



Abundance and spatial attributes of forest remnants differently influence colonization patterns of contrasting oak species

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Abstract

Context Forest remnants in fragmented landscapes may trigger forest recovery after disturbances. Beyond extension of patches and distance to colonization sites, little is known about how the size structure of reproductive trees within patches and past land use/cover shape colonization dynamics in mountainous landscapes.

Objectives To assess the influence of (1) forest remnant abundance, spatial attributes (i.e. distance and

altitude difference to colonization sites), and composition of reproductive trees at the individual level, and of (2) past land use/cover on the colonization of two functionally distinct Mediterranean oaks, the evergreen *Quercus ilex* L. and the deciduous *Quercus faginea* Lam., in a 55-year-old maritime pine (*Pinus pinaster* Ait.) plantation.

Methods We assessed oak juvenile density in 153 plots within a Mediterranean pine plantation established on cropland and shrubland. We geolocated and measured the diameter at breast height of reproductive oaks (n=5020) within a 500 m-radius buffer around each plot.

Results *Q. ilex* showed higher colonization than *Q. faginea* after accounting for remnant abundance. For *Q. ilex*, remnant abundance was the most influential factor, whereas colonization by *Q. faginea* was primarily driven by distance and altitude difference between reproductive trees and colonization sites. Tree size did not affect recruitment. Former cropland exhibited higher oak colonization than former shrubland.

Conclusions In this study, *Q. ilex* was a more efficient colonizer than *Q. faginea*, likely leading to evergreen oak dominance in pine plantations in the mid-term. Spatial attributes influenced recruitment of both oak species differently and independently of tree size. These findings help to identify high-regeneration areas more accurately, which supports the optimization of pine plantation diversification in Mediterranean mountain areas.

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Introduction

Forest cover has increased in the Northern Hemisphere since the second half of the twentieth century (McMahon et al. 2010). This re-greening is primarily attributed to two factors: the implementation of large-scale afforestation policies (Doelman et al. 2020) and the natural expansion of second-growth forests on abandoned agricultural land (García et al. 2020; Sheffer 2012). These new forests are changing under unprecedented conditions linked to global change, including increased tree mortality and reduction in canopy cover, especially in planted forests, which reflects their vulnerability to stress factors (McDowell et al. 2020). These shifts highlight the need to understand the processes driving forest tree regeneration, which is key to catalyzing secondary succession leading to species diversification and optimizing forest restoration (Crouzeilles et al. 2016; Trumbore et al. 2015).

Regeneration of tree species is a slow process in Mediterranean environments (Cruz-Alonso et al. 2020) due to the interaction of multiple factors such as harsh climatic conditions (Gómez-Aparicio et al. 2009), herbivory (Davis et al. 2011) and seed dispersal (Pons and Pausas 2007a). Summer drought is the most limiting abiotic factor in this environment, resulting in high seedling and juvenile mortality (Gil-Pelegrín et al. 2017). In this context, topography can also influence tree species regeneration (Álvarez-Martínez et al. 2014; Martín-Alcón and Coll 2016; Urbieto et al. 2011) by shaping microsite abiotic conditions such as soil moisture or radiation (Ritsche et al. 2021), which directly affect seedling establishment. The legacy of past land use may also affect Mediterranean forest colonization and dynamics (Álvarez-Martínez et al. 2014; Perring et al. 2016). For instance, agricultural use directly affects soil properties by modifying nutrient availability and physical properties (Comita et al. 2010; Martín-Alcón and Coll 2016; Navarro-González et al. 2013), which can facilitate plant colonization after cropland abandonment. Increased nutrient availability may also indirectly shape biotic interactions. For example, it may favor dominant species that suppress

less competitive ones (Kepfer-Rojas et al. 2015), or increase herbivory pressure, as higher soil phosphorus enhances plant palatability (de la Peña et al. 2016). Such impacts can persist for centuries after interruption of human land use (Plue et al. 2008), highlighting the importance of addressing the legacy effect of agricultural land abandonment to better understand and predict forest dynamics (Navarro-González et al. 2013). In this regard, the regeneration pattern of zoochorous plants like oaks, which depends on animals for seed dispersal (Gómez et al. 2003), provides a unique perspective on how multiple factors, including the past legacy and presence of seed sources, interact to shape forest dynamics (Schupp et al. 2010). However, despite this evidence and to our knowledge, no study has examined how past land use/cover legacy interacts with seed availability in the landscape and topography to influence tree species recruitment.

Cropland expansion often occurs at the expense of forest loss and reduced landscape connectivity. In this context, pre-disturbance forest remnants, often persisting as small patches or scattered individuals, play a key role in maintaining ecological connectivity (Herrera and Garcia 2009; Manning et al. 2006) and act as propagule sources that may facilitate forest recovery (Crouzeilles et al. 2020; Wu et al. 2022). The effectiveness of forest remnants in promoting recolonization depends strongly on the abundance and size (often measured as diameter at breast height—hereafter, dbh—, basal area and/or height) of reproductive individuals. These attributes influence seed availability and, consequently, both the likelihood and spatial extent of natural regeneration across the landscape (Andivia et al. 2017; Wimberly and Spies 2002). For instance, Zahawi et al. (2021) found that larger reproductive trees, in terms of dbh and height, in tropical forest patches within abandoned agricultural landscapes correlated positively with seedling recruitment, particularly for large-seeded species. Because tree size serves as a proxy for both age and reproductive output (Greene and Johnson 1994; Moracho et al. 2018), it may be an indicator of a remnant potential to contribute to forest regeneration. Despite this, many landscape-scale studies have estimated propagule pressure based primarily on remnant patch area and distance to colonization sites (Andivia et al. 2017; Bueno et al. 2020; Navarro-González et al. 2013), assuming a homogeneous propagule production. This overlooks the demographic structure

within remnant patches, namely the number and size of reproductive individuals, which could improve predictions of natural regeneration patterns (but see Barber et al. 2022 and Zahawi et al. 2021). Such assessments have been conducted mainly in tropical regions, limiting our understanding in wet temperate and Mediterranean ecosystems.

Beyond the internal structure of remnant patches, the spatial distribution of propagule sources relative to recruitment sites plays also a key role in forest colonization. While distance of remnants to colonization sites often correlates negatively with recruitment abundance (Gómez-Aparicio et al. 2009), this relationship is not always consistent (e.g., Bueno et al. 2020). This is likely due to two reasons. First, colonization patterns are influenced by trade-offs driven by density-dependent processes, such as species abundance and seed/seedling mortality, which in turn depend on context-specific factors such as stand structure (tree density, tree age or dispersers availability); as a result, the influence of distance may vary with study scale (Sheffer et al. 2013). Second, which is related to the first reason, the short distances analyzed in some cases (< 100 m; Barber et al. 2022; Ritsche et al. 2021; Zahawi et al. 2021) may be insufficient to fully understand the dispersal of some zoochorous tree species, such as oaks, whose seeds can travel distances of up to 1 km (Gómez 2003). Unlike distance, the importance of altitude difference between seed sources and colonization sites has been largely overlooked. Altitude difference may hinder forest expansion of zoochorous trees in mountainous areas by limiting the uphill movement of seed dispersers (Li and Zhang 2003; Zamora et al. 2013) due to higher energy expenditure (Shepard et al. 2013). Thus, assessing the effect of the altitude difference along with the distance on the colonization of zoochorous species may improve recruitment prediction patterns.

Oaks encompass approximately 400 deciduous and evergreen trees and shrub species distributed across the Northern Hemisphere (Denk et al. 2017), exhibiting large differences in their ecology. Differences in their functional attributes such as leaf habit (Quero et al. 2006) can influence the colonization capacity of oak species (Gil-Pelegrín et al. 2017). For instance, the evergreen *Quercus ilex* L. colonizes pine plantations (Carnicer et al. 2014; Gavinet et al. 2016) and mixed oak forests (Espelta et al. 2009) more quickly

and abundantly than deciduous oaks. Similarly, *Q. ilex* shows greater colonization efficiency (i.e., a higher rate of colonization per unit of oak cover area in the forest remnant) in shrubland dominated by *Retama sphaerocarpa* (L.) Boiss. compared to the deciduous *Quercus faginea* Lam. (Cruz-Alonso et al. 2020). These differences in colonization between oaks with different leaf habit may be attributed to environmental filters affecting each group, with deciduous species being more impacted by drought (Gil-Pelegrín et al. 2017) and lower soil fertility (Lal et al. 2001; Villar-Salvador et al. 2013), as well as differences in reproductive capacity (Espelta et al. 2009) or acorn preferences by dispersers (Pons and Pausas 2007a; Wróbel et al. 2022). Despite this evidence, it is largely unknown how differences in oak colonization are influenced by the age and composition of reproductive trees within remnants, their spatial distribution in the landscape and the legacy of past land use/cover.

This study assesses how the abundance, spatial attributes, and size of trees within forest remnants affect the capacity of two coexisting and functionally different oaks to colonize a pine plantation established in a mountainous area with contrasting past land use/cover in central Spain. The studied oak species were *Q. ilex*, an evergreen drought tolerant tree, and *Q. faginea*, a deciduous tree that is less tolerant to drought than *Q. ilex* (Rey Benayas et al. 2005; Niinemets and Valladares 2006). We posed the following questions: Q1. Do oak species differ in colonization efficiency? Q2. Do landscape structure of forest patches (abundance, distance and altitude difference of individuals to colonization sites) and tree size modulate oak colonization? And Q3. Does past land use/cover (cropland vs. shrubland) affect oak colonization? We hypothesized that: H1. *Q. ilex* is a more efficient colonizer than *Q. faginea* under limiting environments because of its better adaptation to harsh climatic conditions; H2. Colonization capacity decreases with increasing distance and altitude difference between seed sources and colonization sites because of the increasing effort made by dispersers; H3. Larger reproductive trees within the remnants, which were present in the landscape prior to pine afforestation, contribute proportionally more to colonization than smaller, younger reproductive individuals due to its higher acorn production; and H4. Recruitment will be higher in plots with a legacy of

agricultural use than in those with shrubland cover, because of the nutrient supply in the past and improved soil physical structure, and consequently, differences in colonization patterns among oak species are less pronounced in former agricultural areas.

Material and methods

Study site

The study was carried out in the southeast of the ‘Sierra Norte de Guadalajara’ Natural Park (40° 60′ 00″ N, 3° 11′ 00″ W; central Spain) covering an area over 300 ha. Elevation ranges from 870 to 1100 m a.s.l. The climate is continental Mediterranean, characterized by cold winters and hot summers with a marked summer drought from June to August. Mean annual temperature is 12.4 °C and mean annual rainfall is 754 mm, mainly concentrated in autumn and winter (weather station El Vado, located at 10 km; period 1942–2022). The topography is characterized by slopes that range from 0 to 80% and the presence of numerous ravines.

Around 90% of the study area is dominated by a plantation of Maritime pine (*Pinus pinaster* Ait.) established in 1969 as part of the afforestation efforts to mitigate soil erosion (Vadell et al. 2016). Pine forest understory is composed by different shrub species including *Cistus ladanifer* L., *C. laurifolius* L., *Salvia rosmarinus* Schleid., *Crataegus monogyna* Jacq., *Rubus ulmifolius* Schott., *Rosa canina* L., *Daphne gnidium* L. and *Erica* spp. Scattered individuals of *Juniperus oxycedrus* L., *Q. ilex* L. subsp. *ballota* (Desf.) Samp and *Q. faginea* are also present in some areas, along with herbaceous vegetation dominated by grasses and legumes. The pine plantation is crossed by a firebreak with N-S direction that was established in the highest part of the study site. This study site is representative of many landscapes of the Mediterranean basin characterized by a matrix of pine plantations colonized by mid- and late successional woody species with scattered preexisting forest patches and isolated trees of oak species. At the west and south-west of the site there are several patches of mixed oak stands (Fig. 1). There are also oaks of different size scattered on the slopes, inside the pine forest and especially in the ravines. According to orthophotos from American Flight B Series (1956–1957; CNIG

2022), two main land use/cover existed in the study area before the pine plantation, namely cropland and shrubland.

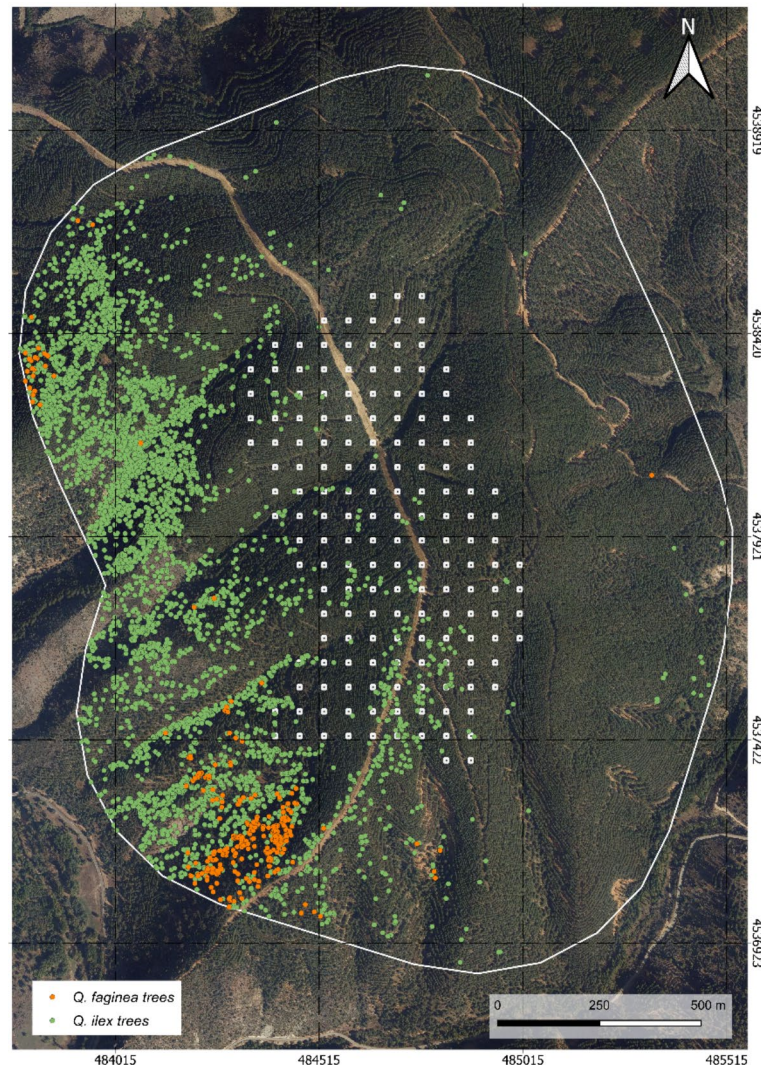
Density of oak juveniles and characteristics of reproductive oak trees

We measured the density of recruits of both *Quercus* species inside the pine plantation by establishing a systematic sample grid design of 153 plots—10×10 m in size—located in the central part of the study area. Plots were separated 50 m among them (Fig. 1). In each plot, we counted the number of recruits of both oaks, mostly seedlings (height < 30 cm) and saplings (height > 30 cm and < 150 cm).

We thoroughly surveyed the study site to identify and measure all reproductive oaks to assess the effect of individual adult oaks on the density of oak recruits. The limits of the surveyed area were defined by delimiting 500 m from the most external plots (Fig. 1). This distance covers most acorn dispersals carried out by the Eurasian jay (*Garrulus glandarius* L.), the main oak disperser in Mediterranean woodlands (Gómez 2003; Pérez-Camacho et al. 2023; Pons and Pausas 2007a), which is also present at the study site (Lorente-Casalini unpublished observations). We classified an oak as reproductive if we observed acorns in their crown during the autumn and/or the presence of acorn cupules under its crown on the ground during the rest of the year. All reproductive trees were geolocated with a hand-held GPS receiver (Garmin GPSMAP® 78 s, Olathe, Kansas, USA; error ± 5 m) and their diameter at breast height (dbh) was measured. When a tree had multiple stems below breast height, we measured all stems with dbh > 10 cm.

We identified the pre-existing oak trees in the landscape prior to the establishment of *P. pinaster* plantation using orthophotos from the American Flight B Series (1956–1957; CNIG 2022; Fig. S1). According to their presence in 1956 and current dbh, reproductive trees were classified into three dbh categories with thresholds of 15, 50 and 160 cm. To distinguish between younger and recently reproductive trees, we used a 15-cm dbh threshold based on previous studies (Arasa-Gisbert et al. 2024) and field observations. Individuals < 15 cm showed minimal seed production (1–5 acorns). The 50-cm dbh threshold corresponds

Fig. 1 Orthophoto of the study site and the *P. pinaster* plantation. White dots indicate the locations of sampled plots used to measure density of *Q. ilex* and *Q. faginea* recruits. Green (*Q. ilex*) and orange (*Q. faginea*) dots are the reproductive oaks measured in the 500-m radius buffer around each plot (white line delimits the buffer)



to the smallest trees visible in the American Flight B Series; this size represents the only confirmed individuals present approximately 70 years ago, which likely are the founders of the current population. Finally, the upper threshold of 160 cm was set as a descriptive reference, corresponding to the largest old-growth trees observed in the sampled area.

Spatial analysis and landscape characterization

We calculated the basal area and the Euclidean distance to the centroid of all plots for each oak species and each category of reproductive oak trees separately. These variables were used as indicators of potential seed availability (Moracho et al. 2018). To

measure the influence of the distance and basal area of oak trees in the density of oak recruits, we included all reproductive oaks growing inside a 500 m-radius buffer around each plot centroid. To measure the influence of the altitude difference between reproductive oak trees and target plots with oak recruitment, we used a digital terrain model (DTM) with a spatial resolution of 2 m. We also calculated the Topographic Wetness Index (TWI, a hydrological indicator of the potential of each plot to accumulate water) with SAGA GIS (7.8.2; Conrad et al. 2015) following the algorithm indicated in Mattivi et al. (2019). TWI is a function of the slope, aspect and curvature of the terrain (accounting for water and nutrient soil availability and radiation exposure). As the DTM had a

grid cell size of 2 m, each plot contains 25 cells and therefore we calculated the average value in each plot. High TWI values indicate wetter areas. TWI can be used to characterize forest site quality, species assemblage, vegetation spatial patterns and other ecological features (Álvarez-Martínez et al. 2014; Kopecký et al. 2021; Sørensen et al. 2006).

To assess the influence of each type of reproductive tree on recruit density, we calculated the Seed Pressure Potential on a plot j (SPP; Andivia et al. 2017) as:

$$SPP = \sum \frac{BA_i}{d_{ij}^{1.65}} (m^2 \cdot m^{-1})$$

where BA_i is the basal area of each reproductive tree (i) within the 500 m-radius buffer around each plot (j) and d_{ij} is the distance from reproductive tree i to plot j . As seed dispersal usually declines exponentially with distance, d_{ij} is raised to the power of 1.65 based on previous studies of acorn dispersal by European jays (Gómez 2003).

To assign a past land use/cover type to each plot, we used the American Flight B Series (1956–1957; CNIG 2022), with a spatial resolution of 1 m. Plots were classified into cropland and shrubland types. When plots shared both types, they were assigned to either category based on the predominant number of pixels on each land use/cover type (Fig. S1). All the spatial information and analysis were performed with Quantum GIS (v 3.22).

Data analysis

To assess the colonization efficiency of each oak species and the influence of past land use/cover (Q1, Q3; H1, H4), we used a Generalized Linear Model (GLM) with a log-link function and negative binomial distribution of errors. The response variable was the juvenile density in each plot (discrete count data) and the explanatory variables were SPP, oak species, and past land use/cover. Given the imbalance in the number of plots between cropland ($n=64$) and shrubland ($n=89$), we used bootstrapping as a resampling method. For that, we first generated 1000 datasets randomly sampled with replacement from the original dataset. In each of these datasets, we selected 64 observations of both land use/cover types. Secondly, we applied the GLM in each dataset. Finally, we

obtained the mean parameter estimates and CIs for each variable.

To assess spatial autocorrelation among plots based on measured oak juvenile density, we conducted a Moran's I test distinguishing between oak species. There was not autocorrelation for *Q. faginea* data ($I=0.001$, $p=0.164$), but there was for *Q. ilex* ($I=0.123$, $p<0.001$). The density of *Q. faginea* juveniles was analyzed using zero-inflated Poisson regression models as the number of observed zeros in the response variable exceeded the expected frequency after adjustment. The density of *Q. ilex* juveniles was analyzed using a Generalized Least Square model (GLS) with a spherical spatial correlation structure to account for spatial autocorrelation. For each model, TWI of each plot, mean distance and altitude difference between the reproductive trees and the colonization point (i.e., the plot centroid), and total basal area of all reproductive trees located inside the 500-m radius circle at each plot were used as explanatory variables (Q2; H2). Continuous variables (i.e., basal area, distance, altitude difference, and TWI) were standardized through the subtraction of the mean from each value and dividing by the SD. Standardization of variables allows comparisons among model-estimated parameters and test interactions (Zuur et al. 2009). Model selection was performed according to a backward stepwise procedure following the principle of parsimony, comparing fitted models by AIC. Finally, we obtained parameter estimates and 95% confidence intervals (CI) of the best-supported model.

To assess the influence of each type of reproductive oak on the density of oak juveniles (Q2; H3), we first checked Pearson's correlations among SPP of the three types of reproductive individuals. For *Q. faginea*, the three types were highly correlated ($r>0.95$ in all cases), but were not for *Q. ilex* ($r<0.50$ in all cases). Thus, we could not perform the analysis for *Q. faginea*, but for *Q. ilex* we used a Generalized Linear Mixed Model (GLMM) with a log-link function and Poisson distribution of errors. We established juvenile density as the response variable and mean SPP and tree size as the explanatory ones. We grouped medium and small reproductive trees versus old-growth trees according to their presence in the landscape before the pine plantation took place. The coordinates and the identifier of each plot were included as random terms to account

for spatial autocorrelation and lack of independence, resulting from repeated measurements within each plot. All data wrangling and statistical analysis were performed using the packages ‘tidyverse’, ‘nlme’, ‘MASS’, ‘stats’, ‘pslc’, ‘glmmTMB’ and ‘DHARMa’ in R v 4.3.2 (R Core Team 2023).

Results

Oak abundance

A total of 5020 reproductive trees were censused. The predominant species was *Q. ilex* (n=4701; old-growth: 258, medium size: 1593, small size: 2850) compared to *Q. faginea* (n=319; old-growth: 17, medium size: 217, small size: 85). The abundance of oak juveniles in sampled plots, mostly seedlings and saplings, was also greater for *Q. ilex* (n=1279) than for *Q. faginea* (n=104).

Colonization efficiency and past land use/cover

Colonization efficiency, measured as oak juvenile density after controlling for species SPP differences in the landscape, differed between oak species (Table 1; $R^2=0.18$). On average, predicted juvenile density of *Q. ilex* was 12-fold higher than the density of *Q. faginea*. Juvenile density was on average 44% higher in plots where the past land use before pine planting was cropland as compared to shrubland cover (38% higher for *Q. faginea* and 50% higher for *Q. ilex*; Fig. 2). However, we found no significant interaction between oak species and past land use/cover type.

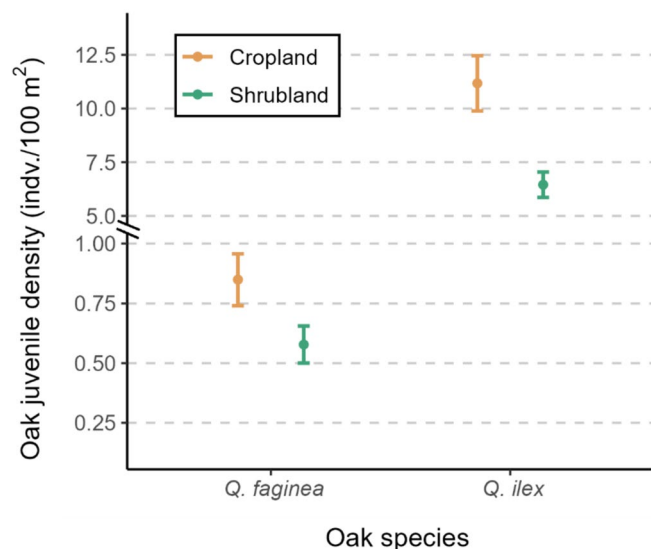
Effects of oak remnant abundance, landscape distribution and tree size

The factors that affected recruitment showed differences between oak species. For *Q. ilex*, the most parsimonious model included the basal area and

Table 1 Mean and 95% confidence intervals (CI) for estimated parameters included in the adjusted GLM to explain the differences in juvenile density between both oak species (SPP is Seed Pressure Potential)

Parameter	Mean estimate	CI
Intercept [‘Cropland’ and ‘ <i>Q. faginea</i> ’]	−0.19	−0.51, 0.09
Oak species [‘ <i>Q. ilex</i> ’]	2.34	2.04, 2.67
Past land use [‘Shrubland’]	−0.36	−0.59, −0.14
SPP	49.0	26.4, 87.5

Fig. 2 Predicted juvenile density ($\pm$ SE) of *Q. ilex* and *Q. faginea* in the pine plantation on sites that were cropland or shrubland before the pine plantation took place. Predicted values account for differences in SPP of reproductive oaks in the landscape. Note the scale change due to a break in the Y-axis



the distance of reproductive trees to plot centroid (Table S2; $R^2=0.21$), with a positive and negative influence, respectively (Fig. 3). For *Q. faginea*, the most parsimonious model included the interaction between distance and altitude difference to plot centroid (Table S2; $R^2=0.17$). Both factors reduced oak juvenile density (Table 2), with density peaking at shorter distances and lower altitude differences from the reproductive tree to the plot centroid. The effect of altitude difference on oak density decreased or disappeared at intermediate distances (Fig. 4). TWI did not have a significant effect on the density of juveniles in any oak species (see Table 2).

We found no significant differences between the type of reproductive trees on the recruit density of *Q. ilex* (see parameters in Table S3; $R^2=0.20$), with old-growth trees contributing in the same proportion than younger and smaller trees established after the pine plantation (Fig. 5).

Discussion

This study assessed how the characteristics and landscape structure of forest remnants affected colonization of two functionally contrasting oak species in a pine plantation with different past land use/cover types. Our results provide insights into the importance of characterizing forest remnants patches at fine-scale to assess the colonization of oak species. The evergreen oak (*Q. ilex*) showed a markedly higher colonization efficiency than the deciduous oak (*Q. faginea*; Q1 and H1). In addition, the role of remnants abundance and position in the landscape on juvenile recruitment differed between oak species (Q2 and H2), whereas the size of reproductive remnant trees did not affect recruitment in either oak species (Q2 and H3). Finally, the past land use/cover—cropland vs. shrubland—had a key role in determining the intensity of colonization (Q1 and H4), with similar effects on both oak species.

Fig. 3 a) Predicted *Q. ilex* juvenile density as a function of distance and b) basal area of reproductive trees measured in the 500-m radius buffer around the plot centroid

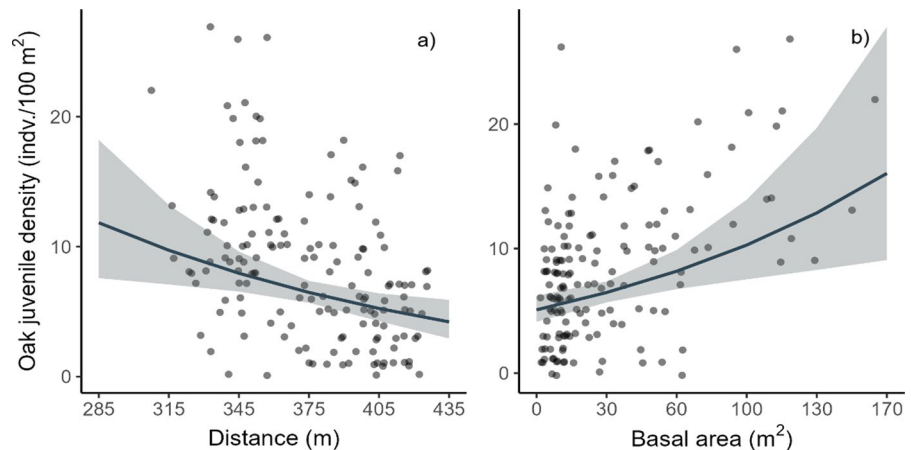


Table 2 Mean and 95% confidence intervals (CI) for each estimated parameter in the selected models explaining the recruitment of *Q. faginea* and *Q. ilex* juveniles

Parameter of selected models	<i>Q. faginea</i>		<i>Q. ilex</i>	
	Mean estimate	CI	Mean estimate	CI
Intercept	0.43	0.11, 0.75	2.01	1.90, 2.12
Basal area	–	–	0.21	0.08, 0.33
Distance	–0.53	–0.87, –0.19	–0.18	–0.31, –0.05
Altitude difference	–0.36	–0.62, –0.10	–	–
TWI	–	–	–	–
Distance × Altitude difference	–0.30	–0.52, –0.08	–	–

Fig. 4 Predicted density of *Q. faginea* juveniles as a function of distance and altitude difference

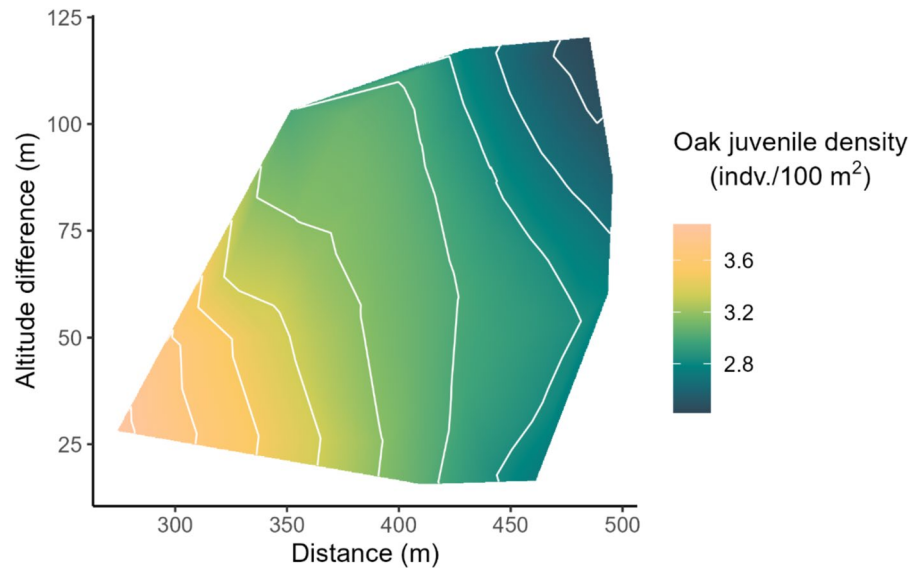
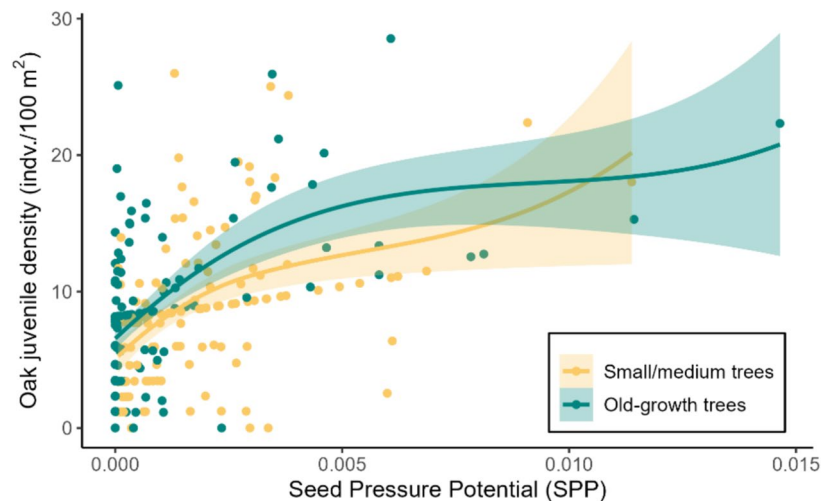


Fig. 5 Predicted *Q. ilex* juvenile density as a function of each type of reproductive remnant tree. Old-growth trees are those established before the pine plantation took place whereas small/medium trees are those established after it



Coexisting oaks differ in colonization capacity

In absolute terms, *Q. ilex* has greater colonization capacity than *Q. faginea*. These differences persist after accounting for differences in propagule pressure between species, indicating that *Q. ilex* is inherently more efficient at colonizing pine plantations than *Q. faginea*, consistent with our first hypothesis. Similar differences in colonization between these oaks have been reported in shrublands (Cruz-Alonso et al. 2020). Consequently, the greater dominance of the evergreen oak in Mediterranean landscapes may be attributed to its higher colonization capacity, which

can be explained by several processes. First, *Q. ilex* acorn production *per capita* is higher (Montserrat-Martí et al. 2009) and more stable over time than in *Q. faginea* (Sánchez Humanes 2009). Second, the Eurasian jay (*Garrulus glandarius*), the primary long-distance disperser of oaks, prefers removing *Q. ilex* acorns than those of *Q. faginea* (Pons and Pausas 2007b). This preference, together with the higher acorn production, enhances acorn dispersal of *Q. ilex* across the landscape. Finally, the evergreen habit of *Q. ilex* results in more scleromorphic leaves with lower nutrient concentration than the malacophyllous marcescent leaves of *Q. faginea* (Castro-Díez et al.

1997; Gil-Pelegrín et al. 2017). These characteristics confer *Q. ilex* juveniles a greater tolerance to drought stress (Quero et al. 2006; Rey Benayas et al. 2005) and herbivory (Davis et al. 2011), potentially providing them a competitive advantage over *Q. faginea* (Martín-Alcón et al. 2015; Montserrat-Martí et al. 2009; Sánchez de Dios et al. 2009). Other less-studied processes, such as differences in post-dispersal predation (Pérez-Ramos and Marañón 2008), acorn desiccation sensitivity and germination capacity (Amimi et al. 2020), and dispersers' selection of microsites to cache acorns (Woziwoda et al. 2018) may also influence the recruitment differences between the two oak species.

The importance of forest remnant characteristics for colonization differs between oak species

The attributes of forest remnants that drive colonization efficiency differed between oak species, with remnant abundance in the landscape playing a critical role in these differences. For *Q. faginea*, which showed 15 times fewer reproductive individuals in the landscape than *Q. ilex*, the distance and altitude difference of remnants relative to colonization sites were key for recruitment. In contrast, the distance to colonization sites had a smaller effect for *Q. ilex*, while altitude difference showed no effect. These results partially confirm our second hypothesis regarding the negative effect of remnant distance and altitude difference on colonization capacity of oaks.

The spatial distribution of forest remnants plays a crucial role in the colonization capacity of several species, including oaks (Barber et al. 2022; Downing et al. 2019; Perea et al. 2021; Wu et al. 2022). Many studies have shown that the likelihood of oak species colonizing new sites decreases with distance to propagule sources (Gómez-Aparicio et al. 2009; Kepfer-Rojas et al. 2015; Nathan and Muller-Landau 2000; Zahawi et al. 2021), illustrating how spatial patterns influence ecological processes such as forest regeneration. Our findings, however, indicate that the importance of spatial distribution of remnants may be even more critical in landscapes where propagule sources are scarce, as for *Q. faginea* in our study area. Fewer reproductive trees in the landscape may result in a smaller seed shadow due to lower seed production (Nathan and Muller-Landau 2000), which may reduce species' colonization capacity. This limitation,

however, can be partially offset by the location of oak reproductive trees, which may influence how easily dispersers can access them (Gómez 2003; Schupp et al. 2010). In contrast, *Q. ilex* is much more abundant across the landscape and likely has a broader seed shadow. As a result, the effect of spatial distribution of remnant trees may be less pronounced, since their high abundance increases the likelihood that dispersers will find and disperse acorns. In this regard, Wu et al. (2022) found similar results, showing that remnant location of many species, oaks among others, had a greater influence on post-disturbance colonization than remnant abundance through simulation of forest recovery. In contrast, Zahawi et al. (2021) found that abundance of tropical large-seeded forest remnants positively influenced colonization over short distances (<100 m), even for less abundant species in the landscape. Thus, the effect of remnant abundance on colonization seems highly context dependent. Sheffer et al. (2013) highlighted that the influence of abundance varies at different study scales (local, landscape, or regional), underscoring the complexity of scale-dependent dynamics. Furthermore, patterns of oak colonization exhibit context-dependent effects shaped by microclimate related to where the seeds are deposited (Cruz-Alonso et al. 2020), the availability of seeds and dispersers (Schupp et al. 2010) or predation pressure at early life stages, as mentioned before. This indicates that colonization capacity cannot be predicted solely by species abundance in the landscape.

Interestingly, for *Q. faginea* altitude difference between the remnants and colonization sites also influenced colonization intensity. Movement limitations by dispersers have been observed at smaller scale in rodents (Li and Zhang 2003) and suggested for jays (Zamora et al. 2013), but to our knowledge, the importance of elevation differences on tree colonization at the landscape scale has not been observed to date (but see González-Moreno et al. 2011). This result suggests uphill movement limitations in acorn dispersers. The steep terrain in the study area likely makes Eurasian jay to make uphill flights that are energetically more demanding since they involve high and constant flapping and significant take-off effort compared to downhill or straight flights (Butler 2016).

The different size of mother trees, a surrogate of age, had a similar influence on the recruitment of

holm oak, contrary to our third hypothesis. This lack of difference contrasts with the results of Zahawi et al. (2021), who observed that larger mother trees close to abandoned tropical agricultural fields contributed more significantly to recruitment. In our study, however, this pattern may be masked by the high abundance of small and medium-sized trees. This effect could reflect a demographic compensation mechanism as the great number of reproductively active individuals compensates for their lower *per capita* contribution. Similar compensatory patterns have been observed in herbaceous plant populations, where most recruitment is often attributed to the most abundant individuals, not necessarily the most fecund ones (Chambers and Aarssen 2009). This suggests that recruitment is influenced not only by the fecundity of individual trees but also by population structure. Under certain demographic configurations, the reproductive output of few large individuals may be diluted by the contribution of many smaller ones. Such patterns align with studies indicating that variation in fecundity among individuals does not always translate into differential recruitment (Clark et al. 2004; Schreiber and Beckman 2020).

Effect of land use legacy

The legacy of the past land use/cover in the areas converted to pine plantations had a long-lasting influence on the colonization capacity of the two oak species even 55 years after pine planting. Sites with a history of cropland use showed higher regeneration densities for both oak species compared to former shrubland sites, even after accounting for variation in propagule pressure potential across the landscape, confirming our fourth hypothesis. However, we found no support for smaller colonization differences between oak species in areas of former cropland use as compared to shrubland. Our observations could be explained by several factors. First, soil improvement practices traditionally implemented for cropping such as fertilization or structural amelioration (Abadie et al. 2018; Cramer et al. 2008) can persist for over a century, significantly influencing the growth of trees established after cultivation has ceased (Dupouey et al. 2002; von Oheimb et al. 2014). Second, shrubland and pastureland usually had lower soil quality than cropland, negatively affecting oak colonization after abandonment (Abadie et al. 2018). In line with our findings of

higher recruitment in previous cropland, Vilà-Cabrera et al. (2017) reported that newly established forests (conifers, deciduous and sclerophyllous) on abandoned agricultural land during the twentieth century showed higher growth rate and carbon storage compared to those on shrubland or grassland.

Variations in TWI, mediated by topographic differences across the landscape, did not significantly influence the colonization capacity of oak species. This may be because TWI, while closely related to soil moisture content (Kopecký et al. 2021), does not account for other key factors affecting juvenile recruitment such as light competition (Martín-Alcón et al. 2015; Rey Benayas et al. 2005), facilitation processes (Cruz-Alonso et al. 2020) or herbivory (Davis et al. 2011), which were beyond the scope of this study.

Ecological and restoration insights

The higher regeneration efficiency of *Q. ilex* compared to *Q. faginea* has ecological implications, especially in the context of climate change. Dense, unmanaged pine plantations, which cover millions of ha across the Mediterranean basin (Pausas et al. 2004), often show poor pine regeneration (Gómez-Aparicio et al. 2009; Ruiz-Benito et al. 2012). Consequently, in regions where remnants of both oak species coexist near pine plantations, regeneration in the mid-term is expected to be dominated by the evergreen oak. This transition toward oak-dominated systems is not a novel phenomenon; rather, it is a widespread process in the Iberian Peninsula (Carnicer et al. 2014). Our findings contribute to this broader understanding by providing insight into the ecological mechanisms that facilitate the increasing dominance of *Q. ilex* in these environments. In contrast, given its ecology, regeneration of the deciduous oak will likely remain confined to areas with higher moisture availability, such as ravines and north-facing exposures, and close to remnants at similar altitudes.

The findings of this study can enhance predictions of recruitment spatial patterns and have practical implications for modelling oak expansion and guiding future research. Importantly, the spatial distribution of forest remnants used for modelling oak colonization capacity, distance and altitude difference between trees and colonization sites, must

account for species specificities. Prediction of regeneration hotspots also provides crucial information for designing effective landscape restoration and management programs. For instance, identifying areas with high potential for passive oak restoration (i.e., natural regeneration) can optimize resource allocation for active restoration efforts such as seedling plantings by targeting areas with low regeneration potential. Moreover, in places where passive restoration measures are planned, our results highlight the importance of not only considering the presence of seed sources but also their spatial accessibility. Thus, the size and relative position of seed sources in relation to the location of areas intended to be restored can guide more effective natural regeneration of oaks, and seed sources such as woodland islets can be strategically planted in the landscape to assist tree regeneration (Rey Benayas et al. 2008). In addition, preserving all potential seed sources, regardless of the age of the individuals, remains crucial to catalyze the regeneration of these species.

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Data availability Processed data are openly available in Zenodo at <https://doi.org/10.5281/zenodo.15986932>.

Declarations

Competing interests The authors declare no competing interests.

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