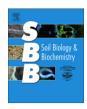
Contents lists available at SciVerse ScienceDirect

Soil Biology & Biochemistry

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



Recovery of soil macrofauna after wildfires in boreal forests

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ARTICLE INFO

Article history: Received 16 January 2012 Received in revised form 2 July 2012 Accepted 8 July 2012 Available online 28 July 2012

Keywords:
Boreal forest
Forest fire
Edge effect
Recovery
Soil macroinvertebrates

ABSTRACT

Forest wildfires can severely affect the soil faunal community. We hypothesised that the recovery of soil animals after a fire would occur through (1) immigration from the unburnt forest into the burnt area and (2) survival in less-burnt patches or deep soil layers. To test the rate of recovery, and whether immigration or survival was the main recovery factor, we studied soil macrofauna after two wildfires occurring in 2001 in central Sweden and north-western Russia. The animals were studied up to 2007 by taking soil and litter samples including unburnt and burnt forest plots 20 and 60 m from the edge of the unburnt forest. Total abundance and species richness was 1.5-5 times higher in the unburnt than in the burnt areas shortly after fire. Animals in deep soil layers had a better survival after fire than surfacedwelling species. The burnt area was colonised within a few months by flying insects, mostly dipterans. When the post-fire vegetation had established after 1-2 years, plant-feeding groups like aphids, cicadellids and thripses became even more abundant than in the unburnt forest. Millipedes established faster in the area close to the forest edge than in the central part of the fire area indicating migration from the forest edge, but most slow-dispersing soil animals seemed to recover through survival in the burnt area. The biomass of both microbi-detritivores and predators showed a delayed recovery in the burnt area and had only reached 40-60% of that in the unburnt forest six years after the wild-fire, indicating reduced habitat quality for the former and food shortage for the latter group.

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1. Introduction

Boreal forest fires are recurrent impacts changing habitats and influencing living organisms (Crutzen and Goldammer, 1993; Niklasson and Granström, 2000; Wardle et al., 2003). The severity of the fire is affected by current weather, soil properties, forest stands and presence of fuel (O'Lear et al., 1996; Fisher and Binkley, 2000; Ojeda et al., 2010; Lehmann et al., 2011). Intensive fires damage litter layers and sometimes burn down soil organic layer with all inhabiting animals (Wikars, 1997; Phillips et al., 2000; Malmström, 2010, 2012).

However, several organisms in the boreal forest depend on fires for their long-term survival (Granström and Schimmel, 1993). A diverse set of insects is regarded as being pyrophilous, and many other insects are favoured by fire (Danks and Footit, 1989; Wikars, 1997). Due to an efficient fire-suppression, the area affected by wildfire has decreased, for example, more than 100-fold during the

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last century in Sweden (Granström, 2001). Many fire-dependent species have experienced range contractions, and a few of them have already gone extinct in Fennoscandia. Prescribed fires are today regularly made for conservation purposes by forest companies and conservation agencies to favour fire-dependent species (Granström, 2001; McKenzie et al., 2004). The baseline information about wildfire recovery in boreal forests is still limited (Metz and Dindal, 1980; Saint-Germain et al., 2004), and quantitative studies on soil macrofauna are particularly scarce (Malmström et al., 2009).

The number of litter organisms has been reported to return to pre-fire values in about 2–13 years after clear-cut fires. Invertebrates are more resilient to single fires than to repeated events, when the recovery takes as much as 17–24 years after the last of several fires (Huhta, 1971; Leonard, 1977). Ground-litter saprophagous arthropods have lower resilience to fire than pollinophagous and zoophagous epigeic groups (Moretti et al., 2006). Recovery is considered to be dependent on the dispersal capacity of organisms and the structure of the remaining community (Bengtsson, 2002). On the other hand, Kiss and Magnin (2003) found that all life forms of land snails appeared in the burnt area a short time after the fire, probably due to heterogeneous burning which created refuges for this kind of immobile fauna.

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The recovery of soil organisms after fire is probably related to the density of the plant cover and the thickness of the organic layer remaining after the fire. The mechanisms beyond the recovery remain poorly understood. It has been suggested that the colonisation begins from the surrounding forest matrix (Broza and Izhaki, 1997; Bezkorovainaya et al., 2007). A gradual immigration of soil animals from the unburnt forest towards the central parts of the burnt areas would probably cause a gradient in animal distribution across the burnt areas, because of a faster recovery close to the forest edge than at a longer distance from the forest matrix. This hypothesis is in line with the ecotone theory (Murcia, 1995; Dutoit et al., 2007), which presumes a higher number of taxonomic groups in the edge zone.

The present study tests the hypothesis that the recovery of soil animals in burnt areas would occur as a gradual inflow from the edges. As an alternative source of recovery, soil animals can survive fire in less-burnt patches (Gongalsky et al., 2012). Here, we compared taxonomic composition, dominance structure and functional groups of soil macrofauna at edge versus central parts of burnt forest areas in central Sweden and in north-western Russia during a 6-year period after fire.

2. Materials and methods

2.1. Study areas

"Tyresta" in central Sweden is situated at the border of the Tyresta National Park and Nature Reserve, which together make up 4700 ha of mostly coniferous forest. The area is situated 20 km south of Stockholm in central Sweden (59°10′ N, 18°20′ E). Longterm annual mean air temperature for the study area is +5.8 °C (-3.5 °C in February, +17.2 °C in July), and mean precipitation is 554 mm. Mean number of days with temperatures above 0 °C is 230. The area consists of undulating rocky outcrops filled with small mires/swamps in the depressions in between. A sparse forest of Scots pine (*Pinus sylvestris* L.) and common silver birch (*Betula pendula* Roth) is growing on the outcrops, whereas the mire elements are to a large extent covered by Scots pine and hairy birch (*Betula pubescens* Ehrh.). The pine forest is dominated by 150–300 year-old trees and has never been affected by large-scale forestry.

In August 2001, 22 ha of the area were burnt in a wildfire. As judged from vegetative re-growth after the fire (Schimmel and Granström, 1996) and from comparisons with the vegetation in unburnt plots, the vegetation in the dry patches before the fire was dominated by Cladonia lichens, Calluna vulgaris (L.) Hull, and Vaccinium vitis-idaea L. The wet patches were tree-covered bogs with Ledum palustre L., Eriophorum vaginatum L. and Sphagnum mosses/ peat in the bottom layer. In November 2001, the mosses Polytrichum commune Hedw., Polytrichum iuniperinum Hedw., Ceratodon purpureus (Hedw.) Brid. and Marchantia polymorpha L. dominated the vegetation in the burnt area. Among the herbs, Epilobium angustifolium L., Rubus idaeus L. and Senecio spp. dominated together with vegetative shoots of recovering C. vulgaris, V. vitis-idaea, and V. myrtillus L. The vegetation remained rather sparse during all observed years after the fire. For example, in a neighbouring burnt area, only aspen (Populus tremula L.) and goat willow (Salix caprea L.) seedlings were observed five years after fire. The area was initially covered by a dense moss and lichen cover. The soil depth varied from a few centimetres on the rocky outcrops to 20–30 cm in the wet depressions. The fire was not very intense, but was strong enough to burn away thin soil layers covered by lichens and mosses on the rocky outcrops. After the fire, the burnt area had a large proportion of bare rocks (60%) intermixed with moist/wet depressions (40%) of 2–10 cm organic layer. Initial pH in the forest was 4.32. It increased to 4.51 in the edge plots and to 4.69 in the central plots two years after the fire (A. Pokarzhevskii, unpublished data).

The study area "Petrozavodsk" in north-western Russia is located 28 km to the north of Petrozavodsk, the capital of the Republic of Karelia (61°59′ N, 34°11′ E). The area is situated on the Baltic shield, which forms the northwestern part of the Russian platform. The climate in Karelia is colder than in central Sweden, with a long winter and a short cool summer. Considerable cloudiness, high humidity, and changeable weather are characteristics of all seasons. Annual mean air temperature for the study area is -2.4 °C (-9.9 °C in February, +16.6 °C in July), and mean precipitation is 600 mm. Mean number of days with temperatures above 0 °C is 125. In Karelia, coniferous forests are the dominant type of vegetation. In the study area, a sparse pine forest (*P. sylvestris*) mixed with silver birch (*B. pendula*) and mountain ash (*Sorbus aucuparia* L.) grows on elevated areas separated by lakes. The depressions are covered by hairy birch (*B. pubescens*).

In early September 2001, a fire affected 24 ha in this area. Similar to the Tyresta site, *C. vulgaris*, *V. vitis-idaea* and *Cladonia* lichens dominated the vegetation at the dry patches before the fire. The first years after the fire, *E. angustifolium*, *R. idaeus* and *Senecio* spp. dominated the ground vegetation together with vegetative shoots of *V. vitis-idaea*, and *V. myrtillus*. Five years after the fire, the soil was covered by a dense moss layer but no complete litter layer. The depth of the moss, litter and humus layers was then approximately 2 cm, while 15–20 cm in the unburnt forest. Topsoil pH was 4.40 in the forest, and pH increased to 4.68 in the edge plots and to 4.77 in the central plots (A. Pokarzhevskii, unpublished data). The severity of the two fires at Tyresta and Petrozavodsk was almost equal as judged by the remaining organic layer.

2.2. Sampling

In both sites, two replicate line transects were established at a distance of about 200 m from each other. Each transect consisted of three 20 m \times 20 m plots, of which one plot was located in the unburnt forest about 30 m outside the fire area (control), one plot was located inside the fire area at a distance of 20 m to the burnt forest edge, and one plot was located in the central part of the fire area, about 60 m from the forest edge.

Five soil samples per plot to collect macroarthropods were taken from the organic (LFH) and the upper 2 cm bleached mineral soil (E) layers with a 100 cm² metal frame that was pressed into the forest floor and mineral soil after cutting off all fine roots with a knife (Tyresta) or a soil corer with a diameter of 9.9 cm (Petrozavodsk). The samples were put into plastic bags in the field and stored at 5 °C for a maximum of one week. The animals in each of the parts were extracted in modified Tullgren funnels equipped with a 20 cm \times 20 cm net (4-mm mesh) basket on which the samples were evenly spread out to a thickness of 1–2 cm. The samples were heated (up to 45 °C at the end of the extraction) and dried for 4 days by means of light bulbs, and the animals extracted were collected in 70–80% ethanol. In Tyresta, the samples were collected during the late autumn in 2001–2007 (with an exception for 2004). The sampling in Petrozavodsk was made in 2004–2007.

All soil animals not belonging to microfauna (mainly Nematoda) or mesofauna (mainly Collembola, Acari, and Enchytraeidae) and being larger than 2 mm in any of its dimensions were ascribed to macrofauna. Due to problematic identification of the juvenile and larval stages of some groups, most identifications were done down to the family level with the help of special literature (Brauns, 1954; Mamaev, 1972; Dindal, 1990; Klausnitzer, 1994, 1996). Macrofaunal groups were sorted and identified under a dissecting microscope.

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