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Impacts of wildfire on soil microbiome in Boreal environments

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Abstract

The temperature changes for the future climate are predicted to be the most pronounced in boreal and arctic regions, affecting the stability of permafrost and fire dynamics of these areas. Fires can affect soil microbiome (archaea, bacteria, fungi, and protists) directly via generated heat, whereas fire-altered soil properties have an indirect effect on soil microbiome. Fires usually decrease microbial biomass and alter microbial community composition. These changes can take decades to recover to prefire states. As the fire occurrence times are expected to change in the future, and the fire return intervals, intensity, and severity are expected to increase in boreal environments, the fire-related changes in the soil microbiome, including its recovery and resilience, are inevitable.

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Fire disturbance, Boreal forest, Microbiome, Soil fungi, Soil bacteria.

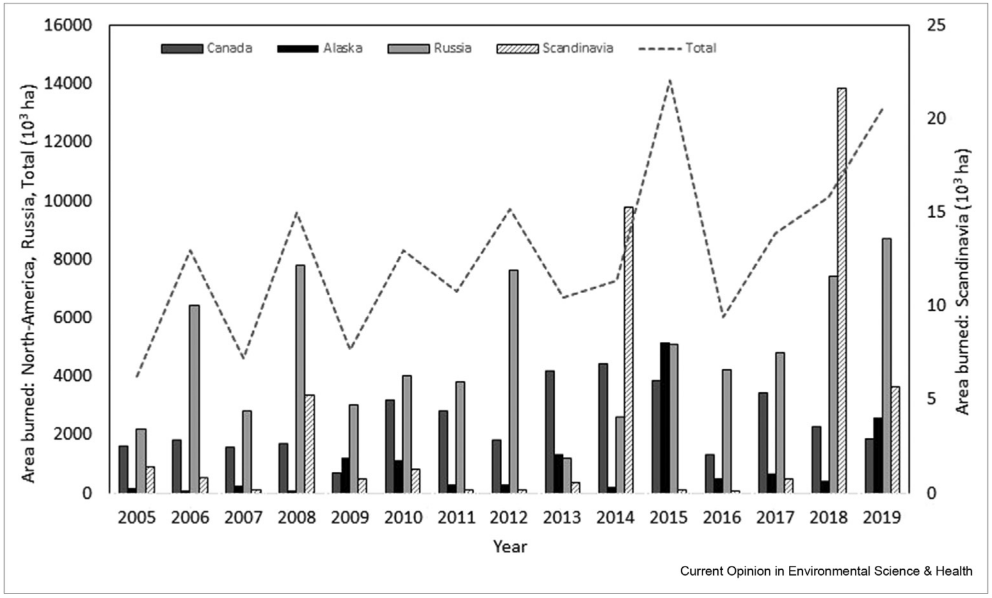
Introduction

Fire is one of the most important natural disturbances in boreal environments, driving carbon (C) cycling and storage [1*], restructuring microbiome [2*], and forest plant species composition [3]. Currently, approximately 1% of the boreal forests is burning annually (Figure 1). As boreal forests comprise roughly one-third of global forested area and terrestrial C stocks, possible climate, vegetation, and fire interactions in that area are of the global importance to the future C dynamics [4]. Various studies have projected changes in future fire regime, including changes in the fire season length [5] and occurrence time (spring vs summer fires) [6], increase in fire frequency (return interval), intensity, and severity [7,8]. In turn, these changes could change also the forest stands domain by shifting the treeline toward the north, increasing the share of deciduous species in the currently conifer governed stands, and affecting the permafrost regime, all contributing to the regulation of climate stability [9,10].

Most of the boreal forest area is underlain by permafrost [15], of which about 25% is predicted to thaw during the 21st century because of climate change [16]. Projected increases in fire activity and subsequent changes in soil properties may reinforce the deepening of the active layer and thawing of the near-surface permafrost [17,18*]. This exposes frozen organic matter to microbial decomposition, causing a positive feedback to global warming and fire activity [16]. The microbial decomposition, in turn, is affected by both permafrost thaw and fire regime.

Soils of boreal forests contain a large diversity of microbes, and the transformation of the soil organic matter (SOM) in these soils depends on the activity of microorganisms, mainly fungi and bacteria [19]. The soil microbiome is one of the main agents responsible for the long-term sustainability of soil ecosystems [20], and compared with soil chemical and/or physical properties, it responds faster to different disturbances through changes in biomass, metabolic activity, and community structure [21]. Wildfires in different ecosystems usually

Figure 1



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Annual burned areas (10^3 ha) in boreal forests (2005–2019): North America, including Canada (data from Canadian National Fire Database and from Hanes et al., [11]) and Alaska (data from Alaska Department of Natural Resources and Moreno-Ruiz et al., [12]); Russia (data from Bondur and Gordo, [6]); Scandinavia (data from Lindberg et al., [13], and San-Miguel-Ayanz et al., [14]).

decrease soil microbial biomass [22–26] and alter the microbial species composition [2*]. The effects of fire on soil microbiome (archaea, bacteria, fungi, and protists) are direct via combustion and generated heat [27**] or indirect through changes in soil properties and vegetation [17]. It can take decades for microbial communities to recover to prefire states [18*,24,26,28].

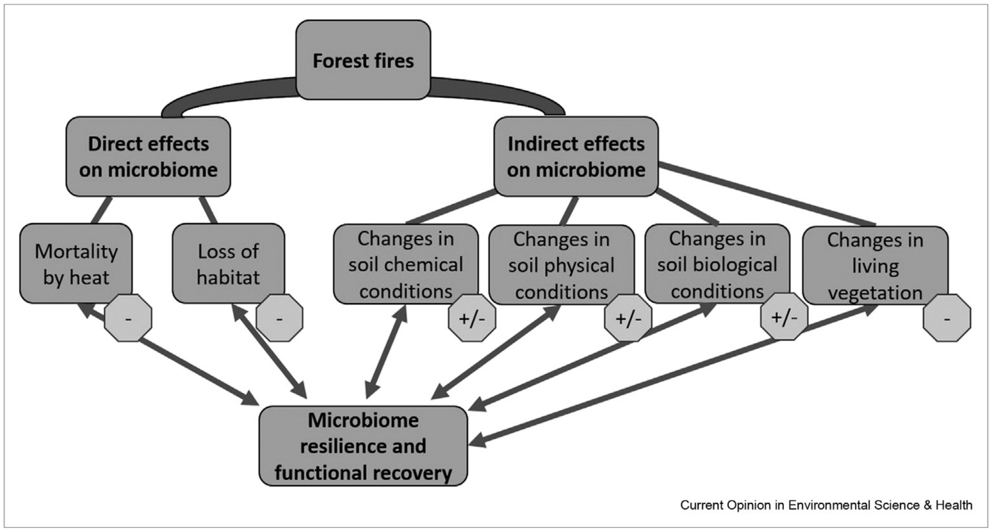
This review aims to synthesize both direct and indirect effects of fires on soil microbial composition and function in boreal forests and to point out the possible prospects for future studies to complement existing knowledge.

Direct effects of fires on soil microbiome

In boreal forests, wildfires range from low-intensity surface fires with no tree mortality (non-stand-replacing fires) to high-intensity fires that kill all trees and remove most of the soil organic layer (stand-replacing fires) [3,29]. Depending on the degree of fire-induced changes to vegetation and soils, fires are divided into low-, moderate- and high-severity fires [2*]. In general, extensive non-stand-replacing (low severity) fires of low- and high-intensity dominate the fire regime in larch (e.g. *Larix sibirica and Larix gmeliini*)- and pine (e.g. *Pinus sylvestris*)-dominated forests of the nonpermafrost regions in Scandinavia, Russia, and Northern China, whereas stand-replacing (high-severity) high-intensity fires predominate in spruce (e.g. *Picea mariana)*- and pine (e.g. *Pinus banksiana*)-dominated forests of Canada and Alaska and in larch forests growing in permafrost soils of Russia [30,31]. A typical fire creates a mosaic of completely burned to scarcely burned or unburned patches, which reinforces the spatial heterogeneity of soil microbial communities.

Direct effects of fires on soil microbiota include consumption of litter and soil humus—that is, loss of habitat and killing living organisms by heat, which often translate into decreased microbial biomass (Figure 2). In theory, most of the living soil microorganisms will die in temperatures close to 50 °C [32] due to the misfunctioning of their enzymes and other essential cell components. Although the soil heating temperature during fire is inversely proportional to microbial survival, with complete sterilization at low soil moisture levels and at temperatures higher than 200 °C [23], longer heating duration may cause significant microbial mortality at much lower temperatures. The effect of heating is also conditional on the microbial taxa, for instance, mycorrhizal fungi are considered to be more sensitive to heat compared with bacteria, due to slower growth, and essential association with living plants [26,33], whereas some thermophilic microbial species such as archaea have a higher resilience toward heating. At the same time, we can find from fire areas fungi that have been surviving fires—these extremophile fungi present after fire can influence C dynamics, as plant—fungal relationships are often species specific [34]. A future increase in the severity of fire could potentially increase local bacterial and saprotrophic fungal competition. Lately, it has been also found that the stand-replacing

Figure 2



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Soil microbiome responses to forest fires. The positive and negative effects of direct and indirect effects on soil microbiome are presented with "+" and "–," respectively.

crown fires in Eurasia have a smaller effect on the soil microbiome than the surface fires [35]. It might be that although the stand-replacing crown fires have much higher burning temperatures, they are moving really fast, and the high temperatures are not on the soil surface but in the upper parts of the canopy. Although in case of slowly moving surface fires, the burning temperatures are lower, but fire has more time to affect different soil properties.

Indirect effects of fires on soil microbiome

Although fires may directly cause microbial mortality, the indirect fire effects on soil physiochemical conditions and plant communities may surpass or counteract the direct effects of fire (Figure 2). Currently, one of the most important discussions in changing fire regime is on the microbial sensitivity to fire severity. Although some studies only identified negligible effects of soil severity on bacterial community composition [36], generally, increased fire severity has been observed to reduce the microbial species richness in the microbiome and/or alter the community composition [2*,23,37].

Fire changes the soil environment by combusting and charring the organic matter (Figure 2). At temperatures around 300 °C, it can alter the structure of SOM complexes, producing pyrogenic compounds (e.g. alkaline ash and charcoal) [38]. However, it already results in significant reductions of the structure of SOM, reducing the decomposition ability of microbes, at temperatures lower than 300 °C. Fires also tend to increase postfire soil temperature and decrease soil moisture. Soil microbial communities may respond to fire-caused temperature changes by shifting their distribution in the soil profile, moving deeper in the soil profile if surrounding temperatures are outside of their optimal thermal range [39]. Because of the effect of combined temperature and moisture on microorganisms, postfire microbial activity in warmer soils will change depending on the water availability of the pre- and post-fire soil [27**]. Hydrophobic nature of charred material may also result in faster drying of the soil surface. In addition to hydrophobic material and removal of the protective forest floor vegetation and organic matter, fire exposes surface soils to increasing runoff and/or erosion [40]. If roots are dying and decompose, they no longer bind the soil in place, and the erosion happens both through wind and water.

Soil pH is one of the major drivers of soil microbial diversity and richness [41–43]. It has been observed that presumably because of the increase in postfire pH, soil fungal diversity in boreal forests increased after the fire and then started to decline over time [33]. However, Whitman et al. [2*] and Hui et al. [28] observed that soil bacterial communities were more strongly structured by pH compared with soil C, whereas soil C stock was a stronger predictor for soil fungal communities. In case of low-severity surface fires, the postfire increase in fungal diversity [33] might be associated with a litter pulse from the dead vegetation. In such case, the material is rapidly colonized by fungi specializing to the early stages of substrate decomposition. In later stages of the postfire succession, the remaining organic fractions of C become more recalcitrant, and the mycorrhizal abundance increases as the easily decomposable compounds are consumed. In addition, global-scale studies have found that the fungal-to-bacterial ratios are highly correlated with soil C:N ratio [44]. Although the pyrogenic matter generated after the fire is high in C:N ratio, soil available C:N of the burned forest is lower than that of the unburned, resulting in lower fungal biomass compared with bacteria [18*].

Microbiome resilience and functional recovery

As we presented, fires affect the soil microbiome directly via heat-induced mortality and indirectly by altering the postfire physicochemical and biological environment of soil (Figure 2). Wildfires usually change soil microbiome, and it can take decades to recover to its prefire level. At the same time, soil microbiome shows different levels of resistance (i.e. the degree to which the microbiome remains unchanged) and resilience (i.e. the rate at which microbiome returns to its original composition after being disturbed) [45]. However, microbiome resilience is not studied often probably because of biases in sampling intensity or duration [25**]. Currently, there are not many studies known to us that concentrate on the resilience of microbiome to fire in boreal ecosystems.

For the recovery processes, postfire environmental conditions of the area are critical. If the conditions are not equal compared with prefire, then microbial communities will not recover to the prefire state. This concerns particularly pH-sensitive and host-associated microbial species, such as mycorrhizae. The postfire spatial heterogeneity of the soil environment also plays a major role in the recovery by providing sources of inoculum [46]. As many microbes reproduce rapidly (in hours or days) [2*,46], the setbacks to microbial communities may be short term as long as some individuals are spared. In such cases, the redistribution and spreading of the microbiome in the area, along with improving physicochemical conditions, is the critical phase of functional recovery.

The long-term effects of wildfires on soil microbial community are expected to increase because of increasing fire frequency. For example, a shift in the age of a forest stand will affect dramatically the structure of the microbial community. Despite there are no clear evidence on the recovery trends of microbial community composition within the first 10 years after fire [25**], the recovery of microbial respiration and carbon cycling activities to prefire levels might take decades. In general, fungi are proved to be more sensitive to heat compared with bacteria. At the same time, fungal growth rate after a fire is lower than that of bacteria (bacteria reproduce faster). In boreal forests, ectomycorrhizal fungi are common and have been shown to decline after a fire more drastically compared with other fungal groups [23,33] because of the loss of vegetation. It may take decades for ectomycorrhizal fungi to recover to prefire levels [47,48] along with the recovery of vegetation.

Postfire plant recovery enriches the soil with organic matter, eventually restoring the naturally low levels of bacterial and fungal diversity. Thus, through postfire ecosystem succession, environmental characteristics become dominant drivers of microbial communities. Of course, this trend can persist till we have sufficient time between the fires. If the fire return intervals will shorten, and the areas are not able to recover, there will be less biomass (fuel) for the next burn. This will decrease the burn severity, and studies of fire effects on the soil microbiome face a completely new situation.

Conclusions

Responses of different microbial groups to forest fires have been studied for decades [2*,25**], but only a few studies have considered the long-term recovery of boreal, subarctic, and/or arctic forests after fires or the coupled effect of climate change and more active fire regimes on the soil microbiome.

Predicted changes in climate, such as warmer temperatures, dry summers, and earlier spring snowmelt, are expected to change the fire dynamics in northern ecosystems. Burn severity is predicted to increase in boreal forests, and even greater effects on microbiome are expected to accompany. However, this might be constrained in fire-prone areas where fire frequency is also expected to increase.

As the soil microbiome plays a crucial role in the mineralization of SOM, and the quality of SOM is modified by both fire and soil microbes concomitantly, the predictions rely on the understanding of the dynamics of the soil microbiome in changing fire regime in the future climate. To understand and predict the possible changes, more information is needed on the functionality in the microbial community after the fire and its relation to SOM quality, for example, recalcitrance to decomposition. Also, it is important to understand the fire resilience of soil microbiome and how microbial communities recover in these ecosystems and how they are affected by the possible changes in fire dynamics. Our current knowledge in the field suggests that future studies dealing with forest fires in the northern latitudes should focus on microbiome-relevant subcomponents of burn severity metrics, classification of specific ecological strategies of fire-responsive microbes, postfire successional stages and changes in microbiome through these, and alterations of microbial functions and ecosystem services.

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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* of special interest
* * of outstanding interest

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