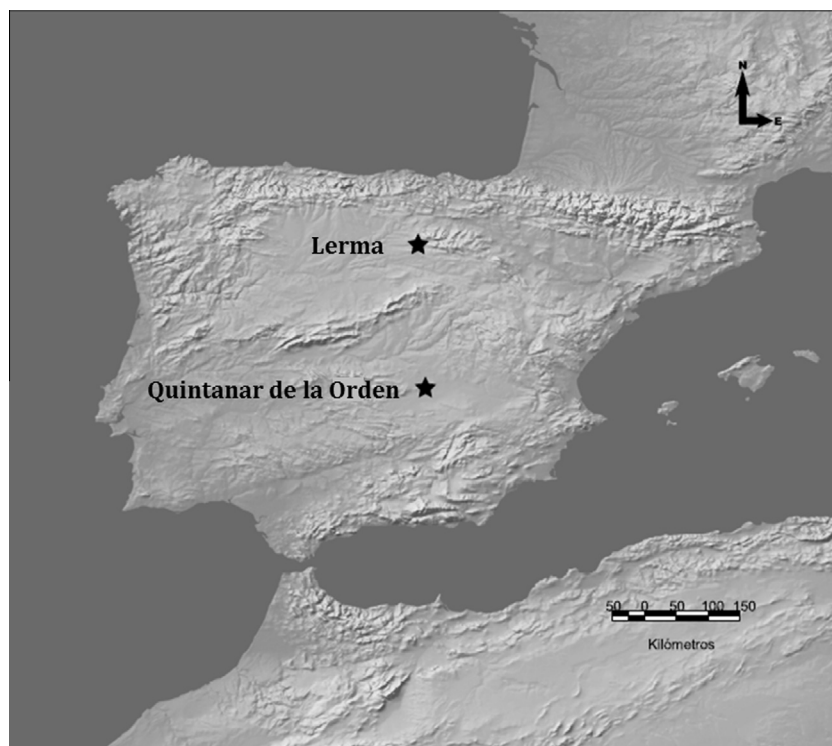
Summary of binomial mixed models to test the effects of predawn water potential (MPa), locality (north and south) and their interaction on the probability of not producing acorns in the (year 2012) and of showing the highest acorn production (year 2013). Non-produc = non-producing trees, highest-prod.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

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

forest fragments in the study area are characterized by higher nutrient availability (Flores-Rentería et al., 2015) and fertilization has been shown to stimulate acorn productivity in dense holm oak stands (Siscart, 1999). Changes in habitat quality in small forest fragments may have acted concomitantly with competition effects.

Contrary to the extended idea of negative effects of forest fragmentation on plant populations, our results show that relaxed tree-to-tree competition in small forest fragments enhance acorn production. In 2012, trees in forest interiors experienced predawn water potentials close to their point of hydraulic failure, while nearby ones located at small forest fragments only suffered a moderate water stress (according to Carevic et al., 2010), which resulted in a much higher acorn production. These results highlight the importance of local environmental conditions in modulating water shortage during the summer and illustrate how fragmentation can override the impacts of climate on acorn production. However, it is necessary to be cautious when interpreting these positive effects of forest fragmentation. Firstly, when scaling up at the population level, the scarcity of trees in extremely fragmented landscapes may supersede enhanced acorn production. For instance,

in the northern locality, where only 49% of trees in forest interiors produced acorns, in ten hectares there would be around 2000 producing trees. In the same locality, it would be only about 40 producing trees in intensively managed agricultural areas (assuming three small forest fragments on average within ten hectares of cropland). Secondly, forest fragmentation constrains acorn dispersal and net positive effects on holm oak regeneration will only occur if there is a higher probability of seedling recruitment in small fragments (Schupp et al., 2010). Eurasian jays (*Garrulus glandarius*) – main acorn disperser in Europe – are absent in small forest fragments (Brotons et al., 2004) and dispersal services provided by wood mice (*Apodemus sylvaticus*) are much poorer (Santos and Tellería, 1997; Morán-López et al., 2015). Besides, seedling dry out in open land microhabitats (Smit et al., 2008), can act as an important post-dispersal recruitment bottleneck in surrounding croplands. Therefore, to assess fragmentation effects on holm oak regeneration in a realistic way, all stages of the regeneration cycle need to be integrated (see Pulido and Díaz, 2005 for a similar approach in dehesas). Thanks to the wealth of studies on key processes of oaks regeneration cycle, we now have the pieces in place to develop such a global approach.



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

## 5. Conclusions

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

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## Appendix A

See Fig. A1.

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