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Short communication

Habitat complexity and individual acorn protectors enhance the post-fire restoration of oak forests via seed sowing

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ABSTRACT

Oak reforestation via direct sowing has advantages over planting for economic and plant-morphological reasons, but the risk of high acorn predation usually dissuades land managers from using this method. In a previous study we hypothesised that overcoming acorn predation would require both large-scale solutions to reduce predation by large mammals – which we had effectively obtained through ecosystem management leading to greater habitat complexity – and small-scale protection to tackle predation by small mammals – which we had been unsuccessful to encounter. In this study we aimed to test this hypothesis under the same management areas but with a new acorn-scale protective device named seed shelter. We carried out an acorn predation experiment in Sierra Nevada (S Spain), in a burnt area with three replicates of each of two post-fire management treatments: non-intervention (NI), with high habitat complexity due to the abundance of lying burnt trees, and salvage logging (SL), with low habitat complexity due to the previous felling and piling of the tree trunks and chopping of the branches. In each replicate we sowed 50 acorns with seed shelter and 50 acorns without (N = 600 acorns). After 129 days, predation by rodents averaged 17% for control acorns, while the seed shelter reduced this to nil. Predation by boars (17.5% overall) was not affected by the seed shelter but was reduced to one-sixth in the NI treatment (5% vs 30% in SL), so we obtained the lowest overall predation rates in the combined NI + seed shelter treatment (5%). We thus corroborated our hypothesis that combining large-scale management with an acorn-scale protection can greatly increase the success of sowing. We expect these outcomes to increase the effectiveness of direct sowing and to raise the share of this practice in reforestation, especially for species that develop best with direct sowing such as oaks.

1. Introduction

Millions of hectares of land are reforested every year to counteract deforestation and the degradation of natural ecosystems. Oaks (*Quercus spp.*) are frequently used for reforestation (e.g., EEC regulation no. 2080/92), as they are widely distributed across the Holarctic. Oaks provide numerous ecosystem services (Marañón et al., 2012), but they are encountering population decline and difficulties in their regeneration in many parts of their distribution range (Dey et al., 2008; Pulido and Díaz, 2005; Thomas et al., 2002). Much hope, effort, and money are thus placed into reforestation with oaks, yet stories of low success are very common (Dey et al., 2008; Navarro Cerrillo et al., 2005; Rey Benayas et al., 2005).

Seedling planting and seed sowing are the two possibilities for reforestation with oaks. While planting oaks has the advantage of using already-established seedlings, it often renders high seedling mortality and/or low-quality plants (Rey Benayas et al., 2005 Zadworny et al., 2014), as nursery-grown seedlings often present root architectures that are suboptimal for field conditions (Tsakaldimi et al., 2009). In contrast, sowing has the advantage of producing seedlings that are better acclimated to local conditions, besides having about one-half to one-third of the economic cost of planting (Bullard et al., 1992; King and Keeland, 1999; Madsen and Löf, 2005). However, sowing is usually opted out because of the frequent high levels of acorn predation and the uncertainty that results from oscillations in predator populations (Dey et al., 2008; Madsen and Löf, 2005). Finding a way to reduce acorn predation could thus increase the success and reliability of acorn sowing and of forestation practice in general.

Reducing seed predation can be achieved by taking advantage of habitat features that affect the activity of seed predators. For example, areas covered by shrubs or coarse woody debris can

Abbreviations: BWM, burnt-wood management treatment(s); SL, salvage logging treatment; NI, non-intervention treatment.

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represent a physical obstacle for foraging by ungulates (Ripple and Larsen, 2001), although they can also provide food and shelter for rodents (Gómez, 2004). Due to such contrasting effects of habitat on different predator guilds there is hardly any optimal solution to increase acorn survival to predation. In a previous study in an area where the management of wood after a forest fire in Sierra Nevada (S Spain) generated areas with low or high habitat complexity (Leverkus et al., 2013) we concluded that combining high habitat complexity at a large scale (which reduced foraging by wild boars; Leverkus et al., 2013; Puerta-Piñero et al., 2010) with some small-scale protection from rodents might effectively increase acorn survival. However, such small-scale protection was yet to be discovered – we tested deeper burial and a chemical repellent but without much success (Leverkus et al., 2013).

Devices designed to represent a barrier for seed predators are usually ineffective, large, expensive, difficult to handle, or a combination of those (Dey et al., 2008; Madsen and Löf, 2005; Pemán et al., 2010; Reque and Martin, 2015). In this short communication we test the effectiveness of a new, simple device – named seed shelter (Castro et al., 2015) – designed to protect individual acorns from small predators in areas where different management schemes have led to greater or lower habitat complexity due to the presence or absence of deadwood. For this we performed an acorn predation experiment in the above-mentioned post-fire habitats. Our working hypotheses were that: (i) the seed shelter device would represent a physical barrier that would reduce acorn predation by rodents, and (ii) the use of the seed shelter in areas with greater habitat complexity would yield the greatest acorn survival due to the cumulative effect of the seed shelter on reducing predation by rodents and of habitat complexity on reducing foraging by ungulates (wild boars). Overall, we expect to find a way to turn acorn sowing into an effective and reliable method to produce high-quality oak seedlings.

2. Materials and Methods

2.1. Study site

This study was carried out in the Sierra Nevada National Park (S Spain), in an area of the Lanjarón municipality where a fire burned about 1300 ha of pine afforestations in September 2005. The area has Mediterranean climate, with hot, dry summers and mild, wet winters. Holm oak forests (*Quercus ilex* subsp. *ballota* (Desf.) Samp.) are the main climax vegetation in the area (Valle, 2003). The main acorn predators are wild boars (*Sus scrofa*) and rodents like *Apodemus sylvaticus* and *Mus spretus* (Gómez and Hódar, 2008; Puerta-Piñero et al., 2010).

In spring 2006, an experimental site was established in a burnt *Pinus pinaster* and *P. nigra* afforestation at 1477 m a.s.l. to test the effects of burnt-wood management on different processes related to ecosystem restoration (37°57′ N, 3°29′ W; see supplementary kml file). This site included three replicates of each of two burnt-wood management (BWM) treatments, which had an area of 2.0 ± 0.2 ha (Leverkus et al., 2012). The treatments were: (a) salvage logging (SL), where the burnt tree trunks were felled, separated from their main branches and piled, and the remaining woody debris was mechanically masticated; (b) non-intervention (NI), where no action was taken and all the trees had fallen by 2010. The physical structure of the SL treatment was an open area easily accessible by humans, while the NI treatment was covered in branches and trunks that complicated movement (Leverkus et al., 2013; Puerta-Piñero et al., 2010). For further details on the study area and the experimental site, see Castro et al. (2012) and Leverkus et al. (2012, 2013).

2.2. Acorn predation experiment

In January 2014 we began an experiment to test the effects of habitat complexity and individual acorn protection on seed predation. For this, we established 50 sowing points per BWM replicate (6 replicates), and in each point we sowed two *Q. ilex* acorns 30 cm away from each other: one with and one without seed shelter (600 acorns in total). The seed shelter (patent #201331441, University of Granada; Castro et al., 2015) consists of two identical truncated cones or pyramids joined at their larger opening and filled with substrate. The rationale is that a large seed could be held in the wide middle of the seed shelter and that the small upper and lower openings would be large enough to allow the stem and the roots to grow out, yet small enough to prevent the entrance of a rodent. For the present study we used prototypes made of polypropylene (Fig. 1).

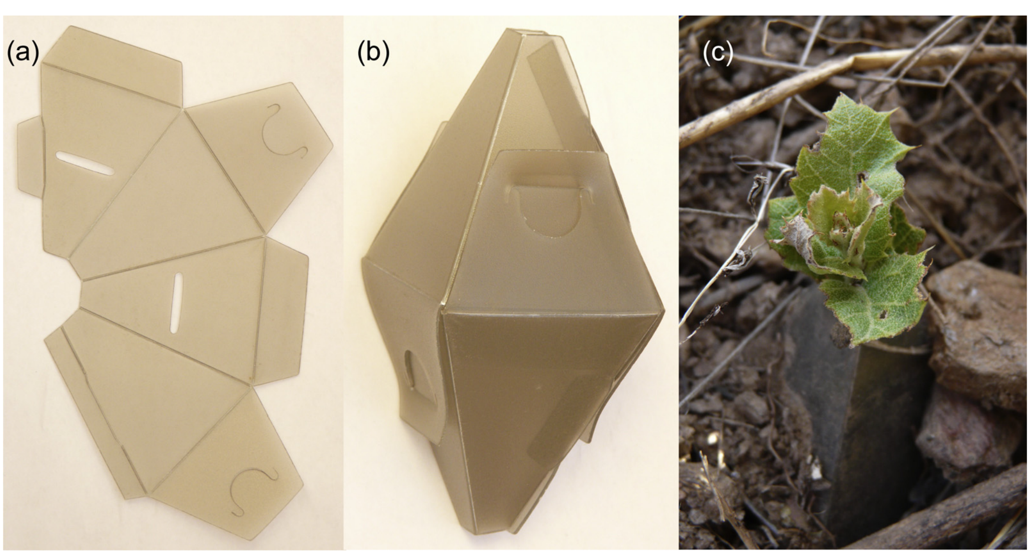

Fig. 1. Photos of the seed shelter prototype used for this study. Two identical flat shapes, punched out of 0.8 mm polypropylene sheets (a), were folded together to create truncated pyramids, which were then assembled with simple folds and slots to create the complete seed shelter (b). Before joining the two parts, they were filled with substrate [1/3 sand and 2/3 peat (Kekkilä Garden Brown 025 W)] and an acorn was placed in the middle. The entire device was then placed belowground in the field with its upper opening at ground level (c), which left the acorn within at 5–6 cm depth. The acorns without seed shelter were placed at the same depth.

We visually inspected each sowing point after 8, 25, 81, and 129 days to identify whether acorns were predated or not and, if predated, to establish the guild of the predator (as described in Leverkus et al., 2013). Acorns with seed shelters that were unburied by wild boars but not opened (i.e., where the acorns were not consumed) were marked as predated because they would likely not produce viable seedlings anymore. During the last revision we dug up all the points to be certain of the fate of all acorns, to record the germination of non-predated acorns, and to remove the devices from the field. We assumed that removed acorns were depredated because studies in the area found that >98% of the acorns handled by the main secondary acorn dispersers are consumed (Gómez et al., 2008).

2.3. Habitat complexity

We sampled the complexity of the habitat in both BWM treatments with linear transects. In each BWM replicate we randomly placed four transects of 25 m and established sampling points one metre to each side at every metre of the transect. At each point we defined five height classes (1–10, 11–25, 26–50, 51–100, 101–200 cm) and estimated the percentage of these ranges contacted by live vegetation or woody debris.

2.4. Statistical analyses

For all analyses we used R version 2.15.0 (R Development Core Team 2012).

To analyse habitat structure relative to BWM treatment, we fitted hierarchical ANOVA models for each cover type (plant or wood) and height class separately. We specified transects within the replicates as the random effects. To reduce the percentage of zeros in the data, we averaged the values of the left and right side of each point of the transects. For each transect we also calculated the percentage of points with cover of bare soil, and we used ANOVA to assess the possible effect of BWM treatment. Cover data were arcsine, square root transformed previous to analysis (Crawley, 2013).

To test the effects of *BWM* and *Seed shelter* on final acorn predation, we fitted a generalized linear mixed model (glmm) with binomial errors, using the lmer function from the lme4 package (Bates et al., 2012). In these models we specified the spatial structure of the experiment (sowing points located within BWM replicates) as random effects, and *BWM*, *Seed shelter*, and the *BWM* x *Seed shelter* interaction as fixed effects. To analyse predation by the individual predator guilds (boars or rodents) we considered the acorns predated by the other guild as “non-predated” and repeated the analysis. For computational reasons we had to simplify the specification of the experiment’s spatial structure with only BWM replicate as a random effect in the predator-specific models. Finally, to test the effect of *BWM* and *Seed shelter* on the germination of non-predated acorns, we fitted a glmm with binomial errors, considering the replicate of BWM as a random effect.

We tested for the significance of the terms in the mixed models through likelihood ratio tests, with model simplification (Crawley, 2013).

3. Results and discussion

3.1. Habitat structure

The cover of live plants did not significantly differ among treatments, although there was a trend of greater cover in NI for all height classes (Table 1). The cover of woody debris was significantly greater in NI than in SL in all height classes above 10 cm (Table 1). In contrast, the cover of bare soil was greater in SL (34.3%) than in NI (21.2%) but not significantly so ($F_{1,22}$ = 1.84, P = 0.19). The lying logs and branches thus created a more complex habitat structure in the NI treatment than in SL, as found in previous sampling (Leverkus et al., 2013), and this may influence the foraging behaviour of acorn predators (Leverkus et al., 2013; Puerta-Piñero et al., 2010).

3.2. Acorn predation

Acorn predation averaged 26% across all the sown acorns, an extremely low value compared to other studies in the same area in previous years, in which overall predation reached up to 90% (Leverkus et al., 2013; Puerta-Piñero et al., 2010). In particular, predation by rodents was surprisingly low (17% for acorns without seed shelters) compared to those previous studies, when rodents generally consumed >80% of the acorns. Wild boars, on the other hand, consumed 17.5% of the acorns, thus more than in previous years when this value ranged from negligible to about 10% (Leverkus et al., 2013; Puerta-Piñero et al., 2010). These results highlight the strong fluctuations that can occur in the populations of acorn predators, especially rodents (Ostfeld and Keesing, 2000). Although it could be tempting to overemphasize this case and others as general successes of sowing due to high acorn survival, such events usually come at times of low rodent population densities (Dey et al., 2008), and the unpredictability that surrounds them turns sowing into a high-risk activity usually avoided by land managers.

Rodents consumed more acorns in the NI treatment (22.0%) than in SL (12.0%; χ^2 = 5.06, P > 0.01; values and analysis for acorns without seed shelters) and, contrarily, boars consumed more acorns in the SL treatment (30%) than in NI (5%; χ^2 = 4.97, P > 0.05; Fig. 2). As previously found (Leverkus et al., 2013; Puerta-Piñero et al., 2010), the greater habitat complexity generated by the lying logs and branches in the non-intervention treatment had opposing effects on the two main predator guilds. Large mammals, in this case wild boars, likely found the areas without post-fire intervention difficult to transit, as the fallen trees acted as physical barriers

Table 1
Effects of burnt-wood management on habitat complexity at the different height classes.

Height (cm)	Live Plants				Wood			
	$F_{1,22}$	P	Mean NI	Mean SL	$F_{1,22}$	P	Mean NI	Mean SL
1–10	1.03	0.32	28.2 ± 1.9	20.4 ± 1.6	1.94	0.18	9.7 ± 1.1	12.4 ± 1.4
11–25	2.11	0.16	19.3 ± 1.6	12.3 ± 1.3	9.43	<0.01	5.5 ± 0.7	3.6 ± 0.7
26–50	1.43	0.24	15.4 ± 1.5	9.6 ± 1.2	86.57	<0.001	2.9 ± 0.3	0.3 ± 0.1
51–100	2.71	0.11	8.9 ± 1.0	4.7 ± 0.7	26.31	<0.001	1.3 ± 0.2	0.0 ± 0.0
101–200	0.51	0.48	1.8 ± 0.4	1.3 ± 0.3			0.4 ± 0.1	0.0 ± 0.0

Habitat complexity was measured as the percentage of the height range covered by either live plants or wood averaged across transects. Values indicate the mean ± 1 SE of the mean for all transects. Due to the lack of points contacting wood at the highest class in the SL treatment, no statistical test was performed for this treatment comparison. Treatments were SL = Salvage Logging; NI = Non-Intervention.

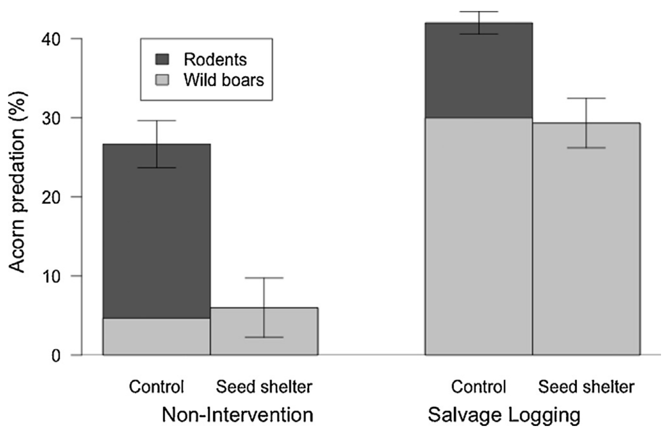

Fig. 2. Acorn predation by the main predator guilds in the experiment as affected by burnt-wood management and the use of the seed shelter. Error bars indicate ± 1 SE of the mean of total acorn predation between the three replicates.

to their movement (Puerta-Piñero et al., 2010). And, on the other hand, smaller animals like rodents may have found more resources and protection below the branches, resulting in greater rodent populations and/or activity (Herrera, 1995; Muñoz and Bonal, 2007). What arises from the present study is that the net effect of the management of habitat complexity on acorn consumption greatly depends on the relative abundance and activity of these predator guilds. In the present study, with low rodent activity, overall predation was much lower in the high-complexity NI treatment (16%) than in SL (36%; Fig. 2) due to the positive effect of SL on predation by boars, while in previous years, with much greater rodent activity (Leverkus et al., 2013), predation was always greater in NI (up to 99%) than in SL, this being due to the positive effect of NI on predation by rodents. Thus, habitat complexity alone cannot be used to predict whether greater or smaller overall levels of acorn consumption will occur because this will also depend on the relative abundance of the different predator guilds.

Not a single acorn within a seed shelter was consumed by a rodent, suggesting that we might have come across an effective solution to the long-lasting problem of predation of sown seeds by small mammal predators (Bullard et al., 1992; Dey et al., 2008; Herrera, 1995; Leverkus et al., 2013; Puerta-Piñero et al., 2010; Pulido and Díaz, 2005). On the other hand, wild boars consumed acorns irrespectively of the seed shelters ($\chi^2 = 0.01$, $P = 0.90$; Fig. 2), as they were able to dig up the devices easily and even break them and consume the acorns within them in many cases. The use of the seed shelters consequently does not entirely solve the problem of acorn predation, as wild boars and other wild and domestic ungulates can cause great acorn losses too (Gómez and Hódar, 2008; McCreary, 2009; Muñoz and Bonal, 2007). A potential solution arises from the significant interaction effect of burnt-wood management and the use of the seed shelter on overall predation ($\chi^2 = 7.90$, $P < 0.01$): the device had a greater proportional effect in NI (where the relative effect of rodents was also greatest and the seed shelter reduced predation by 77%) than in SL (where boars had the greatest relative effect and the seed shelter reduced predation by only 30%). As a result, only 5% of acorns in NI with a seed shelter were consumed (Fig. 2). The efficacy of the seed shelters may thus be greatest in situations where low predation is expected by large animals. In post-fire restoration, a way to achieve this, as shown by our results, is by favouring ecosystem management that leads to greater habitat complexity – i.e., with little or no intervention after the fire –, with the additional advantage that the deadwood remaining after such management may improve microclimatic conditions and provide nutrients that altogether enhance seedling establishment, survival and growth (Leverkus et al., 2012; Marañón-Jiménez et al., 2013; Marzano et al., 2013).

3.3. Germination

Significantly more of the non-predated acorns with seed shelters germinated (82%) than without seed shelters (51%; $\chi^2 = 34.42$, $P > 0.001$), while BWM had no significant effect on germination. We believe that the positive effect of the device on germination could be related to the quality of the substrate included inside the device, or to potentially higher moisture retention or enhanced microclimatic conditions inside the device (Castro et al., 2015). Thus, the seed shelter seems to provide an additional advantage for reforestation although further research on the underlying mechanisms is necessary.

4. Conclusions

In this study the seed shelter, a physical device, proved effective to prevent seed predation by rodents, while it did not reduce predation by wild boars. Although predation by rodents was low during the study compared to other years, our results confirm that the use of a device such as the one tested here – which may eliminate predation by small rodents – in combination with a complex habitat structure – which can greatly reduce predation by larger mammals – could lead to an effective use of direct sowing for reforestation. The seed shelter has high potential for reforestation with many large-seeded species, for which post-sowing seed predation rates are usually high and whose production under nursery conditions may impose limitations for seedling development. These include many late-successional species in forests of different parts of the world, such as the Fagaceae in the Holarctic. Although more research into the use of biodegradable materials and the cost-effectiveness of this method as compared to planting are needed, our results strongly support the usefulness of individual seed protectors for oak forest restoration via direct acorn sowing provided that features of the landscape reduce the access of larger animals.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecoleng.2015.06.033.

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