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Fire impacts on soil microorganisms: Mass, activity, and diversity

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Abstract

The ecosystem response to fire is often linked to fire severity and recurrence, with potentially large consequences on both aboveground and below–ground processes. Understanding the fire impact has become increasingly important in the light of recent changes to disturbance regimes due to climate change. Although the impacts on the above vegetation and the below soil physical and chemical properties are well documented, it remains unclear how fire affects the fine-scale microorganisms. Microbial communities are responsible for driving essential ecosystem processes and particularly sensitive to changes induced in soil quality by wildfire or prescribed fire disturbances. This work is a review of the last three years' literature, dealing with the fire impact on mass, activity, and diversity of soil microorganisms from soil A horizon.

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Keywords

Wildfires, Prescribed fire, Severity, Microbial biomass, Activity and diversity, Short-, medium- and long-term effects.

Introduction

Wildfire is the primary abiotic disturbance in forest ecosystems and closely linked to deforestation. The historical fire regimes, partly due to global changes (climate changes, land use and land cover changes, social changes), have been replaced by larger fires known as 'megafires' or extreme fires [1]. More than 30% of the land surface has a significant fire frequency, the distribution of population and land cover, especially the proportion of cropland and grassland areas, being of vital importance [2]. Global change influences key factors that determine fire regimes, namely biomass growth, fuel availability, fire weather, and ignitions [3]. The extreme fires are the result of the more extreme conditions, high fuel availability, low humidity, high temperature, and high wind speed [4] and can have catastrophic damages on water-plant-soil systems and the loss of human lives [5]. The complexity of the phenomenon and the severe impact of the fires required an integrated fire management approach [6]. The most obvious impact of a wildfire is the loss of vegetation, but in addition, the soil ecosystem is also severely affected by the fire provoking its degradation and hence the loss of soil quality. The different soil properties (physical, chemical, and biological) are affected differently depending mainly on fire severity, which relates to the environmental factors involved in the combustion processes: quantity, nature, and moisture of the dead and living combustible, wind speed, and site topography [7-9].

Soil microorganisms are key components of the edaphic ecosystem because they drive 80-90% of the soil process and being the main responsible agents of the soil fertility and quality [10]. The impact of the fire on the soil microorganisms will determine in great extent the postfire soil recovery. This impact can be analyzed with different methods, from the classic number of the viable cell counting to the determination of several parameters related to its biomass, activity, and diversity [11]. Previous reviews have described a decrease in microbial biomass after a fire event [7,12], with a higher impact on the fungal biomass [13], and its recovery may require months or even years. Long-term shifts in the composition of ectomycorrhizal fungal communities have been described after wildfires and prescribed fires [14]. The fire impact on soil and the following postfire recovery of the microbiota can differ depending on the fire recurrence. For example, a decrease in ectomycorrhizal fungal diversity [15] or alteration of the microbial community structure and no effect on microbial biomass [16] have been described as a consequence of changes in the fire recurrence.

The evaluation of fire impacts on microbial properties requires the comparison of the burnt soil with the corresponding unburnt soil, being necessary to separate the fire effects to those due to the influence on environmental conditions (spatial and temporal variation) [11]. Recently, different reviews have addressed the impact of fire on soil physicochemical properties [17,18], vegetation, soil, hydrology, and geomorphology [19], the effect on sediment and nutrient exports [20], and wildfire impacts on postfire soil management [21]. The fire impact on the soil microbial biomass, activity, and diversity under different climate has been studied during the last years, but, to our knowledge, only in 2018, a meta-analysis study that reveals contrasting responses of soil microorganisms and mesofauna to fire has been reported [22].

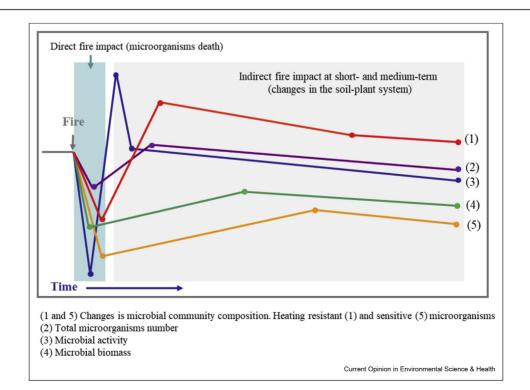
Microbial soil properties can experience immediate, short-term, medium-term, and long-term or permanent fire-induced changes depending chiefly on the type of property, severity, and frequency of fires and postfire climate conditions. Fires affect living organisms directly (causing their death) and indirectly, transforming their living environment (affecting food availability and quantity, heterogeneity of the environment, and pH increase). The direct effects are evaluated immediately after the fire (before first rain events, <1-3 months) and the indirect ones at a short term (1-3 months to 1 year), medium term (1-3 months to 1) 3-5 years), and long term (>3-5 years) [$23,24^*$]] (see Figure 1).

Fire immediate impacts

The direct fire impact on soil microorganisms depends on the fire severity, in other words, on the temperature reached and its duration during the heating as well as the initial soil moisture [7]. However, most studies about wildfire impacts do not take into account these factors in the data interpretation because these data can only be recorded under control conditions. Recently, laboratory studies demonstrated clearly that the initial water content [25] and fire severity (temperature, time) are determinant factors in the response of microbial communities to soil heating treatments. The soil heating at high temperatures (>120 °C) provokes negative effects and/or the death of soil microorganisms. The effect of fire on microbiota is not the same for all the microbial groups. In general, studies of several authors have shown that fungi and microorganisms of the C cycle are more sensitive to heat than bacteria and microorganisms of the N cycle [8,11,23] (Figure 1).

An immediate fire negative impact on properties related to mass, activity, and diversity of microorganism has been recently reported (Tables 1 and 2). As expected, the magnitude of this effect was inversely correlated

Figure 1



Fire-induced changes on different microbial parameters over the time. Modified from Bárcenas-Moreno and Díaz Raviña (2013) [23].

Table 1

Summary of results from the reviewed articles concerning the fire effects on soil properties of samples taken mainly in the 0-5 cm of the A horizon top layer (part 1).

Fire type/ecosystem/climate	Time after fire	Microbial parameter	Change (respect to unburned)	Reference
Wildfires				
Forest/Mediterranean climate	3 days/10 months	Enzyme activities: Acid and alkaline phosphatases, arylsulfatase, beta- glucosidase, and leucine- aminopeptidase	Decrease, recover after 10 months	Borgogni et al., 2019 [24*]
		Bacterial and fungal communities (DNA)	Decrease, recover after 10 months	
		Microbial biomass	None	
Peatland/equatorial climate	14/28 days	Soil respiration	Decrease	Wasis et al., 2019 [32]
		Viable cells (plate counting)	Decrease	
Conifer catchment/alpine	18 days	Enzyme activities:		Fairbanks et al., 2020 [27**]
climate		α-glucosidase, β-xylosidase, leucine- aminopeptidase, acid phosphatase	None	
		β-1,4-glucosidase, β-D- cellobiohydrolase, β-1,4,N- acetylglucosaminidase	Decrease	
Pine forest/Mediterranean	1 month/1-3 years	Viable bacteria and fungi (plate counting)	Increase	Rodriguez et al., 2018 [31*]
climate		Bacterial diversity (DNA)	Decrease (recovery 1 year)	
		Soil respiration (SIR)	Increase	
		Enzyme activities: glucosidase, cellulase, invertase, urease, β-N- acetylglucosaminidase, acid and alkaline phosphatases	None/increase (phosphatase)	
Forest and shrubs/ Mediterranean and temperate climate	2 months	Richness and diversity of bacterial communities (DNA)	Decrease	Sáenz et al., 2020 [38]
Wetland/subtropical wet	2 months	Microbial biomass (PLFA)	Increase (decrease in Fungi)	Zhang et al., 2019 [36]
climate	2 montho	Microbial C utilization (CLPP)	Increase	
Forest/temperate monsoon climate	6 months	Bacterial and fungal richness, diversity (DNA)	Decrease (fungi more sensitive)	Qin and Liu, 2021 [39]
Forest/temperate oceanic climate	1 year	Bacterial and fungal communities (DNA)	Change in structure, bigger impact in bacteria than in fungi	Brown et al., 2019 [40**]
Forest/boreal climate	1 year	Fungal richness and diversity (DNA)	Decrease	Day et al., 2019 [41*]
Wetland/semiarid climate	1/2 years	Enzyme activities: invertase, urease, catalase	Decrease	Semenenko et al., 2020 [35]
Oak-pine forest/humid subtropical climate	1/14 years	Enzyme activities: cellobiohydrolase, β- glucosidase, leucine aminopeptidase, phenol oxidase, peroxidase, urease	None/decrease (urease)/ increase phenol oxidase	Huffman and Madritch, 2018 [33
		Soil respiration Bacterial and fungal diversity (DNA)	Decrease (1 year) Decrease	
Pine forest/semiarid climate	2 years	Soil respiration Microbial biomass (SIR)	Decrease Decrease	Allam et al., 2020 [34]
Pine forest/semiarid climate Forest/boreal climate	3 years 3 years	Viable bacteria and fungi (plate counting) Fungi/bacteria (DNA)	Decrease in bacteria None	Olejniczak et al., 2019 [48] Zhou et al., 2019 [49]
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Fable 1. (*continued***)** Fire type/ecosystem/climate

Time after fire

Pine forest/Mediterranean and oceanic climate	4 years	Microbial biomass (fumigation) Microbial C, N, P Enzyme activities: β-glucosidase, urease Acid-phosphatase Microbial biomass C	None Decrease Increase/decrease (site specific) Increase Increase/decrease (site specific)	Fernández-García et al., 2020 [46
Forest/boreal climate	50 years	Microbial biomass (PLFA)	None	Cavard et al., 2019 [50]
PLFA: Phospholipid fatty acids; CL	PP: Community Level Phys.	PLFA: Phospholipid fatty acids; CLPP: Community Level Physiological Profiling; SIR: Substrate Induce Respiration.		

*****9

Reference

Change (respect to unburned)

Microbial parameter

with the fire severity. A decrease in the enzyme activities one [26], three $[24^*]$, and eighteen days $[27^{**}]$ after a prescribed fire or wildfires was found. Laboratory soil heating experiments showed a decrease in the bacterial activity [25], as well as in the enzymatic activity and the viable N-fixing bacteria [28], but a slight increase the microbial C utilization [16*] after the heating. Likewise, Armas-Herrera et al. (2018) [26] found that the microbial biomass and soil respiration decreased immediately after a prescribed fire. Under laboratory conditions, soil heating at high temperatures reduced notably microbial biomass [16*,25,28], whereas no effect was detected at low temperatures (50 °C). With respect to the diversity of soil microorganisms, Borgogni et al. (2019) [24*], observed that bacterial and fungal diversity decreased three days after a wildfire. Under laboratory conditions, changes in the bacterial composition after low heating temperatures (<100 °C) [29] and in microbial community structure at high temperatures (150 °C - 400 °C) [16*] were observed. No legacy impact of fire was detected on the fungi associated with pine trees [30].

Fire short-term impacts

After the initial microbial activity decrease, the surviving microorganisms (resistant to high temperatures) favored by postfire conditions grow rapidly using as substrate the labile C and nutrients derived from the dead microorganisms (sensitive to high temperatures). Thus, in principle, a rapid increase in the microbial activity, which is inversely related to the fire severity, can be observed at a very short term. This increase is transitory and tends to disappear when the availability of C and nutrients decreased. In some cases, this behavior is not to be observed, and low microbial activity values were found after high severity fires. Therefore, variable results can be observed depending on fire severity, postfire conditions, and time passed after the fire event (Tables 1 and 2). Thus, although the study of Rodríguez et al. (2018) [31^{*}] has shown an enhanced soil respiration one month after a wildfire, other authors found that soil respiration values decreased around one month [32] or even one [33] or two years [34] after a wildfire event, as well as the enzymatic activity can be negatively affected two years after a wildfire [35].

A reduced microbial biomass is observed at the short term as consequence of wildfire or prescribed fire impact (Tables 1 and 2). This fact is attributed to the abundance of the two main decomposer microbial groups (fungi and bacteria) because under postfire conditions, fungi, which contribute more to biomass than bacteria, are not favored. In accordance with this, in tropical climate, it was found that bacterial biomass increased 1-2 months after a wildfire, whereas fungal biomass decreased [32,36]. Likewise, it was observed

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Table 2

Summary of results from the reviewed articles (part 2).

Fire type/ecosystem/climate	Time after fire	Microbial parameter	Change (respect to unburned)	Reference
Prescribed fires				
Shrubland/mountain climate	1 day/1–5 years	Microbial biomass C Enzyme activities (β-D- glucosidase, acid phosphatase), soil respiration	Decrease (recovery after 5 years) Decrease	Armas-Herrera et al., 2018 [26]
Forest/Mediterranean climate	2/6 months	C-substrate utilization	Increase	Moya et al., 2020 [43]
Pinus plantation/subtropical climate	1 year	Bacterial fungal diversity Bacterial-fungal relative abundance	None Shift	Wang et al., 2019; 2020 [37,42]
		Microbial biomass C	Decrease	
Larch forest/boreal climate	3 years	Microbial diversity and richness	Decrease	Kang and Park, 2019 [51]
Shrubland/Mediterranean climate	4 years	Fungal community composition	Decrease mycorrhizal fungi	Castaño et al., 2020 [52]
Shrubland/temperate climate	4 years	Microbial biomass (PLFA) Enzyme activities (β- glucosidase)	Decrease None	Díaz-Raviña et al., 2018 [47]
		Enzyme activities (urease)	Decrease	
		Microbial biomass C	Decrease	
		Soil respiration	Decrease	
		Bacterial growth	None	
Pine forest/semiarid climate Controlled experiments	15 years	Ectomycorrhizal fungi	None	Hart et al., 2018 [53]
Arable land/humid continental climate (laboratory heating, degree-hour	1 day	Enzyme activities: catalase, dehydrogenase	Decrease	Kazeev et al., 2020 [28]
method)		Microbial biomass	Decrease	
		Viable N fixing bacteria	Decrease	
Pine forest/temperate climate (laboratory	1 day/1 month	Microbial biomass	Decrease	Barreiro et al., 2020 [25]
heating under different soil water content, degree-hour method)		Bacterial activity	Decrease	
Shrubland/temperate climate (laboratory	1 day/2 months	Microbial C utilization (CLPP)	None/increase (soil specific)	Lombao et al., 2020 [16*]
heating, severity and recurrence, degree-hour method)		Microbial biomass (PLFA) Microbial community structure (PLFA)	Decrease Shift	
Pine forest/Mediterranean climate (heating	7 days	Microbial biomass	None	Lucas-Borja et al., 2019 [29]
of soil monoliths)		Bacterial composition	Modified	, , , , , , , , , , , , , , , , , , , ,
Pine forest/boreal climate (greenhouse)	1 year	Fungal communities associated to pines	None	Beck et al., 2020 [30]
Postfire management				
Forest/temperate climate (mulch material amendment)	2 months	Bacterial activity Fungal activity, soil respiration Microbial biomass	Increase (straw)/decrease (initial with eucalyptus Increase/none (coconut fiber) Increase (fungi)	s) Barreiro et al., 2016 [44]
Forest/Mediterranean climate (logging)	6 months	N cycling bacteria abundance	Decrease	Pereg et al., 2018 [45]
Grassland/continental climate (fertilizer	1 year	Bacterial and fungal biomass	None	Carson and Zeglin, 2018 [54]
application after yearly prescribed fire)		Bacterial community composition	Decrease/increase (specific phyla)	

that the total microbial biomass decreased one month after fire in a soil under Mediterranean climate [24*] and two years after a wildfire in an Algerian forest [34]. Prescribed fire had also a negative effect on the microbial biomass one year after the fire [37].

The microbial diversity is very sensitive to the shortterm impact of the fire (Tables 1 and 2). Saenz et al. (2020) [38] observed that fire severity triggers a reduction in the diversity of soil bacterial communities of three different Mediterranean ecosystems that persists two months after the fire. Qin and Liu (2021) [39] showed that bacterial and fungal richness and diversity decreased six months after the fire, with the fungi being more sensitive to fire than bacteria. In contrast, Brown et al. (2019) [40**] also detected an impact on the bacterial and fungal communities one year after the fire, the effect being more pronounced for bacteria than for fungi. In the boreal forest of Canada, a reduced richness and diversity of fungal soil communities was observed one year after the fire [41*]. A shift in the abundance of fungi and bacterial but not in the bacterial and fungal diversity was detected one year after a prescribed fire [42]. An increased physiological diversity, measured by the C utilization pattern, was observed two months after a wildfire [36] or a prescribed fire [43]. Soil microbial communities can be also affected by different postfire management practices such as seeding and mulching treatments. The short-term amendment of mulching material to burn soil increased the bacterial and fungal activity and favored the fungal biomass [44]. The postfire salvage logging practices decreased the N cycling bacteria abundance [45].

Fire medium- and long-term impacts

The negative effects of the fire on the microbial communities observed in the short term can be reduced with time until the microbial parameters reach the prefire values (soil recovery) or can persist in the medium term and long term, and hence, the microbial parameters exhibited lower values than those in the unburnt control soil (Figure 1). The soil recovery process depends on the severity of the fire, the resilience of the soil, and the postfire conditions. After the impact of low- or moderate-severity fires, in areas where the vegetation that fixes the soil and provides C and nutrients has been regenerated, the impact of fire may disappear after 1 or 2 years. However, when indirect soil effects persist and long-term C and nutrient availability has dramatically decreased (drastic modifications of the content and composition of organic matter that present a predominance of the recalcitrant fractions over the labile ones), in other words, in high-severity fires with a slow regeneration of the vegetation or in areas susceptible to postfire erosion, a negative effect of fire on soil microorganisms is observed. The negative effects

can persist even 5-10 years after the fire, and the situation can be irreversible; therefore, soil recovery will not take place [8,23].

Field studies concerning the medium- and long-term impact of wildfires and prescribed fires on microbial properties (mass, activity, and diversity) are scarce and show divergent results (Tables 1 and 2). Fernandez-García et al. (2020) [46*] analyzed the fire impact four years after wildfires in pine ecosystems along a Mediterranean-transition-oceanic climatic gradient and found that enzymatic activities can be negatively or positively affected depending on the environmental conditions. The negative impact of prescribed fires has been described four and five years after the fire for the soil respiration and for the urease, β -glucosidase, and acid phosphatase enzymatic activities [26,47] in shrublands. Similarly, a decrease in the bacterial growth was detected four years after a prescribed fire [47]. The microbial biomass in the medium term can increase or decrease depending on the specific environmental conditions [46^{*}], but in general, the values recovered in the long term (Tables 1 and 2). Inconsistent results concerning the soil microbial biomass were observed by different authors 3-5 years after wildfires or prescribed fires [26,47-49]. On the long term, soil microbial biomass can be recovered, as indicated by Cavard et al. (2019) [50] fifty years after the fire in a boreal forest.

Regarding the impact of fire on the soil microbial diversity, it can persist at the medium term and long term (Tables 1 and 2). In the medium term, Kang and Park (2019) [51] detected a decrease in the microbial diversity and richness three years after a prescribed fire, with an increase in the relative amounts of β -proteobacteria and firmicutes and a decrease in acidobacteria. The fungal community diversity is also affected in the medium term. Castaño et al. (2020) [52] observed a decrease of the relative abundance of ectomycorrhizal species four years after a medium-severity prescribed fire. In the long term, a decrease in the bacterial and fungal diversity was found 14 years after a wildfire [33]. However, other studies did not find differences in the fungi/bacteria ratio of a permafrost soil at the medium term and long term after a wildfire [49] or in the ectomycorrhizal fungal diversity in a pine forest 15 years after a prescribed fire [53]. As consequence of the combination of long practices of prescribed burning and application of fertilizer, no effects on the bacterial and fungal biomass and changes in specific phyla of the bacterial community composition were observed [54].

Conclusions and prospects

The fire impact on soil microorganisms and the subsequent soil recovery depends on different factors such as the fire severity, the soil resilience, and the environmental conditions. The current situation of climate change favors more extreme environmental conditions (high fuel availability, low humidity, high temperatures, and high wind speed) that shift the fire regimes to more severe fires with large impact on the soil microorganisms. During the last two years, several studies, mainly concerning activity and diversity of some microbial groups (bacteria and fungi), have been published. However, information on fire impact on microorganisms, especially on diversity, is based on few studies. Most studies assessed the impact of fire in forest ecosystems, under specific vegetation and Mediterranean, boreal, and temperate climate, whereas other land uses and climatic conditions are often not considered.

The data interpretation is very complex and involves the comparison of the burnt soil with the unburnt one, which requires the characterization of diverse microbial aspects in relation to its environment, in other words, studies with an ecological perspective. The laboratory experiments simplify data interpretation, but they are not fully comparable with field studies because of the higher complexity of the latter (additional influence of plant and climatic conditions). In the last years, studies have been focused on the wildfire impact on soil after the sampling at one fixed time, which makes the data interpretation very difficult. In contrast, a small number of heating laboratory studies and/or experimental fire field investigations under controlled conditions, with more concise conclusions, have been performed.

The different microbial properties (related to mass, activity, and diversity) showed a different sensitivity to detect fire impact as well as different trend over time (immediate, short-, medium-, and long-term). In general, microbial activity and biomass changes can be transitory, and their values can reach prefire ones. However, diversity changes seem to be maintained at a longer time. Microbial soil diversity is often related to soil capacity to recover after the stress and the maintenance of soil functionality.

Studies on susceptibility resilience of soil to fire events (ability of soil to withstand the heat stress without losing its quality and intrinsic capacity of soil to return to its equilibrium state or a new state after the heat stress) in relation to microbial diversity and hence soil quality should be performed. This knowledge can help us understand the microbial response to fire and the subsequent implementation of rehabilitation and restoration strategies at the short term, medium term, and long term.

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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