

Salvage logging alters microbial community structure and functioning after a wildfire in a Mediterranean forest

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ABSTRACT

Salvage logging is one of the most common post-fire management strategies, known for trigger soil degradation processes. Soil compaction, the major disturbance associated with logging operations, could seriously hamper the resilience of soil microorganisms after the perturbation produced by fire. The main objective of this work was to assess the impact of post-fire salvage logging on the composition and structure of soil bacterial and fungi communities, as well as to correlate these findings with the changes in soil physicochemical properties. The management severely affected the soil physicochemical and microbial properties. Whereas an increase of alpha diversity was detected in the treated soils for the microbial community, the microbial functionality registered was lower when compared to control soils. Salvage logging profoundly altered the structure and composition of the microbial communities, being modifications in soil structure the main driver in the microbial community shifts. Soil degradation induced by logging operations resulted in new niches related to anoxic habitats, being Proteobacteria and Firmicutes families, capable of anaerobic respiration, families with high abundance in the affected soils. In addition, the depletion in C and N nutrients as a consequence of the soil erosion reduced the microbial populations sensitive to substrates availability, e.g. Actinomycetales. Ascomycota increased proportionally in managed soils, which might be due to the removal of host plants dependent on ectomycorrhizal fungi. This study demonstrated that physical soil disturbance performed by the post-fire salvage logging profoundly impacted the soil microbial community and associated functions. A deeper understanding of the relationship between disturbances caused by forest management and resilience of soil biodiversity is required.

1. Introduction

Fire is a common environmental perturbation in Mediterranean ecosystems. Many soil physical, chemical, and biological properties can be altered by wildfires, being fire severity, climate, topography, vegetation type, and soil type, the main factors that control the impacts on the soil system (Certini, 2005; Fernández-González et al., 2017; Whiteman et al., 2019). Fire can lead to major shifts in highly heat-sensitive soil microorganisms; direct effects of fire provoke cell death, reduction in microbial biomass, and changes in microbial community composition and diversity (Dooley and Treseder, 2012; Weber et al., 2014). While bacteria have developed several mechanisms to deal with heating, the fungi kingdom has been found to be less resistant to fire disturbance

(Ferrenberg et al., 2013; Pressler et al., 2019). Despite the protective mechanisms expressed in fire-adapted systems, post-fire soil conditions ultimately mediate the soil microbial community composition shifts (Li et al., 2019; Prendergast-Miller et al., 2017). Soil pH, which usually increases due to ash incorporation to the soil, as well as soil nutrient state, have been described as major drivers in soil microbial populations (Adkins et al., 2020; Pérez-Valera et al., 2019). Indeed, the post-fire vegetation recolonization indirectly affects microbial communities by influencing soil properties, which is of special relevance in the Mediterranean ecosystem in which numerous plant species exhibit adaptive mechanisms to persist the fire and regenerate after it (Moya et al., 2021; Pausas et al., 2009). Moreover, ecosystem functions performed by microbial communities are tied to the soil status after the fire (Pérez-Valera

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et al., 2020), and tend to recover quickly thanks to resistance and resilience of soil biota to abiotic disturbances and the functional redundancy of microbial taxa (D'Ascoli et al., 2005; Mendes et al., 2015). However, further disturbances such as post-fire management practices may place additional pressure on the recovery ability of the ecosystem.

Salvage logging (SL), one of the most common management strategies after wildfire, and primarily used to recover timber values, has numerous benefits as the economics, the reduction to fire recurrence, or the reduction in safety hazards (Lucas-Borja et al., 2020). However, by increasing soil compaction and modifying the hydrological response during the logging operations, negative impacts affecting vegetation structure and soil degradation have been often reported (Morgan et al., 2015; Slesak et al., 2015). Alterations in the microbial properties have been also registered after post-fire logging operations, e.g. lesser microbial activity and biomass (García-Orenes et al., 2017), impact on CO₂ emission (Hartmann et al., 2014), and adverse consequences for microorganisms involved in N cycling according to Pereg et al. (2018). Soil compaction, the major disturbance associated to salvage logging, implies the collapse of soil structure reducing water and air conductivity, and ultimately the loss of multiple microenvironments that ensure long-term microorganism proliferation and diversity (Rabbi et al., 2016). Consequently, the soil system can suffer substantial and persistent alterations, which ultimately reduce forest productivity and ecosystem functionality via modifications in the microbial community composition and diversity (Chen et al., 2015; Hartmann et al., 2014). However, the effects of post-fire management on microbial community composition and structure, and its consequences for ecosystem recovery, remain partially unknown, being especially important in Mediterranean forests where soils are prone to degradation.

Ecosystem resilience is tied to its disturbance history. Increasing disturbance stress could lead ecosystems to lose the adaptive capacity and threaten their toleration to further perturbations (Villnäs et al., 2013). Therefore, a combination of wildfire and an aggressive post-fire management might shift the ecosystem to another state, exceeding the capacity for the ecosystem recovery (Ammitzboll et al., 2021). In a context of increasing frequency and severity of forest fires and climate change (Moreira et al., 2020), understanding how shifts in soil microbial communities contribute to the ecosystem functioning could help to evaluate the capacity to recover of a system after a disturbance and also guide the post-fire restoration strategies.

The use of high-throughput sequencing approaches can be suitable to assess the effects of the forest management on soil microbial communities in soils previously affected by a wildfire. It was hypothesized that the salvage logging management, additional pressure to fire disturbance, will cause a shift in soil microbial community resulting in a less diverse community. In addition, the microbial functionality in the post-fire managed soils will diminish in comparison to those of non-intervention where all burnt trees were left standing. Therefore, the objectives were: (1) to ascertain the effects of SL post-fire management on the composition and structure of soil bacterial and fungal communities and their associated functions, and (2) to identify the soil factors related to shifts in soil microbial communities and their functionality.

2. Material and methods

2.1. Study site

The study area is located in “Sierra de Mariola Natural Park” in Alcoy, Alicante, in E Spain (38°43'59" N, 0°29'16" W). Climate in the area is Mediterranean, 3–4 months of summer droughts, dry-hot summer, and wet-warm spring, autumn and winter. The precipitation concentrates in October–November with an annual average of 490 mm, and mean temperature is 15.2 °C. The soil is classified as a Typic Xerorthent (Soil Survey Staff, 2014) developed over marls with low depth, very vulnerable to erosion and degradation processes, characterized by clay

loam texture with 40, 25 and, 35% of sand, silt and clay respectively, and 40% of carbonates. The landscape is characterized by terraced hillslopes. The forest is composed mainly of *Pinus halepensis* Mill. trees, around 40 years of age, together with an understory of typical Mediterranean shrubs species such as *Quercus coccifera* L., *Rosmarinus officinalis* L., *Thymus vulgaris* L., and *Brachypodium retusum* (Pers.) Beauv.

The forest fire occurred in July 2012 affected a total of 546 ha. Fire severity was moderate according to Keeley (2009); as all understory plants were charred or consumed, fine dead twigs on soil surface were consumed and log charred, also the pre-fire soil organic layer was largely consumed. The forest lacked any pre-fire management. Seven months after the wildfire, in February 2013, salvage logging (SL) was carried out, consisting of a complete extraction of the burned wood using heavy machinery. The burnt trees were cut down with a chainsaw and dragged with chains at the top of the slope where a processor removed limbs and treetops. After an extreme rainy event in September 2013 (50 mm in less than 3 h), some gullies were formed as a consequence of the vulnerability of soils to erosion where the trunks were dragged.

2.2. Experimental design and soil analysis

Soil sampling was conducted in May 2014, just after 22 months had passed since the fire and 15 months since the implementation of the salvage logging management (SL). Sampling plots were established the same day of SL implementation as a part of a previous study to monitor plant and soil recovery after the wildfire and post-fire management (García-Orenes et al., 2017). Six sampling plots (3 m × 3 m), with a minimum distance of 15 m between them, were randomly established in a burnt affected area of 2500 m² where SL was carried out. Another six sampling plots in a nearby-burnt area comprising the same area and aspect where burned wood remained for investigation purpose were established as the untreated control (C). Within each plot, one composite sample comprised of five subsamples were randomly collected from the A horizon mineral (5 cm depth). The selection of the sampling depth was decided after estimations of the averaged mineral soil depth directly affected by the SL treatments (García-Orenes et al., 2017). According to the vegetation survey carried out in the same area, a significantly higher recovery of plants in terms of evenness in control plots was reported after 15 months since the SL operations (for further details see García-Orenes et al., 2017).

For each soil sample, a first portion was frozen at –20 °C for DNA extraction and a second one was kept at 4 °C for biochemical analysis. The remainder was dried at room temperature and sieved a part between 4 and 0.25 mm for aggregate stability tests and the remaining at 2 mm for the rest of the physicochemical analyses. Soil pH and electrical conductivity were measured in a 1:2.5 and a 1:5 (w/v) aqueous extract, respectively. Soil organic carbon was determined by the potassium dichromate oxidation method (Nelson and Sommers, 1983); total nitrogen was analysed by the Kjeldahl method (Bremner and Mulvaney, 1982); and available phosphorus was determined by the Burriel-Hernando method (Burriel and Hernando, 1950; Díez, 1982). Aggregate stability was measured using the method of Roldán et al. (1994) based on the method of Benito and Díaz-Fierros (1989). This method examines the proportion of aggregates that remain stable after a soil sample is subjected to an artificial rainfall of known energy (279 J min⁻¹ m⁻¹). In a 1:5 (w/v) aqueous extract, water soluble carbohydrates were determined in using the anthrone method as reported by Brink et al. (1960). Soil moisture was analysed from field wet soils by gravimetry after heating for 24 h at 105 °C.

Soil microbial biomass carbon was estimated by the substrate-induced respiration (SIR) method using glucose (3 mg per gram of soil) as the available substrate (Anderson and Domsch, 1978). Soil basal respiration was measured by incubating soil moistened to 60% of its water holding capacity. The amount of CO₂ emitted during both incubations was determined by an automated impedance meter (BacTrac

4200 Microbiological Analyser, Sylab, Austria) based on the changes in the impedance of a KOH solution (2%).

Urease and protease activities were determined as described by Kandler et al. (1999) using as substrates urea or N- α -benzoyl-L-arginine amid, respectively (Nannipieri et al., 1981). β -Glucosidase and alkaline phosphomonoesterase activities were quantified colorimetrically as the p-nitrophenol produced during the incubation of soil with the substrates p-nitrophenyl- β -D-glucopyranoside (Tabatabai, 1983) and p-nitrophenyl phosphate disodium, respectively (Naseby and Lynch, 1997). Dehydrogenase activity was determined by colorimetric estimation of the reaction product INTF (iodonitrotetrazolium formazan) formed by reduction of the substrate INT (2-p-iodophenyl-3-p-nitrophenyl-5-phenyl-tetrazolium chloride), following the procedure described by García et al. (1997).

2.3. DNA extraction, amplification, and sequencing

DNA was extracted from 0.25 g of each soil sample using the DNA PowerSoil kit (Mo Bio, Carlsbad, USA), with the following modifications to the manufacturer's instructions: initial vortexing was at 300 rpm for 20 min (STD 3500 Shaker VWR) and DNA was eluted with 65 μ L elution buffer. The selected primers for DNA metabarcoding library preparation were 341F and 806R to amplify a bacterial 16S rRNA fragment from the V3-V4 region; and ITS1F and ITS2 to amplify the complete fungal ITS1 region. The Illumina sequencing primers were attached to their 5' ends. A mixture of 2.5 μ L of the DNA template, 0.5 μ L of the corresponding primers and 12.5 μ L of Supreme NZYTa2 \times Green Master Mix (NZY-Tech) were contained for each PCR, and were diluted with ultrapure water to a total volume of 25 μ L. For the PCR incubation program, an initial denaturation was fixed at 95 $^{\circ}$ C for 5 min, followed by 35 cycles of 95 $^{\circ}$ C for 30 s, 55 $^{\circ}$ C for 30 s, 72 $^{\circ}$ C for 30 s and a final extension step at 72 $^{\circ}$ C for 10 min. To multiplex different libraries in the same sequencing pool, the barcodes identifiers were attached in a second PCR round with identical conditions but only five cycles and 60 $^{\circ}$ C as the annealing temperature. The amplified DNA in equimolar amounts from each library was pooled according to the Qubit dsDNA BR Assay (Thermo Fisher Scientific, Waltham, MA, USA) results. Previously, each library was purified using the Mag-Bind RXNPure Plus magnetic beads (Omega Biotek Inc., Norcross, GA, USA) following the manufacturer indications. Finally, the equimolar pool was sequenced using an Illumina MiSeq sequencing platform (Illumina Inc., San Diego, CA, USA) with 2 \times 300 base pair paired-end chemistry at the Australian Genome Research Facility (Brisbane, Australia).

Paired-ends reads were assembled by aligning the forward and reverse reads using PEAR (version 0.9.5) (Zhang et al., 2014). Primers were trimmed using Seqtk (version 1.0). Trimmed sequences were processed using Quantitative Insights into Microbial Ecology (QIIME 1.8) (Caporaso et al., 2010) USEARCH (version 8.0.1623) (Edgar, 2010; Edgar et al., 2011) and UPARSE software. Using USEARCH, tools sequences were quality filtered, full length duplicate sequences were removed and sorted by abundance. Singletons or unique reads in the data set were discarded. Bacterial and fungal sequences were clustered followed by chimera filtered using "rdp_gold" database and "Unite" database as reference, respectively. To obtain number of reads in each OTU, reads were mapped back to OTUs with a minimum identity of 97%. Taxonomy was assigned using Greengenes database (Version 13.8, Aug 2013) (DeSantis et al., 2006) for bacterial sequences and using Unite database (Unite Version7 Dated: 02.03.2015) (Köljalg et al., 2005) for fungal sequences by QIIME.

2.4. Statistical analysis

The adjustment of data to a normal distribution was checked by Shapiro-Wilk's test and variables were transformed when necessary in order to assume statistical parametric assumptions. Analyses were performed using the RStudio (RStudio Team, 2020). The effect of the post-

fire management (SL and C) in the variables was tested by *t*-test ($p < 0.05$), and Pearson's correlation coefficients were calculated to quantify the linear relationship between the physico-chemical and biological and biochemical soil properties using the RStudio function "cor".

Concerning microbial communities' datasets, the number of sequences per sample was rarefied to the lowest one and rarefaction curves were calculated (Fig. S1, Supplementary material). The α -diversity estimators, including Shannon and Inverse Simpson, were calculated using the resultants OTUs after rarefying the number of sequences per sample, and *t*-test was used to assess significant differences between managements, both for bacteria and fungi (Fig. S2, Supplementary material).

To analyse the β -diversity, non-metric multidimensional scaling (NMDS) was performed for bacterial and fungal communities in order to obtain the spatial distribution of their communities. With this aim, the "metaMDS" function implemented in "vegan" package for R was used. The effect of the management factor on the microbial communities' composition and structure were confirmed by permutational multivariate analysis (perMANOVA) with the "adonis" function using 9999 permutations.

To assess the relationships between the structural variability of bacterial or fungal communities and soil physicochemical and biochemical properties, canonical correspondence analyses (CCA) were carried out. In order to avoid multicollinearity, the variance inflation factor (VIF) was calculated and variables with a $VIF > 10$ were sequentially removed, and the remaining variables were then subjected to a forward selection procedure to select the subset of constraining variables that better explain the communities' variation in the CCA final model. The significance of the CCA final models was tested by Monte-Carlo permutational test (999 permutations).

An indicator species analysis (ISA) was conducted with the "indicspecies" package for R in order to identify indicator taxa characteristic of the bacterial and fungal communities (Pérez-Izquierdo et al., 2020; Rodríguez-Caballero et al., 2017). The relative abundances of microbial families and OTUs in each sample were used to calculate the Indicator Value (IndVal) and its significance.

3. Results

3.1. Soil physico-chemical, biochemical, and biological properties

The results showed a significant effect of the SL management on all the soil parameters (Table 1). The SL management provoked a decrease in the soil nutrients, a reduction of 60% of organic matter and nitrogen,

Table 1
Physical-chemical, biological and biochemical properties of control (C) and salvage logging (SL) soils.

	Control	Salvage logging
pH (H ₂ O, 1:5)	8.12 \pm 0.07b*	8.35 \pm 0.09a
Electrical conductivity (μ S/cm)	216 \pm 53b	151 \pm 10a
Soil moisture (%)	5.5 \pm 0.6	4.8 \pm 0.5
Organic matter content (%)	7.25 \pm 1.36b	2.80 \pm 0.87a
Total nitrogen (%)	0.29 \pm 0.05b	0.12 \pm 0.02a
Available phosphorus (mg kg ⁻¹)	37 \pm 14b	6 \pm 3a
Aggregate stability (%)	85.9 \pm 2.0b	70.8 \pm 4.5a
Water soluble carbohydrates (mg kg ⁻¹)	62 \pm 26b	37 \pm 12a
Basal soil respiration (μ g C-CO ₂ h ⁻¹ g ⁻¹ soil)	2.37 \pm 0.54b	1.52 \pm 0.38a
Microbial biomass carbon (mg C kg ⁻¹ soil)	1160 \pm 162b	568 \pm 85a
Dehydrogenase (μ g INTF g ⁻¹)	30.0 \pm 4.4b	16.7 \pm 1.6a
Urease (μ mol N-NH ₄ ⁺ g ⁻¹ h ⁻¹)	1.12 \pm 0.38b	0.57 \pm 0.21a
Protease (μ mol N-NH ₄ ⁺ g ⁻¹ h ⁻¹)	0.74 \pm 0.22b	0.38 \pm 0.12a
β -Glucosidase (μ mol PNP g ⁻¹ h ⁻¹)	2.12 \pm 0.44b	0.73 \pm 0.23a
Alkaline phosphomonoesterase (μ mol PNP g ⁻¹ h ⁻¹)	5.64 \pm 1.43b	2.32 \pm 0.41a

* Mean \pm standard deviation. Values in rows sharing the same letter do not differ significantly ($P < 0.05$) as determined by the *t*-test.

around 80% for the available phosphorus, and in the soil structure with lower aggregate stability. Additionally, the microbial biomass carbon and basal respiration showed the negative impacts of SL management with lesser values for both parameters. The same pattern was found for all the enzymatic activities measured in this study, dehydrogenase, urease, protease, alkaline phosphomonoesterase, and β -glucosidase. Most of the biological and biochemical soil properties were highly influenced by the soil physico-chemical properties, positively correlated with the soil nutrients and the aggregate stability of soils, and negatively correlated with the pH (Table 2).

3.2. Bacteria diversity and community composition

Bacterial α -diversity was significantly different between managements (p -value < 0.05 in Shannon and Inverse Simpson indices, Fig. S2), with higher values for SL soils. In addition, the perMANOVA test on β -diversity confirmed that the soil bacterial community composition and structure were significantly different between the SL and C managements ($F = 3.98$, p -value = 0.006). The spatial ordination of the bacteria communities (stress value of 0.046) showed that the communities of SL and C soils clustered separately along the X axis (Fig. 1.a).

The taxonomic profile at the phylum level (Fig. 2) showed Actinobacteria and Proteobacteria as predominant phyla, altogether representing around 70% of the total abundance. At the order level, Actinomycetales (Actinobacteria) was the most abundant followed by the abundance of Solirubrobacterales (Actinobacteria), Sphingomonadales and Rhizobiales (Alphaproteobacteria). At the family level, Sphingomonadaceae and Streptosporangiaceae were the most abundant (Fig. S3, Supplementary material). The relative abundance of the main phyla shifted after SL application. A significant decrease in Actinobacteria (44.94% in C, 37.62% in SL), Firmicutes (9.47% in C, 4.96% in SL), Bacteroidetes (4.31% in C, 3.10% in SL), and Verrucomicrobia phyla (1.62% in C, 1.11% in SL) were observed in SL soils with respect to C soils, whereas an increase of relative abundance was detected for Acidobacteria (4.02% in C, 8.06% in SL), Chloroflexi (4.45% in C, 7.34% in SL), and Gemmatimonadetes (3.75% in C, 4.79% in SL).

The indicator species analysis (ISA) showed higher number of indicator taxa in SL soils, at OTU level with 235 for C and 589 for SL, and at the family level, 40 and 154 for C and SL of bacterial indicator families (Table S.1). The most abundant indicator families for the bacterial community of C soils were Streptosporangiaceae (12.6%), Bacillaceae (5.2%), Oxalobacteraceae (2.7%), Cytophagaceae (3%), Conexibacteraceae (1.3%), and Bifidocacteraceae (1%). Among the indicator families for the bacterial community of SL soils, those with the most relative abundance were Gaiellaceae (3%), Hyphomicrobiaceae (1.4%), Rhodospirillaceae (1.4%), and C111 (1%).

3.3. Fungal diversity and community composition

The α -diversity analyses for the fungal communities showed

significant differences for the Shannon and Inverse Simpson indices between the managements, reaching the highest values in SL soils (p -value < 0.05, Fig. S2). The β -diversity was also significantly different between the managements according to the perMANOVA test ($F = 9.83$, p -value = 0.002). In the NMDS analysis (stress value of 0.060), the fungal communities cluster differently by the management along the X axis (Fig. 1.b).

At phylum level, the fungal taxonomic profile dominance was reduced in both soils to two phyla, Ascomycota and Basidiomycota, representing together more than 90% of the relative abundance (Fig. 2). The dominance of the main phyla was shifted due to the SL management; whereas the Ascomycota increased after the SL management (41.53% in C, 78.08% in SL), a strong decrease was registered for the Basidiomycota (53.58% in C compared to 14% in SL).

According to the indicator species analysis (ISA) performed (Table S.2) higher number of indicator taxa were found at the family level for SL soils. Two fungal indicator families were found in C soils, being Thelephoraceae (2%) the most representative, while 31 indicator families were statistically relevant in SL. The most abundant families included Trichocomaceae (27%), Chaetomiaceae (7.6%), followed with less abundance by Lasiosphaeriaceae (1.1%), Pezizaceae (1%), and Inocybaceae (1%).

3.4. Influence of soil properties in microbial communities

After a forward selection of the constraining variables, the CCA final model for the bacterial communities included the aggregate stability (AS) as the most explanatory environmental variable in the model (Fig. 3.a). The CCA final model explained 40.9% of the total inertia and the first two axes accumulated 57.7% of the variance in the bacterial communities, being the first CCA axis highly related to aggregate stability. The bacterial community from the C management clustered on the left-hand side of the plot, exhibiting higher values of AS than the SL management.

Concerning the fungal communities, the forward selection procedure reduced the constraining variables to aggregate stability (AS) and water soluble carbohydrates content (WSCH) (Fig. 3.b). The CCA final model explained 42.2% of total inertia, and the first two axis explained 64.7 and 35.3% of the constrained inertia, respectively. The constraining variables showing the most important relationship with the fungal community distribution along the first CCA axis were aggregate stability and water soluble carbohydrates. The fungal community of C soils was clustered on the left-hand side of the plot, some samples significantly influenced by higher AS and other samples with higher WSCH.

4. Discussion

The post-fire management based on salvage logging (SL), conducted seven months after the wildfire in a coniferous forest ecosystem, profoundly affected the structure and composition of the microbial

Table 2

Correlation coefficients (r values) for relationships between the physical-chemical soil properties and the biological and biochemical soil properties.

	pH	Electrical conductivity	Water soluble carbohydrates	Aggregate stability	Available phosphorus	Organic matter	Total nitrogen
Basal soil respiration	-0.64*	ns	ns	ns	0.69*	0.78**	0.70*
Microbial biomass	-0.81**	0.72**	ns	0.92**	0.81**	0.79**	0.85**
Dehydrogenase	-0.71**	0.77**	0.74**	0.86**	0.77**	0.85**	0.90**
Urease	ns	0.66*	0.69*	0.70*	ns	ns	ns
Protease	-0.64*	0.82**	ns	0.79**	0.64*	0.62*	0.72**
β -Glucosidase	-0.90**	ns	ns	0.82**	0.80**	0.81**	0.83**
Alkaline phosphomonoesterase	-0.86**	ns	ns	0.78**	0.73**	0.74**	0.78**

ns: not significant.

* Significant at $P < 0.05$.

** Significant at $P < 0.01$.

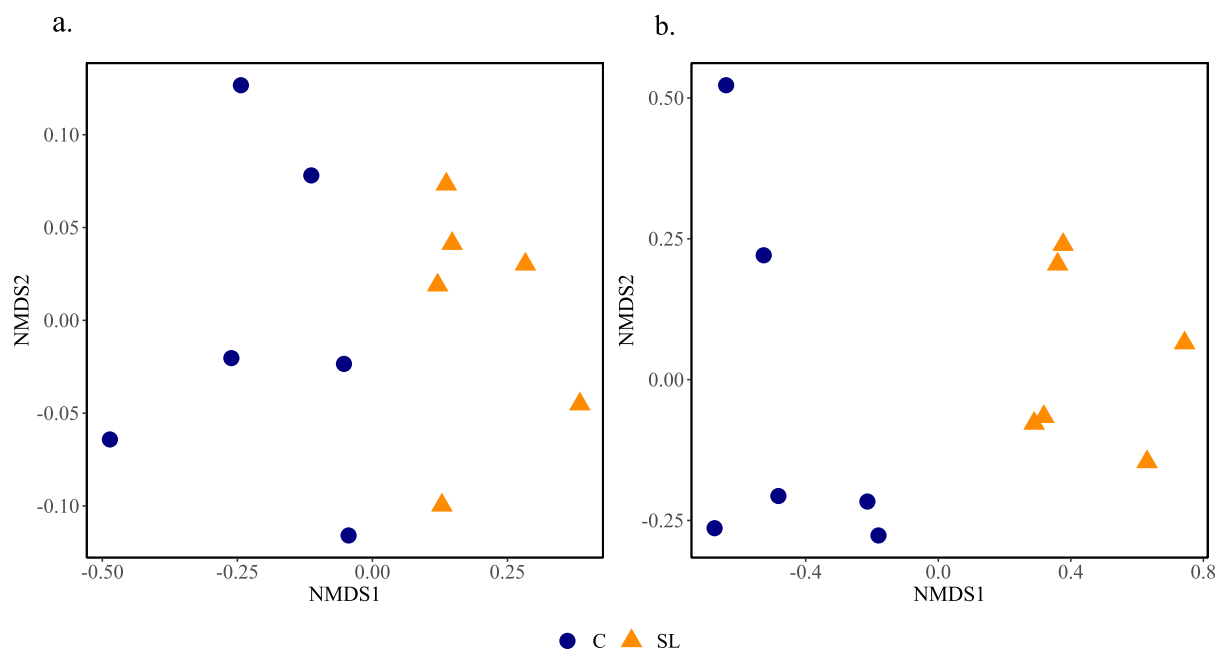


Fig. 1. Two-dimensional non-metric multidimensional scaling (NMDS) ordination based on Bray-Curtis dissimilarities at OTU level for bacterial (a) and fungal communities (b) of control (C) and salvage logging (SL) soils.

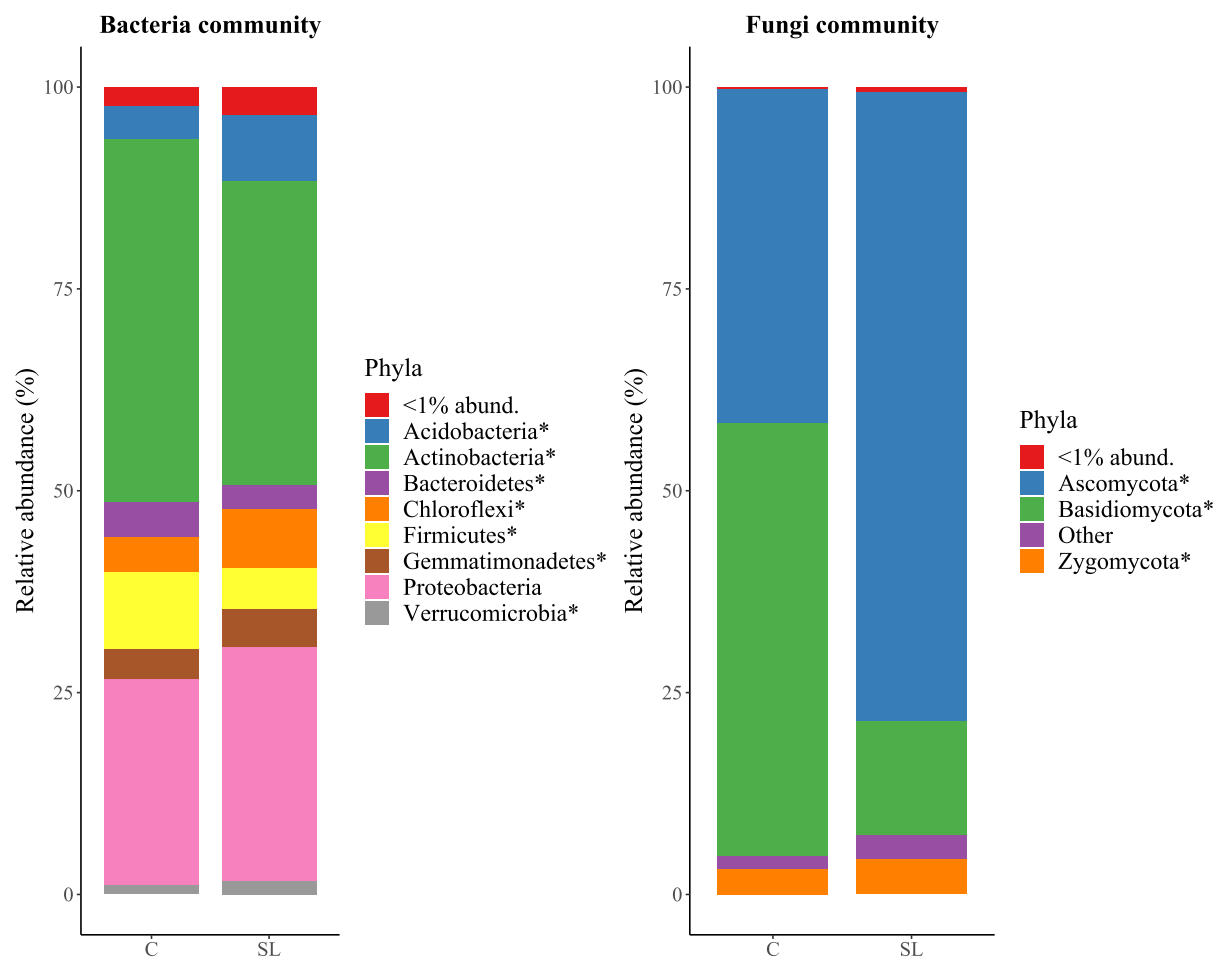


Fig. 2. Relative abundances of the dominant bacterial and fungal phyla of control (C) and salvage logging (SL) soils. For each phylum, significant differences were assessed by the *t*-test calculated at $p < 0.05$ and indicated by an asterisk.

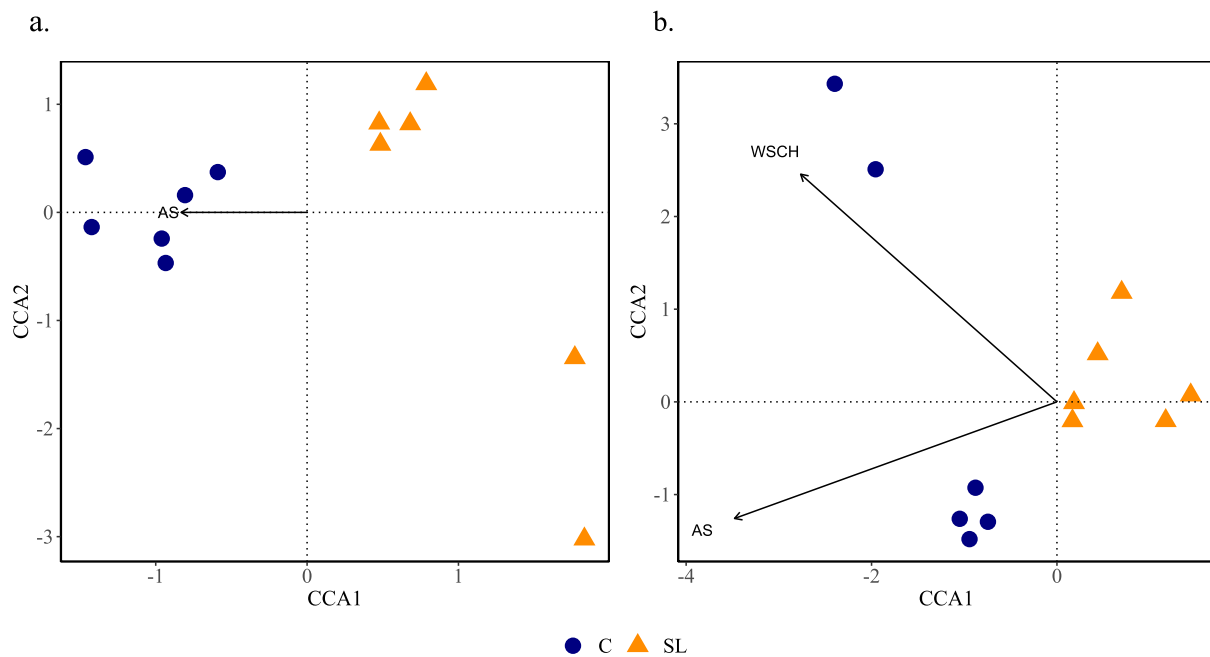


Fig. 3. Canonical correspondence analysis (CCA) at OTU level for bacterial (a) and fungal communities (b) of control (C) and salvage logging (SL) soils. The explanatory variables (arrows) are AS = aggregate stability and WSCH = water soluble carbohydrates.

communities placing additional pressure on the recently disturbed microbial communities. After a fire, the recolonization is pioneered by spore-formers or fast-growth strategies microorganisms adapted to the high release of nutrients of a post-fire environment, principally oxidizable carbon and inorganic nitrogen (Bárcenas-Moreno et al., 2011; Choromanska and DeLuca, 2002; Goberna et al., 2012). This fact might be related to the high dominance of Actinobacteria and Firmicutes bacteria phyla and Ascomycota and Basidiomycota fungi phyla in the soils unaltered by SL (C), all described as positively influenced by fire disturbances (Ferrenberg et al., 2013; Pérez-Izquierdo et al., 2020; Prendergast-Miller et al., 2017). Moreover, the mosaic of soil patches, that offer the burned wood distribution, provides a variety of carbon substrates that promote specialization strategies (Goldfarb et al., 2011; Miller and Chesson, 2009), and simultaneously softens microclimatic conditions facilitating microbial development (Marañón-Jiménez et al., 2013). Thus, the patchiness (heterogeneity) of C soils was revealed by the higher dispersion of the bacterial community among their replication samples, as shown in the NMDS ordination plot. The high presence of Actinomycetales (Actinobacteria) in C soils, known as highly specialized in organic matter degradation, supports the idea of a profound specialization in response to a higher resource availability induced by the burned wood retention. It has been registered that microbial diversity tends to increase after a fire disturbance due to the alteration in resource supply and new habitat creation (Ferrenberg et al., 2013; Shen et al., 2016). After 22 months since the fire, the control soils registered lower α -diversity compared to soils where the salvage logging carried out. This practise, conducted seven months after the fire, might be increased the pressure in the affected-soil and lead to the microbial communities to a stage dominated by species more tolerant to disturbance (Tanentzap et al., 2013).

The implementation of salvage logging management triggered severe soil physico-chemical degradation with a critical decrease in the nutrient content and soil structure deterioration, favoured by the high vulnerability of soils developed over marls. García-Orenes et al. (2017), who studied the soil evolution affected by SL management in the same study area, registered an increase in bulk density and a decrease in aggregate stability, pointing out the low resistance and resilience of soil structure to mechanical stresses. The degradation of soil structure - promoted by

the decrease in organic matter content and reduced plant development (Mataix-Solera et al., 2011) - resulted in the main driver in microbial community composition and structure shifts. Our findings are in accordance with Hartmann et al. (2014), who found soil compaction induced by logging operations provoked lower microbial abundances but increasing bacterial and fungal diversity associated with new niches related to anoxic habitats. In this sense, families with anaerobiosis characteristics Hyphomicrobiaceae, Hyphomonadaceae (Middleton et al., 2020), Syntrophobacteraceae (Liu and Conrad, 2017), or Koelethrixaceae (Astorga-Eló et al., 2020) were more abundant in soils under SL management than in soils under C management. In addition to the soil physical deterioration, the depletion in C and N compounds as a consequence of the erosion triggered by the SL reduced the microbial populations sensitive to substrates availability (e.g. lower abundance of Actinomycetales in SL) and promoted instead certain phylotypes highly competitive in oligotrophic systems (e.g. Saprobian fungi, especially the Trichomaceae family) (Bastida et al., 2017; Fultz et al., 2016). Studying the microorganisms involved in N cycling in the same study area, Pereg et al. (2018) found that the lower abundance in soils affected by SL was strongly related to the microaggregate fraction, described as a hotspot for nitrogen cyclers and bacterial biodiversity (Rabbi et al., 2016). The better vegetation development in C soils (García-Orenes et al., 2017) might have enhanced the soil structure recovery, influenced as well by the microbial biomass growth (De Gryze et al., 2005; Hart et al., 2005). The removal of host plants dependent on ectomycorrhizal fungi (mainly Basidiomycota) by SL management altered the fungal community composition (Kennedy and Egger, 2010). On the contrary, Ascomycota increased proportionally in SL soils, possibly as a result of plant detritus and woody debris supply to the soil after logging operations (Chen et al., 2017; Fraterrigo et al., 2006; Rasmussen et al., 2018).

Whereas an increase of the alpha diversity was detected for the soil microbial community affected by SL, lesser microbial functionality was registered compared to soils with burned wood maintenance (C). Values for the parameters that act as indicators of general microbial activity, as microbial biomass carbon and basal respiration, as well as the specific parameters of microbial performance, the enzymatic activities, suggest a loss in the ecosystem functions performed by the soil microorganisms. In fire-adapted Mediterranean ecosystems, short-time recovery of soil

microbial community, and the ecosystem functions they deliver, are usually reported (Pérez-Valera et al., 2019; Prendergast-Miller et al., 2017; Rodríguez et al., 2018). However, subsequent disturbances are susceptible to alter profoundly the soil microbial community and then the ecosystem functioning (Allison and Martiny, 2008; Hooper et al., 2005). It is well known that the biodiversity is key to maintain ecosystems functioning (Mendes et al., 2015), however ecosystems are valued for multiple ecological functions (i.e., multifunctionality) and other major microbial drivers of soil biodiversity are responsible as well for ecosystem functioning, e.g. species abundance or species composition (Delgado-Baquerizo et al., 2017; Maestre et al., 2012). According to that, Villnäs et al. (2013) argued the effects on ecosystem functioning after multiple disturbances depends on the specific species lost and the functional traits they express in the environment. In this regard, a greater number of microbial indicator taxa associated with SL soils were largely unidentified or unclassified taxa, and thus not known functions are associated to them. Although their functions are yet to explore, rare taxa could be driving the functional response in SL disturbed soils, acting as a reservoir that can rapidly respond to environmental changes (Lynch and Neufeld, 2015).

The fire-affected soils with burned wood maintenance presented higher contents of nutrients and a more stable structure than the soil under SL management, which was associated with a greater abundance of microorganisms with the ability to degrading the organic matter compounds. In this sense, the presence of Actinomycetales (Actinobacteria) in C soils was highly representative thanks to their important role in decomposition of labile (Goldfarb et al., 2011) and recalcitrant organic substances (Mokni-Tlili et al., 2020). Families found as relevant were Streptosporangiaceae as cellulose destructor (Wei et al., 2020), the Microbacteriaceae as lignocellulose decomposer (Argiroff et al., 2019); and the Coriobacteriaceae both labile carbon and cellulose decomposer (Goldfarb et al., 2011). Other Actinobacteria taxa, reported as pioneers in extreme environments, were representative in C soils, e.g. Geodermatophilaceae (Xing et al., 2020) and Cellulomonadaceae after wildfires (Aanderud et al., 2019). Firmicutes phyla reached high relevancy in C soils with special dominance of family Bacillaceae, whose species have reported the ability to degrade hydrocarbons accumulated during fires (Xiang et al., 2014) and fix nitrogen (Yeager et al., 2005). The families of Bacteroidetes Cytophagaceae and Sphingobacteriaceae, both indicators taxa in C soils, are related to organic matter enrichment in soils (Fierer et al., 2012; Hellequin et al., 2018). Among indicator taxa of Proteobacteria in C soils, Burholderiales and Oxalobacteraceae (Betaproteobacteria) are families positively affected by fires with the ability to degrade labile and recalcitrant carbon substances (Aanderud et al., 2019; Puentes-Téllez and Salles, 2020; Stinca et al., 2020), and Desulfovibrionales (Deltaproteobacteria) as lignin degrader.

Bacterial taxa positively associated with the SL management were assigned mainly to families of Acidobacteria, Chloroflexi, and Alpha-, Delta- and Gamma-proteobacteria. Among the families with recognized functions, bacteria associated with anaerobic respiration significantly increased in SL soils, highly represented by Gram-negative bacteria (Fraterrigo et al., 2006). Bacteria families with these characteristics in SL soils were the nitrate reducers and denitrifiers Hyphomicrobiaceae and Hyphomonadaceae (Alphaproteobacteria) (Middleton et al., 2020); the sulfate reducers in anoxic environments Syntrophobacteraceae (Deltaproteobacteria) (Liu and Conrad, 2017); the anoxygenic but potential N fixer Chloroflexaceae (Chloroflexi) (Xun et al., 2018); and Kouleothrixaceae (Chloroflexi), carbon degrader in anoxygenic environments (Astorga-Eló et al., 2020). Induced by the stressful conditions after SL performance, the families radiation-resistant Deinococcaceae and Trueperaceae (Thermo) prospered (Maier et al., 2018). Gaiellaceae (Actinobacteria) was previously reported as an indicator of specific anthropogenic activities in Hermans et al. (2017), and the predators Myxococcales members (Haliangium) survive in oligotrophic and anaerobic environments (Li et al., 2017; Wang et al., 2020).

After the wildfire, Ascomycota and Basidiomycota were dominant

phyla in soils, but SL significantly shifted the community composition favouring the Ascomycota dominance. Similar results have been previously reported after different forest management (Fraterrigo et al., 2006; Hartmann et al., 2014; Smith et al., 2017). Ascomycetes express high tolerance to environmental stress, playing a dominant role under scarce resource availability (Bastida et al., 2017; Huang et al., 2021). In SL soils, almost all the indicator taxa were saprophytes fungi, except the Pezizaceae family that is an ectomycorrhizal group associated with post-fire environments (Pérez-Izquierdo et al., 2020). Saprophytes play an important role in organic matter decomposition making nutrient available, and some of the indicator taxa associated to low nutrient content and stressful conditions were the family Verrucariaceae (Prieto et al., 2012); the Herpotrichiellaceae and Chaetothyriales families, and Sordiales and Hypocreales orders (Huang et al., 2021; Ma et al., 2018; Praeg et al., 2020). Trichocomaceae, saprobic fungi with a ruderal lifestyle (Houbraken and Samson, 2011), was the most abundant family among all the indicators taxa, together with Chaetomiaceae, cellulosic fungi that degrade plant material (Habtewold et al., 2020). On the other hand, Thelephoraceae was the only indicator family in C soils, found as favoured in fire Mediterranean forests (Buscardo et al., 2014; Pérez-Izquierdo et al., 2020), but negatively related to thinning and frequently after prescribed burning (Rasmussen et al., 2018).

5. Conclusions

Salvage logging as post-fire management is a major problem for vulnerable soils to erosion. Performed seven months after the wildfire, the forest management placed additional pressure on soils recently disturbed, compromising the capacity of the fire-adapted ecosystem recovery. The deterioration of soil structure profoundly and persistently altered the soil microbial community composition and structure. Despite the higher diversity found in soils affected by salvage logging, the indicator species reveal that new habitats related with transient environmental conditions were created due to the logging operations. Indeed, the aggregate stability of soils, better conserved in non-intervention soils, resulted in the best soil variable to predict the microbial communities shifts. Increasing intensity and severity of wildfires in the fire-adapted Mediterranean ecosystem, in a global change scenario, demand a better understanding of the relationship between disturbances caused by forest management and soil biodiversity, thus better predicting the resilience of the soil microbial response to future disturbances.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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This paper is dedicated to the memory of Dr. Lily Pereg (1965–2019), soil scientist.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.apsoil.2021.104130>.

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