

UC Santa Cruz

UC Santa Cruz Previously Published Works

Title

Predation and aridity slow down the spread of 21-year-old planted woodland islets in restored Mediterranean farmland

Permalink

<https://escholarship.org/uc/item/62n4c8c3>

Journal

New Forests, 46(5-6)

ISSN

0169-4286

Authors

Rey Benayas, JM
Martínez-Baroja, L
Pérez-Camacho, L
et al.

Publication Date

2015-06-10

DOI

10.1007/s11056-015-9490-8

Peer reviewed

Predation and aridity slow down the spread of 21-year-old planted woodland islets in restored Mediterranean farmland

José M. Rey Benayas, Loreto Martínez-Baroja, Lorenzo Pérez-Camacho, Pedro Villar-Salvador & Karen D. Holl

New Forests

International Journal on the Biology, Biotechnology, and Management of Afforestation and Reforestation

ISSN 0169-4286

New Forests

DOI 10.1007/s11056-015-9490-8



Your article is protected by copyright and all rights are held exclusively by Springer Science +Business Media Dordrecht. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your article, please use the accepted manuscript version for posting on your own website. You may further deposit the accepted manuscript version in any repository, provided it is only made publicly available 12 months after official publication or later and provided acknowledgement is given to the original source of publication and a link is inserted to the published article on Springer's website. The link must be accompanied by the following text: "The final publication is available at link.springer.com".

Predation and aridity slow down the spread of 21-year-old planted woodland islets in restored Mediterranean farmland

José M. Rey Benayas¹ · Loreto Martínez-Baroja¹ · Lorenzo Pérez-Camacho¹ · Pedro Villar-Salvador¹ · Karen D. Holl²

Received: 27 December 2014 / Accepted: 29 May 2015
© Springer Science+Business Media Dordrecht 2015

Abstract Planted woodland islets act as sources of seed that may accelerate woodland development in extensive agricultural landscapes. We assessed a 1-ha plot that was planted with 16 100-m² islets of holm oak *Quercus ilex* subsp. *ballota* seedlings near Toledo (Spain) in 1993. In spring 2014 we measured (1) acorn predation and (2) seedling emergence from seeded acorns at different distances from and orientations around the islets with half of the acorns protected to prevent predation, (3) survival of emerged seedlings, and (4) natural tree establishment outside of the planted islets. Most (96.9 %) unprotected acorns were removed or predated. Seedling emergence from protected acorns ranged from 42.9 % on the northern side of the islets to 13.2 % on the southern side, suggesting a less stressful microclimate on the northern side. Survival of naturally established seedlings was 28.6 % by the end of first summer; seedling mortality was chiefly due to drought (45.0 %) and herbivory (35.0 %). Density of emerged seedlings, surviving seedlings after first dry season, and established oaks >1-year old was similar at different distances from the islets. Over the 21 year time period, 58 new oak individuals >1-year old have established (an average of 3.3 established individuals per ha per year) at an average distance of 6.3 ± 5.4 m away from the closest islet. We conclude that initial oak regeneration triggered by small planted islets in Mediterranean abandoned farmland is slowed down by high acorn predation, seedling herbivory, and stressful microclimatic conditions. Regardless, these islets are a viable tool for regeneration of Mediterranean oak woodland.

Keywords Acorn predation · Applied nucleation · Herbivory · Natural regeneration · *Quercus ilex* · Seedling survival

Electronic supplementary material The online version of this article (doi:10.1007/s11056-015-9490-8) contains supplementary material, which is available to authorized users.

✉ José M. Rey Benayas
josem.rey@uah.es

¹ Forest Ecology and Restoration Group, Departamento de Ciencias de la Vida, Universidad de Alcalá, 28805 Alcalá de Henares, Madrid, Spain

² Environmental Studies Department, University of California, Santa Cruz, CA 95064, USA

Introduction

Natural forest regeneration or passive restoration of Mediterranean abandoned agricultural land is usually slow due to a number of limiting factors (Maestre et al. 2003; Bonet and Pausas 2004; Vallejo et al. 2006; Rey Benayas et al. 2008a). Key constraints on the speed of regeneration include (1) dispersal limitation because seed sources are remote and dispersal vectors may be rare (Rey Benayas et al. 2008a; Pons and Pausas 2007a; Zamora et al. 2010; Ramos-Palacios et al. 2014); (2) seed predation (Gómez et al. 2003; Gómez et al. 2008; Pérez-Ramos and Marañón 2008; Gómez and Hódar 2008; Leiva and Fernández 2003); (3) biotic limitation such as competition from established woody vegetation and herbaceous vegetation (Rey Benayas et al. 2005; Cuesta et al. 2010a), and herbivory (Gómez et al. 2003; Puerta et al. 2012); and (4) abiotic limitation such as low water availability, extreme temperatures, poor soil structure and low nutrient availability (Rey Benayas 1998; Cuesta et al. 2010b). Intensification of land use has brought remnant areas of natural or semi-natural vegetation into mainstream agriculture and as a result many of such areas have been lost or severely degraded. As a consequence, many agricultural landscapes, particularly those that are highly productive, lack parental trees or shrubs which severely limits seed availability, the first step for natural regeneration in circumstances where the socio-ecological dynamics promote abandonment (Pulido and Díaz 2005; Rey Benayas and Bullock 2012).

In actively farmed fields, strategic revegetation actions can include planting woodland islets (clusters of trees), hedgerows and isolated trees that have the potential to enhance wildlife, agricultural production, and other services at the field and landscape scales since they compete minimally for farmland use (Rey Benayas and Bullock 2015). Rey Benayas et al. (2008a) suggested a new concept for designing restoration of forest ecosystems on agricultural land, which uses small-scale active restoration as a driver for passive recovery over much larger areas. Establishment of “woodland islets” is an approach to designing restoration of woodlands in extensive agricultural landscapes where no remnants of native natural or semi-natural vegetation exist. It involves planting a number of small, dense, and sparse blocks of native shrubs and trees within agricultural land that together occupy a small fraction of the area to be restored. This approach, also called “tree islands”, “applied nucleation” (Corbin and Holl 2012; Zahawi et al. 2013), “dispersion and attraction nuclei” (García and Ferrer 2013), and cluster plantings (Stanturf et al. 2014), facilitates secondary succession by establishing small colonisation *foci*, while using a fraction of the resources required for large-scale afforestation. If the surrounding land is abandoned, colonists from the islets could accelerate woodland development through enhanced seed dispersal. Design of islets at a landscape scale benefits wildlife and provides the potential for larger-scale afforestation if the surrounding land is abandoned (Navarro and Pereira 2012).

We have been conducting an experiment on former cropland, where we introduced holm oak (*Quercus ilex* subsp. *ballota* (Desf.) Samp., hereafter *Q. ilex*) seedlings into 100-m² plots in 1993. *Q. ilex* is a late successional, slow-growing tree with high capacity of resprouting (Zavala et al. 2000). We found that, 21 years after the start of this restoration project, the planted woodland islets have grown in volume and produce large amounts of acorns (Rey Benayas et al. 2008b); however, the islets have not increased in area beyond the original planted surface of 100 m². Moreover, whereas a number of holm oaks of different size have established around the islets, there is a ca. 1.5–2 m wide border at the edge of the islands with minimal grass or herbs (Fig. 1).



Fig. 1 In our 21-year-old experiment, it is noticeable that the planted islets have increased in volume, exported acorns and produced new established oaks (e.g. the one with *red arrow* to the *right* of the figure) but are confined to the original planted surface. Also note the area with minimal herbaceous vegetation immediately outside the islets edge (*red arrow* in the *centre* of the figure)

In this study we assessed several demographic processes affecting early seedling recruitment around the woodland islets based on field experiments and long-term recruitment based on field observations. We hypothesized that biotic limitations (primarily acorn and seedling predation), and stressful microclimatic conditions (primarily water stress) would explain overall observed low initial natural regeneration in this system. It was difficult to predict the effect of distance to the islets on long-term oak establishment as a result of two opposing effects, namely more abundant acorn rain and facilitation but also more intense competition from established oaks for water and nutrients, as well as intense rabbit herbivory close to the islets (Bartholomew 1970). We expected high acorn predation for unprotected acorns (H1), highest seedling emergence and survival at the northern-oriented edges of the islets due to micro-climate amelioration by islet canopy (H2), and high predation of unprotected oak seedlings (H3). Results from this study will be particularly useful to practitioners and land use planners of woodland restoration projects in agricultural landscapes.

Methods

Study site

The study site was located at “La Higuera”, a Consejo Superior de Investigaciones Científicas research station in Toledo, central Spain (4°3′N, 4°24′W, altitude 450 m). We ran our experiment on a 1 ha field on previous cropland which had been cultivated for grain for many years until afforestation took place, and that was surrounded by rain-fed cereal crops in a highly farmed landscape context. In 1993, 1-year old *Q. ilex* seedlings were planted in 16 100-m² plots—the planted woodland islets—at a density of 50 seedlings per plot and a spacing of 2 m between seedlings. Mean distance separating islets is 11.8 m. Planted seedlings were subjected to experimental management summer irrigation and

artificial shading for three consecutive years, after which time shading and irrigation were stopped and there was no further management (Rey Benayas and Camacho 2004). Whereas the initial treatments affected survival of oaks and hence the density of trees (Rey Benayas 1998), by the time of the current data collection the overall cover of islets was similar across treatments (>90 % in all islets; see aerial photo in Fig. 4). At the time of the current data collection oaks in the islets were at an average density of 41.9 oaks per islet and all oaks in the periphery (i.e. at least 20 oaks in each islet) were producing abundant acorns. The climate is continental Mediterranean, characterized by a long summer drought that imposes severe water stress on the vegetation and cold winters. Total annual precipitation averaged 470.2 mm and mean temperature averaged 14.7 °C during the 1993–2013 period. The spring of 2014 was dry and total precipitation from the initiation of the experiment (24 February) through the last spring rainfall in 22 June was 64.1 mm), whereas average precipitation for the same period since 2000 was 153.18 mm. The soil is a relatively fertile, deep luvisol type, and derives from arkoses. The use of the land in the area is mostly agricultural. Potential predators/dispersers of acorns and oak seedlings in the study area are chiefly rodents (e.g. *Apodemus sylvaticus* L. and *Mus spretus* Lataste), magpies (*Pica pica* L.), rabbits (*Oryctolagus cuniculus* L.), and hares (*Lepus europaeus* Pallas) that shelter in the woodland islets. However, the European jay *Garrulus glandarius* L., which is an effective acorn disperser in Mediterranean forests (Gómez 2003) is absent in this highly deforested area.

Predation and germination of seeded acorns

We seeded holm oak acorns in our experimental field around the 16 planted woodland islets on 24 February 2014. All acorns were from the Leonesa provenance region (NW Spain) and acquired at the Centro Nacional de Mejora Forestal “El Serranillo” (MAGRAMA). Prior to seeding, acorns were submerged in water for 12 h and floating acorns were eliminated, as they were assumed to be dead or unfilled. A posteriori test resulted in 71.4 % of acorn emergence. A total of 386 points were seeded, with five acorns buried at a depth of 3 cm at each seeding point. Seeding points were located along two 10-m long transects extending out from each of the four corners of every woodland islet (Fig. 1S in Supplemental material). Most seeding points were located at 0, 1, 5 and 10 m from the woodland islet edge. However, in some cases the distance between adjacent islets and between islets and nearby active crop fields impeded seeding at the 5 and 10 m distances; consequently, for these cases seeding points were located either equidistant between adjacent islets or at the edge of the experimental field. In total, 36 points were located between 1 and 5 m, 23 between 5 and 10 m, and 9 points were at 10 m.

One of the two seeding points located at the same distance of each woodland islet side was protected (Fig. 1S in Supplemental material) with a 25-cm plastic tree shelter buried 10 cm and topped with a 15-mm wire mesh to prevent access by acorn predators. This resulted in 193 protected seeding points and 193 unprotected ones. The protection of seeding points at the same distance from each woodland islet side was randomly assigned. Three protected and three unprotected seeding points were accidentally ploughed and lost from the experiment. We buried a 7-cm iron nail together with the unprotected seeding points to facilitate later detection with a metal detector. We monitored seeding points five times on 14 May, 4–6 June, and on 1, 6 and 19 July for acorn predation and seedling emergence. One-third of emerged seedlings occurred after a late spring rain event (18 mm). As seeded acorns were not marked for radio-tracking, we were not able to assess where moved acorns were placed by dispersers.

Seedling survival

On 22 June, after seedling emergence ended, we carefully removed the plastic protectors at half of the seeding points that contained at least one emerged seedling to leave them unprotected from herbivores. For the other half of seeding points with emerged seedlings, the tree shelter was replaced by a wire cage to prevent the micro-climate effects by tree shelters on seedling performance (Puértolas et al. 2010; Oliet et al. 2012). We monitored seedling survival six times, once every ca. 10 days starting at the beginning of July and ending at the end of August, and a final time on 19 October 2014.

Natural early establishment of holm-oak

To assess natural establishment of holm oak seedlings during the 2014 growing season, i.e. not from our experimental acorn seeding, we sampled 192 rectangular plots and nine squared plots between the islets or between the islets and nearby active crops to count seedling emergence in the spring of 2014 and monitor their survival through the end of summer (mid-October). The rectangular plots were placed at the edge of the woodland islets in all four orientations, two at each corner and one between them (Fig. 1S in Supplemental material). These plots were 1×5 m between adjacent islets or 1×10 m between islets and active crop fields. The squared plots between islets were 5×5 m. The 201 plots, which covered a total area of 1474.9 m^2 (i.e. 17.6 % of the experimental field area that was not occupied by woodland islets), were initially surveyed once between May 17 and June 22 and later on July 6 and October 19 due to rain events after the start of the first seedling counting and to account for final survival after summer, respectively. The emerged seedlings in all plots were tagged for easy later localization. The density of both dead and surviving seedlings in bands at different distance to the islets (0–2, 2.01–4, 4.01–6, 6.01–8, 8.01–10 and >10 m) was measured. Recruitment within the islets was not measured as this study focuses on regeneration outside the islets; additionally, the islets were very dense and shaded and visual inspection hinted new established oaks in them were sprouts.

Mapping and size measurement of naturally established holm oak since islet planting

All naturally established holm oaks, i.e. those at least 1-year old, were located, positioned with a GPS (Garmin DAKOTA 20) and mapped using high resolution imagery taken by a drone-borne visible camera of 2×2 cm spatial resolution pixel that produced an ortho-photo of the 1-ha experimental field. We measured their density in the bands explained above and, for illustrative purposes, their height, basal diameter and crown projected area (Rey Benayas 1998; Rey Benayas and Camacho 2004).

Data analysis

Acorn removal at unprotected seeding points was so high (H1, see below) that we could not statistically test the effects of orientation and distance to the woodland islets on this rate. All subsequent statistical analyses of seedling emergence and survival in relation to orientation and distance (H2) to the islets are thus only based on the protected seeding points.

We analyzed differences in seedling emergence using generalized linear mixed-effects model (GLMM) with a binomial error distribution and a logit link function to test the effects of the woodland islets (random effect), orientation and distance to the islets and their interaction (fixed effects). Akaike's (1987) information criterion (AIC) was calculated for each model; a smaller AIC indicates a better-fitting model as determined from the parsimony in the number of parameters. We used the cutoff of $\Delta\text{AIC} < 2$ units to differentiate models with better explanatory power (sensu Burnham and Anderson 2002). Likewise, we performed a binomial generalized linear model including orientation, distance and their interaction based on previous results from the GLMM to test specific hypotheses in relation to these factors (H2).

Seedling survival from seeded acorns (H3) or naturally established in the Spring of 2014 was assessed by survival analysis based on a Cox's Proportional Hazards semi-parametric model using the maximum partial likelihood as the estimation method (Fox 1993; Allison 1995). Finally, we tested the density distribution of naturally emerged and surviving seedlings after the first dry season and of established oaks >1 year old at the bands of different distance to the islets using contingency analysis. GLMM analysis was performed with packages stats (R core team 2014) lme4 (Bates et al. 2014) and MuMIn (Barton 2014) with R software v. 3.1.2. GLMs and survival analysis were carried out with Statistica 7.0 (Statsoft, Tulsa, Oklahoma, USA).

Results

Predation of seeded acorns

Acorns were not found in 83.7 % of the unprotected seeding points; these acorns could have been moved or predated. Of the rest of the acorns, 13.2 % were predated in situ and only six (3.1 %) out of the 190 unprotected seeding points remained with acorns at the end of the spring.

Seedling emergence

At least one seedling emerged at 51 seeding points (13.5 %), 49 of which were protected and two were unprotected. However, only 6.7 % of all seeded acorns with protection produced a seedling. The two GLMMs that best explained seedling emergence included the interaction between orientation and distance from the woodland islet (AIC = 212.6; $\chi^2_3 = 14.12$, $p = 0.0028$) and the orientation relative to woodland islet (AIC = 213.9; $\chi^2_6 = 21.26$, $p = 0.0016$), respectively, but distance by itself did not have any effect ($\chi^2_3 = 3.07$, $p = 0.38$). Seedling emergence was highest (42.9 %) on the northern side and lowest on the southern side (13.2 %) of islets.

We found 28 naturally established oak seedlings that emerged in 2014 (189.8 seedlings ha^{-1}). Mean distance of these seedlings to islets was 4.1 ± 2.7 m. Density distribution of these seedlings did not show any significant pattern at different distance to the islets ($\chi^2_5 = 10.16$, $p = 0.07$) (Fig. 2).

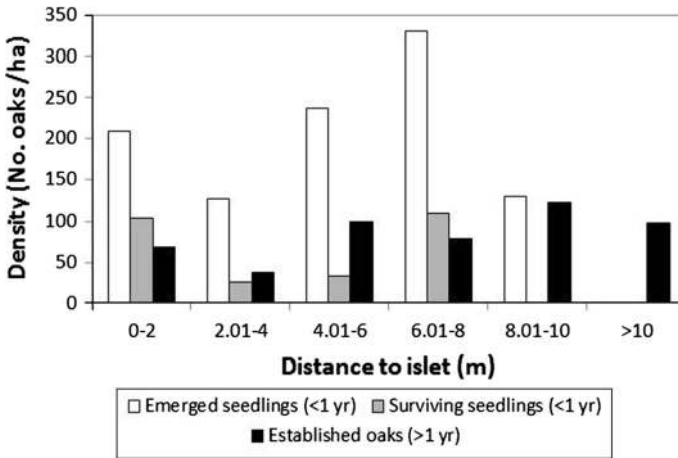


Fig. 2 Oak density (emerged seedlings in 2014, surviving seedlings after the first dry season, and established oaks >1-year old) in 2-m width bands at different distance to the woodland islets

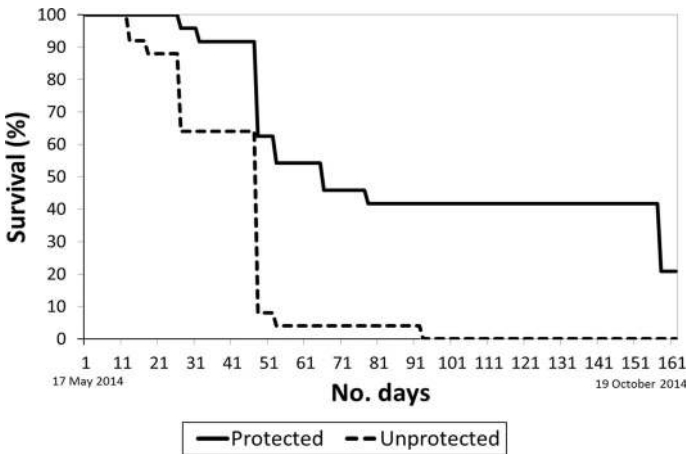


Fig. 3 Changes in survival probability of protected and unprotected *Q. ilex* seedlings through the summer and early fall of the first growing season. These graphs refer to the 31 emerged seedlings from seeded acorns that were monitored since May 17 2014 plus the 18 seedlings that emerged later

Early seedling survival

All emerged unprotected seedlings were predated (i.e. they were found with no aerial organs) while survival of protected seedlings at the end of the first growing season was 33.3 % (protection effect $\chi^2_1 = 13.33$, $p = 0.0003$; Fig. 3). There was a peak of mortality at days 41 to 51 that was much higher for protected than for unprotected seedlings. Neither orientation ($\chi^2_3 = 3.03$, $p = 0.39$) nor distance ($\chi^2_3 = 2.1$, $p = 0.83$) affected seedling survival, but sample size was low ($n = 49$) and the design was highly unbalanced.

Survival of the 28 naturally established oak seedlings that emerged in 2014 was 28.6 % by the end of summer (54.2 seedlings ha^{-1}), and it was independent of orientation



Fig. 4 Position of the 58 naturally established oaks >1 year old in the experimental field

($\chi^2_3 = 1.81$, $p = 0.77$) or distance ($\chi^2_4 = 2.97$, $p = 0.56$) according to the survival analysis. Mean distance of surviving and dead seedlings to islets was 3.0 ± 3.0 and 4.6 ± 2.5 m, respectively (differences in these distances were not significant, t test $p = 0.15$). Density distribution of emerged seedlings that survived after first dry season did not differ among distance bands ($\chi^2_5 = 7.92$, $p = 0.16$). Thirty per cent of dead seedlings dried out, 35 % were predated when they were alive and 15 % once dry, and for the remaining 20 % dead seedlings we could not conclude the cause of death.

Oak establishment after 21 years

Fifty-eight holm oak individuals >1-year old that were developed from dispersed acorns outside the planted islets have established in the experimental field after 21 years (Fig. 4), resulting in a density of 65.1 oaks per ha excluding the area occupied by the islets with an average establishment rate of 3.3 oaks $\text{ha}^{-1} \text{year}^{-1}$. Average distance of these to the closest islet was 6.3 ± 5.4 m (5.8 ± 3.7 m excluding an outlier oak located at 35.7 m from the closest islet), which is similar to half the average distance among islets (5.9 m). The density distribution of these established oaks did not differ among distance bands ($\chi^2_5 = 5.75$, $p = 0.33$; Fig. 2). Height, basal diameter and crown projected area of the established oaks averaged 49.2 ± 64.3 cm, 20.1 ± 31.3 mm, and 0.44 ± 1.09 m^2 , respectively.

Discussion

High acorn predation and low seedling survival

Our results clearly show that acorn predation is a major bottleneck for holm oak recruitment, consistent with our first hypothesis. Similar to our findings, Leiva and Fernández (2003)

reported that only 0–2.4 % of acorns escaped from predation in an oak savanna located in southern Spain, and Pons and Pausas (2007b) found that 98.7 % of acorns were removed and/or predated by rodents in eastern Spain. Rodents and magpies are both predators and dispersers of acorns (Waite 1985), but rabbits and hares, which are abundant in our field site, are only predators (Zamora et al. 1985; Díaz et al. 1996; Leiva and Fernández 2003; Guzmán et al. 2008). We have clear evidence of acorn predation *in situ* for a small fraction of the unprotected acorns but suspect that most of the unfound acorns were either entirely consumed immediately after removal or re-cached and consumed later in other sites (Perea et al. 2011), as the farmland environment where our woodland islets are embedded may exacerbate predation. For instance, Gómez et al. (2008) found in the Sierra Nevada Mountains (SE Spain) that most caches were recovered and consumed, and only 1.3 % of the original experimental acorns were found alive in caches the following spring. Likewise, in another experiment that we conducted for 3 years in old fields in central Spain with tagged acorns, we found that 100 % of remobilized acorns were finally predated (Villar-Salvador and Pérez-Camacho, *unpublished data*). Other studies, however, have documented the spatial patterns and effects of long-distance oak dispersal at the landscape scale and hence the importance of isolated oaks as seed sources (Gómez 2003; Purves et al. 2007). Acorn physical protection against predators is needed in Mediterranean environments to ensure oak establishment after seeding (Adams et al. 1992; Castro et al. 2015), as other methods such as chemical repellents have been shown to be unsuccessful (Leverkus et al. 2013).

We found low rates of seedling survival, consistent with previous studies on *Quercus* establishment in Mediterranean environments (Rey Benayas et al. 2005; Castro et al. 2006; Valdecantos et al. 2006; Del Campo et al. 2010, Cuesta et al. 2010a, b). As we anticipated (H3), most of this mortality was a consequence of seedling predation; all of unprotected seedlings in the seeding experiment and at least 50 % of the naturally established seedlings (which were not protected) were predated by the end of the first growing season. On the other hand, two-thirds of our caged seedlings and at least one-third of the new naturally established seedlings died out probably reflecting mortality due to summer drought, which occurred quickly (Fig. 3). The natural establishment rate we recorded in 2014 (54.2 seedlings ha⁻¹) is lower than those we estimated from data reported by Pulido and Díaz (2005) in oak woodland (123 seedlings ha⁻¹ year⁻¹) and by García-Barreda and Reyna (2013) in gaps of a planted pine forest (120 seedlings ha⁻¹ year⁻¹), but higher than that found by Pulido and Díaz (2005) in an oak savanna (2.8 seedlings ha⁻¹ year⁻¹). Gómez et al. (2003) also found that 98 % of the 1000 experimental seedlings were killed by herbivores, notably wood mice, wild boar, and domestic and wild ungulates.

Low seedling emergence

Seedling emergence was low when compared with results in previous studies of holm oak. For instance, Smit et al. (2009) observed emergence values >90 % while Pulido and Díaz (2005) observed 73 % emergence in their study. Low emergence values in our study are probably a consequence of the dry spring, particularly in the few weeks after seeding. This idea is supported by the emergence peak after a late spring rainy event and by the fact that emergence was highest at the sites with northern exposure where soil desiccation is ameliorated in agreement with our H2 (Montero et al. 2008). Acorns are recalcitrant seeds with their viability dependent upon relatively high water content (Villar-Salvador et al. 2013); hence, *in situ* desiccation is an important cause of acorn mortality (Joët et al. 2013).

Lack of distance effects

The distance to woodland islets at small scales did not affect acorn predation and seedling performance. Lack of distance effect on acorn predation is probably due to the fact that our longest seeding distance (10 m) can be easily reached by all dispersers/predators that may shelter in the islets (Pons and Pausas 2007b; Gómez et al. 2008). Similarly, we did not find higher seedling emergence at closer distances to the islets where we expected higher emergence due to micro-climate amelioration by islet canopy shade. This contrasts with results in Smit et al. (2009) showing higher emergence in shaded microsites than in open microsites and suggests a lack of “safe” microsites for recruitment in our experimental field (Pulido and Díaz 2005). It is possible that microclimatic amelioration by islet canopy was not enough to maintain high soil moisture during the dry spring, but we did not measure soil water content to assess this explanation. The lack of distance effect on seedling mortality from herbivory could be due to the fact that separation between islets is too small to detect a difference in rabbit and hare movement (Gómez et al. 2008), but our observations suggest that consumption of herbs by rabbits is much higher within 0–2 m of the edge of the islets (Fig. 1). It is possible that there is a neutral balance between counteracting effects of established islets on seedling establishment, namely microclimate amelioration facilitating establishment near islets and competition with mature trees and herbivory favoring establishment further away. A final possible explanation for lack of distance effect on seedling emergence and early seedling survival is that we had insufficient power to detect interactive effects between distance and orientation due to low sample size and unbalanced design, due to high predation.

Initial woodland regeneration

We recorded a natural establishment rate of 3.3 oaks $\text{ha}^{-1} \text{year}^{-1}$ along the 21 years of our experiment, which in comparison with the figure of natural establishment found after the first dry season suggests strong future mortality of recently established seedlings in our field site. However, our woodland islets started to produce acorns 7 years after oak seedling plantation and seed production in the first reproductive years was small. This means that the rate above will likely be higher and increase in the future. Leverkus et al. (2014) found a natural establishment rate of 4.18 oaks $\text{ha}^{-1} \text{year}^{-1}$ at a post-fire regeneration site in a Mediterranean mountainous environment with higher precipitation.

We have investigated one case study to address the complex issue of outcomes of relevant techniques, methods and approaches for large scale and long-term efforts for landscape forest restoration (Stanturf et al. 2014). Three limitations of this study are that it was conducted in only one site of 1 ha with planted oak islets, included only 1 year of monitoring acorn removal/predation and seedling emergence/survival, and did not assess dispersal. On the other hand, the age of the introduced islets, the set of recruitment stages and processes studied, and the singularity of the experimental design provide relevant lessons for woodland restoration.

Acorn availability is a bottle-neck that limits vegetation establishment in agricultural landscapes (Rey Benayas et al. 2008a; Rey Benayas and Bullock 2012, 2015), and this limitation was clearly overcome by the introduction of small woodland islets that established successfully in our experimental field. These islets have triggered holm oak regeneration that would have been high unlikely without nearby seed sources (Gómez-Aparicio et al. 2009), but the rate of recruitment is limited by high acorn predation, seedling herbivory, and

stressful microclimatic conditions. Using tree shelters against herbivores that also ameliorate climate harshness (Puértolas et al. 2010) of the naturally established seedlings from acorns dispersed from planted woodland islets would accelerate passive restoration of former cropland and pastureland. Thus, planting woodland islets without further intervention seems not be sufficient to catalyze “fast” initial recovery of Mediterranean woodland on abandoned farmland and restoration will be resource intensive. “Success” or “failure” in restoration efforts like the one investigated here nonetheless depends on the time frame of evaluation, particularly in Mediterranean ecosystems where recruitment is notoriously episodic (Moreno et al. 2011). Overall, we suggest that the woodland islet approach is a low cost and useful technique to speed up woodland restoration in agricultural landscapes.

Acknowledgments Projects from the Spanish Ministry of Science and Education (CGL2010-18312 and CGL2014-53308-P) and the Government of Madrid (S2013/MAE-2719, REMEDINAL-3) are currently providing financial support for this body of research. We are indebted to Aurora Mesa and Paula Meli for their help for acorn seeding and to Laura Fernández and Luis Cayuela for their input with some statistical analyses. The subject editor and two anonymous reviewers provided valuable comments on a former version of this manuscript.

References

- Adams TE, Sands PB, Weitkamp WH, McDougald NK (1992) Oak seedling establishment on California rangelands. *J Range Manag* 45:93–98
- Akaike H (1987) Factor analysis and AIC. *Psychometrika* 52:317–332
- Allison PD (1995) Survival analysis using the SAS® system. A practical guide. SAS Institute, Cary
- Bartholomew B (1970) Bare zone between California shrub and grassland communities: the role of animals. *Science* 170:1210–1212
- Barton (2014) MuMIn: multi-model inference. R package version 1.10.5. <http://CRAN.R-project.org/package=MuMIn>
- Bates D, Maechler M, Bolker B, Walker S (2014) lme4: linear mixed-effects models using eigen and S4. R package version 1.1-7
- Bonet A, Pausas JG (2004) Species richness and cover along a 60-year chronosequence in old-fields of southeastern Spain. *Plant Ecol* 174:257–270
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer, New York
- Castro J, Zamora R, Hódar JA (2006) Restoring *Quercus pyrenaica* forest using pioneer shrubs as nurse plants. *Appl Veg Sci* 9:137–142
- Castro J, Leverkus AB, Fuster F (2015) A new device to foster oak forest restoration via seed sowing. *New Forests* (accepted with pending revision)
- Corbin JD, Holl KD (2012) Applied nucleation as a forest restoration strategy. *For Ecol Manag* 265:37–46
- Cuesta B, Villar-Salvador P, Puértolas J, Peñuelas JL, Rey JM (2010a) Facilitation of oak in Mediterranean shrubland is explained by both direct and indirect interactions mediated by herbs. *J Ecol* 98:688–697
- Cuesta B, Villar-Salvador P, Puértolas J, Jacobs D, Rey-Benayas JM (2010b) Why do large, nitrogen rich seedlings better resist stressful transplanting conditions? A physiological analysis in two functionally contrasting Mediterranean forest species. *For Ecol Manag* 260:71–78
- Del Campo AD, Navarro RM, Ceacero CJ (2010) Seedling quality and field performance of commercial stocklots of containerized holm oak (*Quercus ilex*) in Mediterranean Spain: an approach for establishing a quality standard. *New For* 39:19–37
- Díaz M, González E, Muñoz-Pulido R, Naveso MA (1996) Habitat selection patterns of common cranes *Grus grus* wintering in holm oak *Quercus ilex* Dehesas of central Spain: effects of human management. *Biol Conserv* 75:119–123
- Fox GA (1993) Failure-time analysis: emergence, flowering, survivorship, and other waiting times. In: Gurevitch J, Scheiner SM (eds) Design and analysis of ecological experiments. Chapman and Hall, New York, pp 253–289

- García X, Ferrer P (2013) La creación de núcleos de dispersión y reclamo como modelo de restauración ecológica forestal. In: Martínez C, Lario FJ, Fernández B (eds) Avances en la restauración de sistemas forestales. Técnicas de implantación. SECF-AEET, Madrid, España, pp 149–158
- García-Barreda S, Reyna S (2013) Short-term dynamics of *Quercus ilex* advance regeneration in a *Pinus nigra* plantation after the creation of small canopy gaps. For Syst 22:179–188
- Gómez JM (2003) Spatial patterns in long-distance dispersal of *Quercus ilex* acorns by jays in a heterogeneous landscape. Ecography 26:573–584
- Gómez JM, Hódar JA (2008) Wild boars (*Sus scrofa*) affect the recruitment rate and spatial distribution of holm oak (*Quercus ilex*). For Ecol Manag 256:1384–1389
- Gómez JM, García D, Zamora R (2003) Impact of vertebrate acorn- and seedling-predators on a Mediterranean *Quercus pyrenaica* forest. For Ecol Manag 180:125–134
- Gómez JM, Puerta-Piñero C, Schupp EW (2008) Effectiveness of rodents as local seed dispersers of holm oaks. Oecologia 155:529–537
- Gómez-Aparicio L, Zavala MA, Bonet FJ, Zamora R (2009) Are pine plantations valid tools for restoring Mediterranean forests? An assessment along abiotic and biotic gradients. Ecol Appl 19:2124–2141
- Guzmán JM, Nadal S, Román B (2008) Ensayo preliminar de reforestación con especies facilitadoras: nascencia de encina bajo retama en condiciones semiáridas. Cuadernos de la Sociedad Española de Ciencias Forestales 28:61–65
- Joët T, Ourcival JM, Dussert S (2013) Ecological significance of seed desiccation sensitivity in *Quercus ilex*. Ann Bot 111:693–701
- Leiva MJ, Fernández R (2003) Post-dispersive losses of acorns from Mediterranean savannah-like forests and shrublands. For Ecol Manag 176:265–271
- Leverkus AB, Castro J, Puerta-Piñero C, Rey Benayas JM (2013) Suitability of the management of habitat complexity, acorn burial depth, and a chemical repellent for post-fire reforestation of oaks. Ecol Eng 53:15–22
- Leverkus AB, Castro J, Rey Benayas JM (2014) Regeneración post-incendio de la encina en pinares de repoblación mediterráneos. Ecosistemas 23:48–54
- Maestre FT, Cortina J, Bautista S, Bellot J, Vallejo VH (2003) Small-scale environmental heterogeneity and spatiotemporal dynamics of seedling establishment in a semi-arid degraded ecosystem. Ecosystems 6:630–643
- Montero MJ, Moreno G, Bertomeu M (2008) Light distribution in scattered-trees open woodlands in Western Spain. Agrofor Syst 73:233–244
- Moreno JM, Zuazua E, Pérez B, Luna B, Velasco A, Resco De Dios V (2011) Rainfall patterns after fire differentially affect the recruitment of three Mediterranean shrubs. Biogeosciences 8:3721–3732
- Navarro LM, Pereira HM (2012) Rewilding abandoned landscapes in Europe. Ecosystems 15:900–912
- Oliet JA, Artero F, Cuadros F, Puértolas J, Luna L, Grau JM (2012) Deep planting with shelters improves performance of different stocktype sizes under arid Mediterranean conditions. New For 43:925–939
- Perea R, San Miguel A, Gil L (2011) Leftovers in seed dispersal: ecological implications of partial seed consumption for oak regeneration. J Ecol 99:194–201
- Pérez-Ramos IM, Marañón T (2008) Factors affecting post-dispersal seed predation in two coexisting oak species: microhabitat, burial and exclusion of large herbivores. For Ecol Manag 255:3506–3514
- Pons J, Pausas JG (2007a) Acorn dispersal estimated by radio-tracking. Oecologia 153:903–911
- Pons J, Pausas JG (2007b) Rodent acorn selection in a Mediterranean oak landscape. Ecol Res 22:535–541
- Puerta C, Pino J, Gómez JM (2012) Direct and indirect landscape effects on *Quercus ilex* regeneration in heterogeneous environments. Oecologia 170:1009–1020
- Puértolas J, Oliet JA, Jacobs DF, Benito LF, Peñuelas JL (2010) Is light the key factor for success of tube shelters in forest restoration plantings under Mediterranean climates? For Ecol Manag 260:610–617
- Pulido FJ, Díaz M (2005) Regeneration of a Mediterranean oak: a whole-cycle approach. Ecoscience 12:92–102
- Purves D, Zavala M, Oglel K, Prieto F, Rey Benayas JM (2007) Coupling environmental forcing, metapopulation dynamics, and dispersal of *Quercus* species in central Spain. Ecol Monogr 77:77–97
- Ramos-Palacios CR, Badano EI, Flores J, Flores-Cano JA, Flores-Flores JL (2014) Distribution patterns of acorns after primary dispersion in a fragmented oak forest and their consequences on predators and dispersers. Eur J For Res 133:391–404
- Rey Benayas JM (1998) Growth and survival in *Quercus ilex* L. seedlings after irrigation and artificial shading on Mediterranean set-aside agricultural land. Ann Sci For 55:801–807
- Rey Benayas JM, Bullock JM (2012) Restoration of biodiversity and ecosystem services on agricultural land. Ecosystems 15:883–889
- Rey Benayas JM, Bullock JM (2015) Vegetation restoration and other actions to enhance wildlife in European agricultural landscapes. In: Pereira HM, Navarro LM (eds) Rewilding European Landscapes, Springer International Publishing Switzerland, pp 127–142. doi: [10.1007/978-3-319-12039-3_7](https://doi.org/10.1007/978-3-319-12039-3_7)

- Rey Benayas JM, Camacho A (2004) Performance of *Quercus ilex* saplings planted in abandoned Mediterranean cropland after long-term interruption of their management. *For Ecol Manag* 194:223–233
- Rey Benayas JM, Navarro J, Espigares T, Nicolau JM, Zavala MA (2005) Effects of artificial shading and weed mowing in restoration of Mediterranean abandoned cropland with contrasting *Quercus* species. *For Ecol Manag* 212:302–314
- Rey Benayas JM, Bullock JM, Newton A (2008a) Creating woodland islets to reconcile ecological restoration, conservation, and agricultural land use. *Front Ecol Environ* 6:329–336
- Rey Benayas JM, Cuesta B, Villar-Salvador P, Jaúregui P (2008b) Life-history traits in an evergreen Mediterranean oak respond differentially to previous experimental environments. *Web Ecol* 8:74–83
- R Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL
- Smit Ch, Díaz M, Jansen P (2009) Establishment limitation of holm oak (*Quercus ilex* subsp. *ballota* (Desf.) Samp.) in a Mediterranean savanna–forest ecosystem. *Ann For Sci* 66:511–517
- Stanturf JA, Palik BJ, Williams MI, Dumroese RK, Madsen P (2014) Forest restoration paradigms. *J Sustain For* 33:S161–S194
- Valdecantos A, Cortina J, Vallejo VR (2006) Nutrient status and field performance of tree seedlings planted in Mediterranean degraded areas. *Ann For Sci* 63:249–256
- Vallejo R, Aronson J, Pausas JG, Cortina J (2006) Restoration of Mediterranean woodlands. In: van Andel J, Aronson J (eds) *Restoration ecology: the new frontier*. Blackwell, Oxford, pp 193–207
- Villar-Salvador P, Nicolás JL, Heredia N, Uscola M (2013) *Quercus ilex* L. In: Pemán J, Navarro-Cerrillo RM, Nicolás JL, Prada MA, Serrada R. (Coords.) *Producción y Manejo de Semillas y Plantas Forestales*. Tomo II. Organismo Autónomo Parques Nacionales. Serie Forestal. Ministerio de Agricultura, Alimentación y Medio Ambiente, Madrid, España. pp 226–250
- Waite RK (1985) Food caching and recovery by farmland corvids. *Bird Study* 32:45–49
- Zahawi RA, Holl KD, Cole RJ, Reid L (2013) Testing applied nucleation as a strategy to facilitate tropical forest recovery. *J Appl Ecol* 50:88–96
- Zamora E, Peinado M, Sánchez M, Galleo J, Mata C (1985) Consumo de bellota por conejos en pastoreo continuo. *Archivos de Zootecnia* 34:257–264
- Zamora R, Hódar JA, Matías L, Mendoza I (2010) Positive adjacency effects mediated by seed disperser birds in pine plantations. *Ecol Appl* 20:1053–1060
- Zavala MA, Espelta JM, Retana J (2000) Constraints and trade-offs in Mediterranean plant communities: the case of holm oak–Aleppo pine forests. *Bot Rev* 66:119–149