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Forest fires alter the trophic structure of soil nematode communities

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ABSTRACT

The impact of fires on nematode diversity, abundance and biomass was assessed in 20 burnt forests and 20 adjacent control plots across a 3000-km-long north-south transect in European Russia. The transect covered five main forest types (Mediterranean and broadleaved forests, southern, middle, and northern taiga). In spring 2015, we assessed major abiotic parameters of soil, soil microbial PLFA markers, and nematode community characteristics (genus richness, abundance, biomass and trophic structure) in the burnt and control plots.

Generic richness was the highest in the southern taiga (22 genera) declining both northwards (down to 16) and southwards (down to 13 genera). The highest abundance of nematodes was recorded in the Mediterranean forests (139.4 ± 15.1 ind. g^{-1} soil dwt, control site) and the lowest in the northern taiga (10.8 ± 1.2 ind. g^{-1} soil dwt, burnt site). Biomass followed the same pattern with slight deviations. Abundance and biomass of soil nematodes was not significantly affected by fires in any ecoregion with the exception of Mediterranean forests.

We detected consistent fire effects on the abundance of particular nematode feeding groups. Trophic groups abundance of soil nematode communities were considerably modified in burnt forests due to the increase in abundance of bacterial-feeding nematodes and reduced number of hyphal-feeding, plant-associated and plant-feeding nematodes. This increase in bacterial-feeding nematode biomass coincided with the growth of the ratio between bacterial and fungal biomass in pyrogenic soils. pH of soil solution and actual denitrification rate in the burnt forests correlated with the biomass of predatory nematodes. We conclude that, five years after fire, the structure of the microbial community, pH of soil solution and denitrification activity correlate with the ratio of feeding groups of belowground nematode communities in these forests. Taking into account considerable nematode biomass in soil, shifts in the ratio of trophic groups after fires induced by these factors may potentially lead to changes in the level of ecosystem functions which they deliver in burnt forests.

1. Introduction

The world's forests are prone to fires of varying frequency and intensity (Goldammer and Furyaev, 1996; Whitlock, 2004). Fires change the geochemistry of terrestrial ecosystems by removing nutrients from soil with smoke and post-fire leaching. Change of abiotic conditions in soil after fires inevitably leads to the transformation of the range and quality of belowground ecological niches in the burnt areas (Certini, 2005). Ground fires dramatically alter the ratio of the major groups of soil microflora and result in massive extinctions of not only rare but also common organisms, especially in the topsoil in both boreal and temperate European forests (Moretti et al., 2004; Gongalsky and Persson, 2013). For example, active mycelium practically disappears in the first few years after burning from the microbial community consistently across a wide range of ecosystems (Wang et al., 2012). Then, several years after fires, the abundance of microorganisms of all groups except for micromycetes increases. One of the reasons is that the soil becomes more basic due to ash deposition. Bezkorovainaya et al. (2005) showed that fires in pine stands of the East-Siberian

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middle taiga resulted in an increase in soil pH, and that this was associated with increased bacterial and decreased fungal populations. As soil microflora along with detritus are the main trophic resources for soil animals, fire-induced changes to the soil microbial community will obviously lead to the drastic modification of soil fauna community composition, especially for those taxa that are directly feeding on detritus or soil microbes (Coleman et al., 2004; Bardgett and van der Putten, 2014).

Nematoda is a widespread group of invertebrates, with about 25,000 described (Zhang, 2013) and one million of potentially existing species (Lambshead, 1993). In the soil, nematodes directly or indirectly feed on bacteria, fungi, plants and animals or their metabolic products as well as detritus and carrion. Some soil-dwelling nematodes demonstrate high trophic specialization (for example, Mononchidae are obligate predators), while others consume a wider range of trophic resources (Yeates, 1999).

Reported effects of forest fires on soil nematode communities are controversial so far. Some researchers conclude that the abundance of soil nematodes is higher in unburnt ecosystems (for example, New Mexico, USA, Whitford et al., 2014); however, findings of Fenster et al. (2004) do not support this. Other studies also report higher abundance of nematodes in the burnt areas, while trophic diversity of soil nematode communities was reported to decrease after fires (Čerevkova and Renco, 2009). The reasons for this decrease, according to Yeates (1999) and Viketoft (2013) are the close linkage between nematode taxonomic richness and diversity, on one hand, and the reduction of vegetation productivity on the other hand. However, Čerevkova et al. (2013) found that three years after a fire there was a decrease in abundance of bacterivorous nematodes which were replaced by the other trophic groups (mainly fungal-feeders). This observation is somewhat counterintuitive since the majority of studies (Dooley and Treseder, 2012; Mikita-Barbato et al., 2015) and our own data (Gongalsky et al., 2016) demonstrated that soil microbial communities after forest fires shift from fungi-dominated to bacteria-dominated ones. One can assume that such controversies may be driven by overarching regional differences in their food resource availability and quality, but not much is known on this topic so far (Zaitsev et al., 2016).

All of the abovementioned studies were done either within a limited range of geographic conditions or even in single locations, which severely narrowed the applicability of conclusions that can be drawn from these observations. Obtaining and verifying such data for geographically extensive regions is an important but challenging task due to the issues of fire replication and variability in natural conditions (Zaitsev et al., 2016). The Russian plain offers an excellent opportunity to examine fire effects on nematode communities with particular regard to the importance of climatic gradients and environmental spatial variability. The advantage of this macroregion is its relatively uniform surface topography, which does not provide any significant impact on the local climate, the frequent occurrence of wildfires, and extensive datasets available on the spatial variability of many environmental parameters over the past century (Solntsev, 1962; Dewdney, 2013), as well as the influence of recent climatic change on these parameters (Kislov et al., 2011).

To better understand to what extent the soil nematode community taxonomic and functional composition are modified in burnt forests in different geographic conditions, and which factors drive these shifts, we conducted a study on soil-living nematodes after forest fires along the extensive geographic gradient of the Russian Plain from the Mediterranean to the boreal forests. We anticipated that fire-induced alterations of nematode communities would be driven by shifts in microbial communities more than by actual changes in soil type-specific abiotic characteristics. We hypothesized that (i) the abundance and diversity of soil nematodes would remain lower five years after forest fires of moderate severity regardless of macrogeographic conditions; and (ii) the alteration in the relative representation of different soil nematode trophic groups would be driven by the shift from a fungal-based channel to a bacterial-based one in the burnt forest soil. We studied abundance, biomass, taxonomic richness of nematode trophic groups along with the wide range of soil abiotic and microbiotic variables in five ecoregions along the extensive north-south transect in European Russia.

2. Material and methods

2.1. Study area

The study area covers almost the entire diversity of forest types represented in the European part of Russia (Fig. 1) (Ogureeva et al., 2015). The material was collected along a 3000-km long transect in five ecoregions: 1) The Black Sea coast of the Krasnodar Region, the Crimea-Caucasus Ecoregion, Mediterranean forests (further abbreviated as MD), 2) the Voronezh and Lipetsk Regions, the Dnieper-Volga Ecoregion, broadleaved forests (BL), 3) the Moscow and Tver Regions, the Smolensk-Priuralsky Ecoregion, southern taiga (ST); 4) the Republic of Karelia and the Leningrad Region, the Baltic-Vetluzhsky Ecoregion, middle taiga (MT); 5) the Murmansk Region, the Kola-Karelian Ecoregion, northern taiga (NT).

To harmonize differences in seasonality across a geographically

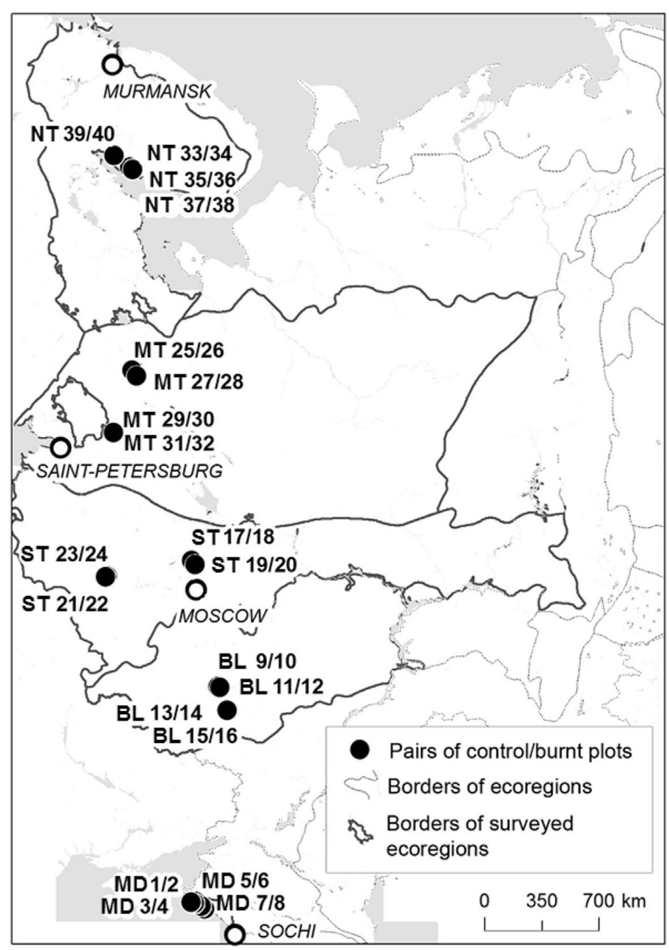

Fig. 1. Location of pairs of control and burnt plots in five ecoregions across European Russia (Ecoregions map: Ogureeva et al., 2015). Plot numbers refer to those in Table S1.