



Post-fire salvage logging alters species composition and reduces cover, richness, and diversity in Mediterranean plant communities



Alexandro B. Leverkus^{a,*}, Juan Lorite^b, Francisco B. Navarro^c,
Enrique P. Sánchez-Cañete^{d,e}, Jorge Castro^a

^a Departamento de Ecología, Facultad de Ciencias, Universidad de Granada, E-18071 Granada, Spain

^b Departamento de Botánica, Facultad de Ciencias, Universidad de Granada, E-18071 Granada, Spain

^c Grupo de Sistemas y Recursos Forestales, Área de Producción Ecológica y Recursos Naturales, IFAPA Centro Camino de Purchil, Camino de Purchil s/n, E-18004 Granada, Spain

^d Departamento de Desertificación y Geo-ecología, Estación Experimental de Zonas Áridas-CSIC, E-04120 Almería, Spain

^e Centro Andaluz de Medio Ambiente (CEAMA), E-18006 Granada, Spain

ARTICLE INFO

Article history:

Received 19 June 2013

Received in revised form

5 December 2013

Accepted 7 December 2013

Available online

Keywords:

Biological legacies

Clear-cutting

Post-fire restoration

Post-fire burnt-wood management

Salvage harvesting

Sierra Nevada National Park

ABSTRACT

An intense debate exists on the effects of post-fire salvage logging on plant community regeneration, but scant data are available derived from experimental studies. We analyzed the effects of salvage logging on plant community regeneration in terms of species richness, diversity, cover, and composition by experimentally managing a burnt forest on a Mediterranean mountain (Sierra Nevada, S Spain). In each of three plots located at different elevations, three replicates of three treatments were implemented seven months after the fire, differing in the degree of intervention: “Non-Intervention” (all trees left standing), “Partial Cut plus Logging” (felling 90% of the trees, cutting the main branches, and leaving all the biomass *in situ*), and “Salvage Logging” (felling and piling the logs, and masticating the woody debris). Plant composition in each treatment was monitored two years after the fire in linear point transects. Post-fire salvage logging was associated with reduced species richness, Shannon diversity, and total plant cover. Moreover, salvaged sites hosted different species assemblages and 25% lower cover of seeder species (but equal cover of resprouters) compared to the other treatments. Cover of trees and shrubs was also lowest in Salvage Logging, which could suggest a potential slow-down of forest regeneration. Most of these results were consistent among the three plots despite plots hosting different plant communities. Concluding, our study suggests that salvage logging may reduce species richness and diversity, as well as the recruitment of woody species, which could delay the natural regeneration of the ecosystem.

© 2013 Elsevier Ltd. All rights reserved.

1. Introduction

Predicting the effects of anthropogenic changes mediated by land uses or disturbances has been a central concern of ecological research (e.g. Grime, 1979; Lavorel et al., 1997). Ecosystems show remarkable differences in their capacity to regenerate after disturbance depending on the type of vegetation, disturbance characteristics, and historical background. After disturbance, large amounts of ecological legacies can remain, which play crucial roles in ecosystem recovery and influence ecosystem processes for decades or centuries (Foster et al., 1998). Ecological legacies are the

residues left after disturbance, and they are composed of both biological and physical components (Turner and Dale, 1998).

Biological legacies left after a wildfire, such as remaining burnt trees, logs and branches, as well as surviving vegetation, aid ecosystem recovery by retaining soil (Reeves et al., 2006), producing nutrient inputs in the short- and the long-term (Brais et al., 2000; Marañón-Jiménez and Castro, 2013), favoring mutualistic plant–animal interactions (Castro et al., 2012), acting as seed traps (Marzano et al., 2013), facilitating survival and population viability in disturbed areas (Castro et al., 2011; Leverkus et al., 2012), and promoting plant and animal (re) colonization by providing habitat features, substrate, and food for many species (Lindenmayer and Noss, 2006; Lindenmayer et al., 2008). However, the ecological role of these biological legacies in post-fire ecosystems has long been neglected by managers and policymakers, associated with the lack of scientific evidence of their importance (McIver and Starr,

* Corresponding author. Fax: +34 958 246166.

E-mail address: leverkus@ugr.es (A.B. Leverkus).

2001). In fact, the removal of some of the biological legacies (i.e. the burnt biomass) is one of the most common post-fire management strategies worldwide, also called salvage logging (McIver and Starr, 2001; Beschta et al., 2004; Lindenmayer and Noss, 2006; Lindenmayer et al., 2008). Post-fire salvage logging consists in the felling and removal of the burnt trunks, often including the elimination of the remaining woody debris. Major motivations for post-fire salvage logging can differ, although the most important are economic (recovering part of the forest capital) or silvicultural (aiding the management and restoration of the burnt site; Lindenmayer et al., 2004, 2008; Donato et al., 2006; Castro et al., 2010). However, there is increasing evidence that biological legacies are components of natural systems that promote ecosystem recovery and diversity, and that their extraction represents a further disturbance which acts synergistically with the original one and may lead to effects that would not be expected by considering one of the disturbances (i.e. fire or logging) alone (Lindenmayer et al., 2004, 2008; Beschta et al., 2004; DellaSala et al., 2006; Hutto, 2006). As a result, there are growing calls to implement post-fire policies of retention of all or at least part of the biomass (DellaSala et al., 2006; Lindenmayer et al., 2008; Castro et al., 2011; Marzano et al., 2013; Marañón-Jiménez et al., 2013a).

Potential reductions in species diversity and changes in community assemblages are among the major concerns about post-fire salvage logging (Franklin et al., 2000). As this management practice can dramatically change habitat structure and other abiotic conditions (McIver and Ottmar, 2007; Castro et al., 2011), these can in turn alter the composition and relative abundance of species, as well as the successional trajectories of plant communities (Purdon et al., 2004; Macdonald, 2007; Beghin et al., 2010; Marzano et al., 2013). The effect of salvage logging on plant diversity has been addressed in some studies, and it often points to reductions in species richness and/or diversity (Sexton, 1998; Purdon et al., 2004; Bradbury, 2006; Marzano et al., 2013). However, the overall trends on plant species richness and diversity are not clear, as some studies have found no effects (e.g. Macdonald, 2007) or even positive effects of salvage logging (e.g. Ne'eman et al., 1995; Kurulok and Macdonald, 2007).

Differing results for salvage logging effects on species richness and diversity can be explained by several factors related to fire characteristics, the nature and timing of the logging operations, or ecosystem features (Lindenmayer and Ough, 2006; Lindenmayer et al., 2008), but it is hard to draw conclusions because most studies have not been performed under controlled and designed experiments. In fact, part of the scientific literature dealing with ecological consequences of post-fire logging predicts effects but without testing them (Van Nieuwstadt et al., 2001; Reeves et al., 2006; Lindenmayer and Ough, 2006). Among experimental studies, most have sampled salvaged sites without the consideration of unsalvaged controls (Greenberg et al., 1992; Greenberg and Mcgrane, 1995), made use of areas that have been differently managed for reasons other than the experiment itself (e.g. Martínez-Sánchez and Ferrandis, 1999; Purdon et al., 2004; Bradbury, 2006; Foster and Orwig, 2006; Kurulok and Macdonald, 2007; Macdonald, 2007), or carried out unreplicated experiments (e.g. Martínez-Sánchez and Ferrandis, 1999; Spanos et al., 2005; Beghin et al., 2010). Altogether, these studies have provided crucial and urgent information about the potential impacts of post-fire salvage logging. However, problems of lack of proper experimental designs and the imperative need of such an approach have previously been pointed out (McIver and Starr, 2001; Lindenmayer and Noss, 2006; Lindenmayer and Ough, 2006) and are common throughout conservation science in general (Sutherland et al., 2004), but studies with an experimental approach remain scarce (but see Ne'eman et al., 1995; McIver and Ottmar, 2007; Fernández et al., 2008).

In this study we seek to analyze the effects of salvage logging on post-fire plant communities. We made use of a replicated experimental design that was set up in a burnt pine reforestation in the Sierra Nevada National Park (Spain) to study the effects of three burnt-wood management treatments (salvage logging, a partial felling treatment without biomass extraction, and non-intervention) on plant community regeneration two years after fire. This experimental design allowed making rigorous assessments of the working hypotheses that burnt-wood management affects plant communities in terms of: i) species richness and diversity, ii) percent cover, and iii) species composition and abundance. Overall, we aimed to investigate whether this silvicultural practice could change the patterns of regeneration of plant communities in a Mediterranean mountain ecosystem.

2. Methods

2.1. Study area and experimental design

The study site was located in the Sierra Nevada Natural and National Park (SE Spain; 37°N, 3°W), where in September 2005 the Lanjarón fire burned 1300 ha of pine reforestations (3420 ha in total) with 35–45 year-old trees. The fire, moderate to high in severity, consumed or totally scorched most of the tree crown (Marañón-Jiménez et al., 2013b). Climate in the area is Mediterranean, with hot, dry summers and mild, wet winters (see Table 1 for details).

Three plots of ca. 25 ha each were established after the fire along an elevational gradient, with similar aspect (SW) and slope (28.7–31.4%). The pine species present in each plot differed according to their ecological requirements along this elevational/moisture gradient (Table 1). All of them are native in the region, although they were extensively planted in the area for soil protection after long-term degradation resulting from human intervention. The area surrounding the plots was dominated by shrublands mixed with scattered individual holm oaks (*Quercus ilex* subsp. *ballota*

Table 1
Main characteristics of the experimental site.

	Plot		
	1	2	3
UTM coordinates (x; y) ^a	456070E– 4089811N	455449E–4 091728N	457244E– 4091551N
Plot area (ha)	17.7	23.9	31.7
Subplot area (ha) ^b	2.0 ± 0.15	2.7 ± 0.18	3.5 ± 0.30
Elevation ^a	1477	1698	2053
Slope (%) ^c	30.3	28.7	31.4
Mean daily min. temp. (°C) ^d	6.8 ± 0.2	5.6 ± 0.2	3.4 ± 0.2
Mean daily max. temp. (°C) ^d	17.1 ± 0.2	16.2 ± 0.2	13.4 ± 0.2
Mean ann. precip. (mm) ^d	501 ± 49	550 ± 40	630 ± 42
Dominant species	<i>Pinus pinaster</i> / <i>P. nigra</i>	<i>Pinus nigra</i>	<i>Pinus sylvestris</i>
Tree density (trees/ha) ^e	1477 ± 46	1064 ± 67	1051 ± 42
Tree basal diameter (cm) ^e	17.7 ± 0.2	18.3 ± 0.1	15.7 ± 0.1
Tree diameter at 1.30 m (cm) ^e	13.3 ± 0.2	14.5 ± 0.2	10.7 ± 0.2
Tree height (m) ^e	6.3 ± 0.1	6.6 ± 0.1	6.2 ± 0.1

^a Coordinates and elevation measured at the centroid of each plot (UTM zone 30N, Datum: ED-50).

^b There was no significant difference in subplot area among treatments (Kruskal Wallis test; $P > 0.05$).

^c Mean slope of the nine subplots.

^d Data obtained from interpolated maps of Sierra Nevada (1981–2010) created at the Centro Andaluz de Medio Ambiente (CEAMA) except precipitation in Plot 1, which is an empirical value obtained at Plot 1 (1988–2011).

^e Measured after the fire. Density sampled in each subplot by counting the trees in four randomly placed 25 × 25 m quadrats. Basal tree diameter was measured on 30 randomly chosen trees in these quadrats, thus 120 trees per subplot.

(Desf.) Samp.) which likely dominated the canopy before human presence (Valle, 2003). Each of the three plots was divided into nine subplots of ca. 2.5 ha each, which were randomly assigned one of the following burnt-wood management regimes:

- 1) “Non-Intervention” (NI).
- 2) “Partial Cut plus Lopping” (PCL), where 90% of the burnt trees were felled, with the main branches also lopped off, and leaving all the cut biomass *in situ* on the ground without chopping.
- 3) “Salvage Logging” (SL), where the trees were felled and the trunks cleaned of branches with chainsaws. Trunks were piled in groups of 10–15, and the remaining branches and woody debris were chopped with a crawler tractor with a mechanical chopper.

Treatments consequently differed both in the time spent on site by machinery and workers, as well as in the resulting habitat structure (Leverkus et al., 2012, 2013). The resulting experimental design corresponds to a generalized randomized block design (Quinn and Keough, 2002) with three blocks each containing three replicates of each of three treatments. All post-fire management treatments were implemented between March and May 2006 (six to eight months after the fire). Subplots did not significantly vary across treatments in terms of pre-fire tree density or dbh (Kruskal–Wallis tests; $P > 0.01$). Pre-fire conditions were likely of low seedling abundance and low species richness and diversity due to the competition imposed by pines (Manor et al., 2008; Gómez-Aparicio et al., 2009; Salvatore and La Mantia, 2012).

2.2. Sampling of species composition and cover

Plant species composition and cover were sampled between May and July 2007 –during the second growing season after the fire–, at bloom peak in each plot. For this, in each subplot we randomly placed 8 linear transects of 25 m with three contact points every 0.5 m: at the center and 1 m to each side of the transect ($n = 150$ points per transect). In one of the PCL subplots of Plot 1 we sampled only 5 transects, so there were 213 transects in total. For each contact point we noted the nature of the contact (soil or vegetation). In case of contact with vegetation, species identity was determined for non-annual plant species (i.e. phanerophytes, chamaephytes, hemicryptophytes, or geophytes, according Raunkjaer’s system; Raunkjaer, 1934), while annual species were noted and used for the calculation of vegetation cover but not classified into species. Non-annual species (hereafter referred to as perennials but also including biennials) were classified according to their post-fire regeneration strategy (seeders, resprouters, or both), in accordance with the literature (Lorite et al., 2007, 2010; Blanca et al., 2009) and expert knowledge (Appendix S1). Nomenclature of species throughout the manuscript follows *Flora de Andalucía Oriental* (Blanca et al., 2009) or *Flora iberica* (Castroviejo et al., 1986–2012).

2.3. Parameters estimated

For each transect we calculated: (1) total percent cover and percent cover of annuals, perennials, phanerophytes, seeders, resprouters, and of each species; (2) plant species richness, as the number of species intercepting at least one point of the transect. (3) Shannon-Weaver diversity index for perennial species, as:

$$H' = - \sum (p_i * \log_{10}(p_i))$$

where p_i is the relative cover of species i (Magurran, 2004).

2.4. Statistical analyses

To test hypothesis (i) (changes in species richness and diversity due to burnt-wood management) we used two approaches. First, we calculated Chao 1 species richness estimators for each treatment in each plot with the EstimateS software (Colwell, 2009). We then compared the treatments (separately for each plot) in terms of the 95% confidence intervals provided by the software. For the computation of the Chao 1 estimators a total of 24 transects were available for each treatment within each plot (8 transects/subplot \times 3 subplots/plot) except in PCL of Plot 1, with only 21 transects. Although estimators generated with different sampling effort should not be compared due to the positive relationship between sampling effort and species richness (Magurran, 2004), in this case the method is conservative because the value for salvage logging was smaller despite the greater sampling effort.

Second, we analyzed species richness and Shannon diversity with mixed modeling in R version 2.15.0 (R Development Core Team, 2012), using the “nlme” package (Pinheiro et al., 2012). Prior to the modeling, we averaged the values of the transects to generate one value per subplot and eliminate pseudoreplication. Wood management treatment was the only fixed factor, and Plot and the Wood management \times Plot interactions were random effects. Model simplification was carried out by eliminating Wood management from the model, and likelihood ratio tests (LRT) assessed for its significance. *Ad-hoc* differences among Wood management levels were assessed by merging two levels of the factor into a single level and performing LRTs among the model with the original and the new factor (Crawley, 2007). The random effects were also assessed through LRTs among models with and without the specified term. Heteroscedasticity at different spatial scales was assessed through the varIdent function, with the use of LRTs (Pinheiro and Bates, 2000). Assumption checking through plotting of residuals and random effects was carried out as suggested by Pinheiro and Bates (2000).

To test hypothesis (ii) (changes in plant cover due to burnt-wood management) we fit linear mixed models in R. Methods were the same as described for hypothesis (i). Total percent cover, as well as the percent cover of annuals, perennials, phanerophytes, seeders, and resprouters, were taken as response variables. Previous to analysis, percent cover data were square root, arcsine transformed (Crawley, 2007).

For hypothesis (iii) (changes in species composition and abundance due to burnt-wood management) we used two complementary approaches: multivariate analyses and indicator species analysis. First, we analyzed the composition of the plant community for the whole dataset and separately for each plot with multivariate methods with CANOCO v. 4.5 (Microcomputer Power, Ithaca, New York), following the recommendations by Ter Braak and Smilauer (2002) and Leps and Smilauer (2003). We used Detrended Correspondence Analyses (DCA) of the species abundance data as an unconstrained ordination method since the gradient of the first axis was longer than four standard deviation units of species turnover (cf. Jongman et al., 1995). These DCAs were detrended by segments, with log-data transformation and down-weighting rare species. Although environmental data did not influence the species and sample ordination in DCAs, nominal variables were included to be projected afterwards onto the ordination diagram (Leps and Smilauer, 2003). After this, we carried out Canonical Correspondence Analyses (CCA) as a constrained ordination method to extract any variation directly explainable by the explanatory variables. These nominal variables were previously converted into a series of zero/one dummy variables. These analyses were carried out with focus scaling on inter-sample distances, biplot scaling, log-transforming species data, and down-weighting

rare species. A Monte Carlo permutation test with 499 permutations was made with these explanatory variables to assess the significance of the first and of all the canonical axes.

Second, to test the effect of Plot, as well as Wood management within each plot, on individual species, we performed indicator species analysis (Dufrêne and Legendre, 1997) in R with the “labdsv” package (Roberts, 2012). This analysis generates an indicator value for each species and group of sites, which is the combination of the specificity and the fidelity of the species for a given group of sites (Dufrêne and Legendre, 1997). Indicator values range from 0 (species not present) to 100 (species always present and always absent from all other groups). A Markov Chain Monte Carlo resampling procedure with 10,000 permutations generated *P*-values for the significance of the indicator values. We first performed the analysis on the whole dataset, with plots as groups of sites, and then analyzed the data of each plot separately, with treatments as groups of sites. We report only those species found to be significant indicators of a plot or Wood management treatment ($P < 0.05$) and with indicator values above 25 (Dufrêne and Legendre, 1997).

3. Results

3.1. Plant species richness and diversity

We recorded a total of 100 perennial species throughout the study area (Appendix S1). The Chao 1 index calculated 103 species, with a 95% confidence interval of 99.8–118.9 species. We recorded 73 species in Plot 1, 66 in Plot 2, and 63 in Plot 3 (treatments pooled). Pooling plots, 87 species were found in NI, 79 in PCL, and 66 in SL. Observed species richness for treatments within plots was within the range of Chao estimates in most cases (Appendix S2).

Chao 1 richness estimators showed significantly lower species richness in SL as compared to both PCL and NI in Plot 1 and compared to NI in Plot 2, but no significant differences in Plot 3 (Appendix S2). Species richness and Shannon diversity at the transect level, analyzed with mixed models, were significantly affected by burnt-wood management (Table 2; Fig. 1). Both variables showed lower values in SL than in NI and PCL, with no significant differences among the latter. Plot was significant for both variables. For Shannon diversity there was a significant Wood management \times Plot interaction (Fig. 1).

3.2. Plant cover

Burnt-wood management significantly affected total plant cover and the percent cover of perennials, phanerophytes, and seeders

Table 2
Results of mixed models and effect sizes for burnt-wood management treatments.

Response var.	Fixed ^d	Random ^a	BWM ^b effect sizes ^c			
	BWM ^b	Plot (P)	BWM \times P	Non-intervention	Partial cut plus lopping	Salvage logging
Species richness	8.5	4.2	0.0	15.3 \pm 0.8 a	14.8 \pm 0.4 a	13.0 \pm 0.7 b
Shannon diversity	10.1	8.1	4.2	0.90 \pm 0.03 a	0.91 \pm 0.02 a	0.78 \pm 0.04 b
Total cover ^d	5.9	0.1	6.0	74.0 \pm 2.7 a	70.7 \pm 2.7 ab	63.2 \pm 3.7 b
Annuals cover ^d	1.3	12.3	3.9	23.1 \pm 3.2	19.9 \pm 2.6	24.6 \pm 5.0
Perennials cover ^d	16.7	27.5	0.2	50.9 \pm 4.4 a	50.8 \pm 3.8 a	38.6 \pm 4.9 b
Phanerophytes cover ^{d,e}	7.4	9.3	0.0	2.2 \pm 0.8 ab	3.9 \pm 1.6 a	0.7 \pm 0.4 b
Seeders cover ^d	15.9	30.7	0.2	48.4 \pm 4.9 a	48.8 \pm 4.1 a	36.7 \pm 5.3 b
Resprouters cover ^d	1.7	10.2	0.0	24.2 \pm 1.8	26.5 \pm 2.9	22.7 \pm 3.9

^a Values correspond to likelihood ratio tests among models with and without the given term. Differences among treatment levels were further assessed by merging two levels into one level and carrying out likelihood ratio tests. Significant effects (at $P = 0.05$) are shown in bold, and non-significant effects in italics.

^b BWM = burnt-wood management treatments.

^c Effect sizes are means and SE's (of the means), based on subplot mean values, averaged across plots. Letters indicate significant differences between treatments.

^d Percent cover data were arcsine-square root transformed.

^e Phanerophytes were the tree and shrub species *Adenocarpus decorticans*, *Berberis hispanica*, *Crataegus monogyna*, *Genista cinerea*, *Pinus pinaster*, *Pinus sylvestris*, *Populus nigra*, *Quercus ilex* subsp. *ballota*, *Rosa canina*, *Salix atrocinerea*, and *Spartium junceum*.

(Fig. 2). In all cases, cover was lower on salvaged sites than in non-intervention and/or PCL (Table 2). The cover of annuals and resprouters were not significantly affected by Wood management. The effect of Wood management on total cover varied between plots (significant Wood management \times Plot interaction) due to a similar interaction affecting the cover of annuals. Overall, all other effects were consistent among plots (Fig. 2, Table 2).

3.3. Species composition and abundance

The projection of the explanatory variables of DCA revealed that plots generated most of the variability in the data (Fig. 3), especially Plot 3, situated at the greatest elevation and with the highest species turnover. Similarities in species composition and abundance between NI and PCL were high overall, and differences with SL were more accentuated. The within-plot analyses showed that these between-treatment differences were mostly evident in Plots 2 and 3 (Fig. 4).

The first CCA canonical axis explained 74.5% of the variance of the species–environment relation in Plot 1, 66.9% in Plot 2, and 73.2% in Plot 3. Nearly all phanerophyte species were related to NI or PCL (*Berberis hispanica*, *Crataegus monogyna*, *Quercus ilex*, *Salix atrocinerea*, *Pinus pinaster*, *P. sylvestris*, *Populus nigra*, *Rosa canina*, *Populus* sp., *Spartium junceum*) but none to SL (Fig. 5). Moreover, earlier-successional species such as *Thymus mastichina*, *Artemisia campestris*, *Andryala ragusina*, *A. integrifolia*, *Picnomon acarna*, *Chondrilla juncea*, *Carthamus lanatus*, *Helichrysum italicum* subsp. *serotinum*, and *Santolina rosmarinifolia* were found near the SL centroids.

Indicator species analysis showed a variety of species indicative of each plot and of Wood management treatments within plots (Appendix S3). Remarkably, two phanerophytes were indicators of specific treatments: *Adenocarpus decorticans* (of NI in Plot 1 and of PCL in Plot 2) and *Pinus pinaster* (of PCL in Plot 1). No phanerophyte was an indicator of SL in any plot.

4. Discussion

Burnt-wood management affected post-fire regeneration. Species richness, Shannon diversity, and plant cover were lowest, and species composition of the plant communities was different, on salvaged sites as compared to the partial cut and the non-intervention treatments. These results make an important contribution to the knowledge of the ecological consequences of post-fire salvage logging because of the experimental design applied and

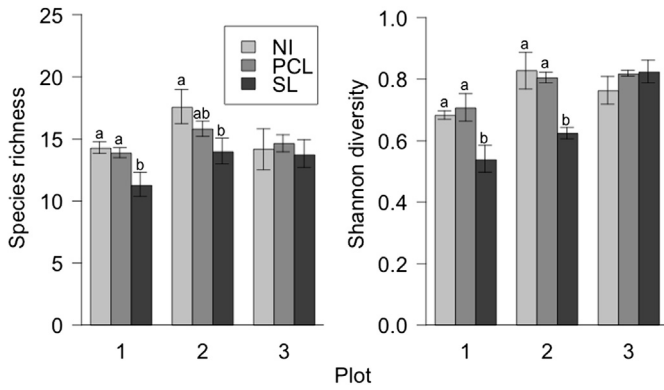


Fig. 1. Mean (± 1 SE of the mean) observed species richness and Shannon diversity per transect for each of the Wood management \times Plot combinations. Means and standard errors were calculated on the basis of subplot means. Letters above bars show within-plot significant differences among Wood management treatments, according to Tukey tests after one-way ANOVA. Treatments are NI = Non-Intervention, PCL = Partial Cut plus Logging, SL = Salvage Logging.

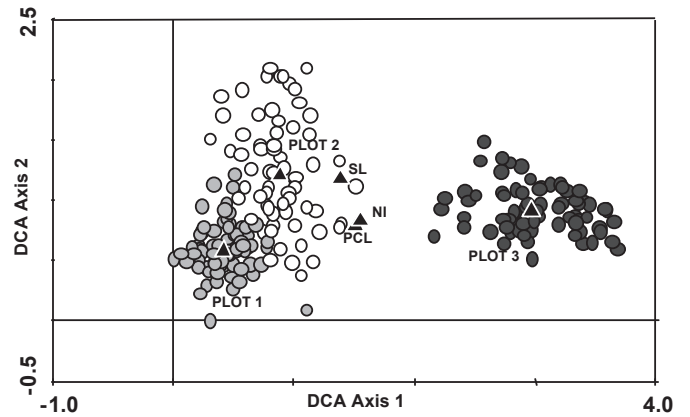


Fig. 3. Two-dimensional DCA ordination diagrams of the first two axes showing the distribution of all transects. Circles symbolize transect centroids obtained from species abundance data (grey circles = Plot 1, white = Plot 2, black = Plot 3), and their proximity means similarity. Triangles show the categorical variables projected *post hoc*. Treatments were: NI = Non-Intervention; PCL = Partial Cut plus Logging; SL = Salvage Logging.

due to the spatial consistency of effects on species richness and diversity even across an ecological gradient.

Overall, salvage logging showed a 12–15% lower number of species at the transect level than the other treatments. This could be explained by several non-exclusive mechanisms. First, the presence of burnt wood in treatments other than SL increased habitat heterogeneity (Lindenmayer et al., 2008; Leverkus et al., 2013), a factor that can prompt species richness (Tilman, 1982;

Kreft and Jetz, 2007). The spatially variable presence of trunks and branches of different sizes and decay levels can have effects on microclimatic conditions and soil properties that vary at the scale of microsites, leading to a heterogeneous light, wind, temperature, moisture, and nutrient environment (Söderström, 1988; Franklin et al., 2000; Castro et al., 2011). Following Tilman's (1982) resource competition theory, under such conditions many microsites with different resource ratios would exist, which would allow

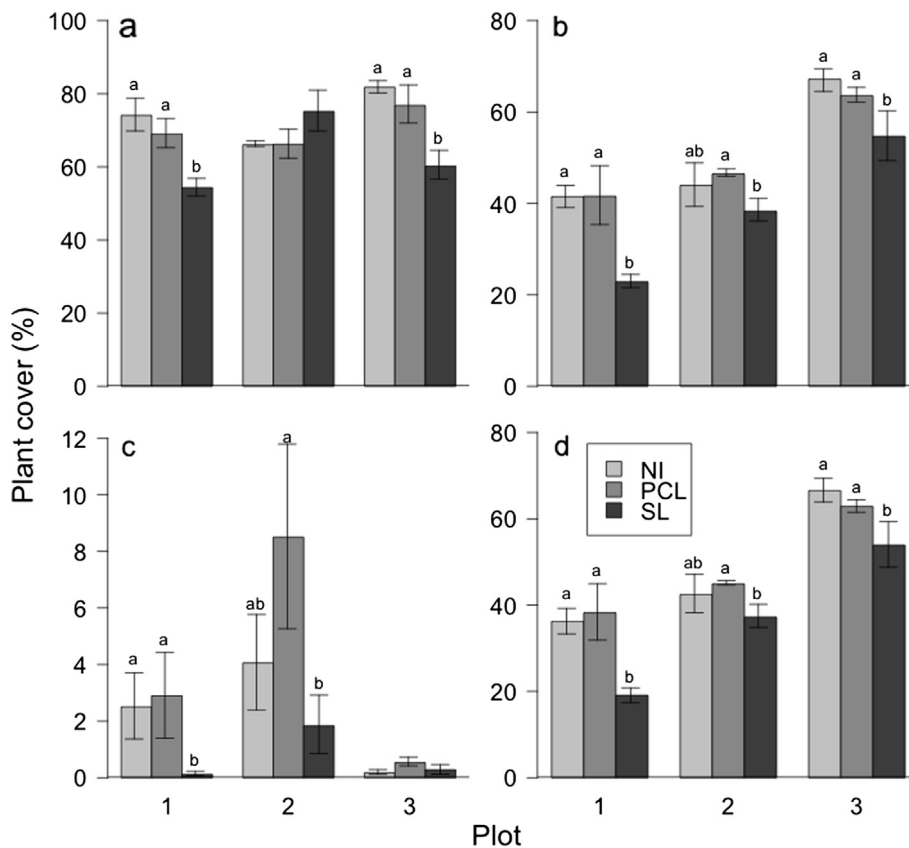
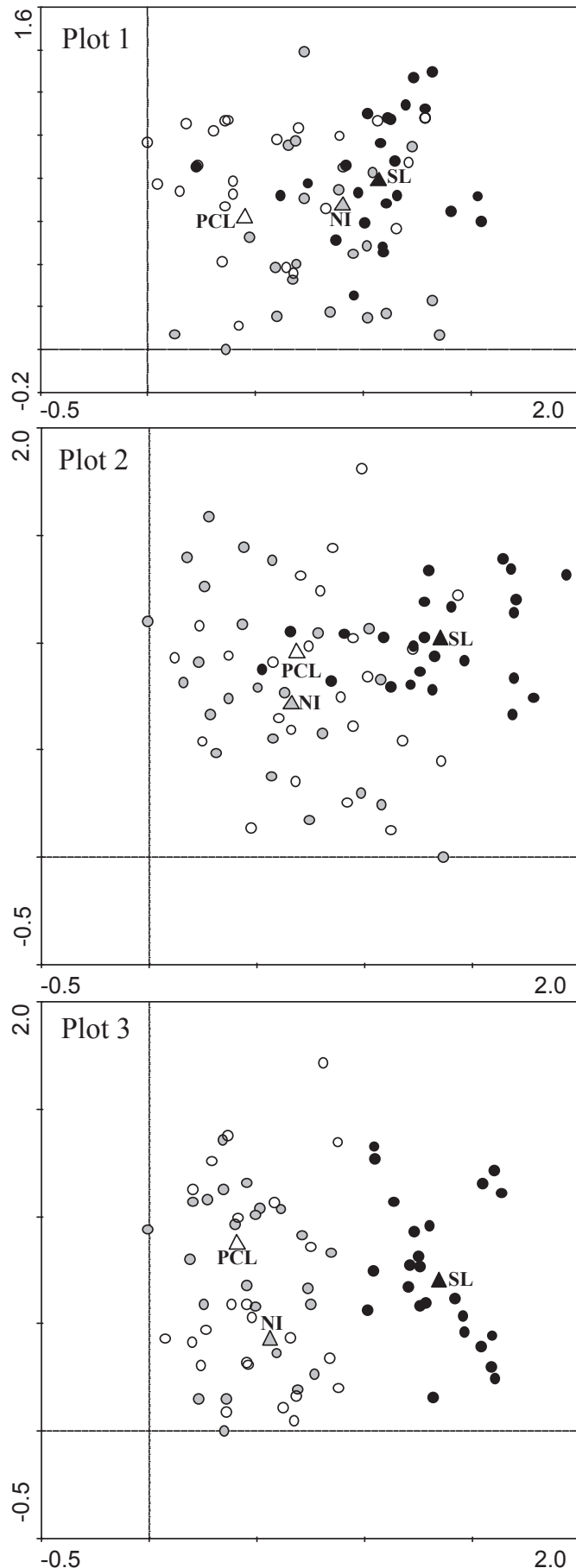


Fig. 2. Mean (± 1 SE of the mean) a) total plant cover and cover of b) perennials, c) phanerophytes, and d) seeders. Letters above bars show within-plot significant differences among Wood management treatments, according to Tukey tests after one-way ANOVA. Treatments are NI = Non-Intervention, PCL = Partial Cut plus Logging, SL = Salvage Logging.



more species to cover their niche requirements and be able to compete with other species. Second, deadwood can reduce microclimatic extremes and generate microsites where drought stress is reduced (e.g. [Marañón-Jiménez et al., 2013a](#)), increasing seedling survival ([Castro et al., 2011](#); [Leverkus et al., 2012](#); [Marzano et al., 2013](#)). As summer drought is a major cause of seedling mortality under Mediterranean climate ([Rey and Alcántara, 2000](#); [Castro et al., 2004](#); [Mendoza et al., 2009](#); [Matías et al., 2012](#)), this microclimatic amelioration would generate a “nursing” effect ([Castro et al., 2011](#)) and allow the establishment of more species. Third, the mechanical disturbance of logging activities can have effects on the recovering vegetation ([Martínez-Sánchez and Ferrandis, 1999](#); [Van Nieuwstadt et al., 2001](#); [Fraser et al., 2004](#); [Beschta et al., 2004](#)). The logging activities are usually associated with heavy machinery working on the ground, which can kill or damage the vegetation ([Van Nieuwstadt et al., 2001](#); [Donato et al., 2006](#); [Lindenmayer and Ough, 2006](#)). In our study, the work of crawler tractors in the salvage logging treatment might have had such an effect ([Castro et al., 2011](#)). This idea is supported by the fact that seed regenerators were particularly affected by the burnt wood treatments but resprouters were not. Seeders are expected to be more affected by salvage logging because of the greater vulnerability of seedlings to trampling. In contrast, resprouters can produce new shoots even if the aerial part is damaged during salvage operations.

Salvaged sites also yielded lower plant cover. This may be a consequence of the above-mentioned factors of harsher microclimatic conditions and the mechanical disturbance. Additionally, burnt wood still contains a large pool of nutrients (e.g. [Marañón-Jiménez et al., 2013b](#)), which can be key to ensure the sustainability of early-successional communities ([Jurgensen et al., 1997](#); [Augusto et al., 2000](#)) especially on nutrient-poor soils as in many areas around the Mediterranean. Wood decomposition had already generated important nutrient inputs to the soil by the year of vegetation sampling ([Marañón-Jiménez and Castro, 2013](#)), which could promote greater plant growth ([Peterson et al., 2009](#); [Marañón-Jiménez et al., 2013a](#)), hence increasing plant cover.

Another key effect of salvage logging was related to plant species assemblages. Overall, salvaged areas showed an increased presence of pioneer species, while late-successional species such as bushes and trees were more common in the other treatments, a result corroborated both by multivariate analysis and indicator species analysis. Mixed modeling also showed a greater cover of phanerophytes in unsalvaged subplots. Some of these phanerophytes can be considered key plant species for the development of the ecosystem. First, fleshy-fruited woody species such as *Crataegus monogyna* and *Berberis hispanica* are among the main species that benefit from reduced radiation and microclimatic amelioration ([Gómez-Aparicio et al., 2009](#)), and they attract avian seed dispersers that can further enrich the plant community ([Zamora et al., 2010](#); [Carlo et al., 2013](#)). This effect is likely to add upon the preference of birds for areas with standing dead trees, which may act as perches for seed dispersers ([Castro et al., 2010](#); [Cavallero et al., 2013](#)), and which have already contributed to a greater recruitment of *Quercus ilex* seedlings at our experimental site ([Castro et al., 2012](#)). Second, some of these species, such as *Q. ilex* and *P. pinaster*, are species of the mature community, indicating that the presence of burnt wood may accelerate succession. And third, *Adenocarpus*

Fig. 4. Two-dimensional DCA ordination diagrams of the first two axes showing the distribution of transects for each plot separately. Circles symbolize transect centroids obtained from species abundance data, and their proximity means similarity. Triangles show the categorical variables projected *post hoc* (NI = Non-Intervention (grey); PCL = Partial Cut plus Logging (white); SL = Salvage Logging (black)).

Innovación. AL had a Ph. D. grant from the Spanish *Ministerio de Educación, Cultura y Deporte* (Ref: AP2010-0272). Two anonymous reviewers provided useful comments that improved the manuscript.

Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.jenvman.2013.12.014>.

References

- Augusto, L., Ranger, J., Ponette, Q., Rapp, M., 2000. Relationships between forest tree species, stand production and stand nutrient amount. *Ann. Forest Sci.* 57, 313–324.
- Beghin, R., Lingua, E., Garbarino, M., Lonati, M., Bovio, G., Motta, R., Marzano, R., 2010. *Pinus sylvestris* forest regeneration under different post-fire restoration practices in the northwestern Italian Alps. *Ecol. Eng.* 36, 1365–1372.
- Beschta, R.L., Rhodes, J.J., Kauffman, J.B., Gresswell, R.E., Minshall, G.W., Karr, J.R., Perry, D.A., Hauer, F.R., Frissell, C.A., 2004. Postfire management on forested public lands of the Western United States. *Conserv. Biol.* 18, 957–967.
- Blanca, G., Cabezudo, B., Cueto, M., Fernández-López, C., Morales, C., 2009. Flora vascular de Andalucía Oriental, 4 vols. Consejería de Medio Ambiente, Junta de Andalucía, Sevilla.
- Bradbury, S.M., 2006. Response of the post-fire bryophyte community to salvage logging in boreal mixedwood forests of northeastern Alberta, Canada. *For. Ecol. Manag.* 234, 313–322.
- Brais, S., David, P., Ouimet, R., 2000. Impacts of wildfire severity and salvage harvesting on the nutrient balance of jack pine and black spruce boreal stands. *For. Ecol. Manag.* 137, 231–243.
- Carlo, T.A., García, D., Martínez, D., Gleditsch, J.M., Morales, J.M., 2013. Where do seeds go when they go far? Distance and directionality of avian seed dispersal in heterogeneous landscapes. *Ecology* 94, 301–307.
- Castro, J., Allen, C.D., Molina-Morales, M., Marañón-Jiménez, S., Sánchez-Miranda, Á., Zamora, R., 2011. Salvage logging versus the use of burnt wood as a nurse object to promote post-fire tree seedling establishment. *Restor. Ecol.* 19, 537–544.
- Castro, J., Moreno-Rueda, G., Hódar, J.A., 2010. Experimental test of postfire management in pine forests: impact of salvage logging versus partial cutting and nonintervention on bird-species assemblages. *Conserv. Biol.* 24, 810–819.
- Castro, J., Puerta-Piñero, C., Leverkus, A.B., Moreno-Rueda, G., Sánchez-Miranda, A., 2012. Post-fire salvage logging alters a key plant-animal interaction for forest regeneration. *Ecosphere* 3, 1–12.
- Castro, J., Zamora, R., Hódar, J.A., Gómez, J.M., 2004. Seedling establishment of a boreal tree species (*Pinus sylvestris*) at its southernmost distribution limit: consequences of being in a marginal Mediterranean habitat. *J. Ecol.* 92, 266–277.
- Castroviejo, S., et al., 1986–2012. Flora Iberica. In: Real Jardín Botánico. CSIC, Madrid.
- Cavallero, L., Raffaele, E., Aizen, M., 2013. Birds as mediators of passive restoration during early post-fire recovery. *Biol. Conserv.* 158, 342–350.
- Colwell, R.K., 2009. EstimateS: Statistical Estimation of Species Richness and Shared Species from Samples. Version 8.2. User's Guide and Application published at: <http://purl.oclc.org/estimates>.
- Crawley, M.J., 2007. The R Book. Wiley and Sons Ltd., UK.
- DellaSala, D.A., Karr, J.R., Schoennagel, T., Perry, D., Noss, R.F., Lindenmayer, D., Beschta, R., Hutto, R.L., Swanson, M.E., Evans, J., 2006. Post-fire logging debate ignores many issues. *Science* 314, 51–52.
- Donato, D.C., Fontaine, J.B., Campbell, J.L., Robinson, W.D., Kauffman, J.B., Law, B.E., 2006. Post-wildfire logging hinders regeneration and increases fire risk. *Science* 311, 352.
- Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol. Monogr.* 67, 345–366.
- D'Amato, A.W., Fraver, S., Palik, B.J., Bradford, J.B., Patty, L., 2011. Singular and interactive effects of blowdown, salvage logging, and wildfire in sub-boreal pine systems. *For. Ecol. Manag.* 262, 2070–2078.
- Fernández, C., Vega, J.A., Fonturbel, T., Jiménez, E., Pérez-Gorostiaga, P., 2008. Effects of wildfire, salvage logging and slash manipulation on *Pinus pinaster* Ait. recruitment in Orense (NW Spain). *For. Ecol. Manag.* 255, 1294–1304.
- Foster, D.R., Knight, D.H., Franklin, J.F., 1998. Landscape patterns and legacies resulting from large, infrequent forest disturbances. *Ecosystems* 1, 497–510.
- Foster, D.R., Orwig, D.A., 2006. Preemptive and salvage harvesting of New England forests: when doing nothing is a viable alternative. *Conserv. Biol.* 20, 959–970.
- Franklin, J.F., Lindenmayer, D., Macmahon, J.A., Mckee, A., Perry, D.A., Waide, R., Foster, D., 2000. Threads of continuity. *Conserv. Biol. Pract.* 1, 8–16.
- Fraser, E., Landhäuser, S., Lieffers, V., 2004. The effect of fire severity and salvage logging traffic on regeneration and early growth of aspen suckers in north-central Alberta. *For. Chron.* 80, 251–256.
- Gómez-Aparicio, L., Zavala, M.A., Bonet, F.J., Zamora, R., 2009. Are pine plantations valid tools for restoring Mediterranean forests? An assessment along abiotic and biotic gradients. *Ecol. Appl.* 19, 2124–2141.
- Greenberg, C.H., Mcgrane, A., 1995. A comparison of relative abundance and biomass of ground-dwelling arthropods under different forest management practices. *For. Ecol. Manag.* 89, 31–41.
- Greenberg, C.H., Neary, D.G., Harris, L.D., Linda, S.P., 1992. Vegetation recovery following wildfire and silvicultural treatments in sand pine scrub. *Am. Midland Natural.* 133, 149–163.
- Grime, J.P., 1979. *Plant Strategies and Vegetation Processes*. John Wiley & Sons, New York.
- Hutto, R.L., 2006. Toward meaningful snag-management guidelines for postfire salvage logging in North American conifer forests. *Conserv. Biol.* 20, 984–993.
- Jongman, R.H.G., ter Braak, C.J.F., van Toger, O.F.R., 1995. *Data Analysis in Community and Landscape Ecology*. Cambridge University Press, Cambridge, p. 324.
- Jurgens, M.F., Harvey, A.E., Graham, R.T., Page-Dumroese, D.S., Tonn, J.R., Larsen, M.J., Jain, T.B., 1997. Impacts of timber harvesting on soil organic matter, nitrogen, productivity, and health of Inland Northwest forests. *For. Sci.* 43, 234–251.
- Koivula, M., Spence, J.R., 2006. Effects of post-fire salvage logging on boreal mixed-wood ground beetle assemblages (Coleoptera, Carabidae). *For. Ecol. Manag.* 236, 102–112.
- Kreft, H., Jetz, W., 2007. Global patterns and determinants of vascular plant diversity. *Proc. Natl. Acad. Sci. U S A* 104, 5925–5930.
- Kurulok, S.E., Macdonald, S.E., 2007. Impacts of postfire salvage logging on understory plant communities of the boreal mixedwood forest 2 and 34 years after disturbance. *Can. J. For. Res.* 37, 2637–2651.
- Lavorel, S., McIntyre, S., Landsberg, J., Forbes, T.D.A., 1997. Plant functional classifications: from general groups to specific groups based on response to disturbance. *Trends Ecol. Evol.* 12, 474–478.
- Leps, J., Smilauer, P., 2003. *Multivariate Analysis of Ecological Data Using CANOCO*. Cambridge University Press, Cambridge.
- Leverkus, A.B., Puerta-Piñero, C., Guzmán-Álvarez, J.R., Navarro, J., Castro, J., 2012. Post-fire salvage logging increases restoration costs in a Mediterranean mountain ecosystem. *New For.* 43, 601–613.
- Leverkus, A.B., Castro, J., Puerta-Piñero, C., Rey Benayas, J.M., 2013. Suitability of the management of habitat complexity, acorn burial depth, and a chemical repellent for post-fire reforestation of oaks. *Ecol. Eng.* 53, 15–22.
- Lindenmayer, D.B., Burton, P.J., Franklin, J.F., 2008. *Salvage Logging and its Ecological Consequences*. Island Press, USA.
- Lindenmayer, D.B., Foster, D.R., Franklin, J.F., Hunter, M.L., Noss, R.F., Schmiegelow, F.A., Perry, D., 2004. Salvage harvesting policies after natural disturbance. *Science* 303, 1303.
- Lindenmayer, D.B., Noss, R.F., 2006. Salvage logging, ecosystem processes, and biodiversity conservation. *Conserv. Biol.* 20, 949–958.
- Lindenmayer, D.B., Ough, K., 2006. Salvage logging in the Montane Ash Eucalypt forests of the central Highlands of Victoria and its potential impacts on biodiversity. *Conserv. Biol.* 20, 1005–1015.
- Lorite, J., Molina-Morales, M., Cañadas, E.M., Ballesteros, M., Peñas, J., 2010. Evaluating a vegetation-recovery plan in Mediterranean alpine ski slopes: a chronosequence-based study in Sierra Nevada (SE Spain). *Landsc. Urban Plann.* 97, 92–97.
- Lorite, J., Navarro, F.B., Valle, F., 2007. Estimation of threatened orophytic flora and priority of its conservation in the Baetic range (S. Spain). *Plant Biosyst.* 141, 1–14.
- Macdonald, S.E., 2007. Effects of partial post-fire salvage harvesting on vegetation communities in the boreal mixedwood forest region of northeastern Alberta, Canada. *For. Ecol. Manag.* 239, 21–31.
- Magurran, A.E., 2004. *Measuring Biological Diversity*. Blackwell Publishing, India.
- Manor, R., Cohen, O., Saltz, D., 2008. Community homogenization and the invasiveness of commensal species in Mediterranean afforested landscapes. *Biol. Invasions* 10, 507–515.
- Marañón-Jiménez, S., Castro, J., Kowalski, A.S., Serrano-Ortiz, P., Reverter, B.R., Sánchez-Cañete, E.P., Zamora, R., 2011. Post-fire soil respiration in relation to burnt wood management in a Mediterranean mountain ecosystem. *For. Ecol. Manag.* 261, 1436–1447.
- Marañón-Jiménez, S., Castro, J., 2013. Effect of decomposing post-fire coarse woody debris on soil fertility and nutrient availability in a Mediterranean ecosystem. *Biogeochemistry* 112, 519–535.
- Marañón-Jiménez, S., Castro, J., Querejeta, J.I., Fernández-Ondoño, E., Allen, C.D., 2013a. Post-fire wood management alters water stress, growth, and performance of pine regeneration in a Mediterranean ecosystem. *For. Ecol. Manag.* 308, 231–239.
- Marañón-Jiménez, S., Castro, J., Fernández-Ondoño, E., Zamora, R., 2013b. Charred wood remaining after a wildfire as a reservoir of macro- and micronutrients in a Mediterranean pine forest. *Int. J. Wildland Fire* 22, 681–695.
- Martínez-Sánchez, J.J., Ferrandis, P., De las Heras, J., Herranz, J.M., 1999. Effect of burnt wood removal on the natural regeneration of *Pinus halepensis* after fire in a pine forest in Tus valley (SE Spain). *For. Ecol. Manag.* 123, 1–10.
- Marzano, R., Garbarino, M., Marcolin, E., Pividori, M., Lingua, E., 2013. Deadwood anisotropic facilitation on seedling establishment after a stand-replacing wildfire in Aosta Valley (NW Italy). *Ecol. Eng.* 51, 117–122.
- Matías, L., Zamora, R., Castro, J., 2012. Sporadic rainy events are more critical than increasing of drought intensity for woody species recruitment in a Mediterranean community. *Oecologia* 169, 833–844.
- Mclver, J.D., Ottmar, R., 2007. Fuel mass and stand structure after post-fire logging of a severely burned ponderosa pine forest in northeastern Oregon. *For. Ecol. Manag.* 238, 268–279.

- McIver, J.D., Starr, L., 2001. A literature review on the environmental effects of postfire logging. *West. J. Appl. For.* 16, 159–168.
- Mendoza, I., Zamora, R., Castro, J., 2009. A seeding experiment for testing tree-community recruitment under variable environments: implications for forest regeneration and conservation in Mediterranean habitats. *Biol. Conserv.* 142, 1491–1499.
- Moro, J.M., Domingo, F., 2000. Litter decomposition in four woody species in a Mediterranean climate: weight loss, N and P dynamics. *Ann. Bot.* 86, 1065–1071.
- Moro, M.J., Domingo, F., Escarré, A., 1996. Organic matter and nitrogen cycles in a pine afforested catchment with a shrub layer of *Adenocarpus decorticans* and *Cistus laurifolius* in south-eastern Spain. *Ann. Bot.* 78, 675–685.
- Ne'eman, G., Lahav, H., Izhaki, I., 1995. Recovery of vegetation in a natural east Mediterranean pine forest on Mount Carmel, Israel as affected by management strategies. *For. Ecol. Manag.* 75, 17–26.
- Peterson, D.W., Dodson, E.K., Harrod, R.J., 2009. Fertilization and seeding effects on vegetative cover after wildfire in north-central Washington State. *For. Sci.* 55, 494–502.
- Pinheiro, J.C., Bates, D.M., 2000. *Mixed-effects Models in S and S-PLUS*. Springer, New York.
- Pinheiro, J.C., Bates, D.M., DebRoy, S., Sarkar, D., the R Development Core Team, 2012. *Nlme: Linear and Nonlinear Mixed Effects Models*. R package version 3.1-103.
- Purdon, M., Brails, S., Bergeron, Y., 2004. Initial response of understorey vegetation to fire severity and salvage-logging in the southern boreal forest of Québec. *Appl. Veg. Sci.* 7, 49–60.
- Quinn, G.P., Keough, M.J., 2002. *Experimental Design and Data Analysis for Biologists*. Cambridge University Press, New York.
- Raunkjaer, C., 1934. *The Life Forms of Plants and Statistical Plant Geography*. Oxford University Press, Oxford.
- Reeves, G.H., Bisson, P.A., Rieman, B.E., Benda, L.E., 2006. Postfire logging in riparian areas. *Conserv. Biol.* 20, 994–1004.
- R Development Core Team, 2012. *R: a Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Austria, ISBN 3-900051-07-0.
- Rey, P.J., Alcántara, J.M., 2000. Recruitment dynamics of a fleshy-fruited plant (*Olea europaea*): connecting patterns of seed dispersal to seedling establishment. *J. Ecol.* 88, 622–633.
- Roberts, D.W., 2012. *labdsv: Ordination and Multivariate Analysis for Ecology*. R package version 1.5-0. <http://CRAN.R-project.org/package=labdsv>.
- Salvatore, P., La Mantia, T., 2012. The impact of *Pinus halepensis* afforestation on Mediterranean spontaneous vegetation: do soil treatment and canopy cover matter? *Eur. J. For. Res.* 23, 517–528.
- Serrano-Ortiz, P., Marañón-Jiménez, S., Reverter, B.R., Sánchez-Cañete, E.P., Castro, J., Zamora, R., Kowalski, A.S., 2011. Post-fire salvage logging reduces carbon sequestration in Mediterranean coniferous forest. *For. Ecol. Manag.* 262, 2287–2296.
- Sexton, T.O., 1998. *Ecological Effects of Post-wildfire Management Activities (Salvage-logging and Grass-seeding) on Vegetation Composition, Diversity, Biomass, and Growth and Survival of Pinus ponderosa and Purshia tridentata*. Master Thesis. Oregon State University.
- Spanos, I., Raftoyannis, Y., Goudelis, G., Xanthopoulou, E., Samara, T., Tsiotis, A., 2005. Effects of postfire logging on soil and vegetation recovery in a *Pinus halepensis* Mill. forest of Greece. *Plant Soil* 278, 171–179.
- Sutherland, W.J., Pullin, A.S., Dolman, P.M., Knight, T.M., 2004. The need for evidence-based conservation. *Trends Ecol. Evol.* 19, 305–308.
- Söderström, L., 1988. Sequence of bryophytes and lichens in relation to substrate variables of decaying coniferous wood in Northern Sweden. *Nord. J. Bot.* 8, 89–97.
- Ter Braak, C.J.F., Šmilauer, P., 2002. *CANOCO Reference Manual and CanoDraw for Windows User's Guide*. Biometris and Wageningen University.
- Tilman, D., 1982. *Resource Competition and Community Structure*. Princeton University Press, New Jersey.
- Turner, M.G., Dale, V.H., 1998. Comparing large, infrequent disturbances: what have we learned? *Ecosystems* 1, 493–496.
- Valle, F. (Ed.), 2003. *Mapa de series de vegetación de Andalucía*. Editorial Rueda, Madrid, ISBN 84-7207-137-5.
- Vallejo, R., Aronson, J., Pausas, J.G., Cortina, J., 2006. Restoration of Mediterranean woodlands. In: van Andel, J., Aronson, J. (Eds.), *Restoration Ecology*. Blackwell Publishing, Oxford, UK.
- Van Nieuwstadt, M.G.L., Sheil, D., Kartawinata, K., 2001. The ecological consequences of logging in the burned forests of east Kalimantan, Indonesia. *Conserv. Biol.* 15, 1183–1186.
- Zamora, R., Hódar, J.A., Matías, L., Mendoza, I., 2010. Positive adjacency effects mediated by seed disperser birds in pine plantations. *Ecol. Appl.* 20, 1053–1060.