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Management of burnt wood after fire affects post-dispersal acorn predation

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ABSTRACT

The management of burnt wood after a fire may affect seed predation by vertebrates due to the change produced in habitat structure. We analyze the effect of burnt wood management on post-dispersal seed predation in the Holm oak. Three plots were established in a burnt forest, with three treatments per plot: (1) non-intervention (NI, all trees left standing), (2) "partial cut plus lopping" (PCL, felling 90% of trees, cutting their main branches, leaving all the biomass *in situ*), and (3) "salvage logging" (SL, felling the logs for their removal and masticating the woody debris). Acorns were buried to mimic dispersal by jays or rodents two and three years after fire, with two trials per year (7200 monitored acorns), and the predation rate was evaluated until the time of seedling emergence. The spatial patterns of acorn predation were assessed by computing a transformed-Ripley's *K* function and Moran's *I* correlograms. There was a large spatial and temporal variability in acorn predation, with differences among trials, plots, and replicates within treatments and plots. Overall, PCL showed the lowest predation values (83.0% versus 87.4 in NI and 88.0 in SL). Predator species (mice versus wild boar) also differed among treatments, wild boar having a negligible effect in PCL, presumably due to the physical barrier of felled logs and branches. The results support that: (1) salvage logging offers no advantage against predators and (2) that post-fire burnt wood management alters the guild of acorn predators and may reshape the pattern of seedling establishment.

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1. Introduction

Seed predation can be a key process for natural population dynamics as well as for applied restoration purposes. Post-dispersal seed predation may reshape the spatial pattern of seedling emergence and thus have strong influence on the regeneration dynamics of natural systems (Rey and Alcántara, 2000; Rey et al., 2002; Forget et al., 2005; Gómez-Aparicio, 2008). In the last decades, many studies have shown that predation may vary among predator agents (García et al., 2005) that differently predate throughout different elements of the landscape (García et al., 2005; García-Castaño et al., 2006; Muñoz and Bonal, 2007; Gómez-Aparicio, 2008). Therefore, in many cases seed predation can determine the final distribution of plants going from the smaller to the larger spatio-temporal scales depending on the case.

Seed predation rate is strongly determined by habitat characteristics. Predator activity can be conditioned by the ability or impediment to forage under different circumstances (Forget et al., 2005), the vicinity of the territories of each species (García-Castaño et al., 2006; Muñoz and Bonal, 2007), or the risk of predation for

seed predators while foraging (Muñoz et al., 2009), among other major factors. It is usually assumed that habitats with scant overstorey complexity, such as open areas or grasslands, will represent a greater risk for seed predators than habitats with a woody overstorey (García-Castaño et al., 2006; Muñoz and Bonal, 2007; Pons and Pausas, 2007). Thus, seed predators are expected to spend less time in open areas than in sites with more refuge, such as dense forest (Muñoz and Bonal, 2007). On the other hand, the amount of stones, debris, and remaining wood in some areas can impede rooting by big predators (Massei et al., 1997; Meriggi and Sacchi, 2000; Gómez and Hódar, 2008). Consequently, less seed predation by ungulates should be expected in dense understory areas. Furthermore, species differ in traits such as body size and home-range, which determine the use of the landscape where they live (Wiens, 2000). Larger predator species such as ungulates are expected to forage at broader spatio-temporal scales than smaller species such as rodents. This species-specific landscape perception within a common area can also lead to differences in seed predation in both spatial and temporal dimensions (García-Castaño et al., 2006; García and Chacoff, 2007; Matías et al., 2009).

Fires provoke a strong alteration of habitat structure and impact resource availability, consequently affecting the abundance of seed predators (Torre and Díaz, 2004; Zwolak, 2009). In addition, burnt wood is usually managed after fires, provoking an additional change in habitat characteristics that can alter the facility of animals to move and forage throughout the burnt area (Zwolak, 2009). A com-

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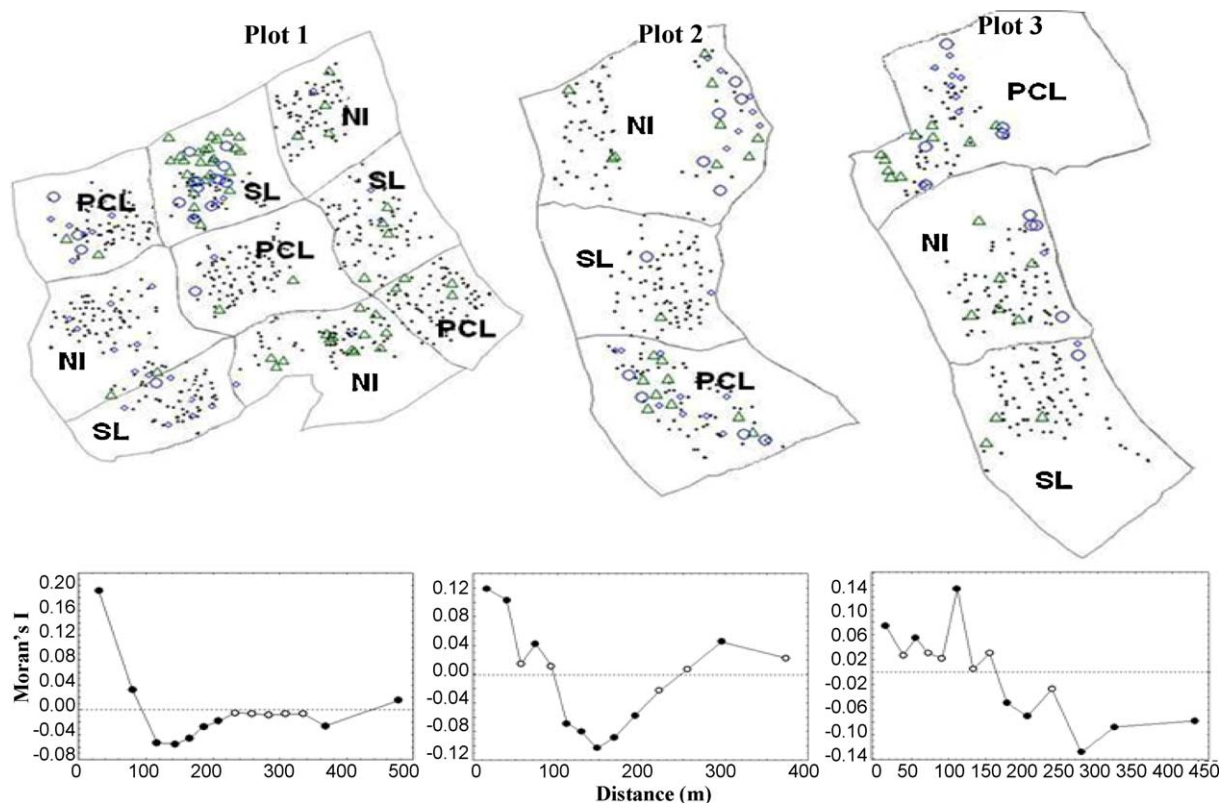


Fig. 1. Spatial patterns of post-dispersal acorn predation. The figure shows the number of predated acorns at each supply point (0–3). Solid black dots correspond to supply points where the three acorns were predated; blue circles to those where one acorn (big circles) or two acorns (small circles) were predated; triangles correspond to supply points where no acorn was predated. At the bottom, the figure shows the auto-correlogram screening the Moran's I in each plot. Solid-black circles correspond to significant distance classes.

mon practice after fires in forested areas worldwide involves the felling and removal of burnt trunks, often eliminating the remaining woody debris (branches, logs, and snags) by chopping, mastication, etc. (Beschta et al., 2004; Lindenmayer and Noss, 2006; Castro et al., 2010a), a practice that is usually termed salvage logging (McIver and Starr, 2000). As a result, the post-fire landscape undergoes a strong transformation driven by a simplification of the habitat characteristics in relation to the situation previous to salvage logging. Despite the common implementation of salvage logging after fires, there is increasing evidence that this practice may have a negative impact on the ecosystem, affecting a wide array of aspects such as the regeneration of plant and animal communities, diversity, water flow dynamics, or nutrient cycling (Beschta et al., 2004; Karr et al., 2004; Donato et al., 2006; Lindenmayer and Noss, 2006; Castro et al., 2010a,b). However, we are not aware of any study on the effect of burnt wood management on the rate of post-dispersal seed predation of tree species with the potential to colonize the burnt area. This is a key question to determine desirable post-fire forest restoration plans that would prompt forest recovery either by natural regeneration or by human intervention via seed sowing.

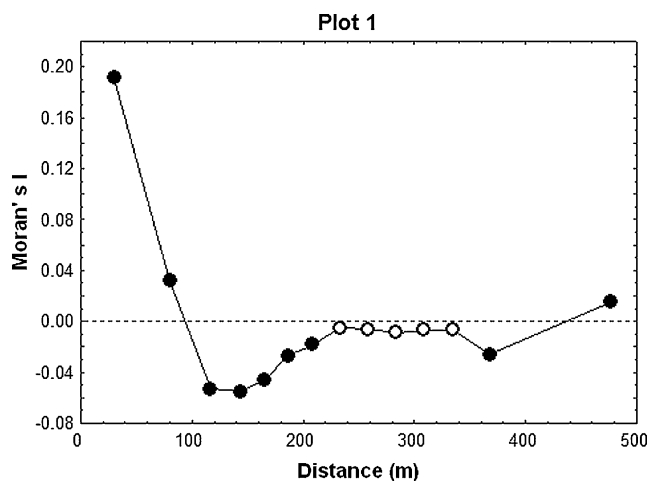
In this study, we analyze the effect of different post-fire burnt wood management on post-dispersal seed predation of the Holm oak (*Quercus ilex* L. subsp. *ballota* (Desf.) Samp.), a widely distributed tree species in the Mediterranean basin. In September 2005, the "Lanjarón" fire burned ca. 3500 ha in the Sierra Nevada National and Natural Park (southern Spain), including around 1300 ha of pine stands planted in the 1960s, mostly in the distribution area of the Holm oak. We established three experimental treatments that differed in the degree of burnt wood management, ranging from the conventional salvage logging to non-intervention. We hypothesize that this will influence the post-dispersal rates of seed predation, as the treatments contrast sharply in habitat

characteristics, ranging from a landscape without tree overstory in salvaged areas to a habitat that still has an overstory of branches and logs in the other treatments, with the potential to affect both seed predators as well as their own predators' activity. The experiments were set up in two consecutive years and at two different times of year (beginning and end of the dispersal period), and a spatial analysis was performed for one of the years. Three questions were formulated: (1) Are there any differences among post-fire burnt wood management in the rates of seed encounter and predation? (2) Are there any differences among predator agents in seed predation in relation to the treatments? and (3) Are there spatio-temporal differences in post-dispersal seed predation?

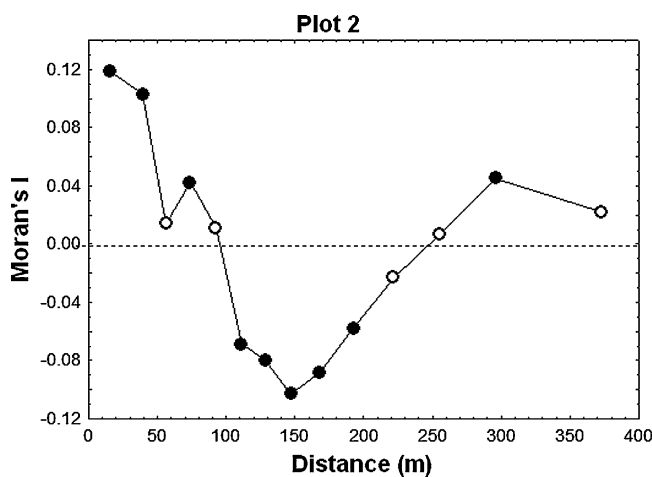
2. Methods

2.1. Study area and experimental design

The study site is located in Sierra Nevada Natural and National Park (SE Spain), where in September 2005 the Lanjarón fire burned ca. 1300 ha of pine reforestations with Trees 35–45 years old, depending on the stand. Three plots of ~25 ha each were established after the fire across an elevational gradient (Fig. 1). All plots were similar in terms of orientation (SW) and slope ($30.1 \pm 1.0\%$; mean \pm SE). Plot 1 was located at 1477 m a.s.l. (UTM positions x, y: 456070; 4089811), Plot 2 at 1698 m (UTM: 455449; 4091728), and Plot 3 at 2053 m (UTM: 457244; 4091551; elevation and position measured at the center of the plot). The pine species present in each plot differed according to their ecological requirements along this elevation/moisture gradient. The cluster pine (*Pinus pinaster*) and the black pine (*P. nigra*) dominated in Plot 1, black pine in Plot 2, and Scots pine (*P. sylvestris*) in Plot 3. All these species are native in the region, although they were extensively planted in the area



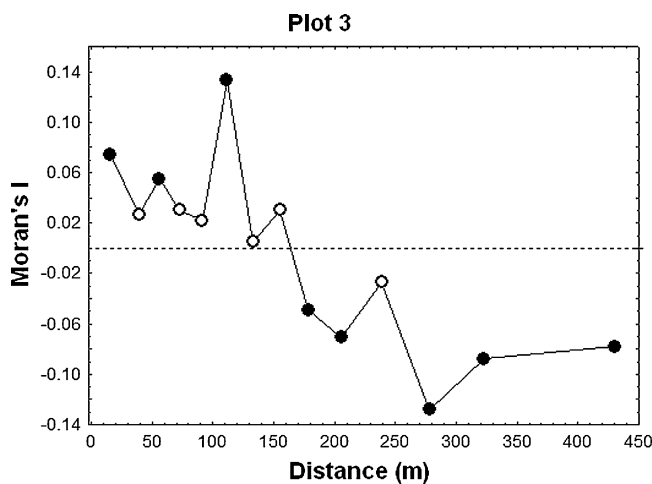
Plot 1.



Plot 2.

for soil protection and wood production. The climate in the area is Mediterranean, with hot, dry summers and wet, mild winters. Mean annual rainfall recorded at a meteorological station next to plot number 1 was 4871 per year (1988–2007 period).

The area surrounding the burnt pine stands is dominated by shrublands with scattered individuals and small clusters of mature



Plot 3.

Holm oak trees. These oaks are acting as sources of acorns, which are recolonizing the burnt area (Castro et al., unpublished data). Acorns are primarily dispersed from October to December, mainly by the European jay (Gómez, 2003). Post-dispersal seed predation is mostly caused by small rodents such as *Apodemus sylvaticus* (Gómez et al., 2008) and *Mus spretus* (Muñoz and Bonal, 2007), and by large ungulates, mainly represented in the area by wild boars, *Sus scrofa* (Gómez and Hódar, 2008). Ongoing acorns then emerge as natural seedlings through spring of the next year (Gómez, 2004; Pulido and Díaz, 2005; Puerta-Piñero et al., 2007).

Within each plot, three replicates of the following management of burnt wood (treatments, hereafter) were implemented following a random spatial distribution:

- (1) "Non-Intervention" (NI), leaving all of the burnt trees standing.
- (2) "Partial Cut plus Lopping" (PCL), a treatment where $\approx 90\%$ of the burnt trees were cut and felled, with the main branches also lopped off, but leaving all the cut biomass *in situ* on the ground.
- (3) "Salvage Logging" (SL), trees were cut and the trunks cleaned of branches with the use of chainsaws. Trunks were manually piled (groups of 10–15) and the woody debris was masticated using a tractor with a mechanical masticator. It was planned to extract the trunks with a log forwarder, but this step was eventually canceled by the Forest Service due to difficulties in operating machinery within the spatial arrangement of experimental replicates.

The treatments therefore differed in the degree of management, NI < PCL < SL. The experimental plots and treatments were implemented by the local Forest Service between 21 April 2006 and 10 May 2006 (ca. 7 months after the fire). Herbaceous vegetation dominated the understory during the years of study, with $74.0\% \pm 1.5$ of cover in treatment NI, 72.3 ± 1.6 in PCL, and 69.3 ± 1.6 in SL (mean \pm 1 SE values for the three plots, data sampled in eight $25\text{ m} \times 2\text{ m}$ transects per replicate of each treatment in spring 2007; Castro et al., unpublished data). For this study we used the three replicates per treatment in Plot 1, and one replicate per treatment in Plots 2 and 3 (Fig. 1). Mean size of experimental replicates is 2.0 ± 0.2 ha for Plot 1, 2.8 ± 0.4 for Plot 2, and 3.4 ± 0.3 for Plot 3.

2.2. Acorn predation experiment

The seed predation experiments were set up in years 2007 and 2008 (2007 and 2008 experiments, hereafter). Acorns were buried at 1–2 cm in depth mimicking primary biotic dispersal by jays or rodents (Gómez, 2003; Muñoz and Bonal, 2007; Gómez et al., 2008). Two experimental trials were performed per year, the first with acorn burial at the beginning of the dispersal period (end of October) and the second with acorn burial at the end of the dispersal period (end of December). For each trial, we established 40 sowing points per treatment and replicate in each plot (Fig. 1). At each sowing point we placed 3 acorns separated ca. 10 cm apart, forming an equilateral triangle. This made a total of $40\text{ points} \times 3\text{ acorns} \times 9\text{ replicates} (=1080)$ buried acorns per trial for Plot 1, and $40 \times 3 \times 3\text{ replicates} (360)$ acorns for Plots 2 and 3 in each trial (1800 monitored acorns per year and trial; 7200 monitored acorns in the whole experiment). Acorns were handled with latex gloves to avoid human-odor traces after sowing (Vander Wall, 1990). We placed a little wooden stick next to each sowing point to ensure finding the acorns later, and attached a colored tag far enough to preclude possible visual identification by seed predators (Vander Wall et al., 2005). In 2009, the UTM coordinates of each sowing point were also recorded (Fig. 1). Before sowing, seeds were floated in water to separate viable seeds from parasitized ones (mainly by curculionid weevils; Puerta-Piñero et al., 2006). The final fate of the

acorns (Predated versus Intact) was recorded until the moment of seedling emergence (spring of the next year). Because prior studies demonstrated that >98% of the acorns handled by rodents are finally predated, and that there is no secondary caching by the main acorn dispersal species in the area (Gómez et al., 2008), we considered removed acorns as having been predated. Whenever possible, predator identity was also identified (wild boars versus rodents). Differences between predators were easily recognized as rodents produce small and clean holes for each buried acorn while boars tend to disturb a larger area due to intense rooting (Puerta-Piñero, in press). In the 2007 experiment, the fate of the acorns was recorded at different intervals since the experiment setting in order to track the speed and rate of seed predation through time. Trial 1 was revisited after 10, 25, 45, 75 and 150 days, while trial 2 after 7, 20, and 105 days. Seed-predation rate was high from the first samplings and reached an asymptote at the end of the experiment in the two trials (Appendix A). Thus, we considered seed predation at the moment of seedling emergence (ca. 5 months after natural seed dispersal and experimental set-up) to be a definitive value for each year. For the 2008 experiment, a single sampling of acorn fate was performed at the end of the experiment.

2.3. Statistical and spatial analyses

Probabilities of acorn predation were analyzed using (1) *Acorn encounter* and (2) *Acorn predation*. *Acorn encounter* was defined as the probability of at least one acorn being removed per supply point, while *Acorn predation* was defined as the proportion of acorns removed once a supply point was found (Hulme, 1998; Puerta-Piñero, in press). Due to the complexity of the model generated with all the factors simultaneously (up to six independent factors, including Replicate nested within plot, with the subsequent decrease in degrees of freedom and stability of the models), we decided to split the full model in order to address and interpret the effect of the main factors on acorn predation. This ensured a better biological comprehension of the results, as well as stable variance-covariance matrixes for these models. First, the effect of Replicate was tested with a spatial analysis (see below), and this factor was not considered for subsequent analyses. Second, the effect of Trial was analyzed independently for each year. Third, the effect of predator Identity (mice versus wild boar) was analyzed using Treatment and Identity as explanatory factors for each year separately. Finally, we constructed a model to determine the effect of plot, Treatment, Year, and the interaction of Treatment with the other factors. We used Generalized Linear Models (GLM) with a binomial response and logit as link function for acorn encounter, and normal and identity link function for acorn predation (Quinn and Keough, 2002).

The spatial pattern of acorn predation was analyzed for the 2008 experiment. For this, we first determined the Cartesian coordinates of each sowing point within each plot using the UTM's (Appendix B). Then, each sowing point was classified by acorn encounter in two categories (found/not found). We joined the encounter information to the coordinates of each supply point. Afterwards, we explored the spatial patterns of acorn encounter within each plot by computing a transformation of the Ripley's K function ($K(d)$) using an edge border correction (Ripley, 1981; Fortin and Dale, 2005), following the equation:

$$L(d) = \sqrt{\frac{K(d)}{\pi}}$$

where d is the distance between any two sowing points of the sample. We then compared the observed distribution at each plot to a random process (null model) with the same area and number of points (H_0 : complete spatial randomness, CSR) to see whether the

spatial pattern of acorn encounter followed a random, clumped, or homogeneous distribution (Fortin and Dale, 2005). Rejection limits were estimated as the envelopes of the simulation, and tests of significance were estimated by a Monte Carlo procedure using 500 permutations (Fortin and Dale, 2005; Rangel et al., 2006). If the observed distribution was above the envelopes, the distribution was considered as clumped, within the envelopes as random, and below the envelopes as homogeneous (Ripley, 1981). To check for autocorrelation among sowing points in acorn predation, we computed a Moran's I correlogram for each plot using the UTM and the number of predated acorns of each sowing point (Rangel et al., 2006). For each computation, we considered equal numbers of distance class pairs, 14 distance classes and a lag distance of 60 m in Plot 1, and 30 m in Plots 2 and 3 (differences in lag distances due to different sampling area; Fig. 1). Significance of each distance class was tested using 500 Monte Carlo permutations (Rangel et al., 2006).

The spatial analysis was performed using the Spatstat 1.8-6 package under R 2.8.0 (Baddeley and Turner, 2005; R Development Core Team, 2007) and SAM 3.0 (Rangel et al., 2006). The rest of the analyses were performed using JMP 7.0 (SAS Institute, SAS Institute, Inc., 2007. Cary, NC, USA). Throughout the paper, mean values are followed by $\pm 1SE$.

3. Results

3.1. Spatio-temporal pattern of acorn predation

Considering Ripley's K , in Plot 1 there were some distance classes where the spatial distribution of acorn encounter was random (at radii = 0.2, 0.5, 0.7, and 1.0 m) while for the rest of distances the distribution was clumped (Appendix C). In Plot 2 many distance classes showed a random distribution for acorn encounter (at radii = 0.8, 0.9, 1.4, 1.8, 1.9, 2.0, 2.2, 2.7, 2.8, 3.1, 3.4, 3.5, 3.6, 4.0, 4.1, 4.2, 4.3, 4.4, 4.9, and 5.0 m) while the rest of the radii considered showed a clumped distribution (Appendix C). Then again, in Plot 3 some radii showed random spatial distribution on acorn encounter (at radii = 0.4, 0.5, 0.6, 0.7, 0.9, 1.0, 1.2, 1.4, 2.7, and 3.0 m) while the remaining radii showed clumped spatial distribution (Appendix C).

Acorn predation also varied at different spatial scales and between plots. Therefore, the correlograms showed that values of Moran's I , regardless of the plot considered, were significantly positive at smaller scales (Fig. 1). Thus, considering distances between 0 and 100 m, values of acorn predation were more similar than expected by random, i.e. within smaller distances the probability of finding the same number of predated (or non-predated) acorns per supply point was higher than expected by random. On the other hand, at larger distances (around 100–200 m) the values of Moran's I were significantly negative. Therefore, the number of acorns predated once a supply point was encountered was more dissimilar than expected by random (Fig. 1). Those negative correlation patterns persisted at larger distances in Plot 3, while in Plots 1 and 2, some distance classes were again significantly positive at a lag distance of 480 m and 300 m, respectively (Fig. 1).

3.2. Differences between trials

Encounter differed between experimental trials in the 2007 experiment, with 84.0% of sowing points encountered for trial 1 and 91.1% for trial 2 ($\chi^2 = 83.5$, d.f. = 1, $P < 0.0001$; all plots pooled). By contrast, encounter did not differ between trials in the 2008 experiment ($\chi^2 = 0.1$, d.f. = 1, $P = 0.7$), with an overall value of 89.5% (all plots pooled). Acorn predation followed the same pattern. There were differences between trials in the 2007 experiment ($\chi^2 = 88.0$, d.f. = 1, $P < 0.0001$), with $78.5 \pm 1.6\%$ of acorns predated in trial 1 and

Table 1

Results of the GLZ model for the differences in acorn encounter and predation of *Q. ilex* in relation to plot, treatment, and year. Results show χ^2 value and *P*-values for each factor using a hierarchical logistic model.

	d.f.	Acorn encounter χ^2	Acorn predation χ^2	Power (1 - β) ^a
Plot	2	21.2***	22.2***	1.0
Treatment (<i>T</i>)	2	17.4**	51.5***	1.0
Year	1	2.3ns	1.0ns	
T* plot	4	79.3***	128.0***	1.0
T* year	2	11.9*	12.0**	0.8
Whole model	11	110.3***	173.6***	

ns, non-significant.

^a Only calculated for significant factors using standard least squares.

* *P* < 0.01.

** *P* < 0.001.

*** *P* < 0.0001.

95.0 ± 0.7% in trial 2. Acorn predation did not differ between trials in the 2008 experiment ($\chi^2 = 0.1$, d.f. = 1, *P* = 0.8), with an overall value of 89.5% of acorns predated (all plots pooled).

3.3. Predator identity

Acorn encounter significantly differed among treatments ($\chi^2 = 10.5$; *P* = 0.01) and predator species ($\chi^2 = 113.9$, *P* < 0.0001), and the same pattern was found for acorn predation (treatment: $\chi^2 = 8.2$, *P* = 0.02; predator identity: $\chi^2 = 155.7$, *P* < 0.0001). While in NI treatment wild boars predated 7.2% and rodents 84.4% of the acorns, in PCL wild boars consumed 1.1% and rodents 82.9% of the acorns, and in SL wild boars predated 9.7% and rodents 78.3% (values for those acorns where the identity of predator agent was clearly assessed).

3.4. Differences across treatments, plots and years

Acorn encounter and predation followed a complex pattern across treatments, plots and years (Table 1). Encounter differed among treatments (highest values in SL [91.6%] followed by NI [90.8%] and PCL [88.6%; all data pooled]) and plots (87.8% in Plot 1; 95.6% in Plot 2; and 87.5% in Plot 3), but there was a significant interaction between the two factors that reflected changes in the pattern among treatments across plots. Acorn predation followed the same pattern (Table 1, Fig. 2), with the highest values in SL (87.8 ± 1.1), followed by NI (87.4 ± 1.1) and PCL (83.0 ± 1.2), and an overall value of 84.9 ± 0.9 in Plot 1, 91.9 ± 1.1 in Plot 2, and 83.8 ± 1.6 in Plot 3. In fact, there was a strong correlation between values of encounter and predation in the two years ($F_{1,13} \geq 165.9$; *P* < 0.0001; $r^2 = 0.99$ for 2007 experiment and 0.92 for 2008 experiment; linear regression made with mean values of encounter and predation per replicate, two trials per year pooled). The same interactions among factors occurred for acorn predation (Table 1, Fig. 2). The year had no effect on acorn encounter or predation (Table 1). However, there was a significant interaction of year with treatment, motivated by different patterns across treatments within years (Fig. 2).

4. Discussion

Post-dispersal acorn predation appears to reshape the seed shadow, as previously found in this oak (Muñoz and Bonal, 2007; Muñoz et al., 2009; Puerta-Piñero, in press) and other species (Rey and Alcántara, 2000; Tomita et al., 2002). This may ultimately be linked to habitat characteristics that influence seed predator activity (Rey and Manzaneda, 2007). In this sense, our results corroborate that the same processes may operate in burnt areas, as burnt wood management affected both the rates of acorn predation and the identity of seed predators. This is a key point for

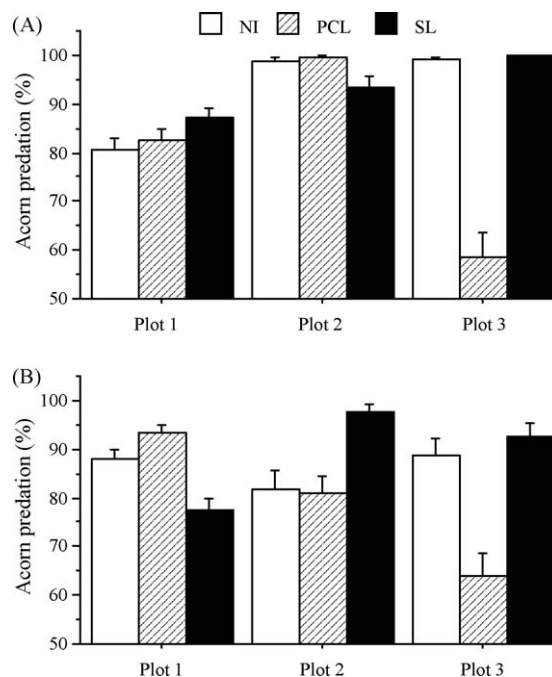


Fig. 2. Mean values of acorn predation in relation to post-fire burnt wood management for each plot in (A) 2007 experiment (predation monitored from autumn 2007 to spring 2008) and (B) 2008 experiment (predation monitored from autumn 2008 to spring 2009). Treatments are NI, no intervention; PCL, partial cut plus lopping; SL, salvage logging. Acorn encounter was highly correlated with acorn predation (see Section 3.4) and followed a similar pattern.

post-fire restoration plans via seed sowing, as acorn predation may be a handicap for oak forest restoration (Pulido and Díaz, 2005; Espelta et al., 2009). On the other hand, post-dispersal acorn predation showed temporal variability and, above all, strong spatial variation. Thus, the landscape appears to constitute a complex, dynamic context-dependent scenario for regeneration purposes (Puerta-Piñero, 2008).

4.1. Spatio-temporal differences in acorn predation

Post-dispersal *Q. ilex* acorn predation after fire significantly varied in space and time. We found significant differences between plots and replicates, as well as differences in the spatial correlations on acorn predation values depending on the distance classes considered. At the smaller distances (0–5 m, thus shorter than distance between consecutive sowing points) the pattern of acorn encounter followed a random spatial distribution. For distances within the same replicate (0–100 m), the probability of having the same number of predated (or non-predated) acorns was higher than the expected by random. By contrast, at larger distances (100–200 m) the number of acorns predated was more different than expected by random. This suggests that movement decisions and population fluctuations among predator agents through the landscape seem to be important for post-dispersal predation rates, as reported in other studies (Gómez, 2004; Muñoz and Bonal, 2007; Pons and Pausas, 2007; Gómez and Hódar, 2008; Muñoz et al., 2009). Furthermore, the correlation between the value of acorn encounter and predation suggests that the most critical step in terms of post-dispersal acorn predation relies on finding the specific point where the acorns are buried. Once it is encountered, either rodents or wild boars track the nearby area and predate most of the surrounding acorns. On the other hand, while some plots and treatments suffer relatively low predation during the first year, they can be the most predated in the following year, and thus be worse for the establishment, and vice versa. Therefore, the success of regeneration seems

to be highly dynamic in time and space, as previously suggested by other authors (Rey and Alcántara, 2000; García and Ortiz-Pulido, 2004; Gómez-Aparicio, 2008; Espelta et al., 2009). Our results can be explained to some extent by the identity of the main predators, the wild boar *S. scrofa* and several species of mice. While boars can move through broad distances in little time (Massei et al., 1997; Meriggi and Sacchi, 2000), the activity of rodents (mainly *M. spretus* and *A. sylvaticus* in the area) can largely vary at short temporal scales due to population fluctuations and to their small movement capacity compared to that of large ungulates (Muñoz and Bonal, 2007; Matías et al., 2009; Puerta-Piñero, in press).

4.2. Effect of burnt wood management on acorn predation

Although the rates of acorn predation were globally high, there were differences related to the burnt wood management. The PCL treatment showed, overall, the lowest values for both encounter and predation. This might partly be because of the effect of the habitat on the predator type. Rodents caused a high predation rate in all the treatments irrespective of the cover of burnt debris. Treatments with an overstorey cover of burnt wood (PCL and NI) may offer a secure site for rodents, but the SL treatment also had a considerable herbaceous cover two years after the fire, which might similarly provide shelter for this guild of predators (Torre and Díaz, 2004; Muñoz and Bonal, 2007; Matías et al., 2009). By contrast, the PCL treatment was highly unsuitable for the foraging of wild boars because of the impediment of logs and branches for rooting. Other ungulates such as goats (either wild or domestic) and sheep also depredate acorns in these systems (Muñoz and Bonal, 2007; Gómez and Hódar, 2008). Although their abundance in the study area was low (without any domestic livestock during the study years), it has been shown that the presence of burnt debris spread on the ground may similarly hamper the activity of these animals (e.g. herbivory; Ripple and Larsen, 2001). Thus, the PCL treatment might reduce acorn predation by ungulates in general in relation to the other treatments.

4.3. Management implications

There is currently an intense debate concerning the appropriate management of burnt trees after forest fires (McIver and Starr, 2000; Beschta et al., 2004; Lindenmayer et al., 2004; Donato et al., 2006). Post-fire salvage logging is widely implemented due to economic, silvicultural, and even aesthetic reasons (McIver and Starr, 2000; Van Nieuwstadt et al., 2001; Lindenmayer et al., 2004; Castro et al., 2010a). However, recent studies are showing that salvage logging may impact ecosystem functioning and regeneration (Donato et al., 2006; Lindenmayer and Noss, 2006; Castro et al., 2010a,b), and consequently there is an increasing appeal for the implementation of post-fire policies of non-intervention or less aggressive intervention (Beschta et al., 2004; Lindenmayer et al., 2004; DellaSala et al., 2006; Hutto, 2006; Castro et al., 2010a). In this context, the results of this study support the idea that alternatives to salvage logging offer similar or even better results regarding post-dispersal acorn predation. Moreover, the activity of a guild

of predators (ungulates) is reduced under an intermediate degree of post-fire management (cutting the trees and main branches and leaving the biomass *in situ*, PCL treatment). In summary, our study shows that salvage logging offers no advantage against post-dispersal acorn predators, supporting the contention that other management policies might also be considered for the regeneration and natural colonization of oak forests.

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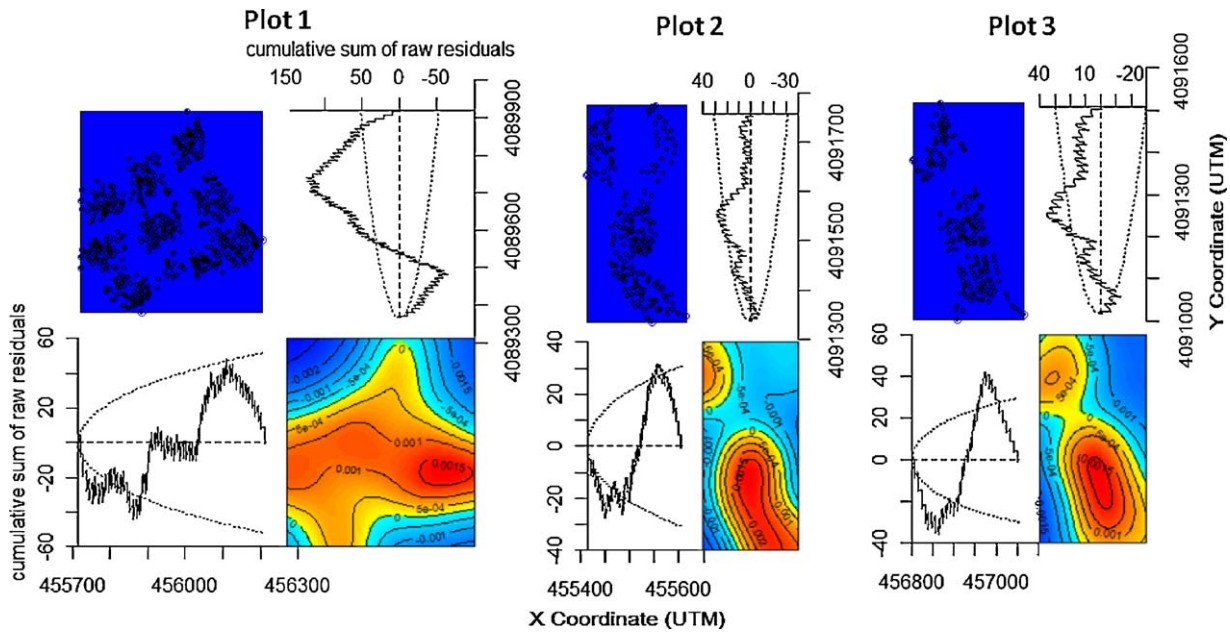
Appendix A.

Summary of the cumulative post-dispersal predation values (% of acorn predation) for the different sampling dates in the 2007 experiment. *Time = days since experimental set-up. Cumulative values approached an asymptote at the end of the experiment in the two trials. Data for acorn encounter followed the same pattern (not shown), as there is a strong correlation between encounter and predation (see Section 3.4). NI, no intervention; PCL, partial cut plus lopping; SL, salvage logging.

	Time*	Treatment		
		NI (%)	PCL (%)	SL (%)
Trial 1	10	61.2	43.5	53.0
	25	71.0	57.8	55.5
	45	72.2	57.7	73.0
	75	74.7	58.7	80.2
	150	82.1	66.0	87.7
Trial 2	7	39.2	54.8	48.8
	20	79.8	90.2	73.2
	105	93.5	95.5	94.5

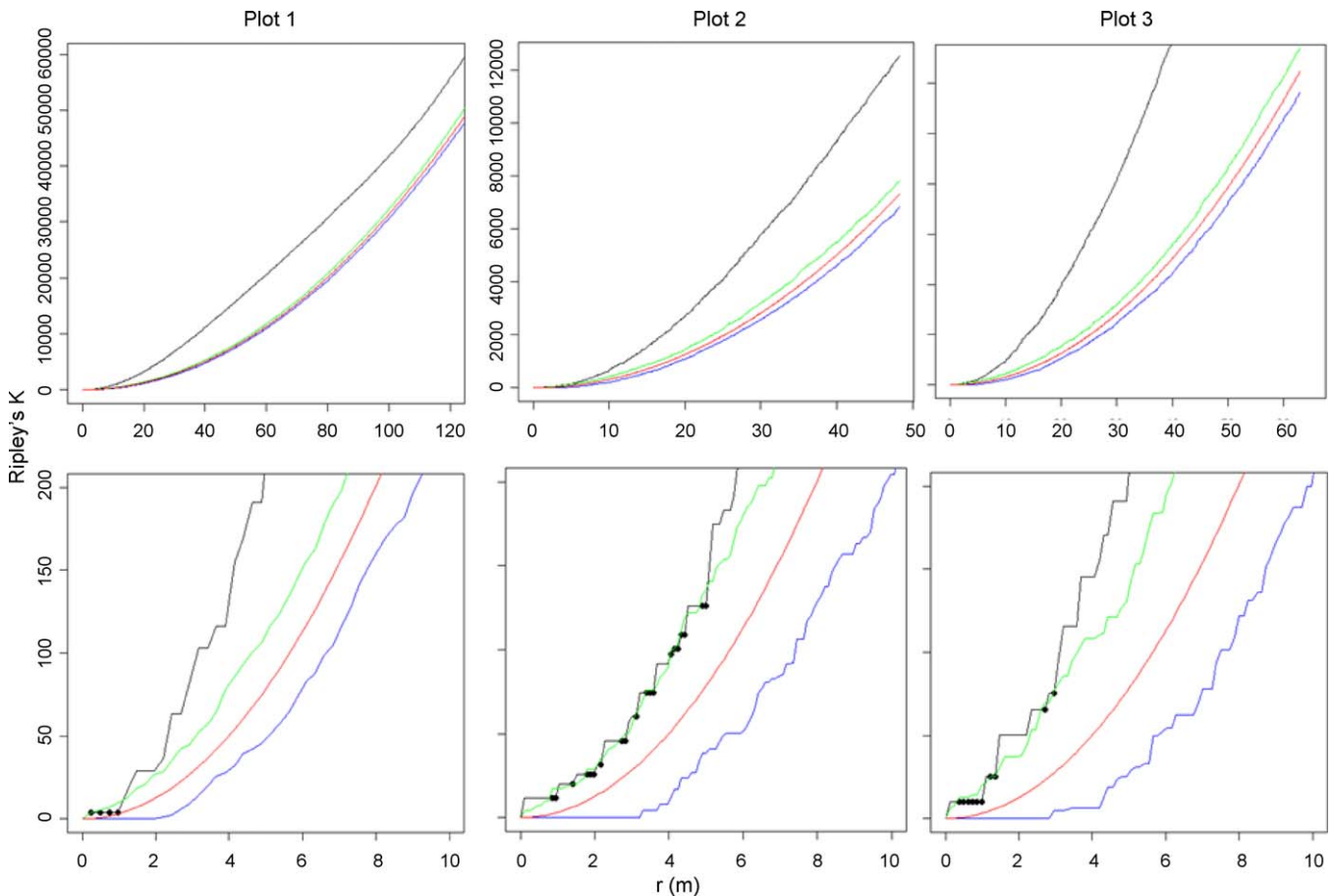
Appendix B.

Representation of the spatial location of the supply points in each experimental plot for the 2008 experiment. The figure shows the X and Y coordinates and the trends of the spatial distribution of the supply points using the cumulative sum of residuals in both dimensions. See Fig. 1 for details on the spatial arrangements of treatments and replicates within plots.



Appendix C.

Spatial patterns of acorn encounter. The figures show Ripley's *K* curves for all the plots. At the top of the template the figures show the whole curve for each plot, at the bottom only the first radii distances where the random distributions were found. Black lines and dots indicate the observed distribution and the points with random distribution respectively. Green and blue lines show the higher and lower limits of the simulated confidence intervals (obtained after 500 simulations). Red lines indicate the theoretical distribution given the points of the studied sample. (For interpretation of the references to color in this figure, the reader is referred to the web version of the article.)



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