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

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Abstract

Aim: 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 higher 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 effectiveness with increasing aridity. Frequency of recruited oaks increased with the total area of woodland remnants located at <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 *R. sphaerocarpa* and dispersal-related processes at local scale are main determinants of the colonization 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.

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 out-compete tree seedlings when colonizing 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 colonize 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.

Plant recruitment is tightly linked to seed availability and dispersal. Low seed input can be a major bottleneck slowing forest recovery after intense forest fragmentation: this is the case, for example, in the Mediterranean region following centuries of intensive land use (Rey Benayas et al. 2008). Many areas in the Mediterranean Basin are a mosaic of different crops with interspersed shrublands, pasturelands and small, if any, forest remnants.

Fast-growing pioneer shrubs has colonized much crop- and pastureland because of rural abandonment over the last 70 yr, while colonization by mid- and late successional forest species has progressed very slowly (Rey Benayas et al. 2015). As a result of the sparse, small forest patches, dispersible seeds are not in abundance and seed dispersion by animals is ineffective (McConkey & O'Farrill 2016); these propagule limitations are probably exacerbated by the harsh mediterranean climate. Seed availability and dispersal are likely to be such strong factors in plant recruitment that can influence nucleation regardless of the fact that nurse plants effectively mitigate stresses (Pausas et al. 2006). This occurs when seed rain is higher under the nurse canopy than in the gaps because animal dispersers disperse the seeds to nurse plants (Jordano & Schupp 2000; Verdú & García-Fayos 1996).

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

In this study, we analysed the relative importance of several factors on the colonization of Mediterranean shrublands by mid- and late successional woody species. These factors included the presence of nurse shrubs, herbivory, rainfall, size of forest remnants and their distance to regeneration sites. Since they operate at different spatial scales, we analysed their importance on the regional, landscape, local and microsite levels. We selected shrublands dominated by *Retama sphaerocarpa* (L.) Boiss (hereafter *Retama*) along an environmental gradient varying in aridity and herbivory. *Retama* is a leguminous shrub native to the Iberian Peninsula and northwest Africa that facilitates both annual herbs and woody species such as oaks (Cuesta et al. 2010; Armas et al. 2011; Rolo et al. 2013), which are the main structural species in many Mediterranean forests. In our study, nurse and beneficiary plant species were the same across the surveyed shrublands. This meant that we could attribute any observed changes in facilitation to changes in stress factors rather than to changes in the functional characteristics of interacting species.

We addressed the following questions: (1) does the recruitment of woody forest species under *Retama* shrubs increase with environmental stress, as predicted by the

SGH; (2) does the size of forest remnants and their distance to *Retama* shrublands affect colonization by forest species; and (3) does an increase in seed propagule pressure outweigh the negative effect of aridity on the colonization of *Retama* shrublands by woody species? We hypothesized that: (1) the relative importance of facilitation by *Retama* shrubs increases with environmental stress; (2) recruitment is enhanced by seed propagule pressure on a local scale (within shrubland), and this recruitment is related to the size of forest remnants and their distance to vegetation remnants that act as seed sources; and (3) the positive effect of seed availability on recruitment increases with decreasing environmental stress.

Methods

Natural history of the study area

The study area lies in the centre of the Iberian Peninsula (40°12′-40°49′ N, 3°20′-4°18′ W) and covers a surface area of *ca.* 6000 km². Altitude decreases southwards from 900 to 600 m a.s.l. The climate is mediterranean continental, with hot and dry summers and cold winters. Annual rainfall increases northwards from 400 to 700 mm, while mean annual temperature decreases from 15.5 to 12.5 °C. Most soils are acid and developed on granites, quartzite and arkose bedrock, although some sites in the southern part of the study area were on limestone and gypsum soils. The landscape is dominated by rain-fed cereal cropland, pastureland and shrubland. Some olive and almond groves occur in the southern part of the study area. Most shrublands are dominated by *R. sphaerocarpa, Cistus ladanifer* L., *Lavandula stoechas* Lam., *Genista hirsuta* Vahl and *Rosmarinus officinalis* L. The shrublands are used mainly for hunting and less frequently for extensive livestock grazing. Woodland occupies a small surface and consists of oak woodland remnants and monospecific pine plantations of variable size. Oak woodland remnants are dominated by *Quercus ilex* subsp. *ballota* (Desf.) Samp. (hereafter *Q. ilex*), *Quercus coccifera* L. and, less frequently, by *Quercus faginea* Lam, while pine plantations are mainly of *Pinus halepensis* Mill. and *Pinus pinea* L. The primary wild herbivores in the area are rabbits, hares, roe deer and wild boar. Abundance of rabbits increases southwards concomitant with decreasing rainfall and increasing temperature (Saldaña et al. 2007).

Recruitment sampling and explanatory factors

We randomly selected 29 patches of *Retama* shrubland (see Appendix S1 for detailed characteristics) using vegetation maps of the Regional Government of Madrid, the Geographic Information System for Agricultural Plots (SIGPAC®, available at http://sigpac.mapa.es/fega/visor/) and the Climatic Atlas of the Iberian Peninsula (Ninyerola

et al. 2005). For each *Retama* shrubland we recorded annual rainfall based on Ninyerola et al. (2005). *Retama* shrublands were considered eligible when they met the following criteria: (1) large enough to fit a 200 m × 5 m transect; (2) a high proportion of healthy adult *Retama* shrubs, i.e. individuals with a minimum height of 1.6 and minimum width of 1.5 m; and (3) <1000 adult *Retama* shrubs·ha⁻¹, ensuring the presence of relatively large gaps among individual shrubs. Mean area and density of *Retama* shrublands were, respectively, 19.0 ± 4.8 ha and 422 ± 28 shrubs·ha⁻¹ (Appendix S1). We discarded patches dominated by decaying *Retama* adults, which may have lower facilitation capacity (Schöb et al. 2013). We also avoided small *Retama* shrubs, since a minimum shrub size is needed for seedling facilitation (Allegrezza et al. 2016).

In each *Retama* shrubland, we randomly established a 200 m × 5 m belt transect and used a hand-held GPS receiver (Garmin 12XL, Olathe, US) to map all *Retama* shrubs with heights >1.6 m and width >1.5 m. We sampled a total of 1263 *Retama* shrubs. The numbers of established woody plants were counted in the area under each *Retama* shrub and in a paired control gap of similar size as the *Retama* shrub. Sampled gaps were located on the north side of the *Retama* shrubs, 1–2 m apart from the canopy. In this study, we refer to each pair of counting plots as a '*Retama* site' ($n = 1263$), and to the counting plots under the *Retama* canopy and gaps as a 'microhabitat' ($n = 2526$). In each microhabitat, we recorded the number of seedlings and saplings of vines, shrubs and tree species characteristic of mid- and late successional stages in oak woodlands. Early successional chamaephytes and shrubs such as *Thymus* sp., *Genista hirsuta* or *L. stoechas* were not considered. To avoid counting plants that had established prior to the establishment of the *Retama* shrub, we discarded saplings taller than one third of the *Retama* height. We also estimated herbivore relative abundance by counting the number of pellet droppings of rabbits, hares and ungulates present on a 50 cm × 50 cm quadrat randomly placed within each counting plot. Counting faecal accumulation has been used to estimate herbivore relative abundance (Marques et al. 2001).

We accounted for the effects of surrounding vegetation on recruitment of mid- and late successional woody species at two scales. At the local scale (within shrublands) we identified every patch of shrubland, olive grove, oak and pine woodland (including isolated trees) within a circular area (radius, 0.5 km) around each *Retama* site. Then we measured the area of each vegetation patch and its distance to the sampled *Retama* site using ArcView 3.2 GIS software (ESRI, New York, US). We chose the 0.5-km radius based on (1) the distance of acorn dispersal by the Eurasian jay (*Garrulus glandarius*), the major disperser of

Quercus seeds in Mediterranean woodlands, which is usually <0.5 km (Gómez 2003; Pons & Pausas 2007); and (2) the dispersal distance for small and medium-size frugivorous birds (Jordano et al. 2007). For each *Retama* site, we calculated an index of seed pressure potential (SPP) as:

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

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

Data analysis

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

Model selection was performed according to a backward, step-wise procedure and the principle of parsimony, in which the AIC and BIC served as indicators of both parsimony and likelihood (Burnham & Anderson 2002). First,

we fitted a saturated model including all fixed effects and the triple interaction to be tested (microhabitat × rainfall × SPP), and we compared the saturated model with a reduced model in which the triple interaction term was dropped (Round 1, Appendix S2). Second, we compared the model selected after Round 1 to models in which each pair-wise interaction was ignored (Rounds 2–3, Appendix S2). Then we compared the selected model after previous rounds with models that ignored main effects (Rounds 4–6, Appendix S2). If the difference in AIC or BIC between the reduced and full models was ≤2, then the simpler model was selected and the model was considered to have substantial support (Burnham & Anderson 2002). Parameter estimates and CIs of the best-supported model were obtained, and the pseudo-R^2 was used to estimate the variance explained by fixed and random factors (Nakagawa & Schielzeth 2013). All statistical analyses were performed using the packages '*lme4*', '*stats*' and '*piecewiseSEM*' in R v 3.2 (R Foundation for Statistical Computing, Vienna, AT).

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

Results

Recruitment survey

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

We recorded a total of 211 juveniles of four mid- and late successional woody species and a crop tree in the *Retama* shrublands, namely *Asparagus acutifolius* L. (96), *Q. ilex* (84 individuals), *J. oxycedrus* L. (27), *Rosa canina* L. (2), and *Prunus dulcis* (Mill) D.A. (2). Five *Retama* patches, corresponding to 17% of shrublands studied, lacked saplings of any woody species; *Q. ilex* saplings were not recorded in 12 *Retama* patches.

Factors influencing recruitment

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

Frequency of *Q. ilex* juveniles correlated positively with rainfall and the SPP of oak woodlands (Table 1, Fig. 3). SPP positively correlated with rainfall for all woodland types ($r = 0.49$, $P < 0.01$) and oak patches ($r = 0.53$, $P < 0.01$). However, the lack of significance of the interaction microhabitat × rainfall × SPP showed that the increasing differences in recruited plants between both microhabitat types (gaps vs under *Retama* canopy) was not confounded by higher potential seed pressure in the *Retama* shrublands located in the wettest sites of the study area. In other words, SPP may determine the extent of recruitment, but not the direction of the interaction between microhabitat and rainfall. When the two components of oak SPP, oak forest patches area and distance, were analysed separately, frequency of *Q. ilex* juveniles correlated positively with total area of oak woodland patches located <0.5 km from *Retama* sites (Fig. 4a). In contrast, no s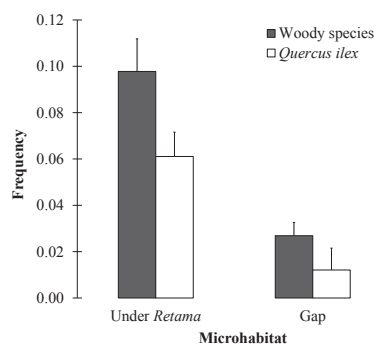ignificant relationship was found between *Q. ilex* juvenile frequency and mean distance to the oak forest patches located <0.5 km from *Retama* site (Fig. 4b).

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

Discussion

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

Facilitation of plant recruitment in *Retama shrublands*

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

Retama can also recruit mid- and late successional woody species by attracting seed-dispersing animals (Verdú & García-Fayos 1996). All recruited woody species found in this study were zoochorous (Pemán et al. 2012). For the endozoochorous species, frugivorous birds may use *Retama* shrubs as perches, which leads to seed rain beneath *Retama* (Verdú & García-Fayos 1996; Aerts et al. 2006). For oaks and other nut-producing species, rodents and some corvids such as the Eurosiberian jay and magpies are major dispersers (Gómez 2003; Pons & Pausas 2007; J. Castro, M. Molina-Morales, A.B. Leverkus, L. Martınez-Baroja, L. Perez-Camacho, P. Villar-Salvador, S. Rebollo, & J.M. Rey-Benayas, unpubl data). Rodents prefer to

Fig. 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 SE.

Table 1. Mean value and 95% CI for each estimated parameter in the selected models for the recruitment of all woody species or only of *Q. ilex* in *Retama* shrublands. For both models, 'under *Retama*' is the reference level for the microhabitat factor.

Selected Model	All Woody Species Microhabitat + Rainfall		Quercus Ilex Microhabitat × Rainfall + SPP$_{oak}$	
Parameter	Mean	CI	Mean	CI
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
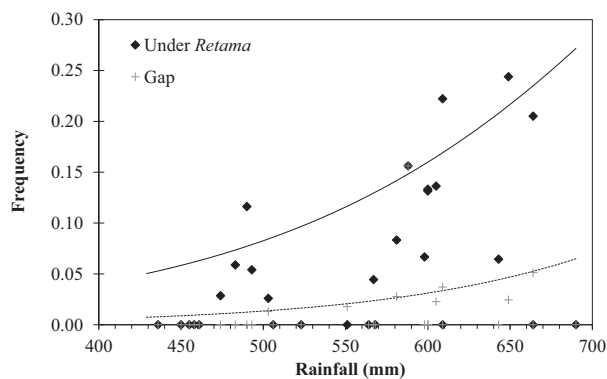
Fig. 2. Relationship between recruitment of *Q. ilex* under the *Retama* canopy and in gaps in the central part of the Iberian Peninsula and rainfall. The black solid and dashed lines depict predicted recruitment under *Retama* canopy and in gaps, respectively. Recruitment was predicted by the best model 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.

disperse acorns to shrubs, but they consume most cached acorns before seedling emergence (Perea et al. 2011). European jays (Gómez 2003; Pons & Pausas 2007) and likely magpies (Castro et al. 2017) cache acorns not only in woodlands but also in open areas in heterogeneous landscapes. We hypothesize that *Retama* shrubs can act as singular landscape elements for acorn dispersal by corvids. Large shrubs such as *Retama* may be safe landmarks (*sensu* Vander Wall 1990) for acorn caching and recovery (Gómez 2003). Future studies are needed to corroborate the role of corvids and rodents in *Q. ilex* colonization of Mediterranean shrublands.

A major finding of our study is that differences in the recruitment of *Q. ilex* between microhabitat types increased with decreasing environmental severity, which does not support our first hypothesis related to the SGH (Bertness & Callaway 1994). Our results also contrast with those reported by Armas et al. (2011) in which facilitation of herbs by *Retama* shrubs increased with aridity. These differences might be explained by functional differences

between beneficiary species (Maestre et al. 2009). Consistent with our finding, Maestre & Cortina (2004) reported that as aridity increases, facilitative interactions decrease between the nurse grass *Stipa tenacissima* and the beneficiary shrub *Pistacia lentiscus*. Similarly, positive plant–plant interactions have been predicted to be more intense and frequent at moderate rather than extreme stress levels (Holmgren & Scheffer 2010). At the same time, our failure to observe the facilitation–stress relationship predicted by the SGH may reflect the action of multiple stress factors acting in different directions, or of changes in the competitive network of the beneficiary plant species (Cuesta et al. 2010; Soliveres et al. 2011a, 2015).

The role of vegetation remnants as seed sources in Mediterranean shrublands

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

At the shrubland scale, recruitment of *Q. ilex* seedlings correlated with the total area of oak remnant patches but not with their distance to *Retama* shrubs (Fig. 4). This indicates that, on a local scale, *Q. ilex* recruitment to Mediterranean shrublands is limited more by the amount of seeds and, probably, seed dispersal (McConkey & O'Farrill 2016)
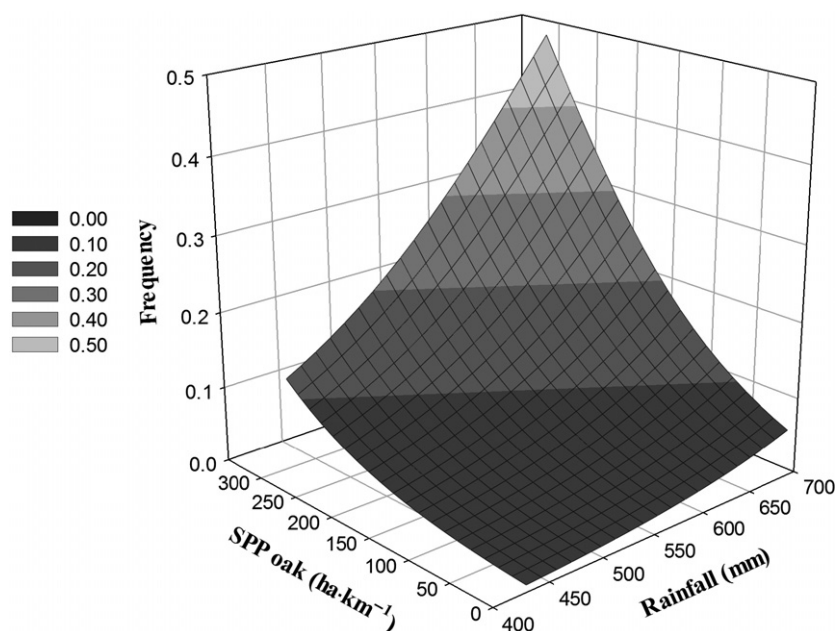
Fig. 3. Predicted *Q. ilex* recruitment under the *Retama* canopy as a function of rainfall and oak seed pressure potential in surveyed *Retama* shrublands in the central part of the Iberian Peninsula.
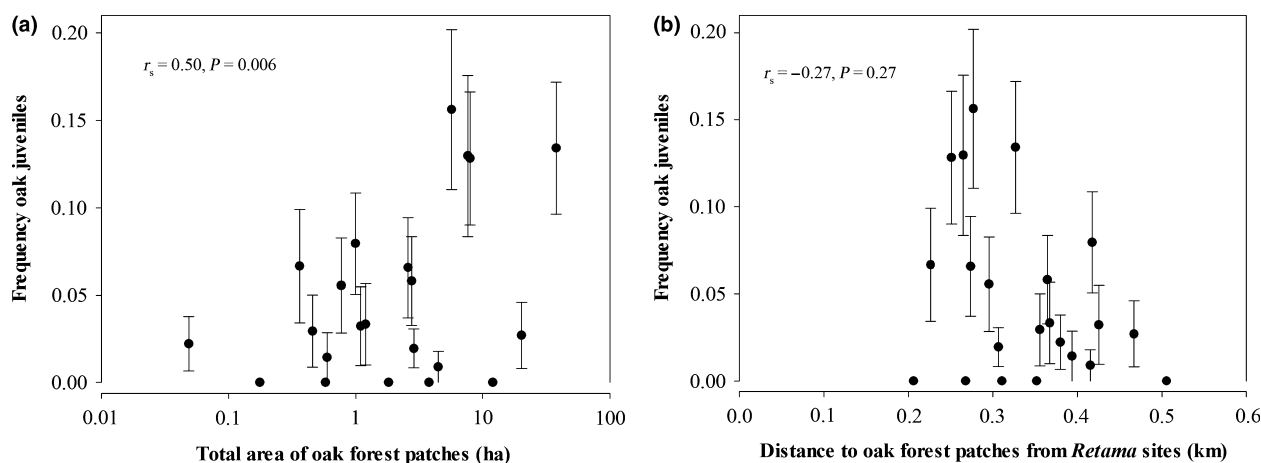

Fig. 4. Frequency of *Q. ilex* seedlings in relation to the two components of *Q. ilex* seed pressure potential (SPP$_{oak}$): (**a**) total area of oak forest patches at distances <0.5 km from *Retama* sites, and (**b**) mean distance of *Retama* sites to oak forest patches located within an area of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

than by the distance to seed sources. In contrast, Verdú & García-Fayos (1998) found that recruitment of the endozoochorous shrub *Daphne gnidium* in an abandoned olive grove decreased with distance to the seed source, although the proposed model failed to explain dispersion at distances >250 m. The discrepancy between this study and our work may reflect differences in the disperser: European jays disperse *Q. ilex* acorns at distances of 250–500 m (Gómez 2003; Sheffer et al. 2013), consistent with the mean distance between *Retama* shrubs and patches of oak remnants.

In contrast to our results for *Q. ilex*, we did not find any relationship between recruitment frequency and SPP when we analysed all woody species together. This suggests different dispersal constraints acting on different woody species colonizing *Retama* shrublands. *J. 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-sized 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 colonization 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).

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

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

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