ARTICLE IN PRESS

Geoderma xxx (xxxx) xxx–xxx

Contents lists available at ScienceDirect

Geoderma

journal homepage: www.elsevier.com/locate/geoderma

Evidence of a trait-specific response to burning in springtails (Hexapoda: Collembola) in the boreal forests of European Russia

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ARTICLE INFO

Handling Editor: Jan Willem Van Groenigen

Keywords:
Soil mesofauna
Wildfire
Taiga
Disturbance
Life-history traits

ABSTRACT

The reaction of soil fauna to forest fires is highly variable in space across large ecoregions, the reasons for which are still not completely documented. We tested regional differences in the response of springtail (Hexapoda: Collembola) taxonomic richness, total abundance and collembolan abundance, which share combinations of the two traits (reproduction mode and vertical distribution), in a pilot study within boreal forests of European Russia. We selected four stands burned five years ago and four respective controls in each of the three boreal forest subregions: northern, middle and southern taiga. Plots were located along a 1500 km-long north-south transect covering most of the existing climatic and edaphic gradient within this ecoregion. The General Linear Model (GLM) results showed that fire had a significant effect on the abundance of collembolans that shared certain trait combinations (sexually reproducing epiedaphic species), while the total collembolan abundance depended on the forest subregion, but not burning. The abundance of sexually reproducing epiedaphic springtails decreased in burned plots by 40%, on average, in comparison with the respective controls. This reduction was positively correlated with the degree of fire severity and negatively correlated with litter thickness and soil water holding capacity. We conclude that fires induce a consistent shift in the composition of the springtail functional trait community, which is driven more by the forest stand level of litter thickness and moisture than by subregional forest differences. Our study revealed the potential of the functional trait composition to be a sensitive and informative tool for tracing the effects of fire in boreal forests, which is relatively independent from regional differences.

1. Introduction

Forest fires act as an important environmental factor that shape the dynamics and composition of flora and fauna in boreal forest ecosystems (Goldammer and Furyaev, 2013; Niklasson and Granström, 2000; Granström, 2001; Ryan, 2002). Boreal forests occupy the largest share of land in Russia, with a total area of approximately 600 million ha (Conard and Ivanova, 1997). The fire regimes in taiga are highly variable in space and time and depend on a diversity of factors such as climate, vegetation, topography and human pressures (Carcaillet et al., 2001; Kasischke and Turetsky, 2006). The resulting fire frequency may vary on average from 14 to 23 years in Central Siberia (Furyaev and Kireev, 1979) to 58–71 years in the European part of Russia (Goldammer and Furyaev, 2013; Vakurov, 1975). The same is true for fire intensity, severity and its type (crown or ground fire) (Shorohova et al., 2009). These differences will undoubtedly imply spatial variability in the pyrogenic recovery patterns of all groups of organisms inhabiting coniferous forests. However, such a spatially explicit analysis has been performed for only a few taxa so far (Butenko et al., 2017; Korobushkin et al., 2017).

Ground fires prevail in European boreal forests (Gromtsev, 2002). They can severely damage vegetation, litter and the top humus horizon (De Bano et al., 1998; Certini, 2005). This consequently affects soil organisms due to direct heat and toxic smoke effects, as well as the destruction of microhabitats. As a result, belowground ecosystems in boreal forests are subject to the strong, and at the same time, complex effects of fires. This is reflected in the short-term reduction in the abundance and species richness of soil taxa and their different rates of recovery after burning (Bezkorovainaya et al., 2007; Malmström et al., 2008; Malmström et al., 2009; Wikars and Schimmel, 2001). Post-fire recovery of soil fauna is not only group-specific but also depends on the pre-fire parameters of their habitats (e.g., hydrothermal conditions, soil type, microhabitat diversity, etc.) as well as a long list of fire properties (e.g., heterogeneity and severity of fire) (Scott et al., 2014; Webb,

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http://dx.doi.org/10.1016/j.geoderma.2017.07.021
Received 10 November 2016; Received in revised form 15 July 2017; Accepted 19 July 2017
0016-7061/

Please cite this article as: Saifutdinov, R.A., Geoderma (2017), http://dx.doi.org/10.1016/j.geoderma.2017.07.021

1994). This results in a spatially complex matrix of interacting factors that determine the resulting soil community structure in pyrogenic forests (Zaitsev et al., 2016). The associated reduction in soil fauna taxonomic and functional diversity may potentially lead to the reduced functionality of detrital food webs and decreases in decomposition rates, nutrient cycling and carbon sequestration after a fire event (de Vries et al., 2013; Gongalsky et al., 2016). However, there is still not much knowledge of the spatial differences of the impact of fire with regard to differences in geographic conditions on the functional composition of different soil animal taxa that constitute belowground food webs. This is particularly true for soil mesofauna, which are hardly studied in this respect (Gongalsky et al., 2012; Zaitsev et al., 2014).

Springtails represent an important component of soil mesofauna and inhabit all types of soils (Hopkin, 1997; Rusek, 1998). Despite their small size and overall relatively low contribution to the total soil biomass (Petersen and Luxton, 1982), they play a visible role in the regulation of decomposition and nutrient cycling processes by controlling microbial communities (Filser, 2002; Seastedt, 1984). They also act as important disseminators of soil microflora and serve as food for many predators, such as carabids, ants, and frogs, etc. (Rusek, 1998). Since they are sensitive to various environmental changes, they are often used as indicators of different types of disturbances (Greenslade, 2007; Henig-Sever et al., 2001; Kuznetsova, 2009). Moreover, the higher colonization and reproduction rates of collembolans in comparison with, for example, oribatid mites (Lehmitz et al., 2012; Walter and Proctor, 2013) make them one of the "pioneer" groups of soil animals that relatively rapidly recolonize disturbed soil (e.g., in burned plots) (Malmström et al., 2008).

The impact of forest fires on springtail communities in boreal ecosystems was studied to some extent but with no special emphasis on the geographic differences between burned forests (Haimi et al., 2000; Huebner et al., 2012; Huhta et al., 1969; Malmström et al., 2008, 2009; Malmström, 2012). Some knowledge exists on the post-fire recovery patterns of collembolans with respect to fire severity (depth of combustion) (Malmström, 2010). It has been shown that in comparison with severe fires, communities affected by fires of light severity can recover within 1–2 years (Čuchta et al., 2012; Malmström, 2010). However, all of these studies mainly used collembolan species abundance and species richness and only in the few instances was the functional structure used (see e.g., Huebner et al., 2012; Malmström, 2012). It is therefore hard to predict to what extent collembolan community composition and especially functional structure can recover a few years after burning at different locations. In this respect, recently several authors highlighted the better perspectives of using trait spectra for springtails instead of taxonomic richness or composition to disentangle their reaction to different types of disturbances, including fires (Huebner et al., 2012; Malmström, 2012; Vandewalle et al., 2010; Widenfalk et al., 2015).

To fill the aforementioned knowledge gaps on the macrospatial heterogeneity of the possible effect of forest fires on collembolan community trait composition, across the larger geographic regions we sampled boreal forests that burned 5 years ago and the respective adjacent unburned forest stands along a 1500-km north-south transect covering the major boreal forest subregions (north, middle and south taiga) in European Russia and compared the composition of springtail community traits in them. We have already studied the impact of fire on the taxonomic composition of springtail communities in exactly the same plots (Saifutdinov et al., 2018). In the current paper, we focus on the shifts in springtail trait composition in response to forest fires in different subregions as a potential indicator of their community functionality. We hypothesized that (i) the abundance and species richness of springtails would recover in the burned plots of studied subregions five years after burning, and (ii) collembolans will demonstrate a trait-specific response to forest fires five years after a burning event. We further assumed that (iii) the degree of modification in the community trait composition after fire would depend on the spatial differences in soil parameters and hydroclimatic conditions, which are presumably nested within different subregions.

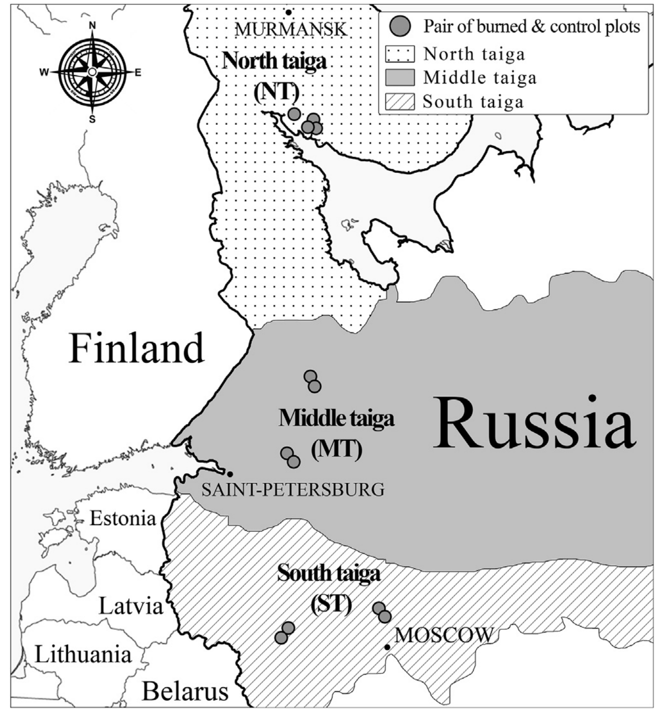

Fig. 1. Schematic map of the studied forest locations within boreal forest ecoregion. Sampling was performed along a 1500 km-long N-S transect in three forest subregions: north taiga (NT), middle taiga (MT) and south taiga (ST). Gray dots indicate investigation plots within subregion.

2. Material and methods

2.1. Study areas

Our study was carried out along a 1500 km-long latitudinal gradient in boreal forests of European Russia (Fig. 1). We selected three subregions across the European taiga: north taiga, middle taiga and south taiga. These subregions vary in climate, soil type and vegetation properties and form a macrogeographic gradient (Supplementary material, Table S1). Study plots were selected among burned sites of approximately the same age in each of the three studied subregions. The majority of fires occurred in 2010, due to the unusually hot summer (Shvidenko and Schepaschenko, 2013; Shvidenko et al., 2011). Four forests were burned in 2009: three in the middle taiga and one in the north taiga. Based on expert assessment in the field, preliminary analysis of the results and our previous experience (Gongalsky and Persson, 2013) indicated there was no drastic difference in the soil community composition between forests burned 5 and 6 years ago. All burned forests suffered from ground fires and some from crown fires. We assessed the fire severity (see Keeley, 2009) based on the remaining soil organic layer (litter thickness) and the height of the fire scars. Hence, all fires were classified as fires of moderate severity (De Bano et al., 1998). Each pair of burned-control plots formed one study block. The minimum distance between the studied blocks was 1 km. Within the block, burned and control plots were approximately 250 m apart, and inside each forest stand, the actual sampling area was ca 10 m × 10 m, placed in the center of the burned forest stand. In total, we examined 12 blocks (pairs) of forest stands.

The north taiga occupies the territory from forest-tundra in the north to approximately 64°N parallel in the south of the Russian plain. Summer in this subregion is cold, with an annual temperature of the warmest month (July) of +13–15 °C and frost-free period of ca. 75–95 days. These forests are dominated by spruce (*Picea abies*) and