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1 **Microsite manipulation in lowland oak forest restoration results in indirect**
2 **effects on acorn predation**

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15

16 **Abstract**

17 Taking advantage of facilitation mechanisms to counteract harsh environmental
18 conditions may prove to be a successful strategy in the restoration of degraded
19 man-made ecosystems. Seed sowing is often a viable and less expensive
20 technique to restore forest cover in environments subjected to heavy anthropic
21 disturbance. In this context, nurse plants and shield objects can improve microsite
22 conditions, enhancing the emergence and growth of seedlings. However, their

23 presence can also create preferred microhabitats for seed predators, and as a
24 result, may alter their movement decisions and foraging behavior. In this study,
25 we investigated whether nurse shrubs and artificial shade structures, with and
26 without previous soil amelioration, could facilitate acorn emergence. We also
27 tested their effects on the predation of acorns by small mammals, within the
28 framework of a larger project aimed at restoring a *Quercus robur* L. forest. The
29 research was conducted in a former roadbuilder's yard located along the
30 Mediterranean Corridor, in Northern Italy. The yard had been in use during the
31 widening of a highway that runs parallel to a stretch of the Corridor. The area was
32 restored in 2014. Mechanical preparation of the soil included two treatments, with
33 and without the addition of compost and zeolite. Acorns were then sown in plots
34 in different microsites, i.e., 1) close to a shrub (*Cytisus scoparius* L., Scotch
35 broom), 2) to the north and 3) south of a shield object (a 30 cm x 30 cm wood
36 particle board), and 4) without any protection element (control). We recorded
37 acorn emergence and predation during the first growing season. At the end of the
38 season, overall acorn emergence was observed to be low, and, surprisingly, was
39 higher in the non-amended soil treatment. The amended soil had a higher
40 temperature and a lower water volumetric content in the summer (JJA). No
41 evidence of direct facilitation on emergence by shield objects or Scotch broom
42 was found, but indirect effects were detected. Acorn predation was generally high
43 (67.45%), but was negatively affected by the presence of *C. scoparius*. The
44 distance of the plot from the rainwater drainage ditch surrounding the study site
45 also influenced winter predation; a larger number of acorns were removed by
46 rodents at longer distances from the drainage ditch. In order to restore degraded

47 sites to lowland oak forests through direct seeding, it is necessary to deal with
48 complex interactions between direct and indirect facilitation mechanisms,
49 competition and predation. Predation was particularly important because of the
50 high predation pressure on acorns.

51

52 **Key words:** *Quercus robur*, acorn; nurse shrub; artificial shield object; facilitation;
53 seed predation.

54

55 **1. Introduction**

56 The ecological restoration of degraded man-made ecosystems usually requires
57 plant establishment and survival in harsh or stressful environments, while limiting
58 restoration costs and further interventions.

59 Seed sowing is often a viable and less expensive alternative to planting nursery-
60 grown seedlings (Madsen and Löf, 2005), with seeds being easier to transport
61 and manage than bareroot and container seedlings. Direct seeding also allows
62 the plant root system to develop naturally, thereby avoiding the root
63 malformations that are generally associated with containers (Stanturf et al., 2000;
64 Dey et al., 2008). Instead, the use of container stock can reduce the stress linked
65 to nutrient or water limitation, the risk of poor survival, and number of operations
66 necessary for site preparation and management, e.g. litter removal, mechanical
67 scarification, repeated mowing to control competing ground vegetation (Smith et
68 al., 1997; Dey et al., 2008). Moreover, after germination, seedlings can show
69 slower development rates than planted trees (Nyland 2007).

70 The early stages of seedling establishment are critical for the regeneration of
71 plant populations. Several mortality factors, including predation, competition and
72 abiotic stress can hamper seed regeneration (Nathan and Muller-Landau, 2000;
73 Castro et al., 2004; Schurr et al., 2004; Davis et al., 2005; Riginos et al., 2005;
74 Kipfer et al., 2009). In addition, excess light, high temperatures and summer
75 drought, which are accentuated in degraded areas without forest cover, can
76 severely limit the survival and growth of seedlings (Castro, 2006; Gómez-Aparicio
77 et al., 2006). Site conditions and mechanisms that operate at a small scale may
78 in particular limit the emergence and performance of seedlings (Collins and Good,
79 1987).

80 Taking advantage of intra- or interspecific facilitation mechanisms and the
81 sheltering effects of abiotic elements in natural environments has proven to
82 produce beneficial effects on the survival, initial growth and fitness of the
83 neighbouring seedlings, particularly in climatically stressing sites (Callaway,
84 2007; Brooker et al., 2008; Marzano et al., 2013). Increasing evidence has
85 pointed out the potential benefits of the application of this nursing effect to
86 improve the success of restoration projects in degraded environments (Padilla
87 and Pugnaire, 2006; Torroba-Balmori et al., 2015).

88 Nurse plants improve the emergence, survival and growth of seedlings (Castro
89 et al., 2004; Gómez-Aparicio et al., 2004; Gómez-Aparicio et al., 2006; Torroba-
90 Balmori et al., 2015) providing a favourable microhabitat in their surroundings.
91 They offer shade, buffering against high radiation and temperatures, and can
92 increase soil moisture and nutrient content (Callaway, 1995; Rey Benayas, 2005;
93 Legras et al., 2010; Leiva et al., 2015).

94 In highly degraded systems, and in particular at the grassland stage, nurse
95 objects, such as woody debris or artificial shade-structures can emulate the
96 beneficial effects of nurse plants by reproducing the shaded environments that
97 can be found under their canopies (Gómez-Aparicio et al., 2005; Rey Benayas et
98 al., 2005; Badano et al., 2011).

99 A key point that influences the recruitment process success is then the interaction
100 among environmental factors that affect regeneration and the behavior of seed
101 dispersal and predation agents (Crawley and Long, 1995; Sunyer et al., 2015).

102 This interaction can actually alter the probability of seed survival and seedling
103 establishment, with the spatial pattern of seed removal usually resulting from
104 predator preferences for certain microhabitats (Clark et al., 1999; Jordano and
105 Schupp, 2000; Pérez-Ramos and Marañón, 2008). Thus, even though nurse
106 plants and shield objects could improve microhabitat conditions and promote
107 seed germination and growth, they could also influence animal behavior, driving
108 seed and seedling predator movements. Their presence, which in particular
109 affects the foraging behavior of animals that usually feed on seeds, could result
110 in increasing predation.

111 It is well known that wild ungulates and granivorous rodents in Europe can
112 predate a large number of seeds and browse saplings, thus reducing the success
113 of direct seeding in restoration projects (Birkedal et al., 2009; Jinks et al., 2012;
114 van Ginkel et al., 2013). The seed predation rate is strongly affected by habitat
115 complexity, which in turn can influence the abundance of ungulates and rodents.
116 For instance, wild ungulates tend to avoid habitats with complex structure that
117 could hamper their movements, while small mammals prefer to forage in habitats

118 with shrubs and rocks, where they perceive a minor predation risk (Gómez et al.,
119 2003; Orrock et al., 2004; Fedriani and Manzaneda, 2005; Pérez-Ramos et al.,
120 2008; Leverkus et al., 2013). The presence of coarse woody debris in forests
121 usually intensifies the removal of seeds by rodents, and the presence of shrubs
122 and shelters lengthens the time that the rodent spends handling and choosing
123 viable seeds (Perea et al., 2011; van Ginkel et al., 2013).

124 In the context of a large lowland oak forest restoration project, we have
125 investigated whether the presence of shelter elements can improve acorn
126 emergence and seedling survival of pedunculate oak (*Quercus robur* L.) or
127 whether it can support the movement decisions and foraging behavior of small
128 rodents, by analyzing the main factors that affect spatio-temporal variations in
129 seed predation.

130 Since acorn germination in *Quercus* species is conditioned by soil moisture
131 (Pérez-Ramos et al., 2013) and can present delayed emergence (González-
132 Rodríguez et al., 2012), using shrubs (Gómez-Aparicio et al., 2004) and artificial
133 shield objects on planting sites could ameliorate microclimatic conditions, and
134 thus enhance emergence rates (Smit et al., 2008). The large size of oak
135 cotyledons can increase the odds of both regeneration success and seed
136 predation. The latter, which is mainly by small mammals (Gómez et al., 2003;
137 Smit et al., 2008), is usually more intense in the post-dispersal phase and is one
138 of the main factors that endangers oak recruitment. The regeneration
139 performance of oak is related to several variables (Annighöfer et al. 2015). Acorn
140 predation before germination largely determines the success of regeneration

141 (Harmer, 1994), with competition, pests, water supply, light availability and
142 browsing being other variables leading to recruitment failure (Nilsson et al., 1996).
143 We have hypothesized that improving the physical and chemical conditions of the
144 soil and facilitating seed germination with nurse shrubs and shield objects could
145 influence oak establishment but also the removal of acorns by small mammals.
146 Our main aims were thus to 1) assess the impact of soil amelioration on acorn
147 emergence and predation rate; 2) evaluate the role of enhanced seeding
148 microsites (close to nurse shrubs and shield objects) on the regeneration
149 performance and acorn predation; 3) determine whether the relative position of
150 sowing sites can modify the predation pattern.

151

152 **2. Materials and methods**

153 **2.1 Study site.**

154 The experiment was conducted in a degraded area in northwestern Italy
155 (45°11'38.60" N, 7°50'38.04" E, ca. 190 m a.s.l.). The site is located along the
156 Rail Freight Corridor 6 (Mediterranean Corridor) (European Commission, 2018),
157 linking the southwestern Mediterranean region of Spain and the Hungarian
158 border with Ukraine. The area, which is bordered by a highway, was formerly a
159 roadbuilder's yard. In November 2014, after the road works ended, the area was
160 restored through both seed sowing and seedling planting (2 year old nursery
161 plants), followed by hand sowing with a grassland species mixture. The tree and
162 shrub species used in the experiment were those that usually grow in the lowland
163 oak-hornbeam Mesophytic deciduous forest, i.e., the natural late seral forest

164 ecosystem of the Po Plain, which is dominated by *Q. robur* and *Carpinus betulus*
165 L.

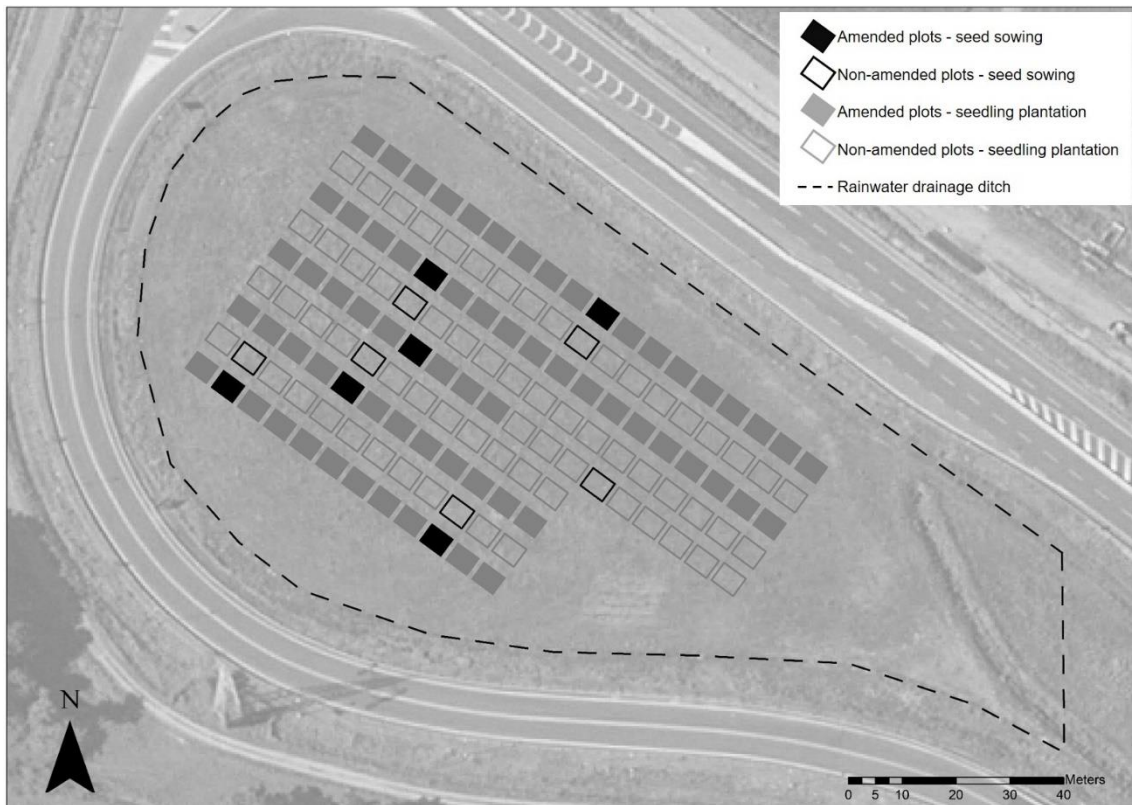
166 No trees were present when the experiment was started. The soil texture was
167 sandy loam. The pH ranged from 7.41 to 8.08 and soil organic matter content
168 ranged from 1.5% to 3%. The cation exchange capacity (CEC) was lower than
169 10 meq/100 g.

170 The climate is temperate, with an annual mean temperature of 11.4 °C and
171 average annual precipitation of 806.2 mm (ARPA Piemonte-Verolengo
172 meteorological station 10 km from the study site, period 1988-2010). The rainfall
173 is not homogeneously distributed during the year, with spring and autumn being
174 the wettest seasons.

175 A rainwater drainage ditch surrounds the area. At the beginning of the
176 experiment, the area was fenced off against the introduced eastern cottontail
177 (*Sylvilagus floridanus*) and wild ungulates to avoid browsing damage to seedlings
178 and seed predation.

179 The experimental design (Fig. 1) included two soil treatments (non-amended and
180 amended). In November 2014, the treatments were applied in rows after a
181 mechanical site preparation. Using a tractor the rows were ripped (to a 70 cm
182 depth) and ploughed (to a 40 cm depth). The distance between rows was
183 approximately 2.5 m. Furrows were then formed along the southern edge of the
184 rows. Half of the rows were just ripped and ploughed (non-amended). Since we
185 wanted to improve the organic matter content up to 3% and raise the CEC to 15
186 meq/100g, the other rows were ripped, ploughed and amended using 4.2 Mg/ha
187 of compost and 43 Mg/ha of zeolite, with a diameter of 3-8 mm. The compost

188 had a pH of 8.7, 24% w/w of organic carbon content on a dry matter basis, and a
189 2.19% total N content. Zeolite was chosen as it is a slow release fertilizer (Allen
190 and Ming, 1995; Campisi et al., 2016). It has a very good cation exchange
191 capacity and retains water and nutrients thanks to its high adsorption ability. In
192 the sampling design, amended rows alternated with non-amended ones (Fig. 1).
193 Rectangular plots (4 m x 5 m) were established, 1.5 m apart from each other,
194 within each row. Six plots per treatment were used for the direct seeding of *Q.*
195 *robur* acorns, while the remaining 60 plots per treatment were used for seedling
196 planting.



198 **Fig. 1.** Sampling design. Plots were established in rows after mechanical site
199 preparation. Rows amended with compost and zeolite (fully colored in grey)
200 alternated with the non-amended ones (no color; grey border). Among the
201 amended plots, the black ones are those used for the direct seeding of *Q. robur*

202 acorns. Among the non-amended plots, those with a black border were used for
203 the direct seeding of *Q. robur* acorns. The rest of the amended and non-amended
204 plots were used for seedling planting (data not reported). A rainwater drainage
205 ditch (black dashed line) surrounds the study site, which is also bordered by a
206 highway.

207

208 **2.2 Acorn facilitation and predation experiment**

209 In order to assess the role of shield and nurse elements in the oak emergence,
210 and their influence on rodent predation, we performed a sowing experiment, the
211 set-up of which included four different treatments within each of the 12 main-plots
212 that were sown (6 x 2 soil treatments). In each soil treatment, acorns were sown
213 1) close to a *Cytisus scoparius* L. (Scotch broom) shrub (B); 2) close to the
214 northern (N) and 3) southern side (S) of a shield object; 4) without protection
215 elements in the surrounding area (control) (C).

216 Scotch broom is a native nitrogen-fixing species, which grows in dense clumps,
217 and has been found to facilitate *Q. robur* recruitment (Muhamed et al., 2015). The
218 nurse shrubs were 2 year old nursery Scotch brooms, with a mean height of 72.5
219 cm (\pm 10.8) at planting time in November 2014. Any dead Scotch brooms were
220 replaced during the experiment. The artificial shield objects consisted of wood
221 particle boards (30 cm x 30 cm), erected vertically in an east-west direction.

222 We established 10 sowing sites (replicates) for each treatment. Three acorns
223 were planted in each site, 5 cm apart, one per hole; they were buried vertically at
224 a depth of 3 cm and covered with soil. The acorns were sown at the minimum
225 possible distance from the wooden boards and *C. scoparius* (2-5 cm). This

226 resulted in a total of 10 replicates x 3 acorns x 4 treatments x 6 plots x 2 soil
227 treatments (= 1440 buried acorns). Before sowing, the seeds were floated in
228 water to exclude any non-viable ones (Gómez et al., 2003). A single batch of
229 acorns was used (Bosco della Mesola, 44°50'20.66" N, 12°15'08.70" E, ca. 0 m
230 a.s.l.). Sowing was performed twice, in winter (December 2014) and spring
231 (March 2015), thus allowing us to test for seasonality in predation. The sowing
232 site position was recorded in order to investigate whether the distance from
233 potential preferential paths (e.g. the drainage ditch and furrows), where rodents
234 would be protected from possible predators, affected their foraging behavior and
235 thus the seed removal rate.

236

237 **2.3 Data Collection**

238 Seedling emergence was recorded 3 times during the experiment, in May, July
239 and September 2015. It was calculated in a cumulative way.

240 The meteorological data that might have influenced emergence (air temperature,
241 precipitation) were obtained from the ARPA Piemonte-Verolengo meteorological
242 station (45°10'54.86" N, 8°1'55.46" E; 163 m a.s.l.). The study year (2015) had a
243 particularly hot and dry summer. Mean summer temperature (JJA) was 1.9 °C
244 warmer than the 1989-2014 period (23.1 °C vs. 21.2 °C), and precipitation
245 amounted to 168.4 mm (mean summer precipitation 1991-2014 was 196.8 mm).

246 The soil temperature and moisture were collected using Lascar EasyLog EL-
247 USB-2 data loggers (n=16) and Spectrum WatchDog 1400 Micro Stations with
248 Spectrum WaterScout SM 100 soil moisture sensors (n=16), respectively. The
249 soil sensors were buried at a depth of 10 cm in each sowing manipulation for the

250 two soil conditions (amended and non-amended). Data were collected from the
251 beginning of June to the end of August 2015.

252 The final fate of the acorns was recorded twice: early spring (March), and late
253 summer (September). By means of a hunting camera, rodents were identified as
254 the main acorn predators. Removed and gnawed acorns were considered as
255 predated.

256 We confirmed the removal of acorns in each survey by digging all the sowing
257 points. During the first survey, acorns were recorded as predated or intact. During
258 the second survey, acorns were recorded as seedlings (epicotyl visible
259 aboveground), ungerminable (empty or unhealthy endosperm/cotyledon), or
260 predated (removed or gnawed seeds) (Birkedal et al., 2010).

261

262 **2.4 Data analysis**

263 We firstly analyzed the role of soil treatments on acorn emergence and predation
264 rate by means of the χ^2 test. As expected, soil amelioration had no effect on
265 predation rates, and was thus not considered in subsequent predation analyses
266 (χ^2 ; $p>0.05$). We then tested the effect of the different treatments on acorn
267 predation by fitting generalized linear models (GLM) in which the presence or
268 absence of shrubs (B), the location south (S) or north (N) of the board, distance
269 from the surrounding drainage ditch (DIST), and the period (TIME) were included,
270 along with all their possible interactions, as explanatory variables. The DIST
271 parameter was computed in a GIS (ArcMap 10.1) environment: eight 5.5 m wide
272 buffers were created and each plot was assigned to a buffer in relation to its

273 distance from the ditch. The control plots were included in the analysis with
274 absence values (0) for all treatments (i.e. no shrubs, no boards).

275 In order to define the influence of different factors on the rate of emergence we
276 ran generalized linear mixed models (GLMM) considering soil amelioration (A),
277 presence of shrubs (B), location south (S) or north (N) of the board as fixed
278 parameters, along with their possible interactions, and plot location defined by
279 distance from the drainage ditch (DIST) as a random factor. GLMM analyses
280 were implemented in the R software environment (2.15.2; R Development Core
281 Team, 2012) using the lme4 package (Bates et al., 2015). The GLM analyses
282 were run using STATGRAPHICS centurion XVII (Statpoint Inc., USA, 2014).

283 Since the predation and emergence data showed a binary response, a binomial
284 error distribution with a logit-link function was adopted in both analyses. Model
285 simplification was accomplished by computing the Akaike information criterion
286 (AIC). Starting from the full model, the minimal adequate GLMM or GLM was
287 obtained by sequentially removing any non-significant model terms until no
288 further reduction in AIC was observed.

289 Multi-comparison tests were run using Kyplot 2.0 (KyensLab Inc.) for the
290 parameters that appeared to significantly affect acorn predation or emergence.

291 We tested the relationship between distance from the drainage ditch (DIST) and
292 predation rate for each plot using a linear regression model. A similar analysis
293 was conducted considering the distance of sowing sites from the furrows on the
294 southern side of the rows.

295

296 **3. Results**

297 The mean summer temperature in the topsoil (0-10 cm) was 28.0 °C, while the
298 mean summer volumetric water content was 6.1%. A significantly higher daily
299 mean temperature of the soil was observed in the amended sowing sites located
300 close to shrubs (B) and north of the boards (N), compared to the non-amended
301 ones (t-paired test; $p < 0.01$), but no difference was found between treatments for
302 both amended and non-amended sites (Table 1; Tukey test, Pairwise multiple
303 comparisons; $p > 0.01$). Both daily maximum temperature and temperature range
304 showed higher values in amended sites than in non-amended ones (t-paired test;
305 $p < 0.01$), except for control sites. No significant differences were detected for daily
306 maximum temperature between sowing treatments for both amended and non-
307 amended sites. The soil in amended sites on the southern side of the board (S)
308 showed the largest mean daily temperature range (compared to C and B; Tukey
309 test, Pairwise multiple comparison; $p < 0.01$), while the daily range was
310 significantly wider in S non-amended sites than in N ones (Tukey test, Pairwise
311 multiple comparisons; $p < 0.01$). The mean volumetric water content in amended
312 and non-amended sites was significantly different for each sowing treatment (t-
313 paired test; $p < 0.01$). No differences were found in amended sites, while N
314 showed a significantly higher water content in non-amended ones (Table 1;
315 Tukey test, Pairwise multiple comparisons; $p < 0.01$).

316

317 **Table 1.** Mean soil temperatures (daily mean, maximum and range) and
318 volumetric water content (\pm standard deviation) for the summer months (JJA) in
319 amended and non-amended sowing sites. Different letters indicate significant
320 differences between treatments according to a Tukey post-hoc test ($p < 0.01$). The

321 treatments are C, control; N, acorns sown north of a shield object (a wood particle
 322 board); S, acorns sown south of a shield object (a wood particle board); B, acorns
 323 sown close to Scotch broom (*Cytisus scoparius* L.).

324

	amended soil				non-amended soil			
JJA	C	N	S	B	C	N	S	B
Soil T mean (°C)	28.26 ^a (±4.34)	27.85 ^a (±4.28)	28.19 ^a (±4.46)	28.16 ^a (±4.34)	27.89 ^a (±4.50)	27.21 ^a (±4.22)	28.30 ^a (±4.79)	27.87 ^a (±4.26)
Soil T max (°C)	33.21 ^a (±5.85)	33.28 ^a (±5.94)	34.29 ^a (±6.45)	33.40 ^a (±6.11)	33.05 ^a (±6.43)	31.87 ^a (±5.79)	33.80 ^a (±6.98)	32.87 ^a (±5.84)
Soil T range (°C)	10.13 ^a (±3.79)	10.87 ^{ab} (±3.72)	12.20 ^b (±4.40)	10.47 ^a (±3.93)	10.32 ^{ab} (±4.20)	9.32 ^a (±3.48)	10.99 ^b (±4.72)	10.01 ^{ab} (±3.60)
Soil Water Content (%)	6.17 ^a (±5.10)	4.37 ^a (±3.86)	4.40 ^a (±3.80)	4.73 ^a (±4.05)	5.12 ^a (±3.84)	11.83 ^b (±8.20)	4.82 ^a (±3.33)	7.00 ^a (±5.99)

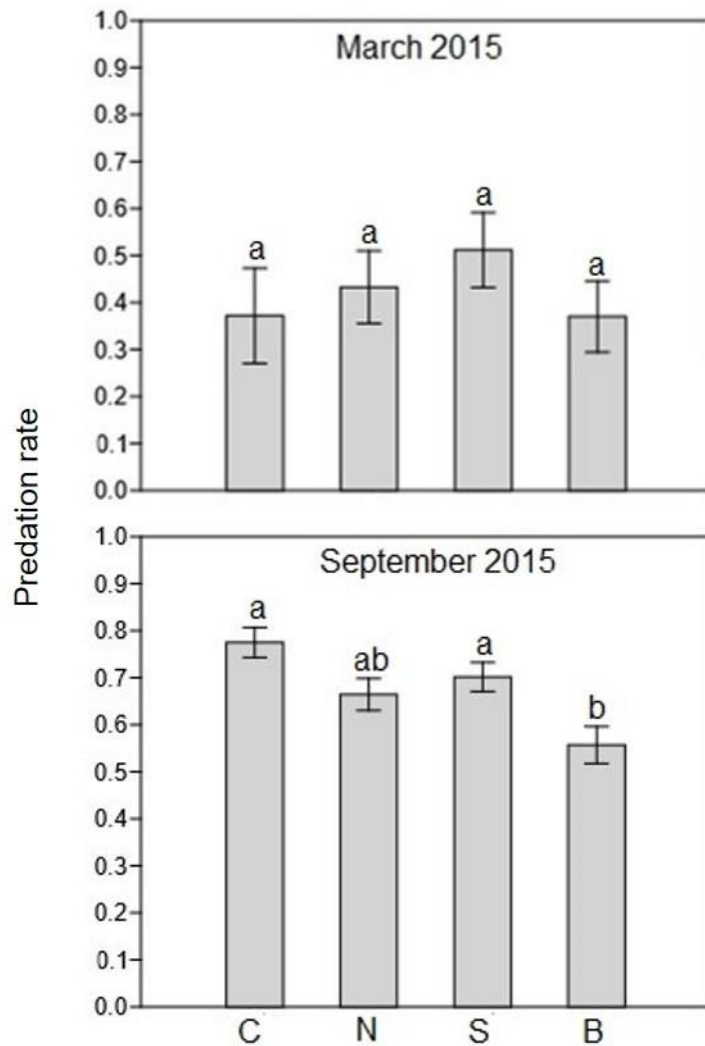
325

326

327 In September, acorn emergence was 7.98% (based on the total sown amount).
 328 No significant difference in emergence rates was observed for the two soil
 329 treatments (χ^2 test; $p>0.05$).

330 Predation rate was high for both periods (42.09% in March; 67.45% in
 331 September). No significant soil treatment effects were observed on the acorn
 332 predation rate for either period (χ^2 test; $p>0.05$). A significant difference between
 333 sowing treatments was instead found in both amended and non-amended sites
 334 (χ^2 test; $p<0.01$). In March no significant difference was found in the number of
 335 predated acorns between treatments. In contrast, predation was significantly

336 lower in September (Steel-Dwass multiple comparisons test; $p < 0.05$) in B
337 (55.56%) than in C (77.50%) or S (70.05%) (Fig. 2).



338

339 **Fig. 2.** Predation rate of *Q. robur* acorns for the two surveys (March and
340 September). Different letters indicate significant differences between treatments
341 according to a Steel-Dwass multiple comparisons test ($p < 0.05$). The treatments
342 are C, control; N, acorns sown north of a shield object (a wood particle board); S,
343 acorns sown south of a shield object (a wood particle board); B, acorns sown
344 close to Scotch broom (*Cytisus scoparius* L.).

345

346 GLM showed that different factors affected predation rate (Table 2). The final
347 model ($F=6.27$; $p<0.001$) showed that only the shrub presence, among the
348 different treatments, significantly affected predation rate, and that distance from
349 the drainage ditch was the most important variable. The period was only
350 important when combined with distance from the drainage ditch and with
351 treatments (B, N, S). This result was confirmed by the linear regression analysis
352 (Fig.3). In March, there was a significant increase in predation rate as distance
353 from the drainage ditch increased ($R^2 = 0.696$, $p = 0.001$). No significant effect
354 was found in September ($R^2 = 0.017$, $p = 0.689$), the predation rate being high
355 and almost constant (always $>50\%$) along the distance gradient (Fig.3).

356

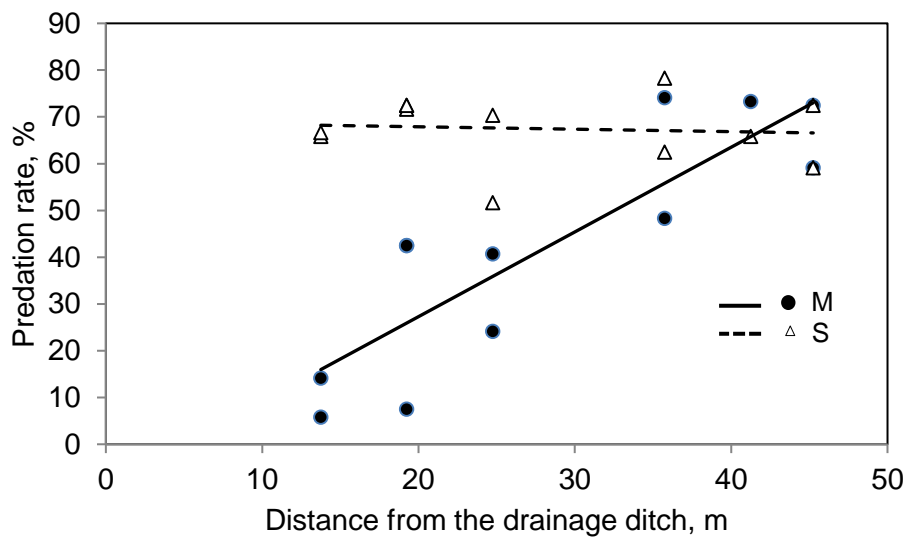
357 **Table 2.** Summary of the GLM for acorn predation. B, acorns sown close to
358 Scotch broom (*Cytisus scoparius* L.); N, acorns sown north of a shield object (a
359 wood particle board); S, acorns sown south of a shield object (a wood particle
360 board); DIST, distance from drainage ditch; TIME period of the survey.

Source	Estimate± S.E.	df	F	P
B	0.064±0.021	1, 69	9.63	0.003
N	0.021±0.021	1, 69	1.06	0.301
DIST	-0.182±0.038	5, 69	8.28	<0.001
TIME	-0.051±0.033	1, 69	2.29	0.135
B x TIME	-0.041±0.024	1, 69	2.76	0.101
N x TIME	-0.031±0.024	1, 69	1.58	0.213
S x TIME	-0.042±0.024	1, 69	2.96	0.090

B x DIST x TIME	-0.032±0.033	5, 69	2.79	0.024
N x DIST x TIME	-0.059±0.033	5, 69	3.69	0.005
S x DIST x TIME	-0.070±0.033	5, 69	3.38	0.009

361

362



363

364 **Fig. 3.** *Q. robur* predation rate in relation to plot distance from the drainage ditch.
 365 $R^2=0.696$, $p=0.001$ in March (M, solid line). $R^2=0.017$, $p=0.689$ in September (S,
 366 dashed line).

367

368 Overall net acorn emergence was computed at the end of the season considering
 369 only non-predated acorns. Just 24.3% of non-predated acorns germinated. A
 370 higher emergence rate was found in non-amended sites (χ^2 test; $p<0.05$), but
 371 there were no significant differences between sowing treatments (χ^2 test; $p>0.05$).
 372 GLMM confirmed that soil treatment was the only factor that affected emergence
 373 (Table 3).

374 The distance between different sowing points in the plot and furrows had no
 375 significant effect on the predation rate in either March or September ($p>0.05$).
 376 Since there was a high predation rate and low germination success, which greatly
 377 reduced the number of emerged seedlings, the growth rate and survival data
 378 were not considered in the subsequent analyses.

379

380 **Table 3.** Model parameter estimates derived from the GLMM models for acorn
 381 emergence at the end of the growing season (net of predation). B, acorns sown
 382 close to Scotch broom (*Cytisus scoparius* L.); S, acorns sown south of a shield
 383 object (a wood particle board); SOIL, acorns sown in amended soil.

384

Fixed effects	Estimate± S.E.	Z-value	P
(Intercept)	-1.45±0.25	-5.81	<0.001
S	0.47±0.29	1.61	0.107
B	0.39±0.31	1.23	0.218
SOIL	-0.83±0.35	-2.35	0.019
B x SOIL	0.61±0.44	1.39	0.165

385

386

387 **4. Discussion**

388 Different biotic and abiotic factors were found to affect the regeneration
 389 performance in our manipulation experiment.

390 Contrary to our expectations, *Q. robur* emergence was low in all treatments.
391 However, the short-term results of the restoration activities were to a great extent
392 influenced by rodent predation.

393 The summer of the study year (2015) was hotter and dryer than average (see
394 also Orth et al., 2016), and this probably reduced the soil moisture, whose
395 influence on acorn germination in *Quercus* species is well known (Löff and
396 Birkedal, 2009; Pérez-Ramos et al., 2013). A rainfall deficit, coupled with high air
397 temperatures, affected the microclimatic conditions in the top soil, and this led to
398 an extremely low water content and high temperatures, far from optimal values
399 for acorn germination and seedling growth.

400 The stressful environment determined by the higher temperatures and lower
401 precipitations in the summer months was also attested to by the high mortality
402 rate of planted seedlings, all of which presented symptoms of drought stress and
403 increased transplant shock (data not shown).

404 Summer drought, the frequency and length of which are predicted to increase in
405 Central Europe due to climate change (Orth et al., 2016; Trnka et al., 2016), can
406 exacerbate the harsh conditions faced by seedlings, particularly in areas
407 undergoing restoration activities. In these areas, its negative effects could
408 potentially be mitigated through microsite amelioration provided by shading
409 elements (Castro et al., 2002; Man and Greenway, 2011). Nurse shrubs and
410 natural or artificial shield objects can affect microsites anisotropically (Lingua et
411 al., 2008; Marzano et al., 2013), thus making the relative location of the seedling
412 crucial. In our manipulation experiment, soil conditions on the two sides of the
413 wooden board differed. Higher maximum temperatures, which lead to an increase

414 in the daily range, are commonly found on the sun-exposed side, as a result of
415 both a lack of shade and an increase in reflected solar radiation.

416 Artificial shield objects have proved important in enhancing microsite conditions
417 in harsh environments, protecting plants from wind, snow, and/or excessive heat
418 (Helgerson, 1990; Carlsson and Callaghan, 1991). Being non-living elements,
419 artificial objects can sometimes induce a net positive effect since they provide
420 benefits to seedlings without competing for resources (e.g. water, nutrients), in a
421 similar way to *in-situ* produced deadwood and woody debris (Castro et al., 2011;
422 Marzano et al. 2013).

423 In our treatments, the amended soil reached the highest daily mean and
424 maximum temperatures, as well as the widest temperature range, since organic
425 matter probably affected solar radiation adsorption and reradiation (Helgerson,
426 1990). The sites located on the southern side of the boards, which were those
427 that reached the highest diurnal temperatures during summer, had the widest
428 temperature range for both soil treatments. On non-amended sites, the
429 temperature on the northern side of the boards was always lower (even if not
430 significantly different from the southern side). However, it should be underlined
431 that the sensors were buried in the soil at a depth of 10 cm, and this probably led
432 to a buffering of the signal at ground level, where the effect of the nurse objects
433 might be higher.

434 The soil water content did not differ among the amended sites. Even though
435 zeolite could improve water retention (Xiubin and Zhanbin, 2001; Polat et al.,
436 2004), the amount applied in the area was calculated only considering soil CEC

437 amelioration and may have been insufficient to affect the soil water holding
438 capacity.

439 Conversely, in non-amended sites the board significantly enhanced the water
440 content in the soil shaded from the midday sun's rays, thus suggesting that in
441 harsh environments even small artificial objects are able to reduce an excess of
442 irradiance and thus influence soil moisture (Egerton et al., 2000), as well as the
443 suitability of a regeneration site.

444 Fabaceae shrubs have been found to facilitate tree regeneration by providing
445 enhanced microsite conditions, but this facilitation probably acts more at the
446 seedling survival stage than at the emergence level (Burrows et al., 2014). In
447 addition, newly emerged oak seedlings depend to a great extent on cotyledon
448 reserves, and are thus probably less influenced by the potential nursing effects
449 of neighboring shrubs (Pérez-Ramos et al., 2010).

450 In our sowing trial, the facilitation provided by the shrubs was not direct in the first
451 year, as a result of microsite enhancement, but was instead indirect, thus
452 protecting the acorns from predation. The presence of shrubs is usually
453 associated with improved microclimate and soil properties (Pugnaire et al., 2004;
454 Smit et al., 2008), as well as the protection of seedlings against herbivory (Smit
455 et al., 2006; Callaway, 2007). On the contrary, the risk of seed predation by
456 rodents is generally first increased by the sheltered conditions created under the
457 shrub (Callaway, 2007), potentially leading to a short-term disruption of the net
458 facilitation effect (Bruno et al., 2003). This complex interaction has still not been
459 exhaustively explored (Chaneton et al., 2010).

460 The crown architecture of our *C. scoparius* transplants was probably not
461 developed enough to create a fully sheltered environment for rodents; moreover,
462 since rodents detect seeds through odorants, i.e., volatile molecules from the
463 seed surface, it is possible that Scotch broom releases substances that mask the
464 smell of acorns buried in their proximity (Vander Wall, 2003). Scotch broom is
465 known to be an allelopathic shrub that produces a set of different alkaloid
466 compounds (Gresser et al., 1996; Grove et al., 2012). Further analyses should
467 be conducted to investigate whether these shrubs can effectively alter the feeding
468 behavior of rodents, as has already been shown for other plants (Curtis et al.,
469 2002; Fischer et al., 2013; Hansen et al., 2016).

470 Seed predation was high in the area in both winter and summer. The presence
471 of the drainage ditch, furrows, shield objects and shrubs could provide protected
472 sites and safe pathways for rodents, thus hiding them from predators. Seed
473 predation rates are usually significantly higher in more complex habitats (Gómez
474 et al., 2003; Madsen and Löf, 2005). Protected by vegetation, rodents can spend
475 more time in finding and removing acorns (Orrock et al, 2004, Pérez-Ramos et
476 al., 2008; Pérez-Ramos and Marañón, 2008; van Ginkel et al., 2013). We
477 therefore expected the acorn predation rate to be higher under shrubs or close to
478 wooden boards since these shelter elements can provide safer sites for foraging,
479 potentially increasing rodent activity (Perea et al., 2011). We also expected a
480 higher predation rate close to the furrows and drainage ditch surrounding the
481 area.

482 Summer acorn predation was instead lower under Scotch broom, thus
483 highlighting that the influence of nurse shrubs on predator feeding habits could

484 result from the interplay of several factors, not merely related to their cover and
485 the resulting sheltering effect. Finding shrub species that are able to both
486 enhance microsite conditions and limit acorn predation would be of great value
487 for forest restoration activities.

488 In winter (Dec-Mar), the distance from the drainage ditch played a key role in
489 determining the predation rate, but it was not inversely related as had been
490 hypothesized. In fact, the observed predation rate increased with distance. A
491 possible explanation for this is the presence of the fence along the highway (and
492 the drainage ditch) enclosing the experimental area. Fence poles provided the
493 only perching sites for rodent predators, given that there was no tall vegetation
494 on the site. The predation pressure of raptors on small mammal populations may
495 depend on the availability of perch sites (Wolff et al., 1999; Meunier et al., 2000).
496 Car and street lights could also have contributed to increasing the perception of
497 danger in the bordering area (Perea et al., 2011). The rodents thus perceived a
498 higher predation risk near the edge of the experimental site rather than in its
499 central part, and modified their feeding behavior accordingly (Diaz et al., 2005).
500 This spatial relationship disappeared in late spring and summer, when tall
501 herbaceous vegetation covered the entire area homogeneously, thus making
502 rodent movements safer over the whole site.

503 Restoring degraded sites to a lowland oak forest through direct seeding requires
504 dealing with the intensive predation pressure that acorns are usually subjected
505 to. With so many animals relying on acorns as a main part of their diet, restoration
506 projects that wish to apply seed sowing must adopt adequate strategies for the
507 direct or indirect protection of acorns (Madsen and Löf, 2005; Leverkus et al.,

508 2015; Torroba-Balmori et al., 2015). Seed protection should not greatly impinge
509 on the total cost of the restoration effort. Cost-effective restoration in highly
510 disturbed areas (e.g. after road, highway or railway construction) is currently a
511 challenge for ecologists and practitioners (Cuperus et al., 1999; Corbin and Holl,
512 2012; Löff et al., 2012; Meli et al., 2014; Stark et al., 2015). Restoring degraded
513 areas, particularly where disturbed site conditions might be made worse by a
514 harsh environment and climate conditions, may require more complex
515 approaches, thus making it necessary to understand the various interactions
516 between direct and indirect facilitation mechanisms, competition, predation and
517 herbivory.

518

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