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Effects of Post-Fire Deadwood Management on Soil Macroarthropod Communities

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Abstract: Dead wood comprises a vast amount of biological legacies that set the scene for ecological regeneration after wildfires, yet its removal is the most frequent management strategy worldwide. Soil-dwelling organisms are conspicuous, and they provide essential ecosystem functions, but their possible affection by different post-fire management strategies has so far been neglected. We analyzed the abundance, richness, and composition of belowground macroarthropod communities under two contrasting dead-wood management regimes after a large wildfire in the Sierra Nevada Natural and National Park (Southeast Spain). Two plots at different elevation were established, each containing three replicates of two experimental treatments: partial cut, where trees were cut and their branches lopped off and left over the ground, and salvage logging, where all the trees were cut, logs were piled, branches were mechanically masticated, and slash was spread on the ground. Ten years after the application of the treatments, soil cores were extracted from two types of microhabitat created by these treatments: bare-soil (in both treatments) and under-logs (in the partial cut treatment only). Soil macroarthropod assemblages were dominated by Hemiptera and Hymenoptera (mostly ants) and were more abundant and richer in the lowest plot. The differences between dead-wood treatments were most evident at the scale of management interventions: abundance and richness were lowest after salvage logging, even under similar microhabitats (bare-soil). However, there were no significant differences between microhabitat types on abundance and richness within the partial cut treatment. Higher abundance and richness in the partial cut treatment likely resulted from higher resource availability and higher plant diversity after natural regeneration. Our results suggest that belowground macroarthropod communities are sensitive to the manipulation of dead-wood legacies and that management through salvage logging could reduce soil macroarthropod recuperation compared to other treatments with less intense management even a decade after application.

Keywords: forest fire; burnt-wood; species richness; soil fauna; post-fire management

1. Introduction

Soil fauna comprises an enormous amount of forest biomass [1]. In forests, soil fauna can amount to millions of individuals of hundreds of species per square meter [1,2], encompassing an array of taxa and functional groups [3,4]. Recently, belowground diversity has attracted special attention due to its importance for ecosystem functions (e.g., decomposition, mineralization, and nutrient cycling [1,5]) and ecosystem services (e.g., pathogen control and soil fertility [6]) and the low amount

of existing knowledge compared to aboveground fauna [7]. As a result, understanding the drivers of soil fauna distribution and diversity represents a priority in soil ecological research [8] and biodiversity conservation [9].

A major current concern in ecological conservation globally is the increase in the frequency of large disturbance events such as wildfires [10]. Fire affects soil insects and other invertebrates by killing individuals directly [11,12], increasing their susceptibility to predation [13], and/or reducing the quantity and quality of food [4,14]. However, some belowground organisms, such as ant communities and mining bees, are often able to survive because underground nesting protects adult individuals, larvae, eggs, and some of their resources from the flames [11,15,16]. Several soil faunal taxa even increase in abundance during the few years after a fire [17,18] as a result of attraction by smoke [11], stimulation of emergence of adults due to increases in soil temperature [14] and, particularly, large pulses in the supply of dead wood [18,19]. An estimated 20%–25% of all forest species are saproxylic, and many of them contribute to soil biota by having at least some life stage belowground [20]. However, while there is a rich body of scientific literature on the effects of fire on arthropods [11,14], most of it focuses on aboveground species [7], and the factors that affect belowground fauna in burnt forests, including factors related to the management of burnt wood, have generally been neglected [21]. Further, the effects of post-fire management on belowground organisms have received very little attention.

Around the world, managing burnt forests frequently involves the removal of large trunks, often including a considerable elimination of smaller woody material by chipping, mastication, or burning. This practice is called salvage logging [22,23]. Salvage logging has generated strong controversy in recent decades because it alters the ecological conditions for secondary succession [24–28]. Less aggressive post-fire interventions, such as partial retention and the cutting of trees without their extraction, have been suggested as alternatives to avoid compromising ecosystem recovery (e.g., [29,30]). The key differences between salvage logging and such alternatives lie in (a) the greater mechanical disturbance of logging operations and (b) the greater reduction in the amount of dead wood under the salvage-logging regime. These differences can affect soil fauna through several non-mutually exclusive mechanisms, including changes in abiotic conditions, such as solar radiation at ground level, and the resulting changes in the biotic environment [31–33]. In fact, some of the main factors that influence soil faunal diversity, such as soil humidity and organic matter [34], are strongly linked to the abundance of dead wood [30,35,36]. The management of burnt wood may thus bring about changes in the abundance and composition of post-fire soil communities, with subsequent alterations in the functions that they perform. However, despite the known effects of salvage logging on many aboveground communities [25] and some evidence pointing out that harvesting undisturbed forest compromises the recuperation of belowground insects [37–39], the effects of different post-fire management treatments on belowground fauna remain poorly known.

To assess the differences in belowground arthropod communities across different dead-wood management treatments, we took soil cores 11 years after a wildfire in southeastern Spain (10.5 years after dead-wood management). We sampled a post-fire management experiment that was replicated within and between two plots located at different elevations (at approximately 1500 and 2000 m a.s.l.). Treatments comprised salvage logging (cutting all trees) and partial cut (90% of trees were cut, and the branches lopped off); within the latter, we sampled soils underneath logs and away from logs. We aimed to analyze the differences between management treatments and the microhabitats therein and to assess whether changes in ecological conditions due to elevation—a key factor affecting macroarthropod abundance and composition [40]—modified the response of macroarthropod communities to management. We hypothesized that: (1) the salvage logging treatment would host the lowest richness and abundance of soil fauna due to the reduction in dead-wood resources at the stand scale, (2) soils in the partial cut treatment would contain more diverse communities than in the salvage logging treatment even under similar microhabitat conditions due to a greater stand-scale species pool, and (3) within the partial cut treatment, the soils sampled beneath lying logs would contain richer soil faunal communities than those in the same stand-scale treatment but away from logs.

2. Materials and Methods

2.1. Study Area

The study was conducted in the Sierra Nevada National and Natural Park (SE Spain), in an area affected by a wildfire that burned 3400 ha of shrublands and pine stands in September 2005 [41]. Two plots were established six months after the fire (Table 1), one at 1477 m a.s.l. (Low Plot, hereafter), and one at 2053 m a.s.l. (High Plot, hereafter). The plots were similar in terms of bedrock (mica schist), orientation (SW), soil type (haplic phaeozems), and fire severity (high according to the local forest service; the fire consumed all the leaves, twigs, and understory vegetation and charred the bark of the trunks [42]). Black pine (*Pinus nigra*) dominated the Low Plot, and Scot pine (*P. sylvestris*) the High Plot, according to each species' ecological requirements and elevational constraints. Both pine species are native to the south of the Iberian Peninsula, yet in our study site they constituted 40–60-year-old plantations (see Table 1 for a detailed description of dasometric parameters of the plots). The pines were situated on terraces established with bulldozers, previously a common reforestation practice on hill-sides in Spain. Climate in the area is Mediterranean, with mild, wet winters and hot, dry summers. In each plot, three replicates (subplots) of the following two burnt-wood management treatments were established (Figure 1):

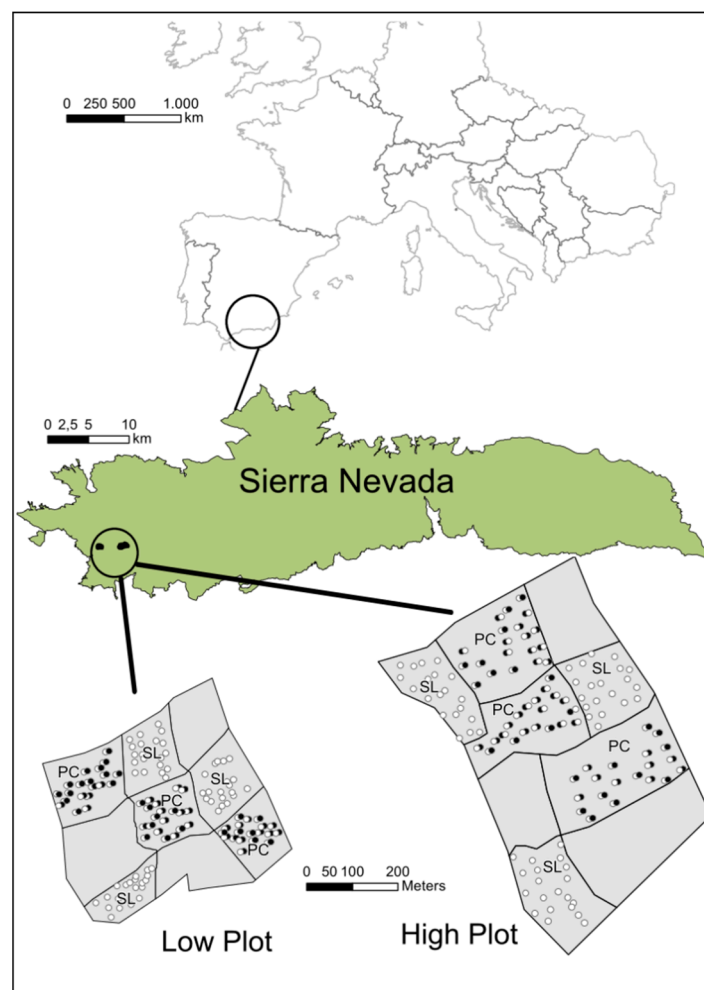


Figure 1. Location of the two study plots within Europe and the Sierra Nevada Natural Park. Each plot contained six subplots, which constituted three replicates of each of two post-fire treatments. SL = salvage logging; PC = partial cut. Black circles correspond to sampling points in the “under-logs” microhabitat and white circles in the “bare-soil” microhabitat.

1. Salvage logging (SL), where all the burnt trees were manually cut and the trunks cleaned of branches with chainsaws. Trunks were manually piled (groups of 10–15 logs), the woody debris was masticated with a tractor, and the slash was spread on the ground. The forest service had planned to extract the trunks with a log-forwarder, but the foresters eventually canceled this step due to difficulties in precisely operating machinery within the spatial arrangement of the plots. Masticated woody material (circa 2–5 cm in diameter) covered 32% of the surface right after treatment implementation [30]. The structure of the habitat was an open landscape with isolated groups of stacked logs covering less than 5% of the treatment area. The most characteristic microhabitat of this treatment was one devoid of dead wood (the logging slash had mostly decomposed by the time of sampling) and with herbs and grasses. Hence, in the SL treatment, we sampled soils in this “bare-soil” microhabitat.
2. Partial cut (PC), which consisted of felling ca. 90% of the burnt trees, lopping off the branches, and cutting the logs in pieces of 2–3 m length. All the biomass was spread over the ground, without chopping. The remaining 10% of the burnt trees were left standing, but they collapsed quickly until 100% had fallen after 5.5 years [43]. This treatment therefore represents a situation that would be reached by a passively managed burnt forest within a few years after the fire. The resulting habitat structure comprised logs and branches spread over the ground with an initial ground coverage of 45% [30]. In this treatment, besides the “bare-soil” microhabitat described above, there was a characteristic microhabitat where the soil was covered by dead wood spread over the flat terrace bed. In the PC treatment, we sampled soils in the “bare soil” and the “under-logs” microhabitats.

2.2. Sampling Design

We sampled soils to study macroarthropod soil communities within each of the twelve subplots in spring 2016 (10.5 years after the fire). GPS positions were recorded for each soil sample (Figure 1).

In each of the subplots, we collected 20 cores from each available microhabitat. Thus, in each SL replicate, we collected 20 cores under “bare-soil”, and in each PC replicate, we collected 40 cores: 20 cores under “bare-soil” and 20 cores “under-logs”. Sampling points in SL were located at least 10 m from each other. In the PC treatment, cores under “bare-soil” were obtained at least 50 cm away from cores “under-logs”, and these pairs were located at least 10 m from each other. This sampling procedure allowed us to address our three hypotheses. Our procedure resulted in 360 samples distributed across the two plots (Figure 1).

The timing of sampling was selected as to make it coincide with the arrival of flowering and the movement of soil invertebrates from lower soil layers, considering the difference in phenology across the two plots [44]. We sampled the Low Plot in May–June and the High Plot in June–July. Soil cores were extracted with soil augers (10 cm diameter, 12–15 cm depth). Samples were put into plastic bags and carried to a laboratory on the same day. In the laboratory, soil cores were broken and sieved by hand. We chose this method because hand sorting has shown to be more efficient than several methods, such as funnels and high-gradient funnels [2]. Furthermore, soil communities comprise a vast amount of life forms, including inactive, sessile, moving, and immature organisms, and sieving soil samples allows the capturing of all possible life forms [2,34,45]. The samples were fractionated meticulously, first at 1 cm mesh size to remove rocks, leaf litter, and roots. They were then sieved at mesh sizes of 3 mm and 1 mm over a clean, white surface, where arthropods were visually sought. Each sample was screened for approximately 40 min. All specimens were conserved in 70% ethanol. Our final database consists of all the organisms identified at the level of orders and at the species level for ants.

Table 1. Location and characteristics of the study plots.

	Plots	
	Low Plot	High Plot
Coordinates ¹	36°57'12" N 03°29'36" W	36°58'06" N 03°28'49" W
Area (ha)	17.7	31.7
Elevation (m above sea level) ¹	1477	2053
Slope (%)	25–30	35
Mean daily minimum temp. (°C) ²	6.8 ± 0.2	3.4 ± 0.2
Mean daily maximum temp. (°C) ²	17.1 ± 0.2	13.4 ± 0.2
Mean ann. precip. (mm) ²	536 ± 41	630 ± 42
Dominant species	<i>Pinus pinaster</i> / <i>P. nigra</i>	<i>P. sylvestris</i>
Tree density (individuals ha ⁻¹) ³	1448 ± 66	1010 ± 49
Basal tree diameter (cm) ⁴	17.7 ± 0.15	15.7 ± 0.13
Tree height (m) ⁵	6.3 ± 0.1	6.2 ± 0.1
dbh (cm) ⁵	13.3 ± 0.2	10.8 ± 0.2
Wood biomass (kg ha ⁻¹) ⁶	55,273	26,166
Representative plants ⁷	<i>Ulex parviflorus</i> , <i>Festuca scariosa</i> , <i>Dactylis glomerata</i> , <i>Euphorbia flavicoma</i>	<i>Vaccaria hispanica</i> , <i>Sesamoides purpurascens</i> subsp. <i>prostrata</i> , <i>Senecio nebrodensis</i> , <i>Heliantemum appeninum</i>

¹ Measured at the centroid of each plot. ² Data obtained from interpolated maps of Sierra Nevada (1981–2010) generated at the Centro Andaluz de Medio Ambiente (CEAMA). ³ Calculated just after the fire (autumn 2005) by counting the trees in four randomly placed 25 × 25 m quadrats for each subplot. Values were statistically higher in the Low Plot than in the High Plot, but there were no differences among treatments within plots (Wilcoxon test; $p > 0.05$ in both cases). ⁴ Calculated from 30 randomly selected trees per each of the 25 × 25 m quadrats used to estimate tree density (360 trees per treatment and plot). Values were slightly different across treatments within each plot ($p < 0.05$ in both plots), but without a consistent pattern, suggesting a spurious effect of the sampling protocol: 16.8 ± 0.2 cm in SL and 19.1 ± 0.2 in PC for the Low Plot, and 16.7 ± 0.2 in SL and 14.8 ± 0.2 in PC for the High Plot. ⁵ From [42]; calculated from 90 randomly selected trees in untreated areas within the experimental plots (which constituted a third treatment, non-intervention, not included in this study and that was representative of the initial conditions in the study area); dbh = diameter at breast height. ⁶ From [42]; estimated from data on tree density, height, and dbh by using the CubiFOR calculation tool (<http://www.cesefor.com/contenido/cubifor-herramienta-descripcion>), a model adjusted for the calculation of wood biomass in pine plantations in the Mediterranean basin [46–48]. ⁷ Sampled two years after the fire [49].

2.3. Statistical Analyses

We analyzed the differences between dead-wood treatments and microhabitats on the diversity, abundance, and composition of soil macroarthropods. Each of the analyses described below was conducted independently for each of our hypotheses, namely:

- Effect of dead-wood treatment (SL vs. PC) at the stand scale, pooling over the greater variety of microhabitats (“bare-soil” and “under-logs”) in the PC treatment. This allowed testing the overall differences between post-fire interventions (Hypothesis 1). Here, the tested factors were plot, dead-wood treatment, and the plot by treatment interaction.
- Effect of dead-wood treatment on the soil fauna found in the bare-soil microhabitat (i.e., PC “under-logs” excluded). With this, we aimed to assess whether stand-scale management affected the communities that were found in an otherwise similar microhabitat (Hypothesis 2). The tested factors were plot, dead-wood treatment, and the plot by dead-wood treatment interaction.
- Difference between the two different microhabitats in the PC treatment. This allowed testing the effect of the presence of dead wood within the same stand-scale treatment on soil macroarthropod communities (Hypothesis 3). The tested factors were plot, microhabitat, and the plot by microhabitat interaction.

To test the effect of dead-wood treatment and microhabitat on the abundance of soil macroarthropods (excluding ants), we used zero-inflated generalized linear mixed-effects models. To deal with the hierarchical sampling design and avoid pseudo-replication, we included an appropriate structure of random effects (soil samples within dead-wood replicates within plots). We generated final models through simplification while testing the significance of terms with likelihood ratio chi-squared tests, which compared the fit of models with and without each term [50]. We fitted these models with the “glmmTMB” function of the “glmmTMB” R package [51].

We compared the diversity of orders of soil macroarthropods by fitting accumulation curves with confidence intervals with sample-based rarefaction and extrapolation with the iNEXT function of the

iNEXT R package [52]. We used this function to assess the increase of order richness with a common sample size and to reveal differences in numbers of orders between dead-wood treatments. This was necessary for the case of Hypothesis 1, as the PC treatment had twice as many samples in this analysis as the SL treatment. Extrapolations were taken to twice the highest number of samples. Due to the high abundance of ants in some individual samples, and the species-level identification of this group, we analyzed ants separately.

We compared macroarthropod community assemblages among treatments and microhabitats using non-metric multidimensional scaling (NMDS). The method does not use absolute abundance; rather, it maximizes rank-order correlation between distance measures in an ordination space, assumes that dissimilarity is monotonically related to ecological distance, and provides a robust and easily interpretable ordination method [53]. We used the “metaMDS” function for adequate dissimilarity measures, scaling several times until reaching a similar minimum stress. This value indicated how well the distribution of points on the plots matches the actual distances between dimensions; stress values were interpreted following the suggestions by Quinn and Keough [53]. We assessed dissimilarities variance to compare differences between community compositions across treatments and microhabitats using the “ANOSIM” function from the “vegan” package [54]. This procedure is based on the difference between average ranked values of distance on abundances among sample replicates. Interpretations were based on R values. R is scaled between -1 and $+1$, where negative values indicate greater similarities across different treatments than those occurring among replicates of the same treatment [55]. Significance was calculated over 1000 permutations.

We used the “vegdist” and “diana” functions from the “vegan” [54] and “cluster” packages [56] for divisive hierarchical cluster analysis to assess macroarthropod groups not defined a priori. This method takes one large set of objects, and then iteratively splits them into consistent groups in which similarity is greatest [53]. Analyses were based on “Bray–Curtis” similarity. Wilcoxon–Mann–Whitney U-tests were used to compare the abundance of the main arthropod taxa across plots, and across dead-wood treatments and microhabitats at each plot, using the “wilcox.test” function. Analyses were made in R version 3.3.1 [57].

3. Results

3.1. Variations in Abundance, Richness, and Diversity

The 360 soil samples yielded 524 macroarthropod individuals belonging to 13 orders. The most abundant orders were Hemiptera (54% of individuals), and Hymenoptera (24%, mostly ants). Among formicids, the most abundant species were *Bothriomyrmex meridionalis* (33% of the 124 ant individuals) and *Proformica ferrari* (22%) (Table A1).

The zero-inflated mixed-effects models—which excluded ants—showed that macroarthropod abundance was affected by an interaction between plot and treatment (Table 2). Abundance was higher in the Low Plot (2.05 ± 0.34 individuals sample⁻¹) than in the High Plot (0.16 ± 0.03), and it was also greater in the PC treatment than in SL (Table 3). However, the effect of treatment varied across plots, as between-treatment differences were greatest in the Low Plot (Table 3). The same trend was found when considering only the bare-soil microhabitat across both dead-wood treatments (i.e., Hypothesis 2; Tables 2 and 3). The comparison of microhabitats in the PC treatment (Hypothesis 3) showed only the negative effect of the High Plot on macroarthropod abundance (Tables 2 and 3).

A different trend was observed for richness, where a significant treatment by plot interaction (Table 2) showed that order richness was similar (~ 0.6 orders sample⁻¹) across treatments in the Low Plot, whereas in the High Plot, the PC treatment had higher values (Table 3). Again, microhabitats in the PC treatment produced no significant effect on richness (Table 2).

Table 2. Model selection for the effects of dead-wood treatment, microhabitat, and plot on the abundance and richness of macroarthropod individuals (excluding ants), estimated with zero-inflated GLMM.

Hypothesis ¹	Macroarthropod Abundance			Macroarthropod Richness		
		χ^2	P		χ^2	P
1	Treatment × Plot	7.34	<0.01	Treatment × Plot	5.5	<0.05
2	Treatment × Plot	6.30	<0.05	Treatment × Plot	9.69	<0.01
	Microhabitat × Plot ²	0.064	0.8	Microhabitat × Plot ²	2.06	0.15
3	Microhabitat ²	0.01	0.891	Microhabitat ²	0.11	0.738
	Plot	7.16	<0.001	Plot	4.69	<0.05

¹ The tested hypotheses were the differences between: (1) dead-wood treatments (SL, PC); (2) treatments but only under similar microhabitat (both treatments under bare soil); and (3) microhabitats in the PC treatment. Significant differences are denoted by boldface at $\alpha = 0.05$. ² Terms excluded from the final model.

Table 3. Mean abundance (number of individuals/sample \pm 1 SE of the mean) of macroarthropods (excluding ants) and richness of orders across burnt-wood treatments and microhabitats.

Response	Low Plot			High Plot		
	Salvage Logging	Partial Cut		Salvage Logging	Partial Cut	
		Bare Soil	Under Logs		Bare Soil	Under Logs
Abundance ¹	1.65 \pm 0.41	2.26 \pm 0.74	2.25 \pm 0.61	0.00 \pm 0.00	0.28 \pm 0.09	0.21 \pm 0.06
Richness ¹	0.61 \pm 0.1	0.51 \pm 0.09	0.7 \pm 0.11	0.00 \pm 0.00	0.23 \pm 0.06	0.2 \pm 0.05

¹ Number of samples per plot: 60 for salvage logging (all under bare soil) and 120 for partial cut (where 60 samples were taken under bare soil and 60 under logs).

3.2. Richness Curves

Sample-based rarefaction and extrapolation revealed significantly higher richness of macroarthropod orders and of ant species in PC than in the SL treatment at the Low Plot (Figure 2a; Hypothesis 1). This trend was also found in the High Plot (Figure A1a), although the results for this plot are less robust because the macroarthropod abundance was very low overall (Table 3). When the two burnt-wood treatments were compared considering only the under-soil microhabitat (Hypothesis 2), there were no significant differences in the number of macroarthropod orders or ant species across treatments at the Low Plot (Figure 2b), although at the High Plot, differences appeared due to the virtual absence of macroarthropods from samples in salvage-logged subplots (Figure A1b). Microhabitats within the PC treatment did not significantly differ in the number of orders (Hypothesis 3), but under-log samples hosted a greater richness of ant species at both the Low Plot (Figure 2c) and the High Plot (Figure A1c).

3.3. Community Assemblages and Cluster Analysis

Non-metric multidimensional scaling ordination of assemblages showed an overall pattern of stratification across treatments at the Low Plot (Figure 3), but the effect of treatments was not significant (ANOSIM $R = 0.02$; $P > 0.05$). Also, microhabitats did not create significant differences (ANOSIM $R = -0.03$; $P > 0.05$). Divisive hierarchical clustering showed that macroarthropod assemblages differed markedly (60% of dissimilarity) between plots and, secondarily, similar microhabitats were more similar in composition (Figure 4).

Differences between treatments in the abundance of individual orders were not significant, except for Lepidoptera, which was significantly associated with the SL treatment (Table 4). When differences between microhabitats were assessed (Hypothesis 3), the two microhabitats did not show characteristic communities (Table A1).

Table 4. Mean abundance (number of individuals/sample \pm 1 S.E. of the mean) of the main macroarthropod taxa across treatments and microhabitats.

Taxa	Low Plot								High Plot							
	Treatment				Dead-Wood Microhabitat				Treatment				Dead-Wood Microhabitat			
	Salvage Logging	Partial Cut	Z	p ^{1,2}	Partial Cut		Z ³	p ^{1,2,3}	Salvage Logging	Partial Cut	Z ³	p ^{1,2,3}	Partial Cut		Z ³	p ^{1,2,3}
					Bare Soil	Under Logs							Bare Soil	Under Logs		
Hymenoptera	0.133 \pm 0.05	0.566 \pm 0.209	-1.11	0.266	0.283 \pm 0.142	0.85 \pm 0.332	-1.689	0.091	0.383 \pm 0.167	0.225 \pm 0.126	-0.244	0.806	0.433 \pm 0.21	0.016 \pm 0.01	1.387	0.165
Lepidoptera	0.216 \pm 0.064	0.008 \pm 0.006	2.25	0.023	0	0.016 \pm 0.011	NA	NA	0	0	NA	NA	0	0	NA	NA
Hemiptera	1.100 \pm 0.217	1.775 \pm 0.378	-0.65	0.513	2.000 \pm 0.524	1.550 \pm 0.396	0.192	0.847	0	0.050 \pm 0.018	NA	NA	0.066 \pm 0.02	0.033 \pm 0.01	0.47	0.638
Aranea	0.016 \pm 0.009	0.008 \pm 0.006	0.5	0.616	0.016 \pm 0.011	0	NA	NA	0	0.008 \pm 0.006	NA	NA	0	0.016 \pm 0.011	NA	NA
Geophilomorpha	0.050 \pm 0.016	0.041 \pm 0.017	0.53	0.59	0.033 \pm 0.016	0.050 \pm 0.026	-0.01	0.98	0	0.008 \pm 0.006	NA	NA	0.016 \pm 0.011	0	NA	NA
Isopoda	0.016 \pm 0.009	0.125 \pm 0.095	-0.006	0.994	0	0.250 \pm 0.165	NA	NA	0	0.008 \pm 0.006	NA	NA	0	0.016 \pm 0.01	NA	NA
Diptera	0.100 \pm 0.029	0.150 \pm 0.043	-0.701	0.483	0.166 \pm 0.063	0.133 \pm 0.04	0.005	0.996	0	0.016 \pm 0.009	NA	NA	0.033 \pm 0.016	0	NA	NA
Coleoptera	0.116 \pm 0.027	0.083 \pm 0.022	0.579	0.562	0.033 \pm 0.016	0.133 \pm 0.035	-1.73	0.082	0	0.141 \pm 0.032	NA	NA	0.150 \pm 0.043	0.133 \pm 0.035	0.004	0.996

¹ P-values are the results of Wilcoxon–Mann–Whitney U-tests. ² Significant differences are denoted by boldface at $\alpha = 0.05$. ³ NA = not applicable.

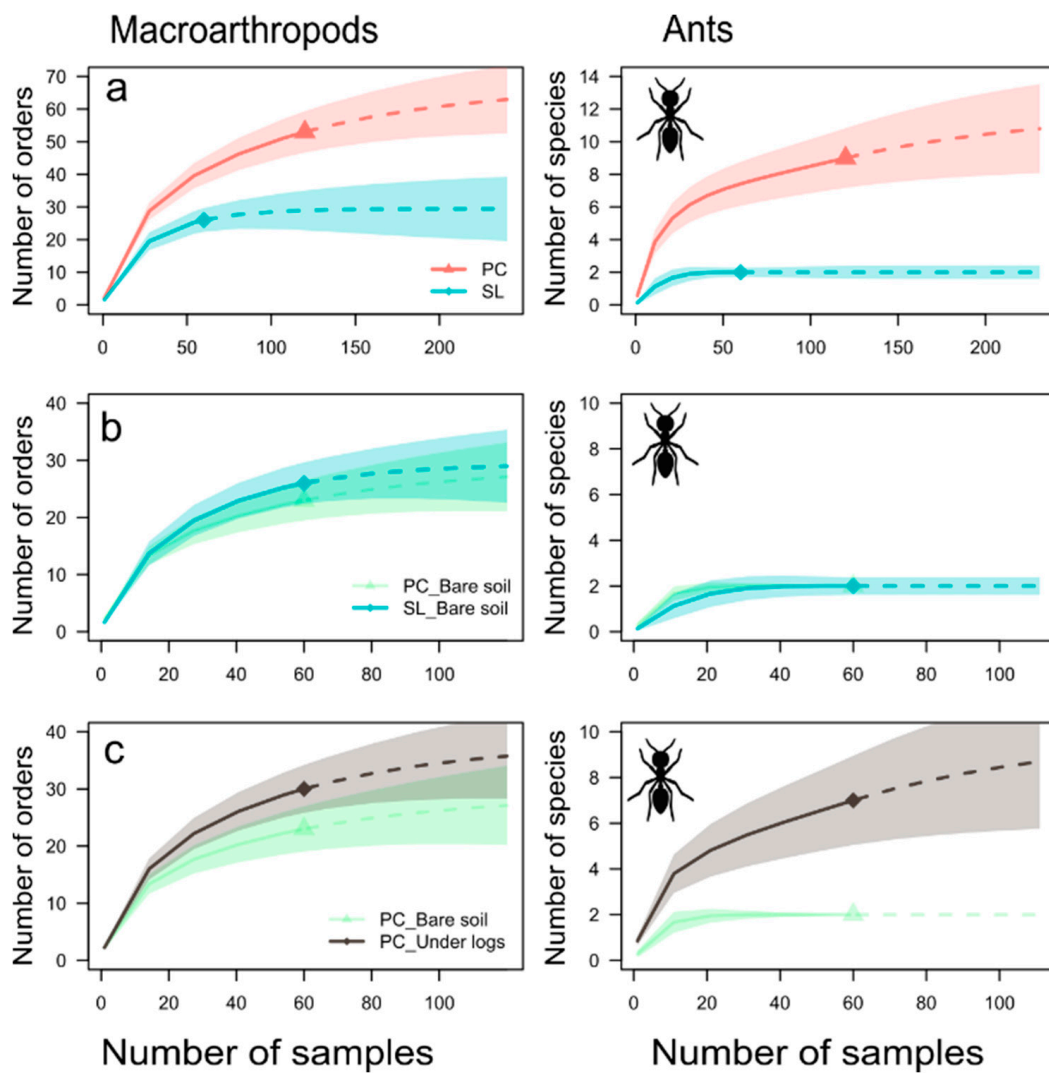


Figure 2. Sample-based rarefaction (solid lines) and extrapolation (dotted lines) until reaching twice the maximum sample size for macroarthropod orders and ant species at the Low Plot. Shaded areas represent 95% confidence intervals. The lettering of the panels indicates the three hypotheses of this study: differences between (a) dead-wood treatments, (b) treatments under the bare-soil microhabitat only, and (c) microhabitats in the PC treatment. Curves for the High Plot are shown in the supplementary Figure A1. Dead-wood treatments are SL = Salvage logging and PC = Partial Cut.

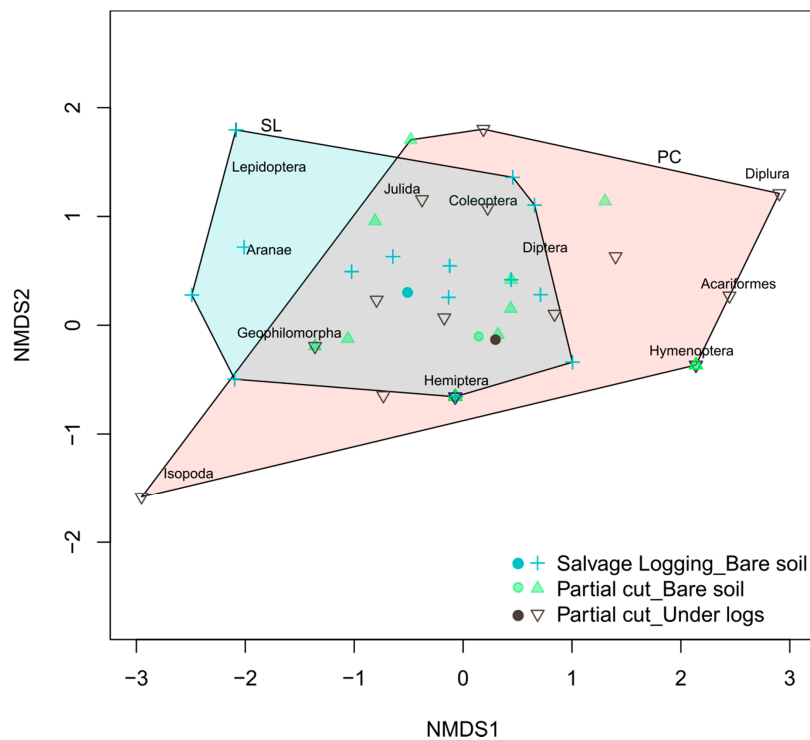


Figure 3. Two-dimensional non-metric multidimensional scaling ordination using Bray–Curtis distance of belowground macroarthropod communities under two different treatments and microhabitats (stress coefficient = 0.088). The solid circles indicate the centroid for each dead-wood treatment by microhabitat combination, and the other symbols indicate each treatment replicate. Polygons are the groups for the salvage logging (blue) and the partial cut (red) treatment. The differences between the treatments and microhabitats were not significant.

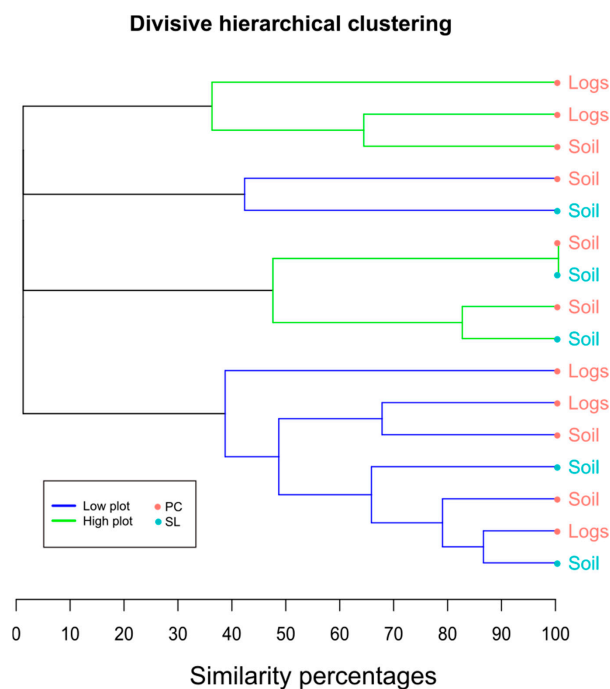


Figure 4. Divisive hierarchical clustering of macroarthropod communities using Bray–Curtis similarity. Branches correspond to plots at different elevations and the microhabitat replicated three times. The two missing branches result from the absence of individuals in two replicates of the High Plot (one in each of PC-logs and SL-soil).

4. Discussion

Our study shows that different landscape-scale management of dead wood after a wildfire produced differences in the abundance and richness of soil macroarthropod communities. In general, the treatment that included microhabitats with dead wood contained greater abundance and diversity of soil arthropods. However, differences were overridden by the effect of the elevation at which dead-wood treatments were applied, and we did not detect significant effects of treatments or microhabitats on composition. This study contributes to understanding the responses of an understudied group of organisms to common management actions after wildfires.

4.1. Overall Abundance and Differences across Elevations

In our study, we found an overall low abundance and diversity of soil macroarthropods compared to other Mediterranean-type ecosystems [17,58,59] as well as other temperate and boreal ecosystems [38,60–62]. Low abundances throughout our study could be attributed to the effects of fire, which can have both direct effects in reducing arthropod abundance through mortality [63], and indirect effects through habitat damage from high soil temperatures [64]. Such changes in habitat quality are a frequent cause of resource depletion and may be an important factor affecting the recovery of soil organisms [65]. Further, the history of the site, characterized by a dense and homogeneous pine afforestation established on terraces made with bulldozers [43,66], could have reduced the initial species pool as well as the spatial heterogeneity in burn conditions at the forest floor, which, in turn, could explain a small proportion of soil animals surviving wildfire [16]. To survive under the environmental conditions prevailing early after fire, particular traits are generally required [67]. For example, wildfire does not only remove pre-existing habitat—it produces new habitat and resources, primarily in the form of dead wood [68,69]. Therefore, saproxylic organisms—those directly associated with dead wood—are generally abundant after fires and other natural disturbances compared to non-saproxylic taxa [20]. However, the link between post-fire dead wood and the fauna that dwells belowground had so far remained less established, and it is likely that more time is required for the full recolonization by soil animals than those living aboveground. Finally, the low abundance of organisms in our study could also be related to the sampling method we used, as hand sorting could have limited the detection of all organisms in our samples.

Belowground faunal abundance and richness were greatest in the Low Plot. This was not surprising, as decreases with greater elevation are a general trend observed across many taxa [40,70]. Interpretations mostly rely on factors such as rough environmental conditions (chiefly temperature), low productivity, shorter vegetative periods, and smaller habitat areas at higher elevation [70–72]. In our study, plot elevation also generated clear differences in species composition, shown by the hierarchical clustering producing its main branches separated by plots. However, a factor that could have influenced our between-plot comparisons was the timing of sampling. We carefully selected the timing to sample according to the phenology at each elevation, yet this could have introduced error. Thus, the primary implications of the effect of plot that we interpret from our study were in its potential to modify the effect of dead-wood treatment and microhabitat.

4.2. Differences between Dead-Wood Treatments

We found support for our first hypothesis, namely that different dead-wood treatments produce differences in macroarthropod abundance and richness. Overall, the abundance of individuals and the number of orders were lowest in the salvage logging treatment, and communities differed between treatments. Similar results have been obtained in previous studies [39,73–75], showing a reduction in the abundance of several invertebrate groups following the large-scale implementation of wood and litter removal treatments (though note that our study did not include an unmanaged control treatment). In fact, the common practice of salvage logging can affect many different groups of organisms, particularly those dependent on dead wood, in a consistent way, as shown by a recent

global meta-analysis [25]. In that global study, the dependence on dead wood of the most negatively affected taxa suggested that major effects likely arise from the removal of the dead-wood resource, rather than other effects such as microclimatic differences among treatments [76], changes in vegetation [49], or direct soil disturbance produced by the harvesting machinery [33]. We should note that, although in our salvage logging treatment the felled trees could not be removed by the log-forwarder, logs were piled, and the branches were masticated, leaving most of the ground without coarse woody debris. In contrast, the partial cut treatment may have enhanced soil fauna, as felling the trees provided a high burnt-wood cover and sped up its contact with the ground, which may have fastened the recovery of soil conditions. In this sense, our results are conservative, as any potential effect of the piled logs on soil fauna (despite being unlikely given that samples were collected at a secure distance from the piles) imply that the differences with respect to the less aggressive treatment would magnify in a situation of complete salvage logging (which includes log removal). In addition, not only the abundance of downed wood over the ground surface differed across the two treatments but also the diversity of microsites, so the results related to our first hypothesis could arise from the existence of the two different microhabitat types sampled in the PC treatment [77].

Our second hypothesis—that stand-scale dead-wood treatment would affect soil communities even when sampling under similar microhabitats—was also supported by our data, although less so. The bare-ground microhabitat differed between the two dead-wood treatments, as in the PC treatment it had an enhanced macroarthropod abundance and richness (although richness only differed in the High Plot). At the Low Plot, the difference between the SL and the PC treatments after hypothesis 1 was, thus, greatly driven by the availability of the under-logs microhabitat in the latter treatment. On the other hand, our results also suggest that the availability of different microhabitats likely yielded a greater species pool in the PC treatment, with more taxa—and more individuals—able to colonize even beyond the reach of the trunks. However, there were no differences between microhabitats (under logs vs. bare soil) in abundance and richness when comparing within the PC treatment, so we did not find support for our hypothesis 3. Although this may be related to the great abundance of zeros in our dataset, the lack of differences across microhabitats could also indicate that the effect of managing dead wood occurred mainly at the spatial scale of management intervention.

The enhancement of soil macroarthropod communities in the PC treatment can be related to several non-mutually exclusive mechanisms, several of which are related to how dead wood can enhance soil biota. First, as the logs decompose, they lose integrity, causing the wood to crumble and increasing the amount and heterogeneity of resources available for taxa involved in wood decay, such as wood-boring beetles (Coleoptera) [78] and termites (Termitoidae) [79]. Logs had lost an overall 23% of their mass at the time of the present study, and they showed a high degree of fragmentation and many tunnels bored by insects [80]. Besides providing shelter, food, and soil nutrients [81,82], dead wood can also ameliorate microclimatic conditions, especially during the long, dry Mediterranean summer [30,83]. Grounded dead wood also provides suitable overwintering habitats for many species, including many that have at least one life stage belowground [84]. It should be mentioned that we lacked data on the total cover of dead wood across treatments (but see [30] for data on ground cover at the beginning of treatment establishment). Differences other than dead-wood abundance may have influenced our results too; for instance, the dead-wood treatments produced markedly different plant communities, which tended to be richer in the PC treatment [49]. Plants change the biophysical environment through facilitative, inhibitory, and competitive interactions, and they thereby enhance soil habitat heterogeneity and ultimately influence soil biota [67]. As a result, the interplay between the aboveground structural complexity produced by burnt wood [85], its effects on the physical and chemical environment, and its contribution to the composition of the plant community may have greatly determined the composition of soil invertebrate communities in our study [34,86], and these factors may have driven the effects of dead-wood treatments.

We did not detect significant differences in community composition across the two treatments. However, such lack of an effect could have resulted from a low overall abundance of organisms,

as dead-wood management can determine the habitat selection of particular groups of organisms. For instance, Lepidoptera were highly associated with the salvage logging treatment in our study. This treatment generated an open habitat with high solar irradiance, which is the kind of habitat sought by some moth species, such as the processionary caterpillar, to burrow and pupate [87]. In contrast, the Hemiptera that we found included several species that suck on the roots of a wide variety of plants [88], and these would likely be more associated with the more diverse plant communities of the PC treatment [49]. Moreover, the high amount of Isopoda, found mostly under logs, likely results from their diet, which consists mostly of decaying wood, and from their preference for moist soils [89]. Finally, the greater richness of ant species found in the PC treatment could result from their preference for dead wood both as nesting habitat [90]—wood provides warmer nesting sites than soils [91], especially important for thermophilic species such as *Cataglyphis velox* and *C. Iberica* [92]—and as feeding habitat for species like *Aphaenogaster* spp. that prey on termites [93].

5. Conclusions

Soil biota is generally overlooked in the setting of management goals and in the evaluation of restoration actions. Our study points out that belowground macroarthropod communities are sensitive to the manipulation of dead-wood legacies after a wildfire. The cumulative effects of repeated perturbations (fire, post-fire management) in already extremely modified ecosystems, such as Mediterranean pine afforestation, may markedly affect the natural development of disturbed areas and ultimately impact important soil processes such as nutrient cycling. In particular, removing burnt wood diminishes the heterogeneity of habitats and the amount of resources available for macroarthropods.

Author Contributions: J.C. designed the experiment, J.C., A.B.L. and C.R.M.-G. conceived the study, C.R.M.-G. conducted the fieldwork, A.G.-M. and C.R.M.-G. classified the organisms, A.B.L. and C.R.M.-G. analyzed the data, C.R.M.-G. and A.B.L. wrote the first draft, all authors revised and approved the draft.

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Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

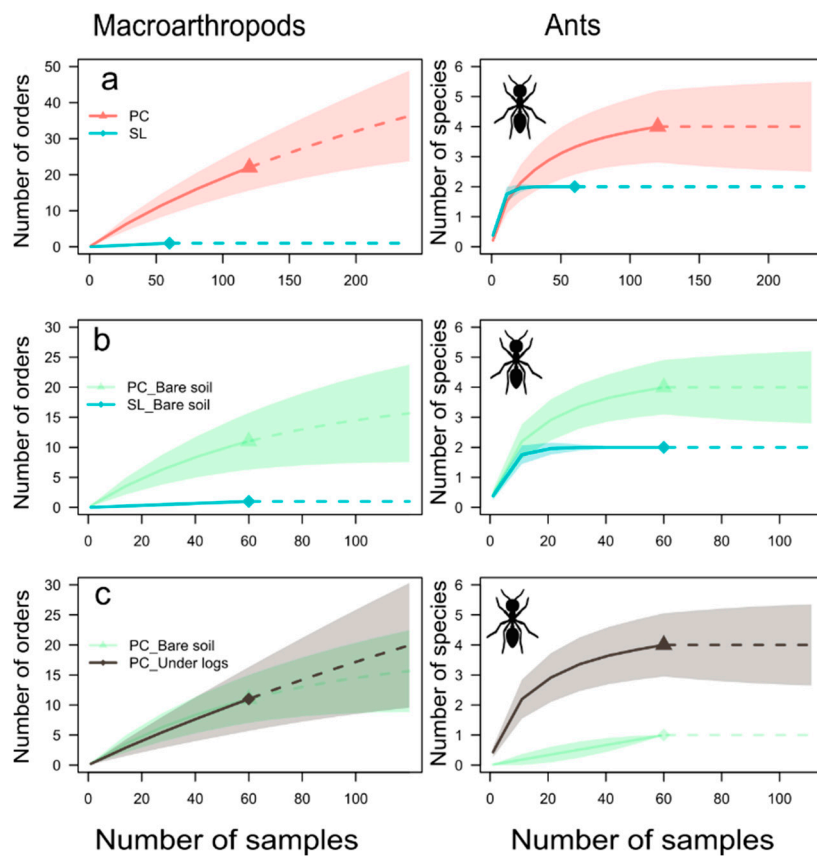


Figure A1. Sample-based rarefaction (solid lines) and extrapolation (dotted lines until reaching twice the maximum sample size) of macroarthropod orders and ant species at the High Plot. Shaded areas represent 95% confidence intervals. Panels show the three hypotheses of this study: differences between (a) dead-wood treatments, (b) treatments under the bare-soil microhabitat only, and (c) microhabitats in the PC treatment. Dead-wood treatments are SL = Salvage logging and PC = Partial Cut.

Table A1. Total number of macroarthropod individuals under two treatments (SL = Salvage logging, PC = Partial cut) and microhabitats (bare soil vs. under logs) collected at the study site ten years after post-fire dead-wood management.

Class	Superorder	Order	Family	Species	Low Plot			High Plot		
					SL	PC		SL	PC	
					Bare Soil	Bare Soil	Under Logs	Bare Soil	Bare Soil	Under Logs
Malacostraca		Isopoda			1	0	15	0	0	1
Diplopoda		Julida			1	1	2	0	0	0
Chilopoda		Geophilomorpha			3	2	3	0	1	0
		Scolopendridae			0	0	0	0	1	0
Arachnida		Aranae			1	1	0	0	0	1
	Acariformes				0	0	2	0	0	0
Hexapoda		Diplura			0	0	2	0	0	0
		Embioptera			1	0	0	0	0	0
		Hemiptera			66	120	93	0	4	2
		Diptera			6	10	8	0	2	0
		Lepidoptera			13	0	1	0	0	0
		Coleoptera			7	2	8	0	9	8
		Hymenoptera			0	0	0	0	0	1
		Hymenoptera	Formicidae	<i>Bothriomyrmex meridionalis</i>	0	0	42	0	0	0
				<i>Cataglyphis velox</i>	2	0	0	0	4	0
				<i>Tapinoma nigerrimum</i>	0	10	0	0	0	0
				<i>Proformica ferrari</i>	0	0	0	7	21	0
				<i>Cataglyphis iberica</i>	0	0	0	0	1	0
				<i>Aphaenogaster dulcinea</i>	0	0	8	0	0	0
				<i>Aphaenogaster gibbosa</i>	0	7	0	0	0	0
				<i>Tetramorium forte</i>	0	0	0	16	0	0
				<i>Tetramorium semilaeve</i>	4	0	0	0	0	0
				<i>Pheidole pallidula</i>	2	0	0	0	0	0

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