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Long-term dynamics of shrub facilitation shape the mixing of evergreen and deciduous oaks in Mediterranean abandoned fields

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ABSTRACT

1. The slow recovery of Mediterranean forests after field abandonment is mainly due to stressful conditions for seedling establishment. In this context, shrubs play a critical role in facilitating tree recruitment, but how this process unfolds after field abandonment is not entirely known. We evaluated the long-term dynamics of facilitation by the nurse shrub *Retama sphaerocarpa* in the recruitment of two ecologically contrasting oaks, the evergreen *Quercus ilex* and the deciduous *Quercus faginea*.
2. Thirty years after field abandonment, we dated shrubs and oak established to calculate the annual recruitment rate and temporal recruitment pattern. For oaks we differentiated oak recruitment at each microsite (i.e., open or under shrub). To assess how nurse shrubs modulated environmental stressors, we modelled oak recruitment as a function of climatic variables. For the evergreen oak, we assessed these effects within each microsite. Finally, we estimated the annual facilitative effect of the shrubs as a function of climatic conditions.
3. Each species showed different recruitment pulses during colonization. Recruitment rate was the highest for the shrub, followed by the evergreen oak. Oak colonization under shrubs was appreciable 20 years after field abandonment when shrub cover reached 2.2% and concentrated under medium and large shrubs older than 7 years. Shrubs not only accelerated evergreen oak colonization but also attenuated the fluctuations of recruitment pulses. For the evergreen oak, the facilitative effect of the shrub was higher in years with more arid summers (precipitation < 47 mm and heat waves longer than eight days) and switched to competition in wetter summers.
4. *Synthesis.* Oak colonization in Mediterranean abandoned fields progressed slowly but two decades after abandonment pioneer shrub population grew to a level in size and number that could effectively trigger facilitation and accelerate tree recruitment. The shrub nurse effect was unbalanced between oak species, only benefiting the evergreen

oak, and was more prevalent in arid years. Our study illustrates the built-up of shrub facilitation during forest recolonization and the varying nature of this process among climatically different years and ecologically distinct species. This information provides insights for assessing and managing Mediterranean forest recovery.

Keywords: colonization, facilitation, forest dynamics, forest recovery, nurse shrub, *Quercus*, recruitment pulses, secondary succession, *Retama sphaerocarpa*

Resumen

La lenta recuperación de los bosques mediterráneos después del abandono de campos agrícolas se debe principalmente a las condiciones de estrés durante el establecimiento de las plántulas. En este contexto, los arbustos juegan un papel crítico en la facilitación del reclutamiento de los árboles, pero no se conoce bien como este proceso evoluciona tras el abandono de los campos. En este trabajo se evalúa a largo de un periodo prolongado la dinámica de facilitación del arbusto nodriza *Retama sphaerocarpa* sobre dos quercíneas de ecología contrastada: la perennifolia *Quercus ilex* (encina) y la caducifolia *Quercus faginea* (quejigo).

Treinta años después del abandono de los campos, datamos los arbustos y quercíneas establecidos para calcular las tasas anuales y los patrones temporales de reclutamiento. Para las quercíneas, diferenciamos el reclutamiento en cada micrositio (es decir, en sitios abiertos o bajo el arbusto). Para evaluar cómo los arbustos nodriza modularon los efectos del estrés ambiental, se modelizó el reclutamiento en función de variables climáticas. Finalmente, estimamos el efecto facilitador de los arbustos en función de las condiciones climáticas anuales.

Cada especie mostró diferentes pulsos de reclutamiento durante la colonización. Las tasas de reclutamiento más altas fueron las del arbusto, seguidas de las de la encina. La colonización de quercíneas bajo los arbustos empezó 20 años después del abandono de los campos, cuando la cobertura de matorral alcanzó el 2.2%, y se concentró bajo los arbustos medianos y grandes, mayores de 7 años. Los arbustos no solo aceleraron la colonización de la encina, sino que también atenuaron las fluctuaciones de sus pulsos de reclutamiento. El efecto facilitador de los arbustos en el reclutamiento de encina fue mayor en los años con veranos más áridos (es decir, con precipitación < de 47 mm y olas de calor más largas de 8 días), pero cambió a competencia en los veranos más húmedos.

Síntesis. La colonización de las quercíneas en campos abandonados mediterráneos progresó con lentitud, pero dos décadas después del abandono, el tamaño de la población de arbustos pioneros y el de sus individuos creció hasta un nivel que permitió desencadenar la facilitación y acelerar el reclutamiento de los árboles. El efecto facilitador de los arbustos fue desigual entre las dos quercíneas, beneficiándose sobre todo la perennifolia y principalmente en los años más áridos. Nuestro estudio ilustra la progresión de la facilitación por arbustos durante la recolonización del bosque y la naturaleza variable de este proceso entre años climáticamente diferentes y especies ecológicamente distintas. Esta información abre nuevas perspectivas para entender y gestionar la recuperación del bosque mediterráneo.

INTRODUCTION

Plants have to overcome several abiotic environmental filters to establish (Harper, 1977; Lortie et al., 2004). Positive and negative biotic interactions, particularly facilitation and competition, modulate the effect of such filters (Connell & Slatyer, 1977; Pulsford, Lindenmayer, & Driscoll, 2016). In forest succession, plant colonizers can facilitate the establishment of mid- and late-successional plant species into the community through environmental modifications (e.g., Butterfield et al., 2010). Generally, the importance of facilitation increases with environmental stress (the so-called Stress Gradient Hypothesis; Bertness & Callaway, 1994). However, plant-plant interactions can be dominated by competition if environmental conditions become very stressful and the abiotic stress is resource driven (e.g., by water shortage, light competition) and (Maestre, Callaway, Valladares, & Lortie, 2009; Maestre, Valladares, & Reynolds, 2005).

In arid and semi-arid ecosystems such as those found in Mediterranean-climate areas, high irradiance and drought are the main abiotic factors affecting early plant establishment (Joffre, Rambal, & Damesin, 2007; Sánchez-Gómez, Valladares, & Zavala, 2006), constraining spring seedling emergence and first-summer survival (Gómez-Aparicio, Zamora, Gómez, Hódar, & Castro, 2004; Mendoza, Gómez-Aparicio, Zamora, & Matías, 2009). Semi-arid ecosystems also show high inter-annual climatic variation that can cause irregular recruitment pulses (Giorgi & Lionello, 2008; Kouba, Camarero, & Alados, 2012; Pérez-Ramos, Padilla-Díaz, Koenig, & Marañón, 2015; Pugnaire, Luque, Armas, & Gutiérrez, 2006). Thus, chronic water stress and inter-annual climatic variation slow down forest recovery after disturbance (Rey Benayas, Martínez-Baroja, Pérez-Camacho, Villar-Salvador, & Holl, 2015).

Under these conditions, shrubs can ameliorate environmental stressors at minimum competitive costs (Gómez-Aparicio, 2009), facilitating the establishment of mid- and late-successional woody species. Nurse shrub can ameliorate abiotic environmental constraints (i.e., direct facilitation; Gómez-Aparicio, Zamora, Gómez, Hódar, & Castro, 2004), but also attract seed dispersers and reduce herbivory or competition with other plants (i.e., indirect facilitation;

Cuesta, Villar-Salvador, Puértolas, Rey Benayas, & Michalet, 2010; Perea, López-Sánchez, & Dirzo, 2017). The facilitative effect of shrubs have been related to specific functional attributes such as plant size (Alday, Zaldívar, Torroba-Balmori, Fernández-Santos, & Martínez-Ruiz, 2015; Navarro-Cano, Goberna, Valiente-Banuet, & Verdú, 2016) and the ability to fix nitrogen into the soil (Gómez-Aparicio et al., 2004).

The presence of nurse shrubs could be particularly relevant in facilitating the recruitment of less stress tolerant and more palatable species (Gómez-Aparicio, Zamora, Castro, & Hódar, 2008; Liancourt, Callaway, & Michalet, 2005), allowing the coexistence of ecologically distinct species (Bruno, Stachowicz, & Bertness, 2003). In Mediterranean forests, like our study system, evergreen and deciduous oaks frequently co-occur (Madrigal-González et al., 2017). Evergreen oaks have more robust leaves with more leaf mass per area and less N concentration than deciduous oaks (Castro-Díez, Villar-Salvador, Pérez-Rontomé, Maestro-Martínez, & Montserrat-Martí, 1997; Gil-Pelegrín, Peguero-Pina, & Sancho-Knapik, 2017). These traits are usually linked to high drought tolerance and low palatability in oak species (Corcuera, Camarero, & Gil-Pelegrín, 2002; Quero, Villar, Marañón, & Zamora, 2006). Thus, we could expect deciduous oaks to be more dependent on nurse shrubs for their recruitment and evergreen oaks establishing earlier than deciduous oaks during forest succession in open environments.

Most research on facilitation has been addressed by short-term studies. However, some works have focused in the shifts of facilitation over ontogenetic stages of the nurse shrub or of the benefactor (Alday et al., 2015; Moreno-Gutiérrez, Battipaglia, Cherubini, Delgado Huertas, & Querejeta, 2015; Navarro-Cano et al., 2016), whereas others have assessed the effect of inter-annual climatic variations on facilitation (Butterfield et al., 2010). Despite these efforts, as far as we know, a long-term and holistic approach evaluating how the facilitative effects may evolve after field abandonment has never been addressed. This knowledge gap hinders our understanding of the dynamics associated with facilitation in plant community recovery (Bertness & Callaway, 1994; Maestre et al., 2005). For example, we know little about how long after field abandonment the nurse shrub community takes to start facilitating recruitment of other species, how the effects of facilitation vary among competing beneficiary species, and how these effects vary with environmental conditions.

To investigate the dynamics of nurse shrub facilitation after field abandonment we studied colonization dynamics of a Mediterranean oak forest over 30 years. Specifically, we assessed the effect of the nurse shrub *Retama sphaerocarpa* (L.) Boiss. (hereafter retama) on the long-term recruitment of the evergreen *Quercus ilex* L. and the deciduous *Quercus faginea* Lam. Our objectives were to: (1) compare the long-term recruitment dynamics of the nurse shrub and the oaks after field abandonment; (2) quantify the time lag between field abandonment and the observed nurse shrub facilitative effect on oak colonization; and (3) evaluate the differential effects of the nurse shrub on the two oak recruitment patterns and the climatic constraints that limit the recruitment. We hypothesised that: (1) recruitment patterns follow temporal pulses that differ among pioneer nurse shrubs and mid- or late successional oaks; (2) there is a time lapse between field abandonment and the acceleration of oak recruitment linked to shrub size and the development of shrub population; and (3) oak recruitment under nurse shrubs is decoupled from recruitment in open sites due to buffering of harsh climate conditions, especially for the deciduous oak which is less drought tolerant. Understanding how climate and facilitation drive the temporal patterns of oak recruitment will allow for more informed assessment of future forest recovery and a better design of restoration efforts.

METHODS

Study area

The studied abandoned fields are located on two flat fluvial terraces of the Jarama river in Uceda, Central Spain (700-750 m a.s.l., UTM X: 462 830; UTM Y: 4 524 000; ETRS89 30N; **Figure 4.1a**). The area has a continental Mediterranean climate, with a mean annual temperature of 13 °C that ranges between 23 and 4 °C in the hottest and coldest months, respectively. The annual rainfall is 500 mm, being *c.* 60 mm during the summer (Tornero Sánchez, 1998). Soils are mainly alfisols and inceptisols, with sandy loam to sandy clay loam textures (Peñuelas-Rubira et al., 1996). Agricultural use ceased in *c.* 1984, although extensive sheep and goat grazing has remained in the area. Since 1985, the fields have progressively changed to a shrubland dominated by retama, a leguminous shrub and a paradigmatic nurse species in the Mediterranean basin (Andivia, Villar-Salvador, Tovar, Rabasa, & Rey-Benayas, 2017; Cuesta et al., 2010; Pugnaire et al., 1996). The abandoned fields are adjacent to mixed forests dominated by *Quercus ilex* and *Q. faginea* in different proportions (**Table S12.1**). In 2017, when our fieldwork took place, the density of *Q. ilex* and *Q. faginea* juveniles were 45 ± 49 and 15 ± 31 individual ha^{-1} [mean ± sd], respectively (Kruskal-Wallis $\chi^2 = 9.17$; $p = 0.002$).

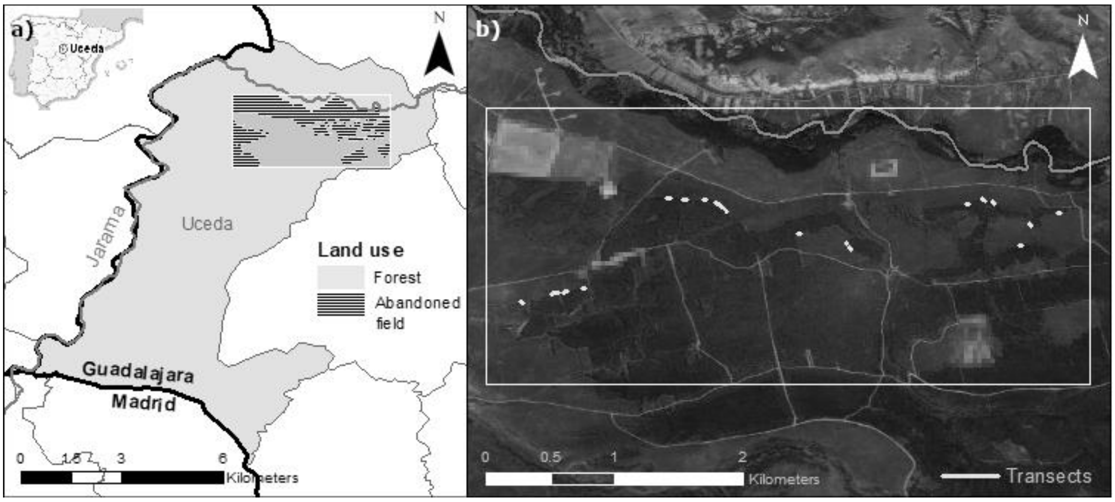

Figure 4.1. a) Location and current land use in the study area (land use categories are modified from the Spanish Forest Map (SFM 1:50000, http://www.mapama.gob.es/). b) An aerial photograph of the study area with the location of the 20 transects where retama and oak recruitment was sampled.

Field work and oak recruitment dating

In the abandoned fields, we surveyed 20 rectangular transects (20 x 60 m) perpendicular to the forest border (**Figure 4.1b**). In the adjacent forest, the diameter at breast height (dbh) of each oak species was measured in one 20 × 35 m plot next to each transect. In each plot, basal area was calculated using individuals with dbh > 8 cm. The location of transects was selected to sample a wide range of shrub covers and abundances of the two oaks representative of the adjacent forest (**Table S12.1**).

In each transect, we located and harvested all juvenile oaks (105 evergreen oaks and 36 deciduous oaks) during early spring of 2017. To harvest the juveniles, we excavated the ground around the upper part of the tap root and cut a transversal section at the root collar, i.e., slightly below the ground level (**Figure S13.1a**). The microsite where oak juveniles grew was recorded as "open" or "under shrub". We then used a dendrochronological approach to date the year of oak recruitment (details in **Appendix S13**) and reconstructed the retama shrubland structure along time using allometric models (details in **Appendix S14**). To ensure that we assigned the right microsite during recruitment, some records under shrub were corrected to open if 1) the oak was older than the shrub (15 cases in 7 transects — 25% of all records -), or 2) the shrub was < 5 years older than the oak and the distance between the oak and shrub stems was less than the predicted crown radius of the shrub in the oak recruitment year (5 cases in 3 transects — 8% of all records -).

Climate data

We downloaded daily weather data for the study period (1985 to 2014) from nine meteorological stations close to our study area (http://www.aemet.es/es/datos_abiertos/AEMET_OpenData; **Figure S12.2**). We interpolated the maximum temperature and the precipitation to our study area using the *meteoland* package (De Cáceres, Martin, Granda, & Cabon, 2018) in R 3.4.3 (R Core Team, 2017). This method interpolates climatic data to a specific area by correcting the original data according to the proximity and elevation differences between the meteorological station and the target area. For each year, we calculated spring precipitation as the sum of April and May precipitation, the summer precipitation as the sum of July, August and September precipitation, and the length of heat waves as the maximum number of consecutive days with maximum temperature ≥ 33 °C.

Data analysis

Long-term dynamics of retama and oak recruitment

We calculated recruitment rate (no. recruits transect^{-1} year^{-1}) of retama, evergreen and deciduous oaks from 1985 to 2014. We used a generalized additive model to analyse the recruitment rate of each species over time. For the evergreen oak we differentiated between microsites, open and under shrub. We could not account for microsite differences for the deciduous oak due to the low number of recruits under shrub. We choose a Poisson error distribution and the smoothing spline method to fit the models with the *gam* package (Hastie, 2018) in R 3.4.3 (R Core Team, 2017). We used the Akaike Information Criterion (AIC; Burnham & Anderson, 2002) to compare models adjusted with different number of knots (i.e. data division points), and we selected the number of knots resulting in minimum AIC (e.g. in Thorson, Punt, & Nel, 2012).

Oak colonization in relation to nurse shrub structure

We studied the relationship between oak recruitment and the structure of the retama shrubland (i.e. density and size structure of shrubs) with a three-step analysis. First, we adjusted generalized additive models for the accumulated recruitment (total and per microsite) of both oak species (recruits transect^{-1}), using the year as explanatory variable and the model details (i.e. error distribution, algorithms and number of knots) described in the previous section. Second, we identified change points over the fitted curves (i.e. the first year of a new regime of variance of accumulated recruitment) using the *cpt.var* function of the *changepoint* package (Killick, Haynes, & Eckley, 2016). The change point was identified with the *PELT* method and the penalty set manually based on the elbow plot criterion (**Figure S12.3**). Change points represented acceleration in the recruitment when they separated curve segments of increasing slope. Third, we compared the change years of the accumulated oak recruitment with the change years in each microsite to assess if the acceleration of the oak recruitment was due to recruitment under shrub (i.e. facilitated recruitment). Then, we described the density and size structure of the shrubland when facilitated recruitment occurred.

To study the relationship between oak recruitment and retama size, we compared (1) the maximum branch diameter of nurse retamas (i.e. with oaks recruited under their canopies) and of retamas without recruits using a Kruskal-Wallis test; and (2) the size structure of the retama populations with and without recruited oaks. For the comparisons, we only used the data of years with oak recruitment under shrub for each transect.

Shrub modulation of the climatic effects on oak recruitment

To assess the effect of climatic variables on the evergreen oak recruitment rates, and how the nurse shrubs might have influenced this process, we used the annual oak recruitment rates estimated since 2005, which was the recruitment year of the oldest oak found under shrub. The deciduous oak had not enough recruits under shrub to make this analysis, so we assessed only the effect of the climate in total recruitment. We focused on climatic conditions during spring and summer, the most limiting periods for seedling survival (Gómez-Aparicio et al., 2004; Mendoza et al., 2009). We selected climatic variables that drive spring emergence (spring precipitation in mm, $SpPrec_i$) and summer survival (summer precipitation in mm, $SuPrec_i$; length of heat waves in no. days, $HtWaves_i$). To control for differences on seed availability among transects, we included the basal area of each target species in the adjacent forest (BA_i, m^2 ha^{-1}). We also considered the year of recruitment as a random variable (YRE) to account for temporal processes not included in the previously explained variables such as masting. For each transect *i* and year *y* the observed number of recruits per microsite ($Count_{i,y,microsite}$) was analysed as:

Likelihood: $Count_{i,y,microsite} \sim Poisson\ (\lambda_{i,y,microsite})$

Process model:

$$\ln(\lambda_{i,y,microsite}) = \alpha_i + \beta \cdot BA_i + \gamma 1_{microsite} \cdot SpPrec_y + \gamma 2_{microsite} \cdot SuPrec_y$$

$$+ \gamma 3_{microsite} \cdot HtWaves_y + YRE_y + \varepsilon_{i,y} \qquad \textbf{Eq. 4.1}$$

We also included an error term $\varepsilon_{i,y}$ to account for over-dispersion in the recruitment rates (i.e., the variance of the number of recruits was higher than the mean; Kéry, 2010).

We estimated the parameters in **Eq. 4.1** with a Bayesian approach and non-informative hyperparameter values (Simpson, Rue, Martins, Riebler, & Sørbye, 2015). We used the *rjags* package (Plummer, 2016) in R 3.4.3 (R Core Team, 2017) and simultaneously ran three Markov chains with a burn-in period of 500000 iterations and a sampling period after convergence of 100000 iterations, during which we recorded the parameter thinning every 100th iteration (see **Table S12.2** for results of convergence diagnosis).

To assess if the effect of the shrub on oak recruitment varied across years as a function of climatic conditions, we estimated the effect size of shrub facilitation on evergreen oak establishment (i.e. facilitative effect). This effect was estimated as the difference between oak recruitment under shrub and recruitment in open sites, in years and transects when at least one oak recruited (Gómez-Aparicio et al., 2004). We could not calculate the facilitative effect for the deciduous oak due to the lack of recruitment under shrub. We then run linear mixed models to ascertain the extent of the facilitative effect; we used quadratic and linear variants, as a function of each climatic variable (i.e., spring precipitation, summer precipitation or length of heat waves, all standardized). We used *lmer* function of *lme4* package in R 3.4.3 to fit the models, with a Gaussian error distribution (Bates et al., 2017; R Core Team, 2017). To account for the higher chances of recruiting under a shrub with increasing shrub cover, we included shrub abundance (i.e., the sum of the basal area of each shrub's widest branch, m^2 ha^{-1}, standardized) as a covariate in the models. We also included transect as a random effect to account for fine grain environmental heterogeneity related to the clustered nature of our sampling.

RESULTS

Dynamics of retama and oak recruitment

All species showed two pulses of recruitment that varied in amplitude (i.e. maximum recruitment rate) and length (i.e. duration of the pulses; **Figure 4.2**, **Table S14.1**). Species recruitment pulses occurred at different years, in 2001 and 2013 for retama, 1994 and 2008 for the evergreen oak, and 1999-2000 and 2008 for the deciduous oak. The second pulse was higher than the first pulse for the three species (**Figure 4.2**). The amplitude and length of retama recruitment pulses were remarkable higher than those of oak species (**Figure 4.2a**). Pulses of deciduous oak recruitment were less ample and more episodic than pulses of the evergreen oak (**Figure S15.1**, violin plots in **Figure 4.2b,c**). Specifically, the deciduous oak had many years with no recruitment at all between 1985 and 1996 and its recruitment became more regular after 1997 but at a lower rate than the recruitment of the evergreen oak.

The observed recruitment of evergreen oaks under shrub started in 2005 (**Figure 4.2b**), 20 years after field abandonment. After that year, evergreen oak recruitment density was 1.5 times greater under shrub than in open areas. This recruitment under shrub represented 38% of total evergreen oak recruitment in the studied period (1985 and 2014). After the peak recruitment in 2008, recruitment rates remained constant under the shrub but considerably decreased in the open areas (**Figure 4.2b**). There were only three recruits of the deciduous oak under shrub (i.e. 9% of total deciduous oak recruitment), all of them in 2008.

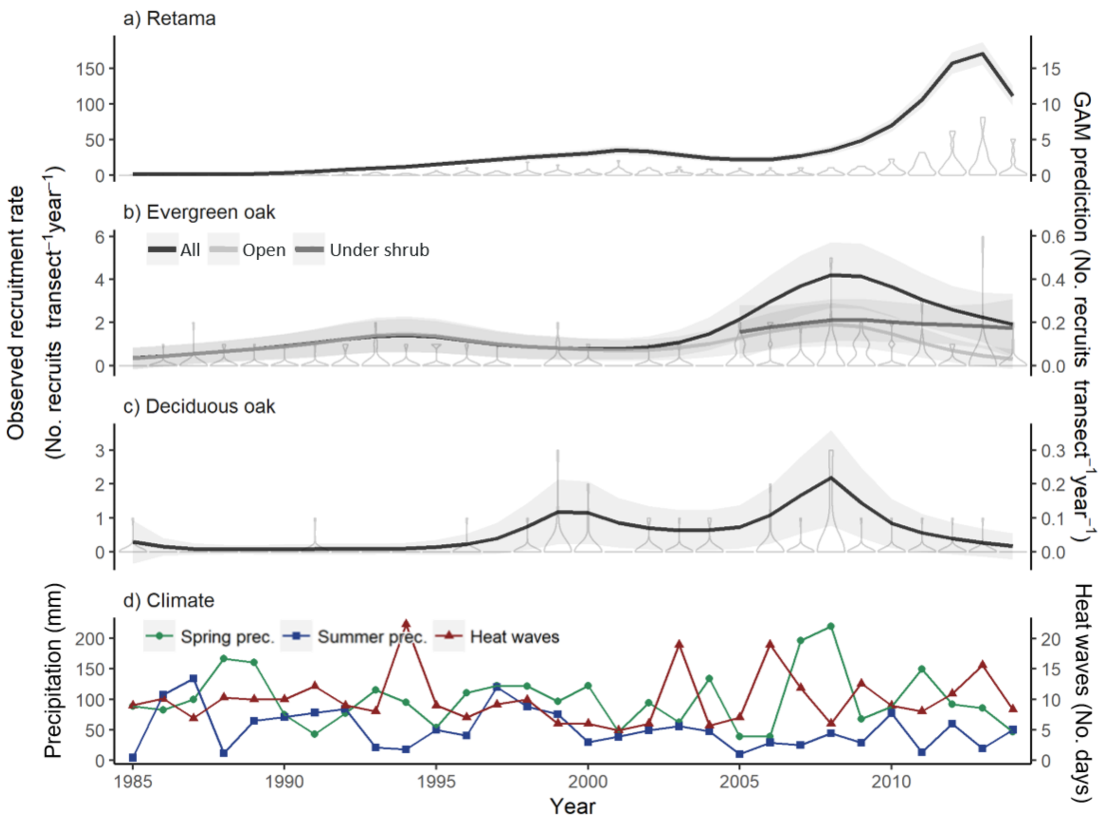

Figure 4.2. Predicted (lines) and observed (violin plots) recruitment rate over time of: (a) the nurse shrub *Retama sphaerocarpa* (retama); (b) *Quercus ilex* (evergreen oak); and (c) *Quercus faginea* (deciduous oak). For the evergreen oak, predicted recruitment rates in open and under shrub microsites is also shown. Note that the scale of recruitment rate differs among species and that all violin plots are represented with the same maximum width. (d) Spring and summer precipitation and length of heat weaves along the study period.

Oak colonization in relation to nurse shrub structure

The change point analysis revealed that total oak recruitment accelerated twice during the study period, between 1991 and 1992 and between 2004 and 2005 (black line in **Figure 4.3a, Figure S4.2**). While the first change coincided with an acceleration of oak recruitment in open areas, the second change coincided with the beginning and acceleration of oak recruitment under shrub (2005-2006; **Figure 4.3a**). By 2005, the estimated retama shrubland density was 276 ± 246 [0-1108] shrubs ha^{-1} (mean ± sd [min-max]), and retama canopy cover was 2.21 ± 1.80% [0-7.16%]. Most of the shrubs were small (branch diameter < 10 mm) or medium (branch diameter 10-40 mm, **Figure 4.3b**).

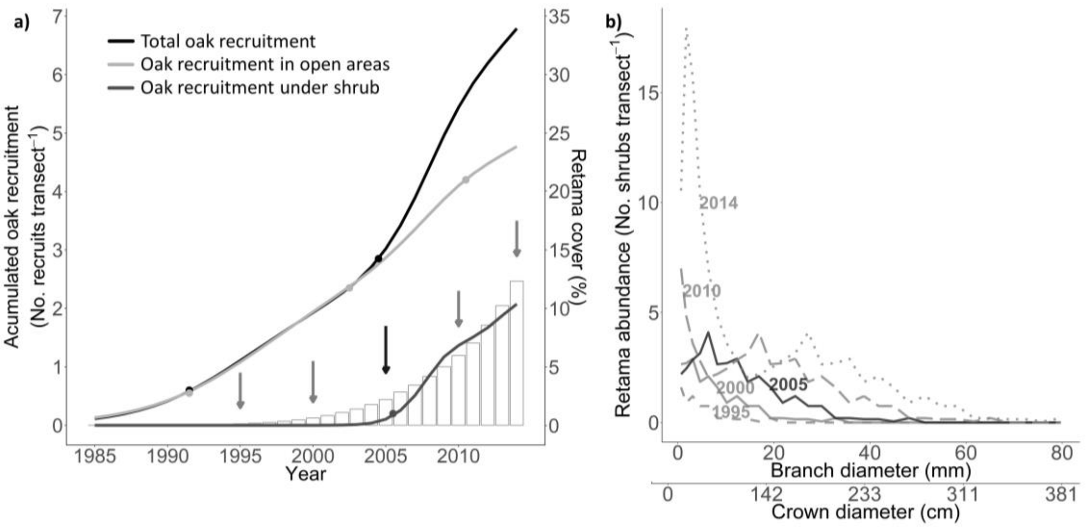

Figure 4.3. a) Accumulated recruitment over time (lines) for both oak species together and cover of the nurse shrub *Retama sphaerocarpa* each year (bars). The dots on lines represent change points in the temporal series of oak recruitment (i.e. acceleration in the recruitment rate when the curve has an increasing slope). The arrows represent the years selected to show the size structure of retama shrubland in panel b. The black arrow represents the change point when oak recruitment under shrub started. b) Size structure of retama shrubland in the abandoned fields for the selected years.

Retamas with recruited oaks underneath were larger (25.4 [8.2-65.1] mm of branch diameter and 168.6 [75.4-329.2] cm of crown diameter; mean [min-max]) than retamas without oaks (14.5 [0.6-76.0] mm and 112.9 [12.4-367.4] cm, respectively; Kruskal-Wallis $\chi^2 = 25.4$; $p < 0.001$). Oak recruitment only took place in a small fraction (3.1% [0.5-9.1]) of the retama population, but this fraction was higher when only big (branch diameter > 40 mm) or medium retamas were considered (15% [0-100] and 5.4% [0-16.7], respectively). Oak recruits were recorded only under retamas that were at least 7-8 years old with branch and crown diameters > 8 mm and 74 cm, respectively (dashed vertical line in **Figure 4.4**). Most of the retamas that contained oaks under their canopy were medium-sized (85.7%; shaded area in **Figure 4.4**), which represented 57.9% of all the shrubs. In contrast, small and big retamas contained only 5.7% and 8.6% of the oak recruits, respectively, and represented 39.3% and 2.8% of the shrubs, respectively.

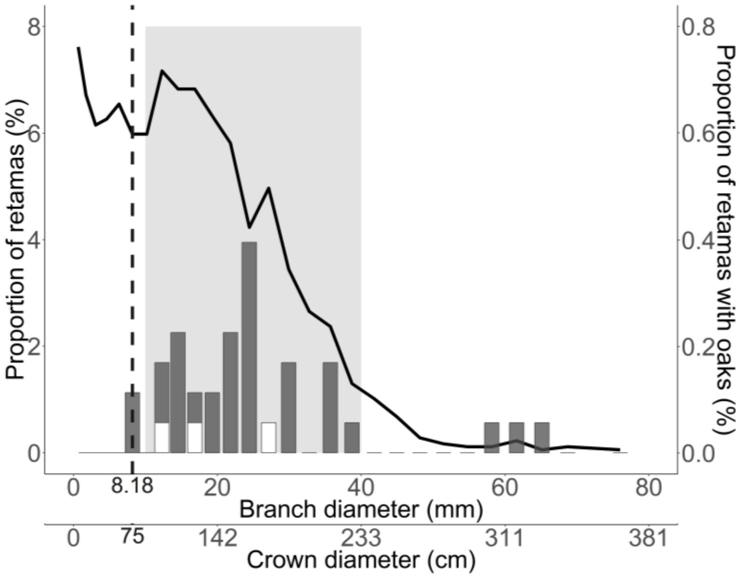

Figure 4.4. Size class distribution of *Retama sphaerocarpa* (retama) population (line). The filled bar portion represents the fraction of retamas with *Quercus ilex* (evergreen oak) and the unfilled portion represents the fraction of retamas with *Quercus faginea* (deciduous oak). The dashed line represents the minimum retama size with an oak underneath. The shaded area represents the medium size retamas.

Shrub modulation of the climatic effects on oak recruitment

The results of the model of **Eq. 4.1** indicated that there were no statistically significant effects of the climatic variables on recruitment rate of evergreen oaks in any of the two microsites (**Figure 4.5a,** model parameters in **Table S15.4)**. Collinearity among explanatory variables in **Eq. 4.1** was low ($-0.27 \leq \rho \leq 0.34$; VIF ≤ 1.20; Dormann et al., 2013), and the fit of the model (R^2) was 0.94 (**Figure S12.4**). There were not either statistically significant effects of the climatic variables on recruitment rate of deciduous oaks (**Figure 4.5b**, model parameters in **Table S15.4**).

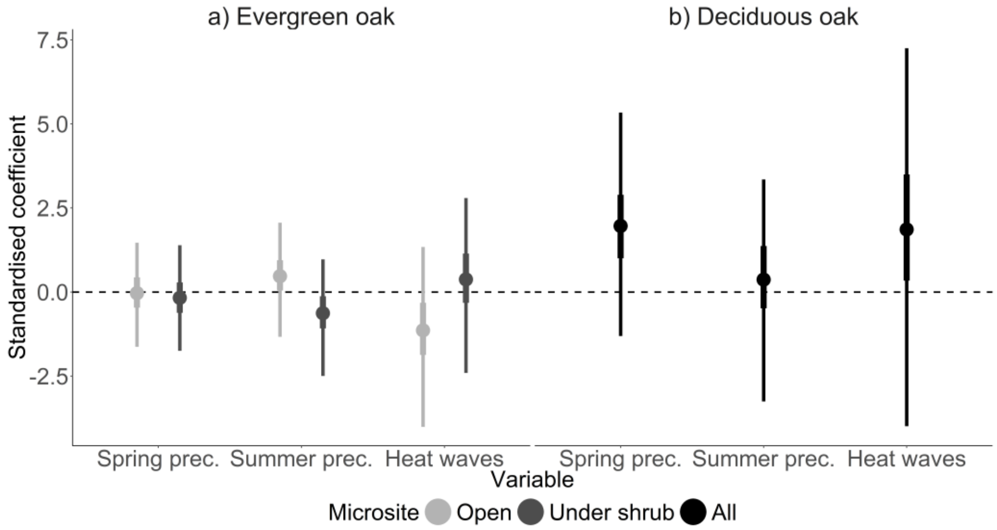

Figure 4.5. Standardised coefficients (parameter × variable mean) of the climatic variables in the model of evergreen oak recruitment (a; Eq. 1 in Data analysis section) and in the model of the deciduous oak recruitment (b). Whiskers represent 95% of the credible interval of the estimated standardized coefficient, and bold whisker segments represent 75% of the credible interval.

The linear model for the facilitative effect of retama on evergreen oak recruitment had the best fit (AIC in **Table S15.4**). Spring precipitation did not have a significant effect on the facilitative effect (**Table S15.5**). However, the facilitative effect of retama on evergreen oak recruitment was inversely related to summer precipitation and directly related to the length of heat waves (**Figure 4.6, Table S15.5**). The facilitative effect turned into competition (i.e., mean effect became negative) when summer precipitation was > 47 mm or the heat waves lasted < 8 days (**Figure 4.6**). Precipitation > 47 mm or heat waves shorter than 8 days occurred in 30% of the studied years each one (see climate from 2005 to 2014 in **Figure 4.2d**).

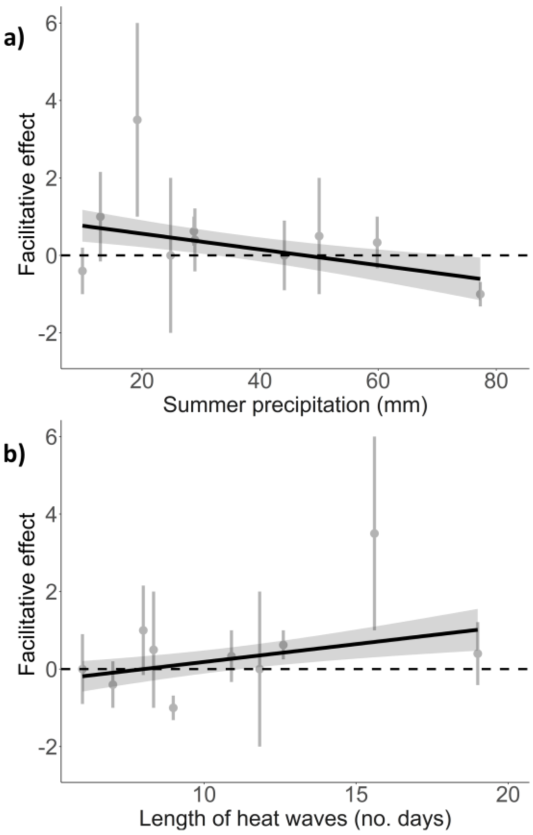

Figure 4.6. Fitted linear model of the relationship between the facilitative effect of retama on evergreen oak (*Quercus ilex*) recruitment and a) summer precipitation and b) the length of heat waves. The dots are the mean facilitative effect observed in the 20 transects per precipitation and length of heat waves level and the whiskers represent the standard errors of the means.

DISCUSSION

Under stressful conditions, the facilitative effect of nurse shrubs is critical to ensure tree colonization, especially in areas that lack woody vegetation like abandoned fields. Despite their relevance in forest recovery, we know little about the dynamics of these effects. Our analysis of long-term colonization dynamics of oaks showed that their recruitment accelerated when oaks started recruiting under shrubs. It took the abandoned field succession 20 years to get to this point, likely when shrub cover and size were large enough to provide a facilitative effect. Our results also showed that evergreen oaks recruited more than deciduous oaks and, against our expectation, only the evergreen species benefited from recruiting under the nurse shrub. Facilitative effects were more pronounced in years with more arid summers, and in wet and mild summers, the interaction between the nurse shrub and the evergreen oak switched to competition.

Long-term dynamics of forest expansion reveal different recruitment pulses of the nurse shrub and oak species

In accordance with our first hypothesis, the temporal trends in pulses of recruitment that we documented indicate distinct regeneration dynamics for the shrub and the two oak species. Retama — a pioneer shrub species - was the earliest colonizer, presumably due to its high dispersion capacity and drought tolerance (Haase et al., 1996; Haase, Pugnaire, Clark, & Incoll, 1999; Padilla & Pugnaire, 2007). The large pulse of retama recruitment towards the end of the studied period is likely due to the beginning of seed production by already established shrubs, as observed for other plant species (Harper, 1977). The oak recruitment pulses were probably caused by a combination of masting cycles (Koenig, Knops, Carmen, & Pearse, 2015; Pérez-Ramos et al., 2015), competition with pre-existing plants (herbs in our study; Rey Benayas et al., 2015), and availability of nurse shrubs (e.g. Navarro-Cano et al., 2016; Perea et al., 2017). The increase in oak recruitment over time could also be attributed to the greater activity of acorn dispersers and to soil improvement after field abandonment (Cuesta, Rey Benayas, Gallardo, Villar-Salvador, & González-Espinosa, 2012; Purves, Zavala, Ogle, Prieto, & Benayas, 2007; Rey-Benayas, Galván, & Carrascal, 2010). In particular, our data show that the facilitative effects of the shrubs started 20 years after abandonment, once the shrub population reached a cover of 2.21%. Climate had a minor effect in recruitment dynamics of both oaks contrary to our expectations (see discussion below).

Comparisons between the two oaks also show differences in their recruitment dynamics, in agreement with hypothesis 1. In consonance with other studies, the evergreen oak recruited more abundantly, and during longer time windows, than the deciduous oak (Gómez-Aparicio et al., 2004; Perea et al., 2017). Differential drought resistance and palatability between species could be the cause (Gil-Pelegrín et al., 2017; Montserrat-Martí et al., 2009). Specifically, sensitivity of stomatal conductance to water stress is lower for the evergreen oak than for the deciduous oak (Acherar & Rambal, 1992; Mediavilla & Escudero, 2004), and the deciduous oak is more heavily browsed than the evergreen oak (Espelta, Habrouk, & Retana, 2006). Moreover, acorn production and dispersion of the evergreen oak is usually higher than the observed for deciduous oak (Pons & Pausas, 2007a, 2007b; Rodríguez-Estévez, García, Perea, Mata, & Gómez-Castro, 2007).

Oak species also differed in their preferential recruitment microsites. Our results show that after 30 years of succession the evergreen oak had higher recruitment under the nurse shrub, while most deciduous oak juveniles recruited in open microsites (91% of recruited deciduous oak). This does not support our third hypothesis and contradicts a previous study that found similar occurrence of juveniles under shrub and in open areas for both evergreen and deciduous oaks (Perea et al., 2017), as well as the notion that facilitation benefits the low stress-tolerant and herbivory-prone species more (Costa et al., 2017; Madrigal-González, García-Rodríguez, & Zavala, 2014; Soliveres et al., 2014). The different recruitment patterns of both oak species in abundance and location could be due to the preference by the main dispersers, *Garrulus glandarius* L. (Eurosiberian jay) and *Apodemus sylvaticus* (wood mice), for the evergreen acorns (Pons & Pausas, 2007a, 2007b), and maybe to a different acorn caching behaviour for both oaks. A higher competition between the retama and the deciduous oak than with the evergreen oak during the less stressful years for establishment would also explain the results. Future experiments should further assess the underlying mechanisms of the recruitment differences between oak species with contrasting leaf traits.

For the evergreen oak, the recruitment under shrub was sustained over time in comparison to the pulse patterns observed in open areas. This dynamic indicates that facilitation can increase the window of opportunity of evergreen oak colonization, a trend that will be critical under the forecasted drier conditions for this region (IPCC, 2018). This effect, together with the scarce recruitment of deciduous oaks observed suggest a more likely future dominance of evergreen oaks in Mediterranean abandoned fields (Perea et al., 2017).

Relationship between retama population structure and oak facilitation

It is likely that direct and indirect facilitative mechanisms increase with nurse size and abundance (Allegrezza et al., 2016; Cuesta et al., 2010; Gómez, Puerta-Piñero, & Schupp, 2008; Navarro-Cano et al., 2016). Our results document the lagged facilitation effect associated with the shrub size and population structure (hypothesis 2). Retama started to effectively facilitate oak recruitment 20 years after shrubland recovery, and shrubs reached a threshold size of 74 cm in crown diameter, reaching the maximum recruitment rate at intermediate shrub sizes. This suggests that facilitation under the shrub saturates once it attains certain size (Navarro-Cano et al., 2016). Shrubs older than 21 years frequently had irregular and open canopies linked to branch senescence (V. Cruz-Alonso personal observation). This canopy opening could deteriorate the microenvironment under the shrub reducing the facilitation capacity of the older and/or larger shrubs (Schöb, Armas, Guler, Prieto, & Pugnaire, 2013). The retama size threshold for oak facilitation was reached when they were 7-8 years old, but the first oak recorded under shrub occurred 20 years after field abandonment. This suggests that recovery of other ecosystem properties, such as soil fertility, may also be needed for recruitment under nurse shrubs (Pugnaire et al., 1996).

Climate modulates the facilitative effect on oak recruitment

We could not find a clear support for the idea that retama buffers the climate effect on oak recruitment. However, our analysis showed that the facilitative effect of retama on the evergreen oak was stronger in years with more arid summers whereas competition prevailed in wet and mild summers. These results support the Stress Gradient Hypothesis (Bertness & Callaway, 1994; He, Bertness, & Altieri, 2013), and are in consonance with the marginally negative effect of summer precipitation on the evergreen oak recruitment under retama that we found. The herb community that usually dries out in summer could grow longer under the retama shade in milder summers, and thus increase competition with oak seedlings (Tielborger & Kadmon, 2000). Surprisingly, we did not find any significant effects of spring precipitation or summer conditions on oak recruitment. This could be due to limitations of our study, which might need additional data and not take into account other processes that might affect recruitment, such us mortality in later years (Debussche & Lepart, 1992). Moreover, modelling results may be affected by the non-inclusion of variables such as acorn production, abundance of dispersers and soil features which vary from year to year (Cuesta et al., 2012; Koenig et al., 2013; Rey-Benayas et al., 2010).

CONCLUSIONS

Long-term forest recovery in the studied Mediterranean abandoned fields exhibited differential pulses of species recruitment. Despite being closely related, oaks with contrasting leaf traits (evergreen vs. deciduous) and drought tolerance showed different patterns of recruitment. The retama shrubland buffered *Q. ilex* recruitment pulses, i.e. recruitment rate under the nurse was maintained during periods of low recruitment in open spaces. We did not document a positive effect of retama on recruitment of the deciduous oak *Q. faginea*, which had lower recruitment than the evergreen oak during the first 30 years of forest succession. The nurse shrub population developed for 20 years before facilitating oak establishment and oak recruits appeared preferably in medium and big shrubs, always older than 7 years. The facilitative effect of retama increased with summer aridity. These results suggest a potential dominance of evergreen oaks in restored secondary forests in the mid-term under more arid climate scenarios and show how less stress tolerant species do not necessarily benefit more from facilitative interactions.

AUTHORS CONTRIBUTION

VCA, PVS, PRB and JMRB conceived the ideas and designed the methodology; VCA and PVS collected the data; VCA, II and PRB analysed the data; VCA and PVS led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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DATA ACCESIBILITY

Data available via Figshare: XXX (Cruz-Alonso et al., 2019)

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