# Post-fire salvage logging alters a key plant-animal interaction for forest regeneration

J. Castro,[1],† C. Puerta-Piñero,[2] A. B. Leverkus,[1] G. Moreno-Rueda,[3] and A. Sánchez-Miranda[1]

[1]*Departamento de Ecología, Universidad de Granada, E-18071 Granada, Spain*
[2]*Smithsonian Tropical Research Institute, Unit 0948, APO AA 34002-0948, Washington, D.C., USA*
[3]*Departamento de Zoología, Universidad de Granada, E-18071 Granada, Spain*

**Abstract.**    Post-fire salvage logging is widely implemented worldwide, but there is an increasing concern about its potential impact on the ecosystem. Moreover, there is scant information about the effect of salvage logging on ecosystem processes mediated by species interactions. We manipulated a burnt pine forest to experimentally analyze the effect of burnt-wood management on the colonization of Holm oak (*Quercus ilex*) mediated by acorn dispersal by Eurasian jays (*Garrulus glandarius*). Three replicates of three treatments were established in an 18-ha plot: salvage logging (SL), non-intervention (NI), and partial cut plus lopping (PCL; felling and lopping most of the trees but leaving all the biomass in situ). We hypothesized that different burnt-wood management could alter jays' landscape perception and thus the pattern of seed dispersal and seedling recruitment. We monitored jay abundance in each treatment for three winters and three breeding periods, and jay flights of potential acorn dispersal between nearby oak trees and the treatments. We also searched for oak seedlings recruited in the experimental plot for five years following the fire. Jays were recorded significantly more times (87%) in NI, and movements to this treatment during the acorn dispersal period were also more frequent (81% of the flights). Oak seedlings were also more abundant in NI (ca. 55%) than in SL or PCL (ca. 25% each), despite a strong effect of small remnants of live pines. The results show that the burnt forest, if unsalvaged, still provides a suitable habitat for jays, while salvage logging reduces the strength of this key plant-animal interaction for oak natural regeneration. Non-intervention policies after a forest fire therefore provide the opportunity for adaptive management that helps reduce restoration costs and increase the resilience of the system.

**Key words:**   *Garrulus glandarius*; jay-oak interaction; oak colonization; *Quercus ilex*; resilience; salvage harvesting; seed dispersal; Sierra Nevada National Park; succession.

† **E-mail:** jorge@ugr.es

## INTRODUCTION

After a forest fire it is customary that the local forest service (whether directly or through private counterparts) removes the burnt logs from the site, a process that is referred to as salvage logging and that often involves the elimination of the remaining woody debris such as branches and snags by chopping, mastication, etc. (McIver and Starr 2000, Lindenmayer et al. 2008). Post-fire salvage logging is widely implemented worldwide (McIver and Starr 2000, Van Nieuwstadt et al. 2001, Lindenmayer and Noss 2006, Mavsar et al. 2011), and renders a

landscape devoid of most of the forest biomass and a simplification of the post-fire habitat (Lindenmayer et al. 2008, Bros et al. 2011). Several reasons are invoked to support this practice, coming from economics (return of economic capital of wood), silvicultural (e.g., greater ease of future reforestation, reduction of fire and pest risk), visitor safety, or even aesthetics (McIver and Starr 2000, Lindenmayer et al. 2008, Mavsar et al. 2011). Many of these reasons are, however, controversial (e.g., Castro et al. 2011), and an increasing number of studies are showing that salvage logging may have strong negative impacts on ecosystem processes, such as a reduction of the natural capacity for the regeneration of tree species (Donato et al. 2006, Castro et al. 2011), lesser diversity of plant and animal communities (McIver and Starr 2000, Castro et al. 2010a), or increases in soil erosion and watershed runoff (Beschta et al. 2004, Karr et al. 2004, Lindenmayer et al. 2008). Consequently, there is a growing appeal for the implementation of post-fire policies of non-intervention or less aggressive intervention, on the basis of the evidence that snags and decaying burnt wood are components of natural systems that promote ecosystem recovery and diversity (Beschta et al. 2004, Lindenmayer et al. 2004, DellaSala et al. 2006, Castro et al. 2010a).

The analysis of the effect of salvage logging on organisms has largely focused on its impact on diversity or on specific groups of species, whereas its effect on ecosystem processes has been focused on abiotic factors such as microclimate, hydrology, erosion, or nutrient cycling (Lindenmayer et al. 2008, Marañón-Jiménez and Castro, in press). However, very little is known about the effect of salvage logging on ecosystem processes mediated by species interactions. It is well known that animal species are affected by intermediate to severe disturbances that modify habitat structure and complexity (e.g., Cody 1985), including the removal of dead trees (e.g., Hutto 2006, Relva et al. 2009, Castro et al. 2010a, Puerta-Piñero et al. 2010). The degree to which post-fire salvage logging changes the habitat could then be of great importance for key plant-animal interactions, as is the case with seed dispersal (Rost et al. 2009, Castro et al. 2010a, Rost et al. 2010). This can affect the resilience of the ecosystem in terms of the time

needed for natural regeneration after fire. The way in which post-fire management affects these interactions will determine the success or failure of other important ecosystem services such as ground cover, carbon fixation, or the scenic view of the landscape, among others (Millennium Ecosystem Assessment 2005, Lindenmayer et al. 2008, Serrano-Ortiz et al. 2011).

In this study, we experimentally analyze the effect of burnt-wood management on the interaction between a tree (the Holm oak, *Quercus ilex* L.) and its main seed disperser (the Eurasian jay, *Garrulus glandarius* L.). Oaks are major components of forests in the Holarctic (Archibold 1995, Breckle 2002). Jays are the main disperser of the oaks as well as other *Fagaceae* species (Bossema 1979). Jays move and cache an enormous amount of acorns during the fall for later consumption, with dispersal distances that average several hundred meters and can reach up to a few kilometers (Kollmann and Schill 1996, Gómez 2003, Pons and Pausas 2007). Part of the cached acorns are not consumed for several reasons (e.g., cached in excess, forgotten, or the death of the jay that cached them), and can therefore emerge as seedlings (Kollmann and Schill 1996, Pulido and Díaz 2005). Furthermore, jays move and cache a large fraction of acorns into conifer forests, either natural or planted (Mosandl and Kleinert 1998, Gómez 2003). As a result, it is common to find an oak seedling and sapling bank in the understory of coniferous forests due to jay dispersal, provided that both jays and mature oaks are present in the area (Mosandl and Kleinert 1998, Lookingbill and Zavala 2000, Puerta-Piñero et al. 2012a).

In September 2005, the "Lanjarón" fire (Sierra Nevada, SE Spain) burned a pine stand located mostly in the potential domain of the Holm oak. The landscape surrounding the burnt pine forest has small clusters of Holm oak as well as isolated individual trees that survived the fire (Fig. 1). Working in cooperation with the local Forest Service, we established three experimental treatments that differed in the post-fire management of burnt trees, ranging from the common salvage logging to non-intervention. We hypothesize that the burnt forest, if not salvaged, might still be a suitable habitat for jays to move and hide acorns, as the basic habitat structure of the forest still persists (high density of standing logs and a
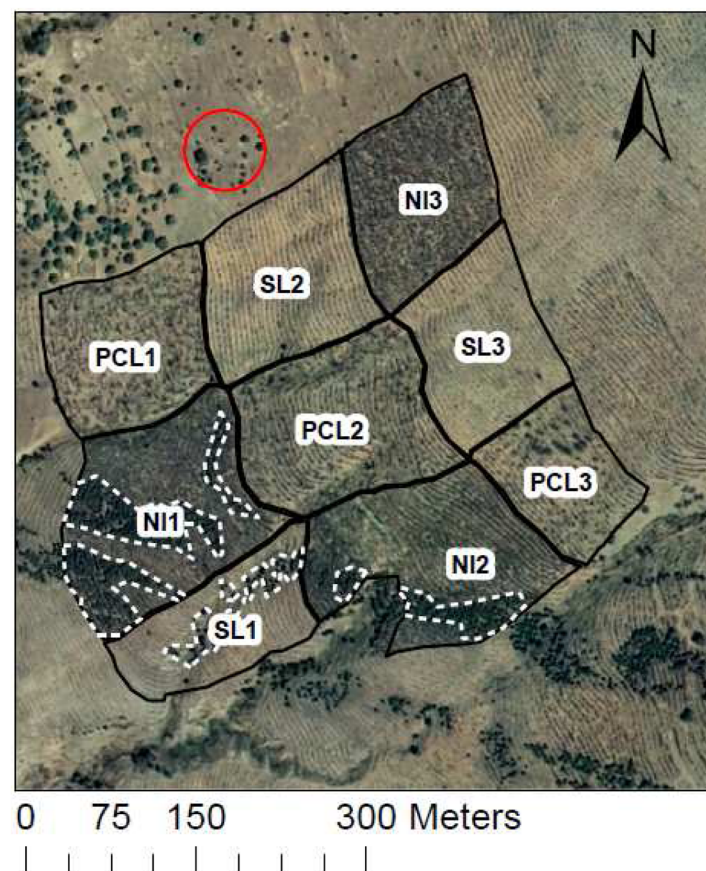
Fig. 1. Orthorectified aerial photograph of the study plot two years after the fire. The polygons indicate the boundaries of the experimental treatment replicates: Non-Intervention (NI), Partial Cut plus Lopping (PCL), and Salvage Logging (SL). One of the clusters of unburnt oaks that did not burn and that are acting as seed source into the study plot is indicated by the red circle. Some trees within the plot partially burned during the fire but survived. As a result, clusters of live pines finally remained in replicates 1 and 2 of NI, and replicate 1 of SL, indicated in the Fig. by the dashed lines. Green trees in the top left corner mainly correspond to chestnut *Castanea sativa* trees. Photo courtesy of the National Park of Sierra Nevada.

relatively high habitat complexity in the overstory), while in the salvaged areas the activity of jays will be reduced given that it is devoid of tree remains. This might translate as an impact of the conventional salvage logging on the natural colonization capacity of the oaks, with potential implications for post-fire colonization of oaks and forest regeneration in large areas of the planet. Our specific objectives are to determine whether: (1) post-fire burnt-wood management alters habitat selection by jays; (2) acorn dispersal by jays is affected by salvage logging; and (3) this behavior translates in differences in the pattern of seedling recruitment among management treat-

ments.

## METHODS

### Study system and experimental design

The study site was located in Sierra Nevada Natural and National Park (SE Spain), where in September 2005 the Lanjarón fire burned ca. 1,300 ha of pine reforestations planted 35 to 45 years ago for forestry purposes (mainly soil protection). A plot of 17.8 ha (UTM $x$, $y$ position at the centroid: 456070, 4089811) was established at 1477 m a.s.l. in the burnt pine stand. At this elevation, oak forests are considered the climax

vegetation according to edaphic and climatic properties as well as historical records (Valle 2003). Pine species present in this plot were *Pinus pinaster* and *P. nigra* (Castro et al. 2010*b*). The area surrounding the experimental plot is dominated by shrublands and patches of almond and chestnut orchards, with scattered individuals and small clusters of mature Holm oak trees that did not burn (Fig. 1).

From 21 April 2006 to 10 May 2006 (ca. seven months after the fire), the Forest Service implemented three replicates of three treatments in the plot, following a random spatial distribution: (1) "Non-Intervention" (NI), leaving all of the burnt trees standing. The trees fell in the course of consecutive years (mostly during the winter). Cumulative tree fall rate (measured in February of each year) was 0.0% by 2006 and 2007, 13.3 ± 0.3% by 2008, 83.5 ± 4.0% by 2009, and 98.3 ± 1.0% by 2010 (measured from 100 marked trees per replicate, mean ± SE in all cases; Castro et al. 2010*b*). Thus, the NI treatment kept a vertical structure of standing trees until autumn 2009. (2) "Partial Cut plus Lopping" (PCL), a treatment where ca. 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. The three treatments therefore differed in the degree of intervention (maximum in SL, minimum in NI) and in the habitat structure generated (low vertical structure in SL, intermediate in PCL, and highest in NI), parameters that may affect habitat selection by jays. Replicate size (2.0 ha in average) was similar among treatments (Kruskal-Wallis test, $P > 0.05$). Pine density before treatment implementation was 1477 ± 46 individuals per hectare (mean ± SE; estimated by counting the number of trees in four 25 × 25 m quadrats per experimental replicate two months after the fire) and did not differ among treatments. Tree size (basal trunk diameter) was 17.7 ± 0.2 cm (estimated for 30 random trees per quadrat, thus 120 trees per replicate) and did not differ among treatments either (Castro et al. 2010*b*).

Salvage logging is the usual post-fire action

taken by the local Forest Service, and it was fully implemented throughout the rest of the surrounding burnt area where the experimental plot was located, including the removal of trunks with a log forwarder. The plan was also to remove the trunks with a log forwarder from the experimental SL treatment. However, the Forest Service eventually cancelled this last step due to difficulties in operating machinery within the spatial arrangement of the experimental replicates. Thus, the logging operation performed in the experimental SL treatment was less intense than the usual salvage logging. On the other hand, small patches of partially burnt but live pines remained after the fire and survived through the rest of the study period (Fig. 1). In particular, there were patches of live pines totaling 0.95 ha in replicate 1 of treatment NI, 0.30 ha in replicate 2 of treatment NI, and 0.26 ha in replicate 1 of treatment SL (Fig. 1). This was expected to affect habitat selection by jays given their preference for conifer forest to hide acorns (Bossema 1979, Pons and Pausas 2007).

Holm oak acorns are dispersed in the area from October to December, mainly by the Eurasian jay (Gómez 2003), and acorns emerge as seedlings through the following spring. Small rodents such as *Apodemus sylvaticus* and *Mus spretus* are acorn dispersers to a lesser extent (Muñoz and Bonal 2007, Gómez et al. 2008), although with a low average distance (below 5 m; Gómez et al. 2008). In addition, rodents finally depredate most (up to 98%) of the acorns they handle (Gómez et al. 2008, Puerta-Piñero 2010). Acorn dispersal by rodents to distances of more than several dozen meters is therefore negligible at the landscape level compared to jay dispersal (Muñoz and Bonal 2007, Pons and Pausas 2007, Gómez et al. 2008, Puerta-Piñero 2010). In our experimental plot, the minimum distance between replicates and the nearest oak patches was 41.0 m, which is further than what would be expected from dispersal by rodents (Fig. 1); thus, we may consider that the seedlings found in the experimental plot originated from acorns dispersed by jays.

### Habitat selection by jays

We monitored habitat selection by jays by point censuses during breeding and winter periods. We located one sampling point at the

center of each replicate of each treatment, and used it permanently as the sampling point. A total of 252 censuses (84 per treatment; 6 min per census) were made during six sampling periods: three autumn-winters (2006, 2007, and 2008; "winters", hereafter) and three breeding seasons (2007, 2008, and 2009), distributed as follows: 4 censuses for the first winter, 6 censuses for the first breeding season, 5 censuses for the second and third winter and second breeding season, and 3 censuses for the third breeding season. We conducted the winter censuses from November to February, and breeding season censuses during May and June. We assessed jay abundance by either visual location or hearing, recording all the individuals detected within the limit of the experimental replicate during the time of census. We considered only jays that were stopped within the limits of the corresponding replicate at the moment of census (thus ignoring those that flew across). Counts started three minutes after the arrival of the observer to each of the sampling points. We only performed censuses under good weather conditions, without rainfall and with low or no wind (Bibby et al. 1992).

### Acorn dispersal by jays

We sampled the spatial pattern of acorn dispersal by jays across treatments in 2008 by observing jay flights during the natural dispersal period (mid-October to mid-November). Two observers (communicating by radio) were simultaneously placed in two strategic positions at a distance that allowed the visual covering of the entire plot and surrounding Holm oak patches, as well as the tracking of flights (Fig. 1). Any jay flight to the plot, from the plot, or between surrounding vegetation was followed with binoculars and noted. Sampling was done during six days, from October 25 to November 13, coinciding with the period of maximum acorn dispersal. They started at 8:00 am (solar time) and lasted for 3–4 hours, depending on jay activity, and only under good weather conditions (without rainfall and with low or no wind). For the observations of jays in the present study, we stayed at sufficient distances to monitor a large area and to track flights to experimental treatments. This precluded the observation of acorn transport in the beak or the gut in some cases. Nonetheless,

jay flights from oak patches to other sites in this period imply acorn dispersal in most of the cases (Gómez 2003, Puerta-Piñero et al. 2012a), so we considered such flights as putative acorn dispersal. Some of the flights occurred between the experimental plot and oak patches located close to the plot (Fig. 1; Appendix A). For those cases, we later calculated flight distances with GIS (as the distance between the centroid of the oak patch and the centroid of the replicate). Mean distance from Holm oak patches to experimental replicates was 373.2 ± 24.2 m, and did not differ among treatments (Kruskal-Wallis test; $\chi^2 = 0.20$, df = 2, $P = 0.90$).

### Holm oak seedling recruitment

We monitored Holm oak seedling recruitment throughout the plot from spring to early summer 2006 to 2010. To accomplish this, we thoroughly searched the surface of each treatment replicate every year, and we marked and noted UTM coordinates of any new seedling (sensu lato, see below) with a GPS system. Holm oak seedlings have the ability to resprout after a fire (Rodrigo et al. 2004). Thus, the 2006 seedlings corresponded either to dispersal in 2005 (thus after the fire but before treatment implementation) or to resprouts of seedlings that were present in the understory before the fire. Because it was difficult to unequivocally differentiate these two categories, we marked them as a single category (2006 cohort). In any case, it is clear that all of them originated from acorns dispersed before treatment implementation, so they were not used for analysis. Seedlings found in spring 2007–10 correspond to acorns dispersed the previous autumn, all after treatment implementation. For seedlings from 2007 onwards, the soil around the root was excavated when necessary to confirm the presence of attached acorn or cotyledon marks as a test of its recent emergence.

### Data analysis

We analyzed habitat selection by jays with a chi-square goodness of fit test using the sum of all censuses per replicate. Potential acorn dispersal by jays was analyzed with two complementary approaches. First, the total number of flights to the experimental plot or from the experimental plot was analyzed with a chi-square test. Second, for those dispersal move-

ments from oak patches to the plot (and thus with known starting and ending point), we used a generalized linear mixed model (glmm) with poisson errors. We constructed and step-wise simplified a full model with treatment, the distance between each oak patch and the experimental replicates, and their interaction as fixed factors. We considered oak patch (three patches were present) as a random factor. Likelihood ratio tests allowed testing for the significance of the change in log-likelihood obtained by the deletion of a term, which would justify the retention of this term in the model. In the minimum adequate model only significant terms were retained. An observation-level random term was included in the model to test for overdispersion. The total number of seedlings in each experimental replicate (seedling recruitment) was also analyzed with a glmm with poisson errors, using burnt-wood management treatment and proportion of replicate area covered by live pines as fixed factors. To account for temporal pseudoreplication, we allowed for a random effect of year on each replicate (with replicates nested within treatments). We further ran the model excluding from the experimental replicates the area of live pine patches and the seedlings they contained in order to explore the results reducing the potential interference of live pines. For this purpose, we similarly used a glmm with the same random effects structure, but with only the factor treatment. Model simplification and overdispersion testing was carried out as described above. Statistical analyses were carried out in R (R Development Core Team 2011), with the use of the package lme4 (Bates et al. 2011).

## Results

### Habitat selection by jays

A total of 23 jay records were made through the three sampled years, 20 of them in the NI treatment (0.25 records per 6 min census), 3 in PCL (0.04 per census), and zero in SL ($P < 0.001$). For the NI treatment, no significant differences were found between periods (winter versus breeding season) in the number of records, nor were there differences among replicates (9, 5 and 6 records for replicates 1, 2 and 3, respectively; $P > 0.05$).

### Acorn dispersal by jays

We registered a total of 167 jay flights (Appendix A), of which 63 were arrivals to the experimental plot and 51 were departures. Among movements into the plot, jays entered the NI treatment in 81.0%, PCL in 15.9%, and SL only in 3.1% of the cases ($P < 0.001$). Jays similarly departed NI in most of the cases when leaving the experimental plot (92.2% of the cases; Appendix A). A total of 28 flights were registered from nearby oak patches to the experimental plot (Appendix A) with a known departure and arrival point. Distance from the oak patches to the experimental replicates did not significantly influence the number of jay flights in a specific route, nor did the treatment by distance interaction. Only the factor treatment affected the number of flights (Table 1), supporting that jays positively selected the NI treatment.

### Holm oak seedling recruitment

A total of 244 seedlings emerged after treatment implementation during the four years of study (28, 38, 140 and 38 in the years 2007–2010, respectively; Fig. 2, Appendix B). Seedlings were more abundant in NI (66.0% of the seedlings) than in PCL (11.5%) or SL (22.5%), although treatment was not a significant factor in the model (Table 2; Fig. 2). The presence of live pines affected post-treatment seedling distribution, as the proportion of replicate area covered by live pines significantly determined the number of recruited seedlings (Table 2; Fig. 2). When seedlings under live pines were excluded from the analysis, the model still did not show a significant effect of treatment on number of recruited seedlings, although significance improved considerably (Table 2). The lack of significance for seedling recruitment could be related to the large variability in number of seedlings among replicates and years. In fact, if data from the replicates were pooled, the number of seedlings greatly differed among treatments, with the highest proportion of seedlings encountered in NI (52.0%), followed by SL (26.0%) and PCL (22.0%; chi-squared test, df = 2, $P < 0.01$).

## Discussion

The analysis of the different phases involved in Holm oak colonization of burnt areas supports a

Table 1. Results for number of acorn-dispersal flights, i.e., flights from nearby oak patches to the experimental replicates during autumn 2008.

| | Number of flights | | |
| --- | --- | --- | --- |
| Explanatory variable | F | df | P |
| Distance† × Treatment‡ | 0.22 | 2 | 0.81 |
| Distance | 0.43 | 1 | 0.52 |
| Treatment | 10.76 | 2 | **<0.0005** |

*Note:* Reported values refer to the changes in log-likelihood obtained by the elimination of the explanatory variable from the model. The minimal adequate model contained only treatment as a fixed factor. Ad hoc analyses showed that among treatments only NI significantly differed from the other two treatments. In the model, 95% confidence intervals showed no significant oak patch-related random effect on jay flights, so the results shown are for a glm with quasipoisson errors. Among the 28 analyzed flights, 24 were to NI, 3 to PCL, and only 1 to SL.

†Distance from the oak patch (flight starting point) to the experimental burnt-wood management replicates (arrival point).

‡Burnt-wood management treatments are: Non-Intervention (NI), Partial Cut plus Lopping (PCL), and Salvage Logging (SL).
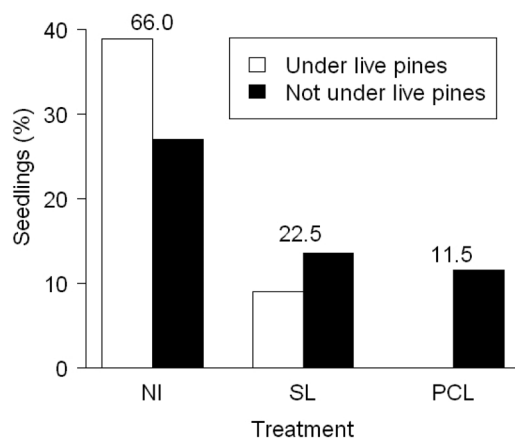


Fig. 2. Percentage of seedlings recruited in the different treatments. Note that jays and other predators consume a huge proportion of the cached acorns, so the reported seedlings are the net result of the mutualistic interaction between jays and the Holm oak. Numbers above columns indicate the total percentage of seedlings per treatment. Treatments are: Non-Intervention (NI), Partial Cut plus Lopping (PCL), and Salvage Logging (SL). Under live pines refers to seedlings located in patches of pines that survived the fire within the replicates of the experimental treatments; these patches were located in 2 replicates of NI and 1 replicate of SL (see Fig. 1 and Appendix B).

strong concordance between habitat selection by jays for foraging across seasons, potential acorn dispersal, and new seedling establishment in the treatment with no post-fire intervention. Jays preferentially used the non-intervention treatment during both the winter and the breeding seasons, still showed a clear preference for movements into this treatment during the acorn dispersal period, and their caching behavior led to the emergence of more seedlings (52% of the total, excluding those below live pines) in non-intervention than in the other treatments. By contrast, salvage logging reduced the natural recruitment of new oaks, as it created a habitat not used by the main seed disperser (Castro et al. 2010*a*). Furthermore, it is likely that the conditions of our experimental salvage logging even produced an over-estimation of the role of jays in the salvage logging treatment, as the permanence of trunk piles could have increased the use of this habitat for caching (see Rost et al. 2009, 2010 for a similar pattern for frugivorous, bird-dependent seed dispersal). In addition, seedling recruitment in the salvaged areas is largely dependent on the presence of live trees that survived the fire (either isolated or in small clusters), as those trees were highly attractive to jays. Patches of live pines might have similarly increased recruitment in replicates of non-intervention, but the results show that when seedlings below these patches were excluded from analysis the significance of the treatment improved considerably. In addition, the replicate of non-intervention that had no live pines registered more records for both jay habitat selection and jay flights during the dispersal period than all the replicates of the other treatments together (Appendix A). Similarly, this particular non-intervention replicate contained more recruited seedlings than any replicate of the other two treatments when live pine patches were excluded (Appendix B). Overall, the non-intervention treatment clearly had a positive effect on jay activity and oak recruitment.

It is well known that the Eurasian jay disperses acorns and other nuts to conifer forests (Gómez 2003), and that this interaction results in an effective oak recruitment in the understory of these forests (Mosandl and Kleinert 1998, Lookingbill and Zavala 2000). In fact, our results show a strong effect of small patches of live pines.

Table 2. Results for number of seedlings recruited in the experimental treatments, for the total amount of seedlings (Total) and for those excluding the seedlings found under live pines (see Fig. 1).

| Category | Explanatory variable | Number of seedlings | | |
| | | $\chi^2$ | df | $P$ |
| --- | --- | --- | --- | --- |
| Total | Treatment† | 0.26 | 2 | 0.88 |
| | Proportion live pines‡ | 5.54 | 1 | **<0.02** |
| Excluding seedlings under live pines | Treatment | 3.80 | 2 | 0.15 |

*Note:* Reported values refer to the changes in log-likelihood obtained by the elimination of the explanatory variable from the model. The minimal adequate model contained only the proportion of replicate area covered by live pines as a fixed factor, as well as the random term (a random intercept and slope of sampling year for each experimental replicate).

†Experimental burnt-wood management treatments: Non-Intervention (NI), Partial Cut plus Lopping (PCL), and Salvage Logging (SL).

‡Percentage of area covered by patches of live pines in a particular experimental replicate, calculated using GIS.

However, the potential use of burnt forests by jays as a suitable habitat for foraging and acorn caching remained untested. Jay selection of live unburnt conifer forest for caching acorns seems to be related to the lower predation risk posed by their own predators, to the suitability of this forest type for breeding (when cached food is more crucial), or to the avoidance of competitors (intra or interspecific) for cached acorns (Andrén 1990, Rolando 1998). Furthermore, jays use visual cues (such as trunks or rocks) to select caching sites that can be memorized for future food recovery (Bennett 1993, Clayton and Krebs 1994, Lanner 1996). All of these characteristics may still be found in a burnt, unsalvaged forest: vertical habitat complexity and tree overstory which may reduce jay predation risk (as opposed to a salvaged area), enough distance to acorn sources to reduce competition, and a large number of visual cues (tree trunks) to hide acorns (see Castro et al. 2010a for similar results of jay habitat selection in the same burnt site across an altitudinal gradient). Our results therefore corroborate our working hypothesis as the burnt forest, if not salvaged, was a suitable habitat for jay activity, likely because of the habitat complexity still provided by the standing, burnt trees. By contrast, in the salvaged areas the activity of jays was reduced given that it was devoid of trees. The low selection by jays of a treatment where most trees were cut and lopped (PCL treatment) supports the relevance of keeping a vertical structure of trees (even burnt) for jay habitat selection.

The maintenance of the jay-oak interaction after a fire provides the opportunity for adaptive management that helps reduce restoration costs.

The ecological and economic role of jays has been demonstrated for oak forest expansion and maintenance at a landscape level (Mosandl and Kleinert 1998, Gómez 2004, Hougner et al. 2006, Purves et al. 2007, Puerta-Piñero et al. 2012b). In our study, the result of the post-treatment activity of jays, spanning only five years after the fire, resulted in the recruitment of 23 oaks per hectare in the NI treatment (sum of oak seedlings divided by the surface of the three replicates). Although low, we should consider that this is the net result after different post-dispersal processes occur, such as seed predation by other predators (that was in fact high in the area during the study years; Puerta-Piñero et al. 2010), germination, or emergence (Gómez 2004, Puerta-Piñero 2010). In addition, the maintenance of the burnt, standing trees after the fire helps to increase the resilience of the system, as it provides a mechanism to accelerate succession and the long-distance colonization and regeneration of the burnt area. Many *Pinaceae* members from the Palaearctic cannot resprout and do not form serotinous cones that resist fire (e.g., most *Pinus* species, *Picea abies*, *Larix decidua* or *Abies* spp.; see Richardson 1998 for *Pinus*), therefore relying on seed dispersal (usually of dozens of meters; e.g., Debain et al. 2007) for regeneration. Jays disperse nuts to larger distances, and thus might accelerate the recovery of a tree cover in burnt coniferous forests.

The effect of post-fire burnt-wood management on the jay-oak interaction reported here might also be common to millions of hectares in the world where oak and conifer forests coexist. First of all, the Eurasian jay is the main disperser of *Quercus* species as well as other *Fagaceae* (e.g.,

*Fagus* spp.) throughout the Palaearctic Region (Bossema 1979). Second, *Pinaceae* and *Fagaceae* species (either oaks or beech) are also species that comprise main forests in the Palaearctic, very often with large ecotone areas between them (Archibold 1995, Breckle 2002). Finally, the positive selection by jays of non-intervened burnt forest is probably a consequence of their niche requirements, as suggested above. Thus, it is likely that an outcome similar to that reported in this study will also apply to large areas of Eurasia wherever mature oak (or other *Fagaceae*) trees (whether forests or scattered individuals) are in contact with a burnt conifer forest.

In conclusion, our results demonstrate that post-fire salvage logging negatively affects a key, positive plant-animal interaction for forest regeneration. Different post-fire treatments altered jay behavior in terms of seed dispersal, which subsequently altered the spatial pattern of seedling recruitment. Recent studies are showing that salvage logging alters other interactions as well, such as herbivory (increasing its impact after log removal; Relva et al. 2009), ungulate-wolf interaction (Hebblewhite et al. 2009), or seed dispersal by frugivorous birds (Rost et al. 2009, 2010). All this supports that salvage logging may interfere with a wide array of species interactions, adding to the growing body of evidence that shows its potential impact at the ecosystem level.

## ACKNOWLEDGMENTS

## LITERATURE CITED

Andrén, H. 1990. Despotic distribution, unequal reproductive success, and population regulation in the jay *Garrulus glandarius* L. Ecology 71:1796–1803.

Archibold, O. W. 1995. Ecology of the world vegetation. Chapman & Hall, London, UK.

Bates, D., M. Maechler, and B. Bolker. 2011. lme4: Linear mixed-effects models using S4 classes. R package version 0.999375-42. http://CRAN.Rproject.org/package=lme4

Beschta, R. L., J. J. Rhodes, B. Kauffman, R. E. Gresswell, W. Minshall, J. R. Karr, D. A. Perry, F. R. Hauer, and C. A. Frissell. 2004. Post-fire management on forested public lands of the western United States. Conservation Biology 18:957–967.

Bennett, A. T. D. 1993. Spatial memory in a food storing corvid 1. Near tall landmarks are prmarily used. Journal of Comparative Physiology A. Sensory, Neural and Behavioral Physiology 173:193–207.

Bibby, C. J., N. D. Burgess, and D. A. Hill. 1992. Bird census techniques. Cambridge University Press, Cambridge, UK.

Bossema, I. 1979. Jays and oaks: and eco-ethological study of a symbiosis. Behaviour 70:1–117.

Breckle, S.-W. 2002. Walter's vegetation of the earth: the ecological systems of the geo-biosphere. Fourth edition. Springer-Verlag, Berlin, Germany.

Bros, V., G. Moreno-Rueda, and X. Santos. 2011. Does postfire management affect the recovery of Mediterranean communities? The case study of terrestrial gastropods. Forest Ecology and Management 261:611–619.

Castro, J., G. Moreno-Rueda, and J. A. Hódar. 2010*a*. Experimental test of postfire management in pine forests: impact of salvage logging versus partial cutting and nonintervention on bird-species assemblages. Conservation Biology 24:810–819.

Castro, J., S. Marañón-Jiménez, A. Sánchez-Miranda, and J. Lorite. 2010*b*. Efecto del manejo de la madera quemada sobre la regeneración forestal post-incendio: desarrollo de técnicas blandas de restauración ecológica. Pages 139–157 *in* L. Ramírez and B. Asensio, editors. Proyectos de investigación en parques nacionales: 2006-2009. Organismo Autónomo de Parques Nacionales, Madrid, Spain.

Castro, J., C. D. Allen, M. Molina-Morales, S. Marañón-Jiménez, A. Sánchez-Miranda, and R. Zamora. 2011. Salvage logging versus the use of burnt wood as a nurse object to promote post-fire tree seedling establishment. Restoration Ecology 19:537–544.

Clayton, N. S., and J. R. Krebs. 1994. Memory for spatial and object-specific cues in food-storing and

nonstoring birds. Journal of Comparative Physiology A. Sensory, Neural and Behavioral Physiology 174:371–379.

Cody, M. L. 1985. Habitat selection in birds. Academic Press, San Diego, California, USA.

Debain, S., J. Chadoeuf, T. Curt, G. Kunstler, and J. Lepart. 2007. Comparing effective dispersal in expanding population of *Pinus sylvestris* and *Pinus nigra* in calcareous grassland. Canadian Journal of Forest Research 37:705–718.

DellaSala, D. A., J. R. Karr, T. Schoennagel, D. Perry, R. F. Noss, D. Lindenmayer, R. Beschta, R. L. Hutto, M. E. Swanson, and J. Evans. 2006. Post-fire logging debate ignores many issues. Science 314:51.

Donato, D. C., J. B. Fontaine, J. L. Campbell, W. D. Robinson, J. B. Kauffman, and B. E. Law. 2006. Post-fire logging hinders regeneration and increases fire risk. Science 311:352.

Gómez, J. M. 2003. Spatial patterns in long-distance dispersal of *Quercus ilex* acorns by jays in a heterogeneous landscape. Ecography 26:573–584.

Gómez, J. M. 2004. Importance of microhabitat and acorn burial on *Quercus ilex* early recruitment: non-additive effects on multiple demographic processes. Plant Ecology 192:287–297.

Gómez, J. M., C. Puerta-Piñero, and E. W. Schupp. 2008. Effectiveness of rodents as local seed dispersers of Holm oaks. Oecologia 155:529–537.

Hebblewhite, M., R. H. Munro, and E. H. Merrill. 2009. Trophic consequences of postfire logging in a wolf-ungulate system. Forest Ecology and Management 257:1053–1062.

Hougner, C., J. Colding, and T. Söderqvist. 2006. Economic valuation of a seed dispersal service in the Stockholm National Urban Park, Sweden. Ecological Economics 59:364–374.

Hutto, R. L. 2006. Toward meaningful snag-management guidelines for postfire salvage logging in North American conifer forests. Conservation Biology 20:984–993.

Karr, J. R., J. J. Rhodes, G. W. Minshall, F. R. Hauer, R. L. Beschta, C. A. Frissell, and D. A. Perry. 2004. The effects of postfire salvage logging on aquatic ecosystems in the American West. BioScience 54:1029–1033.

Kollmann, J. and H. P. Schill. 1996. Spatial pattern of dispersal, seed predation and germination during colonization of abandoned grassland by *Quercus petraea* and *Corylus avellana*. Vegetatio 125:193–205.

Lanner, R. M. 1996. Made for each other: A symbiosis of birds and pines. Oxford University Press, Oxford, UK.

Lindenmayer, D. B., and R. F. Noss. 2006. Salvage logging, ecosystem processes, and biodiversity conservation. Conservation Biology 20:949–958.

Lindenmayer, D. B., D. R. Foster, J. F. Franklin, M. L. Hunter, R. F. Noss, F. A. Schmiegelow, and D.

Perry. 2004. Salvage harvesting policies after natural disturbances. Science 303:1303.

Lindenmayer, D. B., P. J. Burton, and J. F. Franklin. 2008. Salvage logging and its ecological consequences. Island Press, Washington, D.C., USA.

Lookingbill, T. R., and M. A. Zavala. 2000. Spatial pattern of *Quercus ilex* and *Quercus pubescens* recruitment in *Pinus halepensis* dominated woodlands. Journal of Vegetation Science 11:607–612.

Marañón-Jiménez, S., and J. Castro. In press. Effect of decomposing burnt wood on soil fertility and nutrient availability in a Mediterranean ecosystem. Biogeochemistry. doi: 10.1007/s10533-012-9744-x

Mavsar, R., E. Varela, P. Corona, A. Barbati, and G. Marsh. 2011. Economic, legal and social aspects of post-fire management. Pages 44–78 *in* F. Moreira, M. Arianoutsou, P. Corona, and J. De las Heras, editors. Post-fire management and restoration of southern European forests. Springer, New York, New York, USA.

McIver, J. D., and L. Starr. 2000. Environmental effects of post-fire logging: literature review and annotated bibliography. General Technical Report PNW-GTR-486. U.S. Department of Agriculture, Portland, Oregon, USA.

Millennium Ecosystem Assessment. 2005. Ecosystems and human well-being: Synthesis. Island Press, Washington, D.C., USA.

Mosandl, R., and A. Kleinert. 1998. Development of oaks (*Quercus petraea* (Matt.) Liebl.) emerged from bird-dispersed seeds under old-growth pine (*Pinus sylvestris* L.) stands. Forest Ecology and Management 106:35–44.

Muñoz, A., and R. Bonal. 2007. Rodents change acorn dispersal behaviour in response to ungulate presence. Oikos 116:1631–1638.

Pons, J., and J. C. Pausas. 2007. Acorn dispersal estimated by radio-tracking. Oecologia 153:903–911.

Puerta-Piñero, C. 2010. Intermediate spatial variations on acorn predation shapes Holm oak establishment within a Mediterranean landscape context. Plant Ecology 210:213–224.

Puerta-Piñero, C., A. Sánchez-Miranda, A. Leverkus, and J. Castro. 2010. Management of burnt wood after fire affects post-dispersal acorn predation. Forest Ecology and Management 260:345–352.

Puerta-Piñero, C., J. Pino, and J. M. Gómez. 2012*a*. Direct and indirect landscape effects on *Quercus ilex* regeneration in heterogeneous environments. Oecologia. doi: 10.1007/s00442-012-2373-1

Puerta-Piñero, C., L. Brotons, L. Coll, and J. R. González-Olabarría. 2012*b*. Valuing acorn dispersal and resprouting capacity ecological functions to ensure Mediterranean forest resilience after fire. European Journal of Forest Research 131:835–844.

Pulido, F. J., and M. Díaz. 2005. Regeneration of a

Mediterranean oak: a whole-cycle approach. Ecoscience 12:92–102.

Purves, D. W., M. A. Zavala, K. Ogle, F. Prieto, and J. M. Rey-Benayas. 2007. Environmental heterogeneity, bird-mediated directed dispersal, and oak woodland dynamics in Mediterranean Spain. Ecological Monographs 77:77–97.

R Development Core Team. 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Relva, M. A., C. López-Westerholm, and T. Kitzberger. 2009. Effects of introduced ungulates on forest understory communities in northern Patagonia are modified by timing and severity of stand mortality. Plant Ecology 201:11–22.

Richardson, D. M. 1998. Ecology and biogeography of Pinus. Cambridge University Press, Cambridge, UK.

Rodrigo, A., J. Retana, and F. X. Picó. 2004. Direct regeneration is not the only response of Mediterranean forests to large fires. Ecology 85:716–729.

Rolando, A. 1998. Factors affecting movements and home ranges in the jay (*Garrulus glandarius*). Journal of Zoology 246:249–257.

Rost, J., P. Pons, and J. M. Bas. 2009. Can salvage logging affect seed dispersal by birds into burned forests? Acta Oecologica 35:763–768.

Rost, J., M. Clavero, J. M. Bas, and P. Pons. 2010. Building wood debris piles benefits avian seed dispersers in burned and logged Mediterranean pine forests. Forest Ecology and Management 260:79–86.

Serrano-Ortiz, P., S. Marañón-Jiménez, B. R. Reverter, E. C. Sánchez-Cañete, J. Castro, R. Zamora, and A. S. Kowalski. 2011. Post-fire salvage logging reduces carbon sequestration in Mediterranean coniferous forest. Forest Ecology and Management 262:2287–2296.

Valle, F. 2003. Mapa de series de vegetación de Andalucía. Editorial Rueda, Madrid, Spain.

Van Nieuwstadt, M. G. L., D. Sheil, and K. Kartawinata. 2001. The ecological consequences of logging in the burned forest of east Kalimantan, Indonesia. Conservation Biology 15:1183–1186.

## SUPPLEMENTAL MATERIAL

## APPENDIX A

Table A1. Summary of the flights of jays during the acorn-dispersal period in autumn 2008.

| Site | Arrivals | Departures | Arrivals from oak patches# |
|---|---|---|---|
| Treatment NI† | **51** | **47** | **24** |
| NI-1 | 27 | 26 | 12 |
| NI-2 | 13 | 9 | 6 |
| NI-3 | 11 | 12 | 6 |
| Treatment PCL† | **10** | **4** | **3** |
| PCL-1 | 1 | 0 | 0 |
| PCL-2 | 7 | 4 | 2 |
| PCL-3 | 2 | 0 | 1 |
| Treatment SL† | **2** | **0** | **1** |
| SL-1 | 2 | 0 | 1 |
| SL-2 | 0 | 0 | 0 |
| SL-3 | 0 | 0 | 0 |
| Subtotal experimental plot‡ | 63 | 51 | 28†† |
| Subtotal oak patches | 51 | 60 | 5 |
| Subtotal other vegetation patches§ | 44 | 19 | 22 |
| Total¶ | 158 | 130 | 55 |

*Note:* We recorded a total of 167 flights, which we divided into arrivals and departures from/to the experimental plot, oak patches, and other vegetation patches.

†Sums of the three replicates of each treatment (underneath). Treatments are: Non-Intervention (NI), Partial Cut plus Lopping (PCL), and Salvage Logging (SL).

‡Sum of NI, PCL, and SL.

§Flights among patches outside the experimental plot or the oak patches. These movements were mostly to live pine patches not affected by the fire, and to almond tree and chestnut orchards.

¶Arrival or departure was unknown in some of the flights, so the totals are below 167 (the total number of flight registered).

#These arrivals are a subset of the total arrivals.

††These were acorn-dispersal flights from oak patches to the experimental plot with known departure and arrival points (thus with known flight distances). These are the data used for analysis shown in Table 1.

# Appendix B

Table B1. Total numbers of seedlings from acorns dispersed by jays after the fire in each experimental replicate during the sampling period, lasting four years (acorns dispersed from autumn 2007 to autumn 2010).

| Treatment† | Replicate | Altitude (m a.s.l.) | Replicate area (ha) | Area covered by live pines (ha)‡ | Total seedlings | Seedlings under live pines§ |
|---|---|---|---|---|---|---|
| NI | 1 | 1432 | 2.62 | 0.95 | 122 | 85 |
| NI | 2 | 1486 | 2.42 | 0.30 | 14 | 10 |
| NI | 3 | 1533 | 1.89 | 0.00 | 25 | 0 |
| PCL | 1 | 1430 | 1.88 | 0.00 | 11 | 0 |
| PCL | 2 | 1474 | 2.32 | 0.00 | 16 | 0 |
| PCL | 3 | 1516 | 1.29 | 0.00 | 1 | 0 |
| SL | 1 | 1432 | 1.46 | 0.26 | 42 | 22 |
| SL | 2 | 1474 | 2.06 | 0.00 | 6 | 0 |
| SL | 3 | 1522 | 1.73 | 0.00 | 7 | 0 |

†Burnt-wood management treatments are: Non-Intervention (NI), Partial Cut plus Lopping (PCL), and Salvage Logging (SL).
‡Three of the nine replicates had patches of live pines: NI-1, NI-2, and SL-1 (see Fig. 1).
§Subset of the total seedlings in each replicate that were found under live pines. These were zero in the replicates that did not have patches of live pines.