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

3

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9

10 **Abstract**

11 Planted woodland islets act as sources of seed that may accelerate woodland
12 development in extensive agricultural landscapes. We assessed a 1-ha plot that was
13 planted with 16 100-m² islets of holm oak *Quercus ilex* subsp. *ballota* seedlings near
14 Toledo (Spain) in 1993. In spring 2014 we measured (1) acorn predation and (2)
15 seedling emergence from seeded acorns at different distances from and orientations
16 around the islets with half of the acorns protected to prevent predation, (3) survival of
17 emerged seedlings, and (4) natural tree establishment outside of the planted islets. Most
18 (96.9%) unprotected acorns were removed or predated. Seedling emergence from
19 protected acorns ranged from 42.9% on the northern side of the islets to 13.2% on the
20 southern side, suggesting a less stressful microclimate on the northern side. Survival of
21 naturally established seedlings was 28.6% by the end of first summer; seedling
22 mortality was chiefly due to drought (45.0%) and herbivory (35.0%). Density of
23 emerged seedlings, surviving seedlings after first dry season, and established oaks > 1-
24 yr old was similar at different distances from the islets. Over the 21 year time period, 58
25 new oak individuals >1-yr old have established (an average of 3.3 established
26 individuals per ha per year) at an average distance of 6.3 ± 5.4 m away from the closest
27 islet. We conclude that initial oak regeneration triggered by small planted islets in
28 Mediterranean abandoned farmland is slowed down by high acorn predation, seedling
29 herbivory, and stressful microclimatic conditions. Regardless, these islets are a viable
30 tool for regeneration of Mediterranean oak woodland.

31 **Key words:** acorn predation; applied nucleation; herbivory; natural regeneration;
32 *Quercus ilex*; seedling survival.

33

34 **1. Introduction**

35 Natural forest regeneration or passive restoration of Mediterranean abandoned
36 agricultural land is usually slow due to a number of limiting factors (Maestre et al.
37 2003; Bonet and Pausas 2004; Vallejo et al. 2006; Rey Benayas et al. 2008a). Key
38 constraints on the speed of regeneration include (1) dispersal limitation because seed
39 sources are remote and dispersal vectors may be rare (Rey Benayas et al. 2008a; Pons
40 and Pausas 2007a; Zamora et al. 2010; Ramos-Palacios et al. 2014); (2) seed predation
41 (Gómez et al. 2003; Gómez et al. 2008; Pérez-Ramos and Marañón 2008; Gómez and
42 Hódar 2008; Leiva and Fernández 2013); (3) biotic limitation such as competition from
43 established woody vegetation and herbaceous vegetation (Rey Benayas et al. 2005;
44 Cuesta et al. 2010a), and herbivory (Gómez et al. 2003; Puerta et al. 2012); and (4)
45 abiotic limitation such as low water availability, extreme temperatures, poor soil
46 structure and low nutrient availability (Rey Benayas 1998; Cuesta et al. 2010b).
47 Intensification of land use has brought remnant areas of natural or semi-natural
48 vegetation into mainstream agriculture and as a result many of such areas have been lost
49 or severely degraded. As a consequence, many agricultural landscapes, particularly
50 those that are highly productive, lack parental trees or shrubs which severely limits seed
51 availability, the first step for natural regeneration in circumstances where the socio-
52 ecological dynamics promote abandonment (Pulido and Díaz 2005; Rey Benayas and
53 Bullock 2012).

54 In actively farmed fields, strategic revegetation actions can include planting
55 woodland islets (clusters of trees), hedgerows and isolated trees that have the potential
56 to enhance wildlife, agricultural production, and other services at the field and
57 landscape scales since they compete minimally for farmland use (Rey Benayas and
58 Bullock 2015). Rey Benayas et al. (2008a) suggested a new concept for designing
59 restoration of forest ecosystems on agricultural land, which uses small-scale active
60 restoration as a driver for passive recovery over much larger areas. Establishment of
61 “woodland islets” is an approach to designing restoration of woodlands in extensive
62 agricultural landscapes where no remnants of native natural or semi-natural vegetation

63 exist. It involves planting a number of small, dense, and sparse blocks of native shrubs
64 and trees within agricultural land that together occupy a small fraction of the area to be
65 restored. This approach, also called “tree islands”, “applied nucleation” (Corbin and
66 Holl 2012; Zahawi et al. 2013), “dispersion and attraction nuclei” (García and Ferrer
67 2013), and cluster plantings (Stanturf et al. 2014), facilitates secondary succession by
68 establishing small colonisation *foci*, while using a fraction of the resources required for
69 large-scale afforestation. If the surrounding land is abandoned, colonists from the islets
70 could accelerate woodland development through enhanced seed dispersal. Design of
71 islets at a landscape scale benefits wildlife and provides the potential for larger-scale
72 afforestation if the surrounding land is abandoned (Navarro and Pereira 2012).

73 We have been conducting an experiment on former cropland, where we
74 introduced holm oak (*Quercus ilex* subsp. *ballota* (Desf.) Samp., hereafter *Q. ilex*)
75 seedlings into 100-m² plots in 1993. *Q. ilex* is a late successional, slow-growing tree
76 with high capacity of resprouting (Zavala et al. 2000). We found that, 21 years after the
77 start of this restoration project, the planted woodland islets have grown in volume and
78 produce large amounts of acorns (Rey Benayas et al. 2008b); however, the islets have
79 not increased in area beyond the original planted surface of 100 m². Moreover, whereas
80 a number of holm oaks of different size have established around the islets, there is a ca.
81 1.5-2 m wide border at the edge of the islands with minimal grass or herbs (**Fig. 1**).

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

96

97 **2. Methods**

98 *2.1. Study site*

99 The study site was located at “La Higuera”, a Consejo Superior de
100 Investigaciones Científicas research station in Toledo, central Spain (4°3'N, 4°24'W,
101 altitude 450 m). We ran our experiment on a 1 ha field on previous cropland which had
102 been cultivated for grain for many years until afforestation took place, and that was
103 surrounded by rain-fed cereal crops in a highly farmed landscape context. In 1993, 1-
104 year old *Q. ilex* seedlings were planted in 16 100-m² plots – the planted woodland
105 islets– at a density of 50 seedlings per plot and a spacing of 2 m between seedlings.
106 Mean distance separating islets is 11.8 m. Planted seedlings were subjected to
107 experimental management summer irrigation and artificial shading for three consecutive
108 years, after which time shading and irrigation were stopped and there was no further
109 management (Rey Benayas and Camacho 2004). Whereas the initial treatments affected
110 survival of oaks and hence the density of trees (Rey Benayas 1998), by the time of the
111 current data collection the overall cover of islets was similar across treatments (>90% in
112 all islets; see aerial photo in **Fig. 4**). At the time of the current data collection oaks in
113 the islets were at an average density of 41.9 oaks per islet and all oaks in the periphery
114 (i.e. at least 20 oaks in each islet) were producing abundant acorns. The climate is
115 continental Mediterranean, characterized by a long summer drought that imposes severe
116 water stress on the vegetation and cold winters. Total annual precipitation averaged
117 470.2 mm and mean temperature averaged 14.7 °C during the 1993-2013 period. The
118 spring of 2014 was dry and total precipitation from the initiation of the experiment (24
119 February) through the last spring rainfall in 22 June was 64.1 mm), whereas average
120 precipitation for the same period since 2000 was 153.18 mm. The soil is a relatively
121 fertile, deep luvisol type, and derives from arkoses. The use of the land in the area is
122 mostly agricultural. Potential predators/dispersers of acorns and oak seedlings in the
123 study area are chiefly rodents (e.g. *Apodemus sylvaticus* L. and *Mus spretus* Lataste),
124 magpies (*Pica pica* L.), rabbits (*Oryctolagus cuniculus* L.), and hares (*Lepus europaeus*
125 Pallas) that shelter in the woodland islets. However, the European jay *Garrulus*
126 *glandarius* L., which is an effective acorn disperser in Mediterranean forests (Gomez
127 2003) is absent in this highly deforested area.

128

129 2.2. Predation and germination of seeded acorns

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

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

157

158 2.3. Seedling survival

159 On 22 June, after seedling emergence ended, we carefully removed the plastic
160 protectors at half of the seeding points that contained at least one emerged seedling to
161 leave them unprotected from herbivores. For the other half of seeding points with
162 emerged seedlings, the tree shelter was replaced by a wire cage to prevent the micro-
163 climate effects by tree shelters on seedling performance (Puértolas et al. 2010; Oliet et
164 al. 2012). We monitored seedling survival six times, once every ca. 10 days starting at
165 the beginning of July and ending at the end of August, and a final time on 19 October
166 2014.

167

168 *2.4. Natural early establishment of holm-oak*

169 To assess natural establishment of holm oak seedlings during the 2014 growing
170 season, *i.e.* not from our experimental acorn seeding, we sampled 192 rectangular plots
171 and nine squared plots between the islets or between the islets and nearby active crops
172 to count seedling emergence in the spring of 2014 and monitor their survival through
173 the end of summer (mid-October). The rectangular plots were placed at the edge of the
174 woodland islets in all four orientations, two at each corner and one between them (**Fig.**
175 **1S** in Supplemental material). These plots were 1 × 5 m between adjacent islets or 1 ×
176 10 m between islets and active crop fields. The squared plots between islets were 5 × 5
177 m. The 201 plots, which covered a total area of 1474.9 m² (*i.e.* 17.6% of the
178 experimental field area that was not occupied by woodland islets), were initially
179 surveyed once between May 17 and June 22 and later on July 6 and October 19 due to
180 rain events after the start of the first seedling counting and to account for final survival
181 after summer, respectively. The emerged seedlings in all plots were tagged for easy later
182 localization. The density of both dead and surviving seedlings in bands at different
183 distance to the islets (0-2, 2.01-4, 4.01-6, 6.01-8, 8.01-10 and > 10 m) was measured.
184 Recruitment within the islets was not measured as this study focuses on regeneration
185 outside the islets; additionally, the islets were very dense and shaded and visual
186 inspection hinted new established oaks in them were sprouts.

187

188 *2.5. Mapping and size measurement of naturally established holm oak since islet* 189 *planting*

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

196

197 2.6. Data analysis

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

203 We analyzed differences in seedling emergence using generalized linear mixed-
204 effects model (GLMM) with a binomial error distribution and a logit link function to
205 test the effects of the woodland islets (random effect), orientation and distance to the
206 islets and their interaction (fixed effects). Akaike's (1987) information criterion (AIC)
207 was calculated for each model; a smaller AIC indicates a better-fitting model as
208 determined from the parsimony in the number of parameters. We used the cutoff of
209 $\Delta\text{AIC} < 2$ units to differentiate models with better explanatory power (*sensu* Burnham
210 and Anderson 2002). Likewise, we performed a binomial generalized linear model
211 including orientation, distance and their interaction based on previous results from the
212 GLMM to test specific hypotheses in relation to these factors (H2).

213 Seedling survival from seeded acorns (H3) or naturally established in the Spring
214 of 2014 was assessed by survival analysis based on a Cox's Proportional Hazards semi-
215 parametric model using the maximum partial likelihood as the estimation method (Fox
216 1993; Allison 1995). We correlated the volume (*i.e.*, height \times crown projected area) and
217 distance to the closest planted woodland islet of the naturally established oaks > 1 yr old
218 since 1993. Finally, we tested the density distribution of naturally emerged and
219 surviving seedlings after the first dry season and of established oaks > 1 yr old at the
220 bands of different distance to the islets using contingency analysis. GLMM analysis was

221 performed with packages stats (R core team 2014) lme4 (Bates et al. 2014) and MuMIn
222 (Barton 2014) with R software v. 3.1.2. GLMs and survival analysis were carried out
223 with Statistica 7.0 (Statsoft. Tulsa, Oklahoma, USA).

224

225 **3. Results**

226 *3.1. Predation of seeded acorns*

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

231

232 *3.2. Seedling emergence*

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

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

245

246 *3.3. Early seedling survival*

247 All emerged unprotected seedlings were predated (i.e. they were found with no
248 aerial organs) while survival of protected seedlings at the end of the first growing

249 season was 33.3% (protection effect $\chi^2_1 = 13.33$, $p = 0.0003$; **Fig. 3**). There was a peak of
250 mortality at days 41 to 51 that was much higher for protected than for unprotected
251 seedlings. Neither orientation ($\chi^2_3 = 3.03$, $p = 0.39$) nor distance ($\chi^2_3 = 2.1$, $p = 0.83$)
252 affected seedling survival, but sample size was low ($n = 49$) and the design was highly
253 unbalanced.

254 Survival of the 28 naturally established oak seedlings that emerged in 2014 was
255 28.6% by the end of summer ($54.2 \text{ seedlings ha}^{-1}$), and it was independent of orientation
256 ($\chi^2_3 = 1.81$, $p = 0.77$) or distance ($\chi^2_4 = 2.97$, $p = 0.56$) according to the survival analysis.
257 Mean distance of surviving and dead seedlings to islets was $3.0 \pm 3.0 \text{ m}$ and 4.6 ± 2.5
258 m, respectively (differences in these distances were not significant, t-test $p = 0.15$).
259 Density distribution of emerged seedlings that survived after first dry season did not
260 differ among distance bands ($\chi^2_5 = 7.92$, $p = 0.16$). Thirty per cent of dead seedlings
261 dried out, 35% were predated when they were alive and 15% once dry, and for the
262 remaining 20% dead seedlings we could not conclude the cause of death.

263

264 *3.4. Oak establishment after 21 years*

265 Fifty-eight holm oak individuals >1-yr old that were developed from dispersed acorns
266 outside the planted islets have established in the experimental field after 21 years (**Fig.**
267 **4**), resulting in a density of 65.1 oaks per ha excluding the area occupied by the islets
268 with an average establishment rate of $3.3 \text{ oaks ha}^{-1} \text{ yr}^{-1}$. Average distance of these to the
269 closest islet was $6.3 \pm 5.4 \text{ m}$ ($5.8 \pm 3.7 \text{ m}$ excluding an outlier oak located at 35.7 m
270 from the closest islet), which is similar to half the average distance among islets (5.9
271 m). The density distribution of these established oaks did not differ among distance
272 bands ($\chi^2_5 = 5.75$, $p = 0.33$; **Fig. 2**). Height, basal diameter and crown projected area of
273 the established oaks averaged $49.2 \pm 64.3 \text{ cm}$, $20.1 \pm 31.3 \text{ mm}$, and $0.44 \pm 1.09 \text{ m}^2$,
274 respectively.

275

276 **4. Discussion**

277

278 4.1. *High acorn predation and low seedling survival*

279 Our results clearly show that acorn predation is a major bottleneck for holm oak
280 recruitment, consistent with our first hypothesis. Similar to our findings, [Leiva and](#)
281 [Fernández \(2003\)](#) reported that only 0-2.4% of acorns escaped from predation in an oak
282 savanna located in southern Spain, and [Pons and Pausas \(2007b\)](#) found that 98.7% of
283 acorns were removed and/or predated by rodents in eastern Spain. Rodents and magpies
284 are both predators and dispersers of acorns ([Waite 1985](#)), but rabbits and hares, which
285 are abundant in our field site, are only predators ([Zamora et al. 1985](#); [Díaz et al. 1996](#);
286 [Leiva and Fernández 2003](#); [Guzmán et al. 2008](#)). We have clear evidence of acorn
287 predation *in situ* for a small fraction of the unprotected acorns but suspect that most of
288 the unfound acorns were either entirely consumed immediately after removal or re-
289 cached and consumed later in other sites ([Perea et al. 2011](#)), as the farmland
290 environment where our woodland islets are embedded may exacerbate predation. For
291 instance, [Gómez et al. \(2008\)](#) found in the Sierra Nevada Mountains (SE Spain) that
292 most caches were recovered and consumed, and only 1.3% of the original experimental
293 acorns were found alive in caches the following spring. Likewise, in another experiment
294 that we conducted for three years in old fields in central Spain with tagged acorns, we
295 found that 100% of remobilized acorns were finally predated ([Villar-Salvador and](#)
296 [Pérez-Camacho, unpublished data](#)). Other studies, however, have documented the
297 spatial patterns and effects of long-distance oak dispersal at the landscape scale and
298 hence the importance of isolated oaks as seed sources ([Gómez, 2003](#); [Purves et al.](#)
299 [2007](#)). Acorn physical protection against predators is needed in Mediterranean
300 environments to ensure oak establishment after seeding ([Adams et al. 1992](#); [Castro et al.](#)
301 [2015](#)), as other methods such as chemical repellents have been shown to be
302 unsuccessful ([Leverkus et al. 2013](#)).

303 We found low rates of seedling survival, consistent with previous studies on
304 *Quercus* establishment in Mediterranean environments ([Rey Benayas et al. 2005](#); [Castro](#)
305 [et al. 2006](#); [Valdecantos et al. 2006](#); [Del Campo et al. 2010](#), [Cuesta et al. 2010a](#); [Cuesta](#)
306 [et al. 2010b](#)). As we anticipated (H3), most of this mortality was a consequence of
307 seedling predation; all of unprotected seedlings in the seeding experiment and at least
308 50% of the naturally established seedlings (which were not protected) were predated by
309 the end of the first growing season. On the other hand, two-thirds of our caged seedlings
310 and at least one third of the new naturally established seedlings dried out probably

311 reflecting mortality due to summer drought, which occurred quickly (**Fig. 3**). The
312 natural establishment rate we recorded in 2014 (54.2 seedlings ha⁻¹) is lower than those
313 we estimated from data reported by Pulido and Díaz (2005) in oak woodland (132
314 seedlings ha⁻¹ yr⁻¹) and by García-Barreda and Reyna (2013) in gaps of a planted pine
315 forest (120 seedlings ha⁻¹ yr⁻¹), but higher than that found by Pulido and Díaz (2005) in
316 an oak savanna (2.8 seedlings ha⁻¹ yr⁻¹). Gómez et al. (2003) also found that 98% of the
317 1000 experimental seedlings were killed by herbivores, notably wood mice, wild boar,
318 and domestic and wild ungulates.

319

320 4.2. *Low seedling emergence*

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

331

332 4.3. *Lack of distance effects*

333 The distance to woodland islets at small scales did not affect acorn predation and
334 seedling performance. Lack of distance effect on acorn predation is probably due to the
335 fact that our longest seeding distance (10 m) can be easily reached by all
336 dispersers/predators that may shelter in the islets (Pons and Pausas 2007b; Gómez et al.
337 2008). Similarly, we did not find higher seedling emergence at closer distances to the
338 islets where we expected higher emergence due to micro-climate amelioration by islet
339 canopy shade. This contrasts with results in Smit et al. (2009) showing higher
340 emergence in shaded microsites than in open microsites and suggests a lack of “safe”
341 microsites for recruitment in our experimental field (Pulido and Díaz 2005). It is

342 possible that microclimatic amelioration by islet canopy was not enough to maintain
343 high soil moisture during the dry spring, but we did not measure soil water content to
344 assess this explanation. The lack of distance effect on seedling mortality from herbivory
345 could be due to the fact that separation between islets is too small to detect a difference
346 in rabbit and hare movement (Gómez et al. 2008), but our observations suggest that
347 consumption of herbs by rabbits is much higher within 0-2 m of the edge of the islets
348 (Fig. 1). It is possible that there is a neutral balance between counteracting effects of
349 established islets on seedling establishment, namely microclimate amelioration
350 facilitating establishment near islets and competition with mature trees and herbivory
351 favoring establishment further away. A final possible explanation for lack of distance
352 effect on seedling emergence and early seedling survival is that we had insufficient
353 power to detect interactive effects between distance and orientation due to low sample
354 size and unbalanced design, due to high predation

355

356 *4.4. Initial woodland regeneration*

357 We recorded a natural establishment rate of 3.3 oaks ha⁻¹ yr⁻¹ along the 21 years of our
358 experiment, which in comparison with the figure of natural establishment found after
359 the first dry season suggests strong future mortality of recently established seedlings in
360 our field site. However, our woodland islets started to produce acorns seven years after
361 oak seedling plantation and seed production in the first reproductive years was small.
362 This means that the rate above will likely be higher and increase in the future. Leverkus
363 et al. (2014) found a natural establishment rate of 4.18 oaks ha⁻¹ yr⁻¹ at a post-fire
364 regeneration site in a Mediterranean mountainous environment with higher
365 precipitation.

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

374 Acorn availability is a bottle-neck that limits vegetation establishment in
375 agricultural landscapes (Rey Benayas et al. 2008a; Rey Benayas and Bullock 2012,
376 2015), and this limitation was clearly overcome by the introduction of small woodland
377 islets that established successfully in our experimental field. These islets have triggered
378 holm oak regeneration that would have been highly unlikely without nearby seed sources
379 (Gómez-Aparicio et al. 2009), but the rate of recruitment is limited by high acorn
380 predation, seedling herbivory, and stressful microclimatic conditions. Using tree
381 shelters against herbivores that also ameliorate climate harshness (Puértolas et al. 2010)
382 of the naturally established seedlings from acorns dispersed from planted woodland
383 islets would accelerate passive restoration of former cropland and pastureland. Thus,
384 planting woodland islets without further intervention seems not be sufficient to catalyze
385 “fast” initial recovery of Mediterranean woodland on abandoned farmland and
386 restoration will be resource intensive. “Success” or “failure” in restoration efforts like
387 the one investigated here nonetheless depends on the time frame of evaluation,
388 particularly in Mediterranean ecosystems where recruitment is notoriously episodic
389 (Moreno et al. 2011). Overall, we suggest that the woodland islet approach is a low cost
390 and useful technique to speed up woodland restoration in agricultural landscapes.

391

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399

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Fig. 1. In our 21-yr-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).

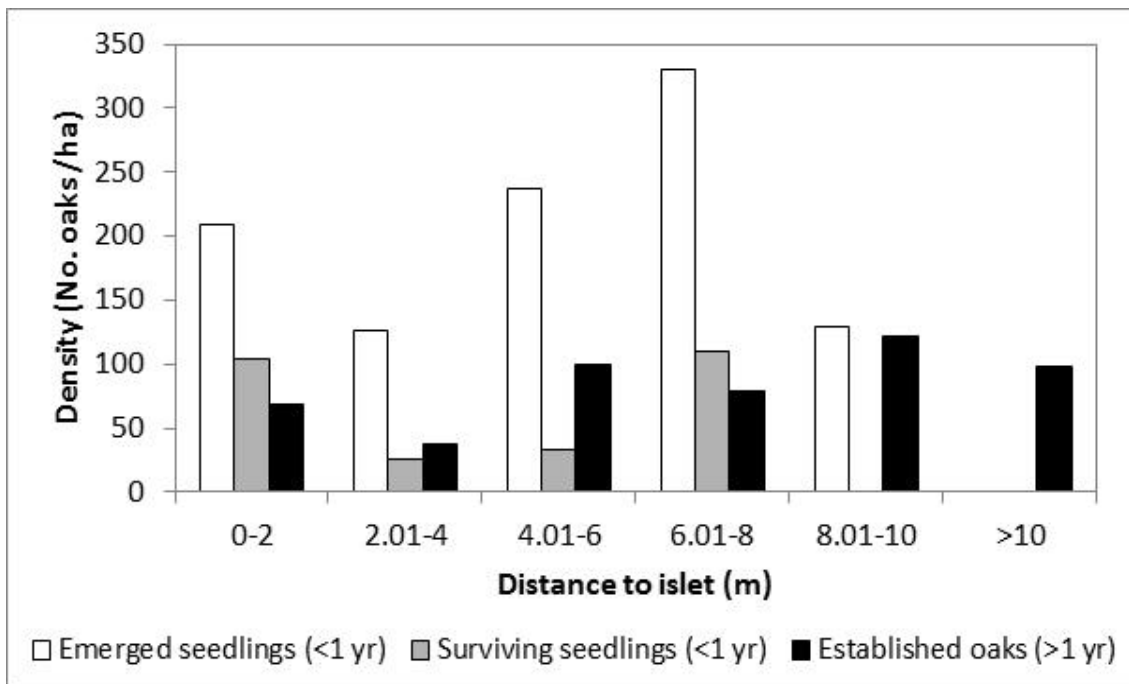


Fig. 2. Oak density (emerged seedlings in 2014, surviving seedlings after the first dry season, and established oaks > 1 year old) in 2-m width bands at different distance to the woodland islets.

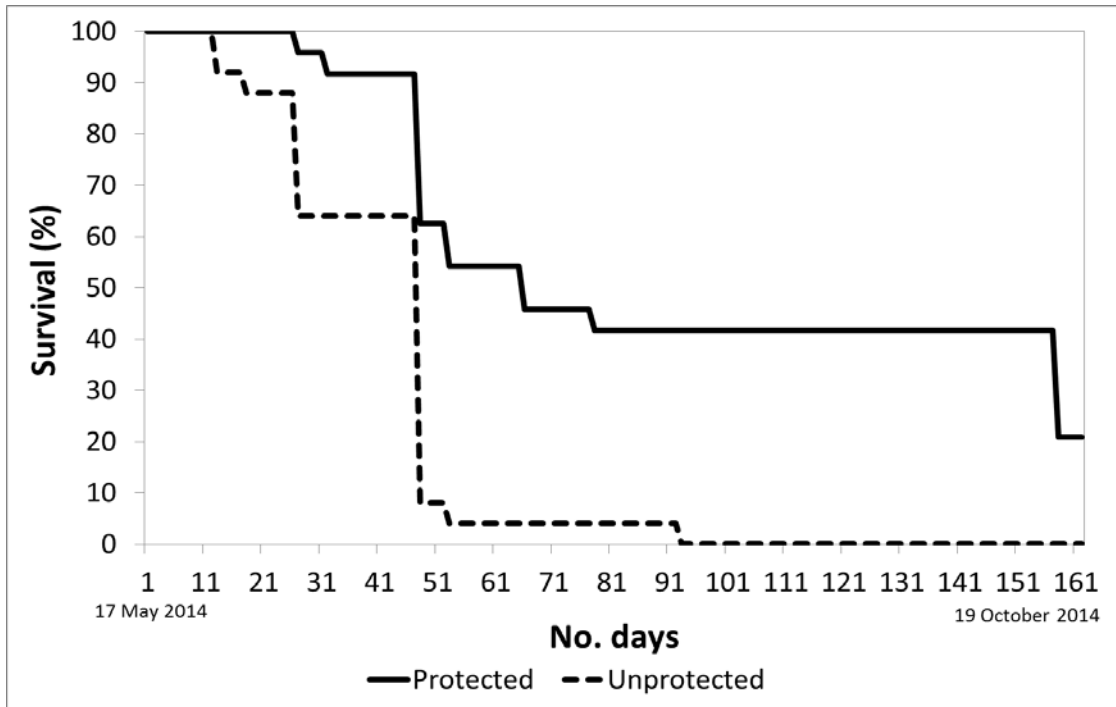


Fig. 3. Changes in survival probability of protected and unprotected *Q. ilex* seedlings through the summer and early fall of the first growing season. These graphs refer to the 31 emerged seedlings from seeded acorns that were monitored since May 17 2014 plus the 18 seedlings that emerged later.

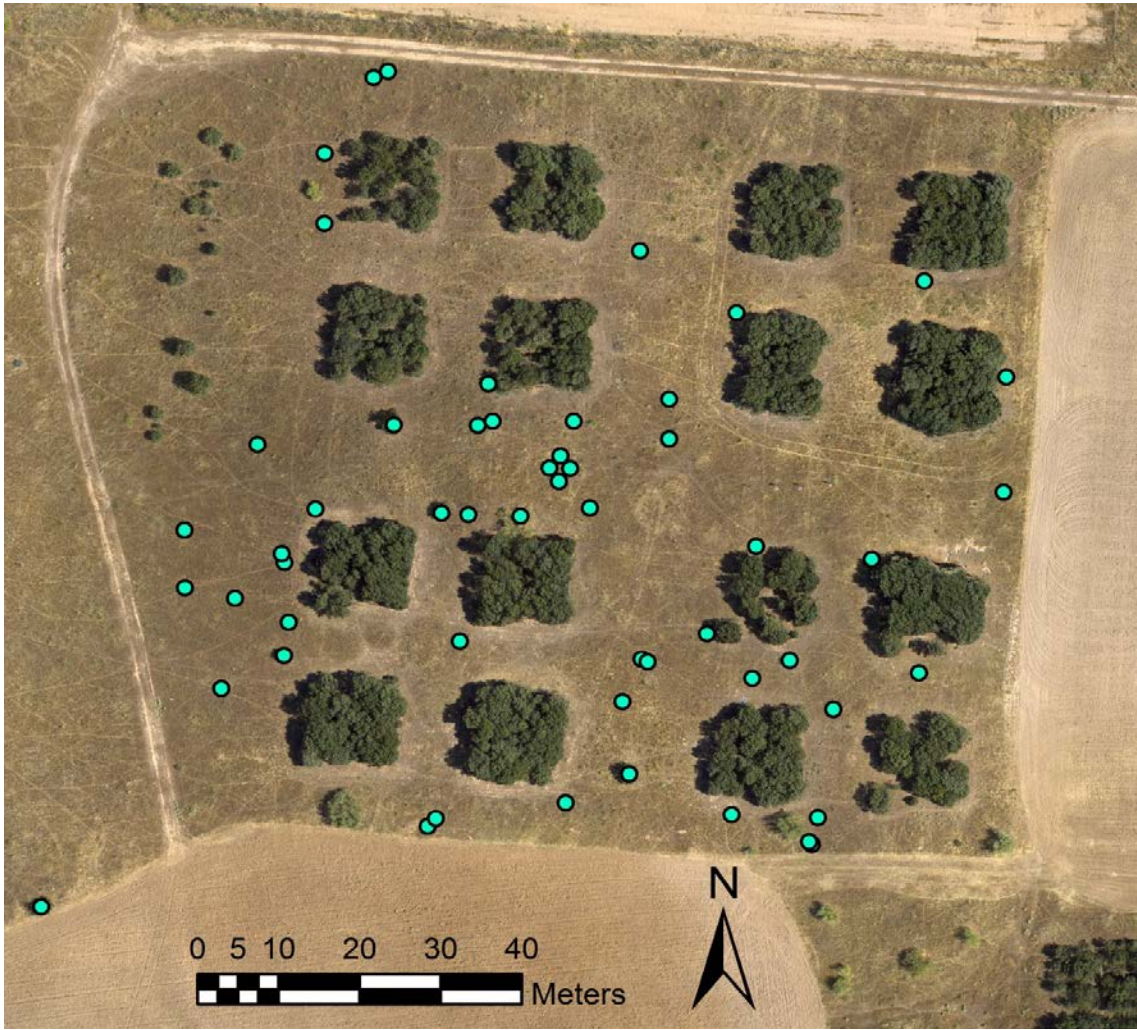


Fig. 4. Position of the 58 naturally established oaks > 1 yr old in the experimental field.

Supplemental material

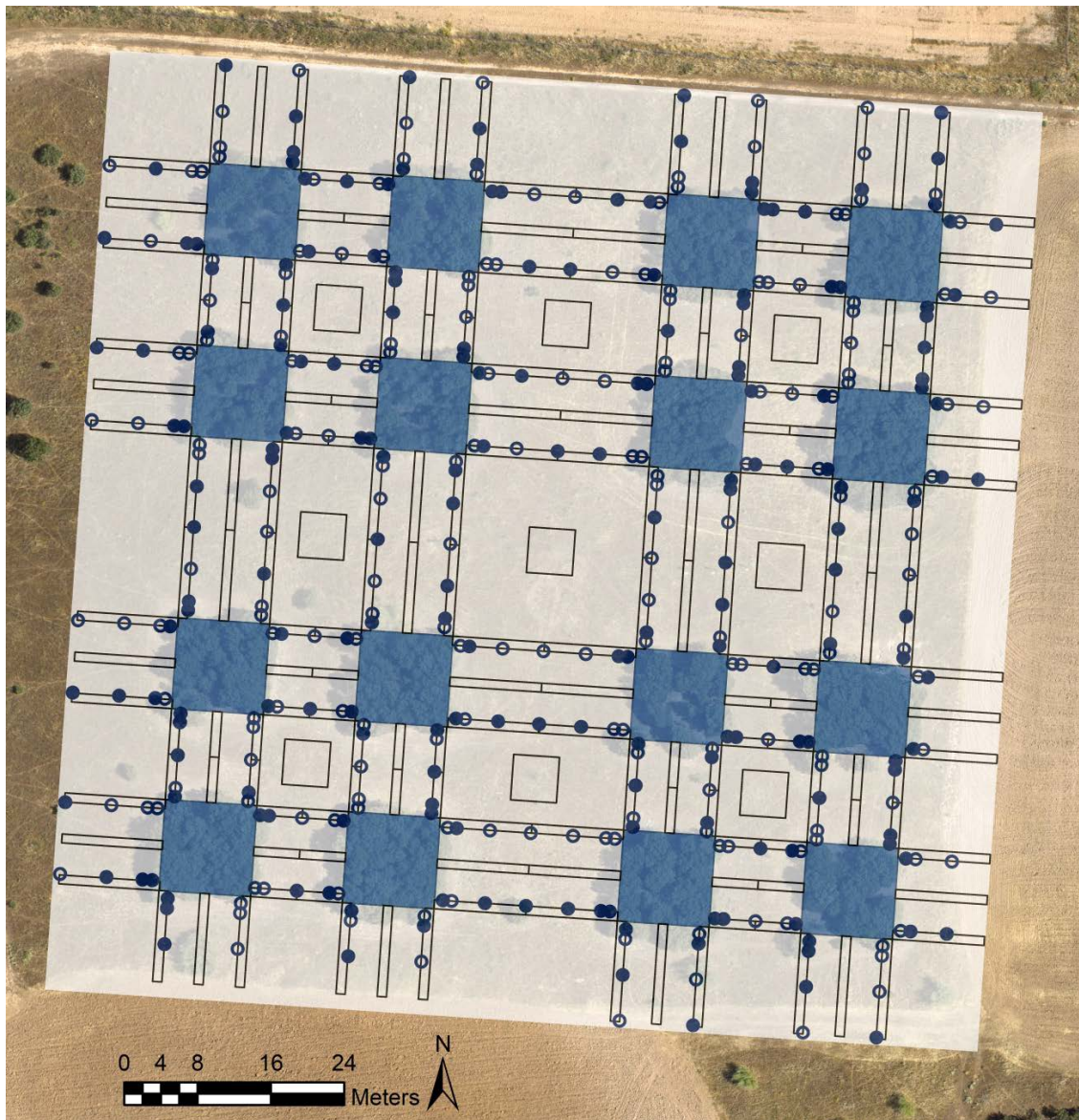


Fig. 1S. Design of the seeding experiment and sampling for assessment of early natural establishment of oak seedlings. Position of (a) 386 acorn seeding points located along two 10-m long transects in each of the four corners of every woodland islet. Open and solid blue circles indicate unprotected and protected seeded acorns, respectively, at 0, 1, 5 and 10 m from the islet edge (see text for a few exceptions to these seeding distances); and (b) 192 rectangular plots and nine squared plots between the islets or between the islets and nearby active crops to count and monitor natural seedling emergence and early survival.