



# Drivers of oak establishment in Mediterranean old fields from 25-year-old woodland islets planted to assist natural regeneration

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## Abstract

Planted woodland islets can provide seeds for restoring forest ecosystems in Mediterranean old fields lacking seed sources, but other factors than seed arrival can also hinder the establishment of woody species. We experimentally examined factors affecting the emergence, survival, growth and recruitment of holm oak (*Quercus ilex*) seedlings juveniles from 25-year-old 100-m<sup>2</sup> oak woodland islets planted in a Mediterranean old field. Wet springs and summers increased seedling emergence and survival. Distance to the islets per se did not affect seedling performance. However, emergence and survival increased in microsites close to the islets in less sun-exposed orientations of the islets and far from the islets in more sun-exposed orientations. Damage by wild boar reduced emergence, and unsheltered seedlings had 26% lower survival than sheltered ones, reflecting herbivory. Herb community biomass and light reduction by herbs increased with distance from nearest islet; the sparse herb cover around islets was due to competition from woodland islets, not to herbivory. There was a mismatch between the pattern of seedling survival and how the abundance of naturally recruited oaks varied with distance from the nearest islet; this suggests that other drivers can counteract the spatial pattern of seedling survival. We conclude that natural regeneration of *Q. ilex* in old fields from planted woodland islets is slow (5.7 seedlings ha<sup>-1</sup> yr<sup>-1</sup>) due to acorn and seedling predation, and drought during spring and summer. Despite their small size, planted islets affected survival of oak juveniles depending on the orientation and distance relative to the islets.

**Keywords** Applied nucleation · Drought · Forest recovery · Herbivory · *Quercus ilex* · Seedling survival

## Introduction

Natural regeneration, also called passive or spontaneous restoration, has restored many woodland and forest areas (Chazdon et al. 2020); for instance, 133 million ha in Europe have been recovered through natural regeneration up to 2010 (FAO 2015). It has been estimated that 0.9 billion ha of woodlands and forests can still be restored globally (Bastin et al. 2019). Passive restoration can help to meet international forest restoration goals such as the 2011 Bonn Challenge (350 million ha of degraded and deforested landscapes

by 2030) and the 2014 UN Declaration on Forests (to halve natural forest loss by 2020 and strive to end it by 2030; Crouzeilles et al. 2016; Meli et al. 2017).

Insufficient seed dispersal, however, reduces the effectiveness of passive forest restoration (Jordano et al. 2008; Navarro and Pereira 2012; Rey-Benayas and Bullock 2012). Various strategic revegetation actions have been applied to accelerate forest restoration in areas without forest remnants such as farmed landscapes (Rey-Benayas and Bullock 2015). These actions differ in their intensity of intervention, from high-intensity intervention named “reconstructive restoration” to lower-intensity “assisted restoration” (Gann et al. 2019; Atkinson and Bonser 2020). The less intensive actions include several forms of nucleation techniques such as planting tree clusters, hedgerows and even isolated trees, all of which not only promote regeneration but also enhance wildlife, agricultural production and other ecosystem services (Manning et al. 2006; Rey-Benayas et al. 2008; Van Vooren et al. 2017).

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The introduction of tree clusters (“woodland islets” approach as a way of nucleation) to assist regeneration was suggested by Rey-Benayas et al., (2008) as an action for restoring forests on old fields. Several small, dense blocks of native shrubs and trees are sparsely planted in agricultural land to trigger secondary succession over larger areas (Navarro and Pereira 2012). Later researchers have referred to this approach as “tree islands” or “applied nucleation” (Corbin and Holl 2012; Zahawi et al. 2013; Piironen et al. 2015), “dispersion and attraction nuclei” (García-Martí and Ferrer 2013) or “tree clumps” (Stanturf et al. 2014). This approach has been implemented in various restoration actions (Robinson and Handel 2000; Dendy et al. 2015; Corbin et al. 2016; Ramírez-Soto et al. 2018; Shaw et al. 2020), yet few studies have addressed the long-term effectiveness of woodland islets for facilitating forest restoration or the factors that may compromise that effectiveness (Rey-Benayas et al. 2015; Rey-Benayas and Bullock 2015; Corbin et al. 2016; Holl et al. 2020).

In Mediterranean old fields, numerous factors slow down passive restoration (Rey-Benayas et al. 2015; Cruz-Alonso et al. 2019a; Martínez-Muñoz et al. 2019); these include seed dispersal limitation by lack of seed sources and/or seed dispersers, seed predation, competition by herbs (Rey Benayas et al. 2005; Cuesta et al. 2010b), herbivory (Gómez et al. 2003; Puerta-Piñero et al. 2012) and harsh abiotic conditions (Cuesta et al. 2010a; Andivia et al. 2017; Martínez-Muñoz et al. 2019). Summer drought and high interannual rainfall and temperature variation can also strongly affect plant performance (Forner et al. 2018); therefore, running multi-year experiments are needed to capture the potential effects of weather variability on dynamics of recruited tree species (Cuesta et al. 2010b; Pérez-Camacho et al. 2012).

The woodland creates a heterogeneous environment for new plants beyond the woodland itself, and factors and processes controlling plant recruitment may operate differently at locations near or far from islets (Rey-Benayas et al. 2015; Benítez-Malvido et al. 2018; Holl et al. 2020). For example, seeds produced by islets can be dispersed at a wide range of distances from them (Corbin et al. 2016). However, the effect of planted woodland islets on the distribution of recruits from the islets depends on the net outcome of several ecological processes, which intensity can change with the distance and orientation from the islets. The islets can facilitate indirectly the establishment of woody plant recruits by reducing the competition of herbs on recruits (Cuesta et al. 2010b). Islet competition with recruits may be stronger in sun-exposed orientations than in shady orientations, which may have a less harsh abiotic microenvironment (Pérez-Ramos et al. 2013). Finally, islets can provide higher mycorrhizal concentration to nearby open areas, which further promotes the establishment of new plants (Dickie et al. 2007). At the same time, at short distances,

islets may compete with new woody plants directly (Morán-López et al. 2018; Gavinet et al. 2020). Moreover, as seed sources (e.g. mature trees) are present only there in an old field matrix, islets may attract seed predators into the area, and thus create a patch (islets plus a buffer) of increased predation pressure as Janzen–Connell’s effect predicts (Janzen 1970; Bogdziewicz et al. 2018). The islets also offer refuge to herbivores such as rabbits (Lombardi et al. 2007) which, in turn, consume herbs, tree seeds and seedlings (Zamora et al. 1985; Leiva and Fernández-Alés 2003).

The goal of the present study was to assess the spatial effects of holm oak (*Quercus ilex* L.) woodland islets on oak recruitment outside the islets 25 years after islets establishment in Mediterranean old fields and to identify factors that influence that recruitment. *Quercus ilex* is a late successional, slow-growing tree (Villar-Salvador et al. 2013). The woodland islets have not expanded beyond their original plantation limits. Some holm oaks of different sizes have become established around the islets (Rey-Benayas et al. 2015) after the islets started to produce acorns in 1999 (Rey-Benayas et al. 2008). A strip approximately 1.5–2.0 m wide around the islets show minimal herbs, suggesting that plant development near the islets may be limited by competition from islets and by herbivory. In a previous study (Rey-Benayas et al. 2015), we analysed long-term recruitment at this site, and we experimentally showed that high acorn predation or removal, seedling herbivory and stressful microclimatic conditions slow down oak seedling establishment from the woodland islets. Nevertheless, we do not know (1) the effect of interannual rainfall and temperature variation, (2) how ecological processes involving the islets and surrounding herb matrix interact at the edge of islets to determine oak regeneration, (3) the effect of herbivory during acorn germination and seedling emergence and later on established seedlings, and (4) if the strip of low herb cover around the islets is due to competition by the islets and/or herbivory. Thus, the present study continued these investigations over multiple years with a longer database to capture potential effects of interannual rainfall and temperature variation and microsite environment around islets.

In this study, we hypothesised that seedling emergence and survival would be highest in years with rainier springs and milder summers (H1); seedling emergence and survival would depend on the orientation relative to islets, being higher at northern, less sun-exposed edges of the islets, where the islet canopy improves the microclimate (H2); and competition by the islets, surrogated by distance from nearest islet, and herbivory would reduce seedling emergence and survival and herb growth near the islets (H3). Our data spanning a quarter century identify mechanisms affecting the success of applied nucleation, which may help guide natural woodland regeneration of Mediterranean old fields and other regions of low productivity.

**Table 1** Spring and summer precipitation, mean temperature, number of days with maximum temperature > 36 °C and consecutive days with maximum temperature > 36 °C per year

Year	Precipitation (mm)			Mean temperature (°C)			No. days	
	Spring	First summer	Second summer	Spring	First summer	Second summer	T > 36 °C	Longest heatwave
2014	45.8	38.1	47.1	14.1	<b>23.4</b>	25.7	<b>26</b>	<b>7</b>
2015	<b>109.2</b>	47.1	19.8	13.8	25.7	25.3	57	47
2016	<b>184.8</b>	19.8	<b>138.7</b>	<b>10.9</b>	25.3	25.9	61	<b>7</b>
2017	56.6	<b>138.7</b>	54.4	13.8	25.9	24.1	51	15
Mean for entire period (2000–2018)	132.03	51.6	51.6	12.5	24.5	24.5	41	16

The first and second summer precipitation refer to the summer precipitation of year, and year<sub>+1</sub>; e.g. 2014: first summer precipitation was the 2014 summer precipitation and second summer precipitation was the 2015 summer precipitation. *Italic numbers* indicate a dry season (below-average precipitation) or hot season (above-average temperature). **Bold numbers** indicate a wet season (above-average precipitation) or a cool season (below-average temperature). Regular numbers indicate seasons with average precipitation or temperature. **Bold and italic numbers** represents the spring when we irrigated acorn seeding points to achieve the precipitation equal to the average spring precipitation for the period 2000–2014

## Material and methods

### Study site

The study was conducted at “La Higuera”, a research station in Santa Olalla, Toledo, Spain (40°3'N, 4°24'W, elevation 450 m), managed by the Consejo Superior de Investigaciones Científicas. We ran our experiments on an old field of 1 ha that had been cultivated for grain for many years, until woodland islets were planted there in 1993. In that year, 16 oak woodland islets of 100 m<sup>2</sup> were established at a density of 50 seedlings per islet, with a mean distance of 11.8 m between the islets. The woodland islets are embedded in a grassland matrix dominated by annuals that have remained from when the islets were planted (Fig. S1). The field is surrounded by rain-fed cereal crops in a highly farmed landscape context. More details about islet establishment and analyses of management and outcomes through 2014 have been described elsewhere (Rey Benayas 1998; Rey Benayas and Camacho-Cruz 2004; Rey Benayas et al. 2015). In 2014, the mean height of trees in the islets ranged between 3 and 4 m.

The climate is continental Mediterranean, characterised by cool winters and a long summer drought that imposes severe water stress on the vegetation. During 1993–2018, annual precipitation averaged 468.2 mm and mean temperature averaged 15.5 °C. Daily weather data were obtained from an in situ weather station. During the period 2000–2018, precipitation and temperature in spring (24 February–14 May) and summer (15 May–31 August), the number of days with high temperature (maximum > 36 °C) and the length of the longest heatwave (defined as consecutive days with maximum temperature > 36 °C) differed substantially across the years. Springs in 2014 and 2017 were particularly dry and hot, spring precipitation in 2015 was close to the average for the period 2000–2018, and spring precipitation in 2016 was higher than the average. The summers of 2014 and of 2016 were dry. Summer precipitation in 2015 was similar to the average for the period, and that of 2017 was higher than the average (Table 1, Fig. S2).

The soil is a relatively fertile, deep luvisol type, and it is derived from arkoses. The major potential predators/dispersers of acorns and oak seedlings in the study area are rodents (e.g. *Apodemus sylvaticus* L. and *Mus spretus* Lataste), Eurasian magpies (*Pica pica* L.) and wild boars (*Sus scrofa* L.), as well as rabbits (*Oryctolagus cuniculus* L.) and hares (*Lepus granatensis* Rosenhauer) that shelter in the woodland islets.

## Experimental design to identify factors affecting seedling emergence and survival

We seeded holm oak acorns around woodland islets on 24 February 2014, 31 January 2015, 8 February 2016 and 23 February 2017. Acorns were from Mediterranean continental-climate provenances from inland Spain acquired in the Centro Nacional de Recursos Genéticos Forestales “El Seranillo”. Prior to seeding, acorns were submerged in water for 12 h. The floating acorns, which had been partially eaten or rotten, were discarded. Mean emergence of acorn lots under laboratory conditions was 79.4% across studied years.

A total of 169 points were seeded and protected in 2014, 206 points in 2015, 198 points in 2016 and 209 points in 2017. Each point had five acorns buried at a depth of 3 cm, which were protected with wire shelters to avoid changing the microclimate around the seeded acorns and emerged seedlings (Fig. S1). We used the same type of wire shelters in 2014, 2015 and 2016 (Fig. S3a), and the shelters were nailed to the ground. Due to high acorn predation by wild boars in 2016 (see Fig. S3c), we used another type of wire shelter in 2017 that was designed to deter predation by wild boars (Reque and Martin 2015; Fig. S3b). Acorns seeded in 2015 were irrigated in spring to the same level as the historical mean spring precipitation.

In all years, seeding points were located along two, 10-m-long transects extending out from each of the external corners of every group of four woodland islets (Fig. S1). Only in 2014, some seeding points were placed among the four islets. Seeding points were located at 0, 1, 5 and 10 m from the woodland islet edge. However, proximity between adjacent islets and nearby active crop fields or trails prevented seeding at some distances of 5 and 10 m. Our analyses did not include equidistant seeding points between adjacent islets because they were not independent of the orientation of the two islets.

We assessed seedling emergence at four times during spring, early summer and fall in each year. When a cluster of five acorns at the same seeding point produced more than one seedling, only one seedling was left to avoid conspecific competition, and the other emerged seedlings were removed by excising the stem at the root collar level to prevent resprouting. Survival of the remaining seedlings was monitored 4–16 times from emergence until the end of the experiment in March 2019.

To assess the importance of seedling herbivory at one year after emergence, we removed the shelters from 40 of the 88 seeding points in 2015 that had live seedlings on 12 May 2016.

## Dynamics of natural establishment

To assess natural establishment of holm oak seedlings during 2014–2017, we counted the emerged seedlings and monitored their survival in 192 rectangular plots and nine square plots located between the islets as well as between the islets and the edge of the study site. The rectangular plots were located along the edges of the woodland islets in four orientations: two at each corner and one halfway between them (Fig. S1). Sampling took place in July 2014, 2016 and 2017, but it was delayed until November in 2015 because of logistical problems. The size of the plots between islets was 1 × 5 m; those between islets and active crop fields or trails measured 1 × 10 m. Square plots between islets measured 5 × 5 m. The 201 sampling plots covered a total area of 1,474.9 m<sup>2</sup> or 17.6% of the experimental field area not occupied by woodland islets. Emerged seedlings in all plots were tagged for later localisation.

We monitored the plots to assess survival of emerged seedling in October or early November, i.e. after the summer dry period and at the start of each autumn. We measured the size of all living seedlings on 14 March 2019.

## Holm oak recruitment and growth assessment

We thoroughly surveyed the entire study site to find all naturally established holm oaks with a minimum height of 5 cm, which were positioned on an ortho-photograph. These individuals represent long-term recruitment after woodland islets had started to produce acorns. We measured the distance of each juvenile to the nearest islet; from 2014 to 2019, we also measured their height, basal diameter and calculated the projected crown area.

On 14 March 2019, we measured the size of all living seedlings and naturally established holm oaks (experiments and observation described in “[Study site and Experimental design to identify factors affecting seedling emergence and survival](#)” section) and calculated mean annual growth rate as:

$$\frac{\text{Plant final size} - \text{Plant initial size}}{\text{Number of years}} \quad (1)$$

When calculating the initial size of the naturally emerged seedlings and established seedlings from sowing points, we assigned 0.5 cm as the initial height and 0.78 cm<sup>2</sup> as the initial projected crown as minimum detectable size in the field. For the naturally established holm oaks, initial size was calculated from the first measurement data.

## Microsite environment around islets

To assess whether islets reduced the growth of the herb community and therefore its competition with oak seedlings, we measured the development of the herb community in two ways. The first was to measure light extinction by the herb community as the percentage of light that herbs reduce by calculating the difference between light levels above the herb canopy under full sun and the light under the herb layer at all seeding points containing emerged seedlings (Fig. S1) in November 2015 and June 2016. Light was measured with a quantum photo-radiometer (HD9021, Delta OHM, Caselle di Selvazzano, Italy) in sunny days. The second was to measure herb biomass in May 2016 in quadrats of 40 × 40 cm located 1 m away from the point where we measured soil moisture (see below). Herbs were dried in an oven at 60 °C for at least 48 h and weighed.

We also studied whether soil moisture differed with orientation and distance from the islet edge by inserting PVC tubes at 45 points in May 2016 (Fig. S1). Soil moisture was measured at depths of 10, 20, 30 and 40 cm and at 1, 5 and 10 m from the islet edge in all orientations. Measurements were taken with a moisture sensor (Profile Probe Type PR2, Delta-T Devices, Cambridge, UK) connected to a moisture meter (HH2, Delta-T Devices). In some cases, moisture could not be measured at 10 m due to the presence of cropped fields or trails. Measurements were taken several times from May 2015 to May 2017.

To ascertain whether strips of sparse herb vegetation around the islet edge were the result of competition from islets or from herbivores living inside the islets (mainly rabbits), we placed on 5 November 2016 a total of 32 wire cages (60 cm deep, 38 cm wide and 29 cm tall) on the ground to exclude herbivores (Fig. S3e). One cage was placed at 1 m from each islet edge on the northern and southern sides. On 7 June 2017, i.e. after maximum herb growth in the spring and before senescence in the summer, we harvested the herb biomass within the cages and in paired plots measuring 60 × 38 cm (Fig. S1), and then processed it as described above.

## Data analysis

Generalised linear models (GLMs) with a binomial distribution and a logit-link function were used to analyse seedling emergence at the experimentally seeded point, as well as the survival of seedlings that had emerged from seeded acorns or were naturally established. We included the year as a categorical variable to test the effect of interannual precipitation and temperature variation in the initial model (fixed effect; H1). The initial model contained orientation, distance from nearest islet, their interaction (H2 and H3) and damage

by wild boar (yes or not) nested within the year as fixed effects. Plot (four groups of four closest woodland islets) was also included as a fixed effect, because our data were spatially aggregated and the plot factor showed only four levels (Crawley 2007). To analyse the effect of herbivory on established seedlings, we added the presence or absence of seedling shelter in 2015 seeding points and its interaction with distance from nearest islet as a fixed effect.

We analysed light extinction by herbs and herb biomass near the points where soil moisture was measured. Orientation, distance from nearest islet, their interaction and plot were included as fixed effects. We also analysed the differences in herb biomass at the islet edges to test the effect of orientation and herbivory exclusion (fixed effects; H3). We used linear models for all analyses except for light extinction by herbs, for which we used GLMs with a gamma error and an inverse link function. We used linear mixed models (LMMs) to analyse the effects of orientation, distance from nearest islet, depth and their double interactions on soil moisture; these models included position and measurement date as random effects. Akaike's (1987) information criterion (AIC) was calculated for each model. We used the cut-off of  $\Delta AIC < 2$  units to identify models with better explanatory power that followed the principle of parsimony (Burnham and Anderson 2002; Crawley 2007).

We used the Chi-squared test to analyse whether the proportion of the established oaks differed between expected and observed values for strips of land at different "distance bins" from the islets. Expected values were calculated by taking into account the proportion of area covered by each strip of land. We used GLM with a gamma error and an inverse link function and LM to analyse the fixed effects of orientation and distance from nearest islet on annual growth rate of living seedlings. These analyses were performed separately for experimentally seeded acorns (with year as fixed effects) and for naturally established oaks. All analyses were performed with R software version 3.5.2 (R Core Team 2018) using the packages *lme4* (Bates et al. 2014), *MuMIn* (Barton 2014), *ggplot2* (Wickham 2016), *effects* (Fox and Weisberg 2018) and *heatwaveR* (Schlegel and Smit 2018).

## Results

### Seedling emergence

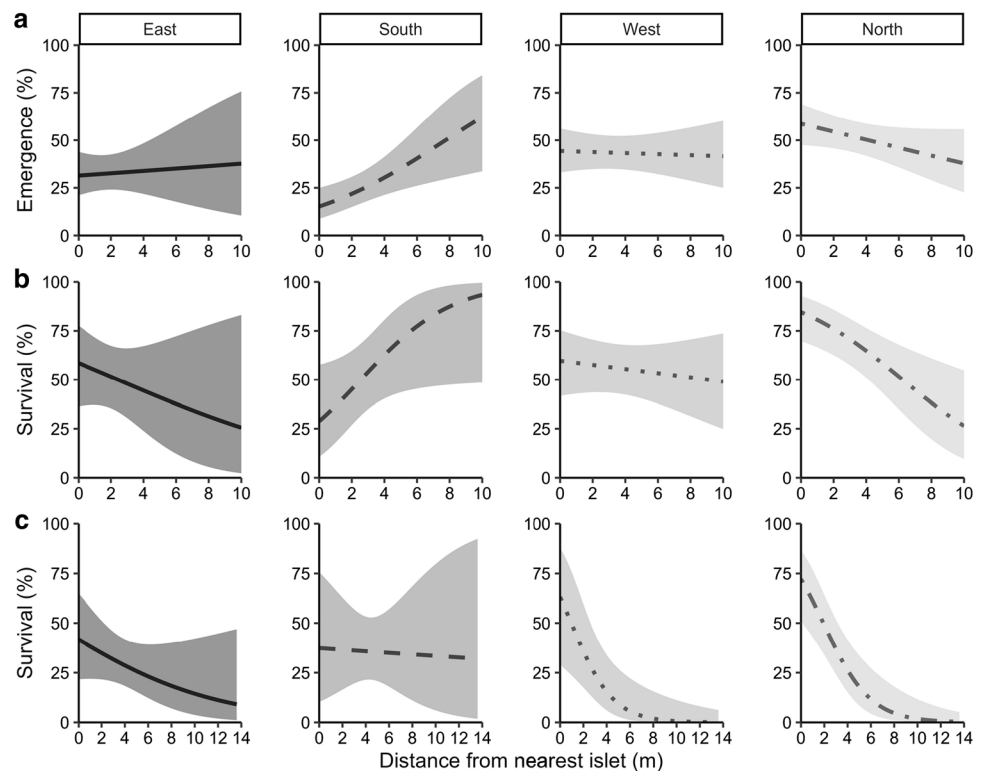
At least one seedling emerged at 41 (24.3%) seeding points in 2014, 134 (65.0%) in 2015, 27 (13.6%) in 2016 and 46 (22.0%) in 2017. For all years, the model that best explained seedling emergence included the orientation × distance interaction, as well as sowing year, damage by wild boar nested by year and plot (Table 2 and S1). Emergence averaged 43.1% on the northern side and 19.8% on the southern

**Table 2** Selection of models of seedling emergence from seeding points and of survival of seedlings that emerged from seeding points or that were naturally established

Study	Sampling time	Model parameters	df	AICc	$\Delta$ AICc	McFadden
Experimental seeding	Seedling emergence	<b>Orientation x distance + year / wild boar damage + plot</b>	<b>16</b>	<b>747.74</b>	<b>0.00</b>	<b>0.268</b>
		Orientation + year / wild boar damage + plot	12	750.54	2.80	0.257
		Null model	1	979.02	231.29	0
	Seedling survival after first summer	<b>Orientation x distance + year</b>	<b>11</b>	<b>273.62</b>	<b>0</b>	<b>0.142</b>
		Distance + year	5	276.48	2.86	0.087
Naturally emerged seedlings	Seedling survival after first summer	Orientation x distance + year + plot	17	289.25	0	0.199
		<b>Orientation x distance + year</b>	<b>13</b>	<b>290.07</b>	<b>0.81</b>	<b>0.168</b>
		Distance + year + plot	9	292.24	2.99	0.133
	Seedling survival after second summer	Null model	1	317.58	28.32	0
		<b>Distance + year</b>	<b>5</b>	<b>82.41</b>	<b>0</b>	<b>0.315</b>
		Distance	2	84.51	2.1	0.231
		Null model	1	106.57	24.16	0

Tested initial models of seeding points: seedling emergence~orientation  $\times$  distance+year / wild boar damage+plot (“/”=variable nested by year); seedling survival~orientation  $\times$  distance+year+plot. Tested initial model of natural regeneration: seedling survival~orientation  $\times$  distance+year+plot. McFadden: McFadden’s pseudo-R-squared, explained deviance by model. Bold: Selected final models and their parameters. Note that, although we tested all possible candidate models, the table only shows models with  $\Delta$ AICc < 2, the next model out of this cut-off and the null model

**Fig. 1** Predicted values of **a** emergence and **b** and **c** survival after the first summer of holm oak seedlings in relation to orientation and distance from the nearest woodland islet. Panel **b** represents survival of experimentally seeded acorns and panel **c** the survival of naturally regenerated seedlings. Shaded areas represent the 95% confidence interval. Note that a different line type and grey colour are consistently assigned to each orientation in all figures



side. It increased with distance from nearest islet in the southern orientation, while the opposite was observed in the northern orientation (Fig. 1a). Distance had a negligible effect on emergence in the western and eastern orientations.

Emergence was higher at seeding points that were undamaged by wild boar than at points that were damaged (42.6 vs. 5.6%).

We found 28 naturally emerged oak seedlings in 2014, corresponding to a density of 190 seedlings  $\text{ha}^{-1}$ . The corresponding values in other years were as follows: 40 seedlings and 271 seedlings  $\text{ha}^{-1}$  in 2015, 152 seedlings and 1030 seedlings  $\text{ha}^{-1}$  in 2016, and 42 seedlings and 285 seedlings  $\text{ha}^{-1}$  in 2017. Across the four study years, these seedlings were located a mean (SE) of  $4.9 \pm 0.18$  m from nearest islets, and mean distance ranged annually from 4.1 to 5.3 m (Fig. S4).

### Seedling survival

After excluding the seeding points damaged by wild boars, survival at the end of the first growing season of the herbivory-protected seedlings was 33.3% ( $n = 7$ ) in 2014, 69.4% ( $n = 93$ ) in 2015, 28.0% ( $n = 7$ ) in 2016 and 54.3% ( $n = 19$ ) in 2017. The model that best explained seedling survival after the first summer included the sowing year and the interaction between orientation and distance from nearest islet (Table 2 and S1). Survival increased with distance from nearest islet in the southern orientation, but it decreased with distance in the remaining orientations, especially the northern one (Fig. 1b). At the last sampling on 14 March 2019, we counted 71 living seedlings at the seeding points, comprising 6 at points seeded in 2014, 47 at sites seeded in 2015, 2 at sites seeded in 2016 and 16 at sites seeded in 2017.

For naturally established seedlings, survival at the end of the first summer were 28.6% for those that emerged in 2014, 50.0% for those that emerged in 2015, 21.7% for those that emerged in 2016 and 35.7% for those that emerged in 2017 (Fig. S5). The model that best explained

the survival of these seedlings included the year of emergence and the interaction between orientation and distance from nearest islet (Table 2 and S1). In general, seedling survival after the first summer was higher nearer rather than farther from the islets, especially in the northern and western orientations (Fig. 1c). At the end of the second summer, survival rates were 14.1% for seedlings that emerged in 2014, 7.5% for those that emerged in 2015, 9.2% for those that emerged in 2016 and 31.0% for those that emerged in 2017 (Fig. S5). The model that best explained seedling survival after the second summer included distance from nearest islet and year of emergence (Table 2 and S1). Seedling survival after the second summer decreased with distance from nearest islet. At the last sampling, we counted 24 living seedlings on the sampled plots, comprising 0 that emerged in 2014, 2 that emerged in 2015, 10 that emerged in 2016 and 12 that emerged in 2017.

In the 2015 experiment designed to assess seedling herbivory, survival after the end of the second summer was higher for protected seedlings (81.2%) than for unprotected ones (55.0%). Survival was lowest in the eastern orientation, and it decreased with distance from nearest islet similarly for protected and unprotected seedlings (Table S2, Fig. S6).

### Light extinction, herb biomass and soil moisture

The model that best explained light extinction in autumn included the plot and the interaction between orientation and distance from nearest islet (Table 3a and S3a). In contrast, the model that best explained light extinction in spring included only distance from nearest islet (Table 3b and S3b).

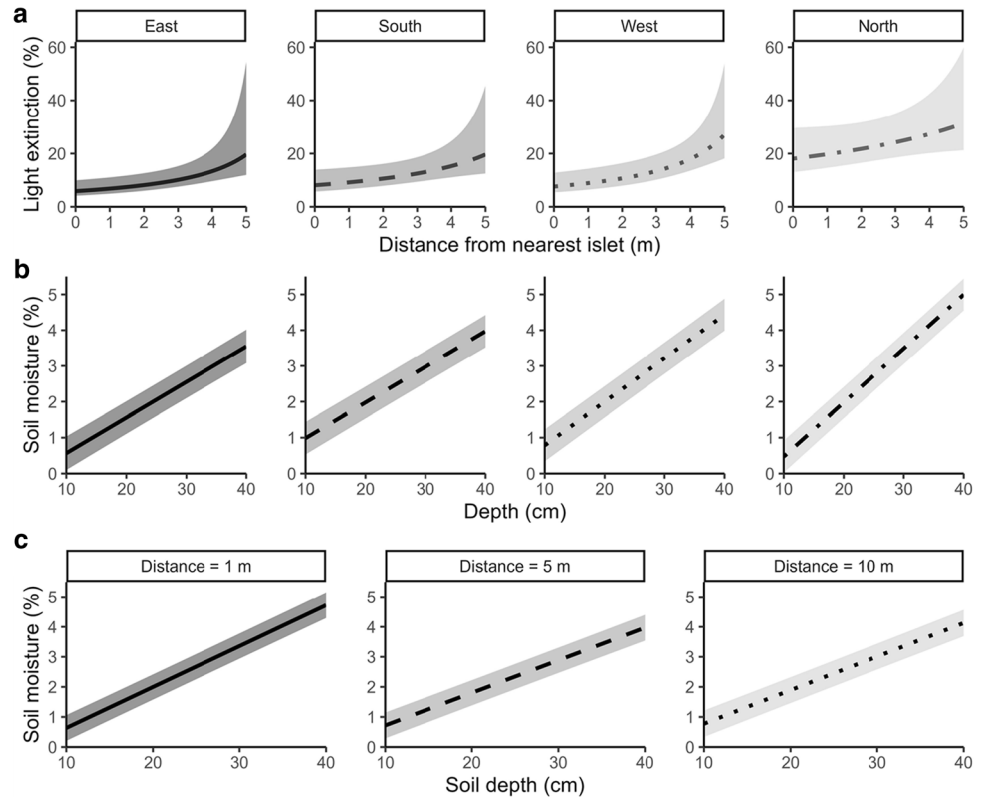
**Table 3** Selection of models of light extinction, herb biomass and soil moisture

Microsite environment characteristic	Model parameters	df	AICc	$\Delta$ AICc	R <sup>2</sup>
(a) Light extinction in autumn (November)	<b>Orientation x distance + plot</b>	<b>12</b>	<b>1292.8</b>	<b>0</b>	<b>0.32</b>
	Orientation x distance	9	1295.3	2.47	0.28
	Null model	2	1338.81	45.99	0
(b) Light extinction in spring (June)	<b>Distance</b>	<b>3</b>	<b>759.18</b>	<b>0</b>	<b>0.299</b>
	Orientation x distance	9	762.35	3.17	0.386
	Null model	2	786.56	27.38	0
(c) Herb biomass near the points of soil moisture measurements	<b>Distance + plot</b>	<b>6</b>	<b>386.59</b>	<b>0</b>	<b>0.764</b>
	Orientation + distance + plot	9	394.10	7.51	0.771
	Null model	2	441.64	55.05	0
(d) Soil moisture	<b>Orientation x depth + distance x depth + plot + (1 partial_n) + (1 date)</b>	<b>18</b>	<b>6001.05</b>	<b>0.00</b>	<b>0.581</b>
	Orientation x depth + plot + (1 partial_n) + (1 date)	14	6006.85	5.80	0.577
	Null model	4	6857.08	856.03	0.261

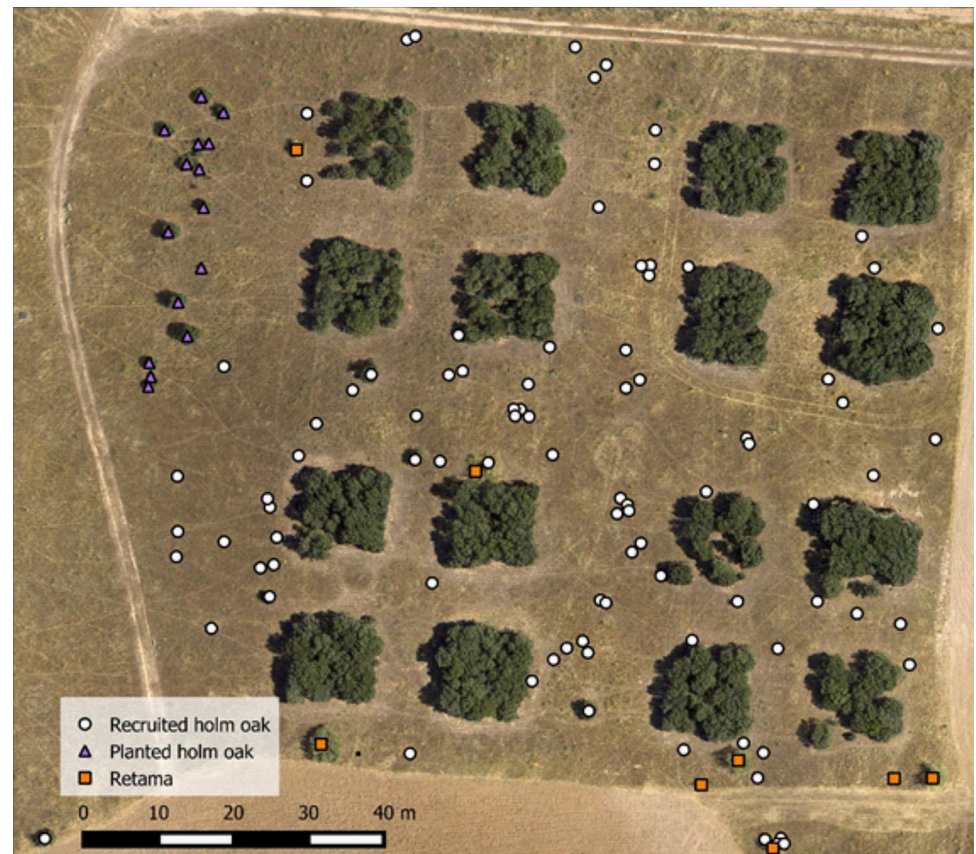
The initial models: light extinction ~ orientation x distance + plot; herb biomass ~ orientation x distance + plot; soil moisture ~ orientation + distance + depth + (orientation: distance) + (orientation: depth) + (distance: depth) + plot + (1|partial\_n) + (1|date)

Bold: Selected final models and their parameters. Note that, although we tested all possible candidate models, the table only shows the models with  $\Delta$ AIC < 2, the next model out of this cut-off and the null model

**Fig. 2** **a** Predicted values of light extinction in autumn 2015 in relation to orientation and distance from nearest islet. Soil moisture in relation to **b** orientation and depth and **c** distance and depth. Shaded areas represent the 95% confidence interval



**Fig. 3** Positions of the 92 naturally regenerated and established holm oaks taller than 5 cm in the experimental field





Light extinction in autumn and spring increased with distance from nearest islet; in autumn, it was highest in the northern orientation (Fig. 2a and fig. S7).

Herb biomass was similar inside and outside the herbivore exclusion cages and was unaffected by orientation or plot (Table S4, Fig. S8). Herb biomass close to the points where soil moisture was measured increased with distance from nearest islet (Table 3c and S3c, Fig. S9).

Soil moisture was affected by the interaction between orientation and depth: it increased with depth, especially in the northern orientation. Soil moisture was also affected by the interaction between distance from nearest islet and depth, increasing with depth especially near the woodland islets and the plot (Table 3d and S3d, Fig. 2b-c).

### Long-term natural regeneration

At 25 years after islet planting, 92 holm oak individuals taller than 5 cm had become established naturally near the islets (Fig. 3). This resulted in a density of 103.3 oaks  $\text{ha}^{-1}$  in areas outside the islets, with an average establishment rate of 4.1 oaks  $\text{ha}^{-1} \text{yr}^{-1}$  on the islets since 1993 or 5.7 oaks  $\text{ha}^{-1} \text{yr}^{-1}$  since the oaks planted in the islets started to produce acorns at the age of seven years. Height, basal diameter and crown projected area of the established oaks averaged  $67.2 \pm 81.2$  cm,  $26.4 \pm 46.4$  mm and  $0.90 \pm 2.66$   $\text{m}^2$ , respectively. The recruits were located an average of  $6.8 \pm 4.8$  m to the closest islet, and each defined strip within different distance bins from the islets contained significantly different proportions of all recruits ( $\chi^2_5 = 21.89$ ,  $p < 0.001$ ; Fig. S10).

### Oak growth

At the last sampling in 14 March 2019, the 95 living seedlings that had emerged either at the seeding points or were naturally established were  $9.1 \pm 0.46$  cm tall, with a basal diameter of  $2.8 \pm 0.18$  mm and a crown projected area of  $25.6 \pm 1.95$   $\text{cm}^2$ . Their mean annual growth rate did not vary with orientation or distance from nearest islet (Table S5a). In fact, the mean annual growth rate of the 92 naturally established individuals taller than 5 cm ( $0.34 \pm 0.15$   $\text{m}^3 \text{yr}^{-1}$ ) did not vary significantly with any variable analysed (Table S5b).

## Discussion

Natural oak regeneration from woodland islets planted 25 years ago progresses slowly and is influenced by herbivory and interannual precipitation and temperature variation. The success of this approach is favoured in wet and mild years. We provide evidence of “islet edge” effects that affect oak seedling emergence and survival and herb

community development, which depend on orientation and distance from nearest islet due to facilitation (namely microclimate amelioration) and competition (namely water extraction) processes. However, the pattern of seedling survival with distance from nearest islet did not match the distance profile of naturally regenerated tree juveniles, suggesting that other important drivers of tree recruitment not addressed in this study could override the pattern of seedling survival.

### Influence of interannual climatic variation and microsite characteristics on seedling establishment

We observed marked interannual variation in seedling emergence and survival, suggesting an important role of precipitation and temperature variability on oak establishment, consistent with previous studies in Mediterranean old fields (Cruz-Alonso et al. 2019b). For instance, emergence was notably higher in 2015 (65.0%) than in 2014 (24.3%), mostly due to interannual spring climate differences (H1). The spring of 2014 was particularly dry and hot, whereas we irrigated in spring of 2015 to achieve the historical mean precipitation for the period 2000–2018 (Table 1, Fig. S2). Our results are consistent with the fact that acorns are recalcitrant seeds (Villar-Salvador et al. 2013) and quite sensitive to spring drought, which hinders seedling emergence (Joët et al. 2013). In addition, holm oak is a masting species, and acorn production depends strongly on interannual climate variation (Bogdziewicz et al. 2017). Consequently, interannual variation in precipitation and temperature can affect acorn availability and seedling emergence in particular years (Fig. S4).

Seedling survival was higher in years in which summer was wet (Table 1, Fig. S2; H1). However, spring rainfall can be as critical as summer rainfall for oak survival in Mediterranean environments (Castro 2006), as indicated by the lower survival in 2017 than in 2015 despite the summer of 2017 was much wetter. The main difference between both years was that the spring of 2017 was drier than the spring of 2015. It is possible that seedlings that emerge in average and wet springs may be more drought-resistant by developing larger and deeper roots during the wet season than seedlings that emerge in a dry spring (Castro 2006; De Luis et al. 2008). Deep and extensive rooting allows plants to avoid drought stress and access to more water resources during the summer drought (Padilla and Pugnaire 2007; Cuesta et al. 2010a).

Woodland islets improved performance of seedlings established in their proximity, but this effect depended on orientation and distance. Emergence and survival decreased with distance from the nearest islet in less sun-exposed orientations, especially the northern orientation (Fig. 1). These results support H3 only in the most sun-exposed orientation.

A similar pattern was shown by O'Donnell et al. (2020), who reported increased seedling emergence and survival up to 3 m from the forest edge. We observed the opposite trend in the most sun-exposed orientation, the southern orientation. This supports our H2 and implies that seedlings did not tolerate the combination of high insolation and water competition from islets in the southern orientation.

The decrease in seedling establishment with distance from the nearest islet and towards northern orientation was opposite to the trends observed for the development of herb community. The lower herb development likely reflected competition from islets in their proximity, in support of H3 and consistent with previous studies in other tree–pasture transitions (Guevara et al. 1992; Belsky et al. 1993). This suggests that better seedling performance close to islets in less sun-exposed orientations could be due, in part, to lower competition from herbs, an indication of indirect facilitation by the islets. Two results support this idea. First, herb biomass increased with distance from nearest islet, especially in less sun-exposed orientations; similarly, light extinction, a surrogate of herb biomass, increased with distance from nearest islet. Second, the herbivore-exclusion experiment (see “[Holm oak recruitment and growth assessment](#)” section) demonstrated that the sparsity of herb vegetation in a strip surrounding the islets resulted from competition from islets rather than from herbivory. This could be due to allelopathy induced by ectomycorrhizal fungi associated with holm oak roots (Menta et al. 2014; Saitta et al. 2018). Low development of herbs close to islets in the less sun-exposed orientations may be due to shading by the islets during the winter and spring (Kunstler et al. 2006).

Lower development of herb community and shading close to islets was associated with increased soil moisture in the northern and western orientations, mainly in the deepest soil layers (Rey Benayas et al. 2002, 2005, 2007). Higher soil moisture with depth, especially near woodland islets, may help explain the better seedling performance in less sun-exposed orientations.

Notably, the spatial pattern of seedling survival relative to islets that was measured after experimental acorn seeding or in naturally emerged seedlings did not match the spatial distribution of spontaneously recruited oaks > 5 cm, which represent long-term natural recruitment. These naturally recruited oak juveniles were more abundant at intermediate distances from nearest islet than close to the islets (Fig. S10). Nevertheless, the spatial variation in the proportion of naturally emerged seedlings in spring with distance from the islet edge matched the spatial pattern observed for the long-term recruitment of oak juveniles (Fig. S4 and S10). This suggests that other main processes involved in the recruitment of oak juveniles are overriding the seedling survival. We can envisage at least three processes explaining the mismatch between the variation of seedling survival and the

proportion of naturally long-term recruited oaks with distance from nearest islet. One is the pattern of acorn dispersal, which is driven by site selection of scatter-hoarders, that could affect emergence and seedling survival and thus determine the final spatial pattern of oak recruitment (Gómez et al. 2019). Consistent with this possibility, rodents disperse acorns at a mean distance of 4–5 m (Pons and Pausas 2007; Morán-López et al. 2018), close to the average distance of oak juvenile regeneration (6.8 m) observed in our study. A second one is acorn predation, which may be higher close to islet edges than in open areas (Villalobos et al., 2020). A third process that may counteract seedling survival is the variation in the interaction between oak juveniles and herbs from negative to neutral along oak ontogeny, due to increased stress resistance of oak juveniles (Cavender-Bares and Bazzaz 2000; Andivia et al. 2020).

Our results showed effective but slow natural oak regeneration in old fields from planted woodland islets, despite the fact that islets provided acorns to accelerate secondary succession. This slowness presumably reflects high acorn predation at the study site, documented here and in a previous analysis (96.9% of unprotected acorns seeded in 2014 were predated; Rey-Benayas et al. 2015), as well as low seedling emergence and survival. The rate of natural establishment in our study was 4.1 oaks ha<sup>-1</sup> yr<sup>-1</sup> since plantation of the islets 25 years ago and 5.7 oaks ha<sup>-1</sup> yr<sup>-1</sup> in the 18 years since the oaks in the islets attained the ability to reproduce sexually and it likely will increase as woodland islets produce more acorns with time. Our recruitment rates are higher than the rates reported for another Mediterranean old field near a big oak forest edge (2 oaks ha<sup>-1</sup> yr<sup>-1</sup>; Cruz-Alonso et al. 2019b) and similar to the rate of natural oak regeneration at a Mediterranean mountainous site after a major fire (4.1 oaks ha<sup>-1</sup> yr<sup>-1</sup>; Leverkus et al. 2014). The differences and similarities among these various studies may depend on distances between the forest edge and open old fields, as well as on abundances of predators and acorn dispersers. Regardless of these variations across studies of forest regeneration, they make clear that such regeneration in Mediterranean climates is a multi-decade process, even when assisted by woodland islets especially when compared with forests of high primary productivity, such as tropical forests, which show recruitment rates of 100 seedlings ha<sup>-1</sup> yr<sup>-1</sup> (Holl et al. 2017, 2020).

### Lessons to improve assisted natural forest regeneration using planted woodland islets

Our long-term experiments provide useful insights for assisting natural forest regeneration based on planted woodland islets. Despite acorn protection, wild boars strongly predated in two of the four sowing years (Fig. S3c-d). The shelters used in 2017, which were specifically designed against

ungulates (Reque and Martin 2015), usually protect acorns from wild boar predation, but they actually destroyed some seeding points by excavating the soil and exposing acorns to the air (Fig. 3d). Wild boar damage probably reflected the increase in the local boar population (Massei et al. 2015), particularly after 2016 (unpublished data). Methods to protect acorns in direct acorn seeding projects need to be improved (Löf et al. 2019).

Shelters should be maintained during the early plant stages. Herbivory reduced survival of holm oak seedlings: thus, survival was substantially higher for seedlings protected with wire shelters than for unprotected seedlings. On the other hand, survival was higher nearer rather than farther from the islets, despite rabbits built their burrows under the islets to take advantage of oak roots (unpublished data). The apparent lack of a distance effect on herbivory may reflect that the home range of rabbits is larger than the distances between islets in our study site (Lombardi et al. 2007). Future studies should clarify the interaction of herbivory and distance from woodland islets by using larger plots and increasing the distance between planted islets.

Plantation of woodland islets resulted in effective oak natural regeneration in a site with little close acorn sources. Nevertheless, the low oak colonisation of the abandoned field matrix from planted woodland islets and the fact that islets did not grow beyond their original size of 100 m<sup>2</sup> (data not shown) at the study site may argue against using woodland islets to restore old fields in dry Mediterranean climate regions and other low-productivity environments. However, we believe that certain interventions can accelerate natural regeneration based on planted and natural woodland islets. Rather than planting mono-specific islets of only one slow-growing, late successional tree species such as oaks, we suggest planting multi-specific islets which are highly attractive to many dispersers, including species of shrubs or trees with fleshy fruits (Martínez and García 2017; Martínez-López et al. 2019). Shrub species colonise old fields faster than oaks and can facilitate oak establishment at latter stages (Debussche and Lepart 1992; Cruz-Alonso et al. 2019b). Additionally, shrubs can be planted around the islets to act as “nurses” to facilitate recruitment of later successional species (Gómez-Aparicio et al. 2008; Andivia et al. 2017; Cruz-Alonso et al. 2019b). Conserving isolated nesting trees or placing new nesting sites for seed dispersers such as the magpie inside the old fields and near islets can increase seed arrival and consequently recruitment (Martínez-Baroja et al. 2021). This study may help increase the effectiveness of woodland islet plantation for restoring Mediterranean old fields and other areas with harsh climates.

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