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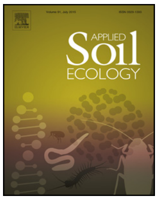

Short communication

Trait-specific response of soil macrofauna to forest burning along a macrogeographic gradient

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ABSTRACT

Fires change physical, chemical and biotic conditions of forest ecosystems. They also strongly affect soil macrofauna including key soil ecosystem engineers and regulators of soil-related processes in forest soils. However, due to a wide range of traits attributable to macroinvertebrates, the effect of forest burning on the macrofauna can be quite contrasting and still has not been quantified. We assessed the impact of forest fires on macrofauna taxonomic richness, abundance, total biomass and biomass of animals belonging to different functional traits in 20 forests burnt five years ago and 20 respective controls plots along a 3000-km-long north-south transect in European Russia which covered five major forest biomes (Mediterranean and broadleaved forests, southern, middle, and northern taiga).

Actual abundance, biomass and taxonomic diversity of the soil macrofauna showed remarkable stability after burning and were specific to forest biome. However, soil macrofauna trait composition was consistently affected by fire. Relatively immobile taxa inhabiting top of the forest floor and sharing saprophagy suffer most from the consequences of fire five years after burning. We have concluded that resident groups of soil macrofauna sharing saprophagy seem to avoid top soil as one of the most damaged "frontiers" of the burnt soil ecosystem possibly due to both unfavorable hydroclimatic conditions in the burnt patches and lack of suitable resources. At the same time damaged soil surface creates a barrier in the way of the resident soil macroinvertebrate taxa distribution due to their inability to quickly transit patches with harsh conditions.

1. Introduction

Forests of the world are prone to fires of varying frequency and intensity. Fires may drastically change resource and habitat availability and diversity. Soil in the burned areas becomes a source for a bioavailable nutrients (N, K, P) and is poorly drained due to reduced evapotranspiration after tree burning. All these factors lead to an instant increase of microbial biomass and rapid development of pyrogenic plant communities (Hart et al., 2005). Following such drastic fire-induced changes in soil, micro biome and above ground plant communities soil macro fauna has to restructure its community composition several years after a fire event. However, it still remains unknown to what extent pyrogenic effects on habitats alter the functional composition of below ground macro invertebrate assemblages. Potentially soil community shifts in pyrogenic forests may be reflected in the proportion of different functional traits as recently suggested for several groups of above ground organisms (Flynn et al., 2011; Clark et al., 2012). So far this approach has been almost completely ignored when explaining the patterns of soil community recovery after fire-related disturbances (but see Moretti and Legg, 2009). This is a serious gap, since trait spectra are now considered to be among the most promising indicators of biodiversity and functional responses to both disturbances and natural gradients (Makkonen et al., 2012; Birkhöfer et al., 2016).

In this paper we compare the functional trait composition of soil macrofauna in the burnt forests across different forest biomes in European Russia. We hypothesize that shifts in soil macrofauna communities five years after fires will be determined by the preferential impact of pyrogenic habitat modification on the animals belonging to certain functional traits. We tested this hypothesis in a large-scale study along a 3000 km-long transect on the Russian Plain, which hosts a very clear and prominent macrogeographic gradient and a diversity of forest biomes: from boreal taiga to Mediterranean stands.

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2. Material and methods

The study area covers almost the entire diversity of forest biomes represented in the European part of Russia (Supplementary material, Fig. S1) (Ogureeva et al., 2015). The material was collected along a 3000-km long transect in five forest biomes: 1) The Black Sea coast of the Krasnodar Region, Mediterranean forests (*Pinus pityusa or Pinus nigra, Carpinus orientalis or Junipers exelsa, Pistacia mutica) on* Leptosols rendzic or Cambisols chromic soils; 2) the Voronezh and Lipetsk Regions, broadleaved forests (*Quercus robur*) on Chernozem chernic or Phaeozem albic or Podbur soils, 3) the Moscow and Tver Regions, southern taiga (*Picea abies, Pinus sylvestris, Betula pendula*) on Albeluvisol soils; 4) the Republic of Karelia and the Leningrad Region, middle taiga (*Pinus sylvestris, Betula pendula*) on leptosols lithic or Podzol Halpic soils; 5) the Murmansk Region, northern taiga (*Pinus sylvestris, Picea abies*) leptosols lithic or Podzol soils.

We sampled respective forest biomes on the annual mean date of the bird cherry tree (*Prunus padus* L.) flowering, which equals the ecologically synchronized late spring period. This approach to the ecological synchronization of the field work is routinely used in soil zoological studies across extensive climatic gradients (Gongalsky et al., 2004). We started from the southernmost region (Mediterranean forests) on April 30, 2015, and sampled each region with a 10-day lag moving northwards. For the same reason the time lag between the two northernmost regions, middle taiga and northern taiga, was 20 days (World atlas . . . , 1964).

In each of the five sampled forest biomes, 4 pairs of plots (burnt and control) were selected. Each day we sampled simultaneously only one pair of plots starting from approximately 10 a.m. It was possible because the burnt forest and adjacent unburnt forest (control) were usually located approximately 250–500 m apart from each other. In total, 20 burned areas and 20 unburned control plots were sampled. For detailed geobotanical descriptions of the sites refer to the project website (http://www.forestfire.biogeo.ru/index.php/en/sites-descritpion).

We obtained five soil samples with the corer of 20 cm in diameter, down to the depth of 15 cm to account for soil macrofauna. The soil samples were delivered to the laboratory in cool boxes at a temperature of ca. +10 °C and were processed within 2-3 days. Extraction of macrofauna was performed using Tullgren extractors into a mixture of alcohol, water and ethylene glycol in a ratio of 80:15:5, for 4 days, the time sufficient to make soil reach an air-dry condition. To extract earthworms from the soil, the formaldehyde method was applied (Römbke et al., 2006). Three 1 × 1 m square areas were selected at each plot. All litter was thoroughly hand-sorted and all earthworms collected. After that, 10 L of a 4% formaldehyde solution was sprayed over the area. All emerging earthworms were collected during a 30 min period after the application of the irritant and fixed in separate jars in 95% alcohol. Animals were sorted out from the samples under a binocular microscope and identified under a light microscope.

Biomass of soil macrofauna was estimated by direct weighing. Animals were lyophilized in a Labconco FreeZone 1 freeze-dryer for a day. Then the animals were weighed on a Mettler Toledo balance with an accuracy of 1 μg. The number of animals in the analysis ranged from 1 to a few individuals for rare taxa to 10 for numerous taxa. Across all taxa and functional groups biomass was expressed in g dry weight m^{-2}.

All taxa were identified at the family level, and some groups (Araneae, Isopoda, Chilopoda, Diplopoda, Elateridae larvae) were further identified at the species level. Soil macrofauna taxa that we identified were allocated to different traits according to their feeding preferences (saprophages, predators, and herbivores) following Gilyarov (1965), predominant vertical distribution (aboveground and belowground) and mobility (relatively mobile and predominantly resident) after Zaitsev et al. (2014). Taxa with biomass exceeding 7% of the total at a plot, were considered dominants, and 1% – subdominants.

The abundance and biomass of soil macrofauna are given as a mean value for burnt and control plots per forest biome ($n = 4$) ± standard error of the mean (SE). Samples within each plot ($n = 5$) were considered pseudo-replicates, and were only used to form a mean value per plot. To test the significance of the effect of forest biome and fire as well as their interactions on macrofauna with different traits we applied the Main effects ANOVA. This analysis was based on the plot-level data. The ANOVA was run on the untransformed data ($n = 4$) because the Kolmogorov-Smirnov & Lilliefors test as well as Shapiro-Wilk's test did not reject normality ($p > 0.05$) for these datasets. Statistical hypotheses were tested at the 0.05 significance *p*-level.

We calculated the biomass of soil macroinvertebrates belonging to each of the possible trait combinations including up to three trait types describing one animal. In total 35 different trait category combinations were examined. All statistical calculations were performed using Statistica 8.0 software.

3. Results

Soil macrofauna abundance, biomass and taxonomic richness across different forest biomes and treatments were barely significant (Table 1). Among all community parameters of soil macrofauna, fire significantly increased the relative spread (ratio of the maximum to minimum values) of biomass (ANOVA: $F = 6.346$, $p < 0.037$). The number of dominant ($F = 1.47$, $p = 0.26$) or subdominant taxa decreased after fires, but insignificantly ($F = 0.02$, $p = 0.90$).

Fires had a significant negative main effect on the biomass of saprophagous macrofauna (ANOVA, $F = 4.32$, $p < 0.05$, Fig. 1), but not of predatory ($F = 0.03$, $p = 0.86$) or phytophagous ($F = 0.13$,

Table 1
Mean abundance (10^3 ind m^{-2} ± SE), biomass (g m^{-2} ± SE) and number of taxa of soil macrofauna in burnt and control plots in the studied forest biomes ($n = 4$). Different letters indicate significant differences between means of forest biomes according to Tukey HSD test. No respective difference between control and burnt plot were observed in each forest biome.

	Mediterranean forests	Broadleaved forests	South taiga	Central taiga	North taiga
	Control plots				
Abundance, 10^3 ind m^{-2}	2066.0 ± 907.6 ab	1290.8 ± 288.8 ab	4996.5 ± 2712.9a	1743.2 ± 304.9 ab	789.8 ± 192.5 ab
Biomass, g m^{-2}	1.9 ± 0.5 ac	6.6 ± 0.8 b	1.7 ± 0.4 a	1.3 ± 0.4 ac	0.4 ± 0.1 c
Number of taxa	29.0 ± 3.0 ac	33.0 ± 1.0 a	30.0 ± 5.0 ac	24.0 ± 1.0 c	15.0 ± 1.0 b
	Burnt plots				
Abundance, 10^3 ind m^{-2}	1129.8 ± 369.6 ab	1395.9 ± 205.9 ab	1542.8 ± 382.9 ab	1375.4 ± 336.7 ab	414.1 ± 67.1 b
Biomass, g m^{-2}	1.0 ± 0.1 ac	5.8 ± 0.9 b	2.0 ± 0.7 a	0.7 ± 0.2 ac	0.3 ± 0.1 c
Number of taxa	25.0 ± 3.0 ac	33.0 ± 2.0 a	31.0 ± 4.0 ac	24.0 ± 3.0 c	12.0 ± 1.0 b