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Plant removal disturbance and replant mitigation effects on the abundance and diversity of low-arctic soil biota

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ABSTRACT

Due to the dependence of soil organisms on plant derived carbon, disturbances in plant cover are thought to be detrimental for the persistence of soil biota. In this work, we studied the disturbance effects of plant removal and soil mixing and the mitigation effects of replanting on soil biota in a low-arctic meadow ecosystem. We set up altogether six replicate blocks, each including three randomized treatment plots, at two distinct fells at Kilpisjärvi, northern Finland. Vegetation was removed in two thirds of the plots: one third was then kept barren (the plant-removal treatment), while the other third was replanted with a local herb *Solidago virgaurea*. The remaining plots of intact vegetation were used as treatment comparisons. The responses of soil microbes and fauna were examined six years later in the early and late growing season. The biomass of bacteria, non-mycorrhizal fungi and mycorrhizal fungi (estimated using PLFA markers) were on average 74%, 89% and 84% lower in the plant-removal and 64%, 74% and 71% lower in the *Solidago* replant plots than in the intact meadow. The positive effect of replanting was statistically significant for fungi, but not for bacteria. The PCA of relative PLFA concentrations further showed that the structure of the microbial community differed significantly among all three treatments. The abundance of nematodes and collembolans was on average 82 and 95% lower, but the total number of nematode genera and collembolan taxa only 27 and 7% lower in the plant-removal plots than in the intact meadow soil. Few disturbance effects on soil fauna were significantly mitigated by the *Solidago* replant (the plant parasitic nematodes being a notable exception) and in the case of the collembolans, the *Solidago* replant plots had even fewer animals than the plant-removal plots. The response of soil biota also varied with locality: the effects on fungivorous nematodes were found at one site only and the replant effects on the number and diversity of collembolan taxa varied with site. Our results suggest that despite drastic reductions in the abundance of soil biota, the majority of animal taxa can persist for years in disturbed arctic soils in the absence of vegetation. In contrast, the alleviating replant effects on the abundance of soil biota appear weak and may only partially reverse the negative effects of vegetation removal and soil disturbance.

1. Introduction

Due to their short growing seasons and low productivity, the arctic and sub-arctic ecosystems can be particularly sensitive to both anthropogenic and natural disturbances. Industry (Kashulina et al., 1997; Walker et al., 1987), reindeer grazing and trampling (Kashulina et al., 1997; Moen and Danell, 2003; Van der Wal et al., 2001) as well as off-road vehicles and tourist activities (Babb and Bliss, 1974) all have impacts on the arctic vegetation and soil. Cryoturbation and landslides further disturb the soil in the arctic ecosystems, and while these disturbances are natural, landslides can also be influenced by human activities and the climate change (Restrepo et al., 2009). Besides affecting the soil structure, disturbances typically reduce the coverage of plants and both of these effects are likely to have an impact on soil communities. It can take fifty years to restore the species composition of the arctic vegetation after a landslide and the recovery of the full plant cover can take even longer (Cannone et al., 2010). How arctic soil

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communities respond to such disturbances, persist in areas with no plant cover and recover along with newly establishing vegetation is poorly known.

Plant biomass not consumed by the herbivores enters the soil as plant litter. Fresh litter is mostly easily decomposable and fuels the microbial and animal activities (Kandeler et al., 1999; Rønn et al., 1996), but the litter also forms the soil organic matter, which is important for soil water retention, formation of three dimensional space and maintenance of soil fertility through absorbing and releasing nutrients (Ehrenfeld et al., 2005; Sturm et al., 2005). Plants also lose a significant proportion of their fixed carbon to soil as root exudates, and in mycorrhizal plants, this carbon is further channeled to the soil community as the exudates and litter of the mycorrhizosphere (Jones et al., 2009). Due to the carbon supply, the activity and abundance of soil organisms are usually several magnitudes higher in the vicinity of roots than in the bulk soil (Cheng et al., 1996; Griffiths et al., 1992; Hamilton and Frank, 2001). It is therefore clear that the abundance of soil biota will decline after plant removal but the effects on the diversity may not be as straightforward (Hirsch et al., 2009) and there are remarkably few field studies of the consequences of long-term plant absence on soil communities. In the arctic soils, microbes act as a strong nutrient sink (Jonasson et al., 1996; Michelsen et al., 1999) and the ability of soil fauna to release nutrients from microbial biomass (Bardgett and Chan, 1999; Setälä et al., 1990) is likely to be particularly important for plant nutrient uptake. As earthworms are few or non-existing in these soils, the relative role of other animal groups, such as nematodes and collembolans, is emphasized (Rusek, 1998). Of these, collembolans are generally considered as fungivores (De Ruiter et al., 1993; Hunt et al., 1987) while nematodes represent several trophic groups (Yeates et al., 1993). To forecast the ecosystem trajectory after a disturbance, as well as to plan the possible remediation actions such as replanting, it is therefore essential to understand the time course of the changes not only in the vegetation, but also in the abundance and diversity of these soil biota.

Here we present results from a study designed for monitoring the response of soil microbes and animals to soil disturbance and long-term vegetation removal. We removed the plant cover and disturbed the soil at several field plots in a low-arctic meadow and kept half of these plots non-vegetated for six years. To examine whether such disturbance could be mitigated by replanting, we planted the other half of the plots with a common local herb, *Solidago virgaurea*. Intact meadow plots were used as references for these two treatments. We chose *S. virgaurea* as the replant species due to its intensive arbuscular mycorrhizal association (Kytöviita et al., 2011), commonness in the meadows and tundra heaths of the northern Fennoscandia and because it is one of the few plant species capable of growing in the early as well as late successional communities. Earlier studies have shown that even rudimentary vegetation, such as plant monoculture, can greatly benefit soil organisms (Johnson et al., 2003). We therefore hypothesized that while the soil disturbance and the absence of plant cover would decrease the abundance, richness and diversity of the soil community, *Solidago* replanting would significantly alleviate this effect through the supply of root exudates and shoot and root litter to soil organisms.

2. Materials and methods

2.1. Study site and experimental design

Two low-arctic meadows, approximately 2.5 km apart and 600 m above sea level, situating on south facing slopes of two fells, Saana (69° 03′ N, 20° 50′ E) and Jehkas (69° 05′ N, 20° 47′ E), were selected at Kilpisjärvi, northern Finland. The two sites were selected relatively far from each other to have higher level replication of experimental sites and better ground for generalizations. Vegetation is at both sites dominated by the grass *Deschampsia flexuosa* and includes sedges and herbs like *Solidago virgaurea*, *Trollius europaeus*, *Potentilla crantzii* and *Bistorta vivipara*. Few species of dwarf shrubs, such as *Betula nana*, *Juniperus communis* and *Vaccinium myrtillus* also occur at the sites. In the area, the long-term mean annual temperature is −2.6 °C and the mean precipitation 422 mm (1961–1985), as measured at the Kilpisjärvi meteorological station, 483 m above the sea level (Järvinen and Partanen, 2008).

The experiment was established at the end of June 1999 and consisted of control, plant-removal and replant plots (each 3.5 m in diameter). The plots were randomly placed 1–10 m apart within three replicate blocks at each site (giving altogether six replicate plots for each treatment) and each plot (including the control plots) was ditched to prevent clonal plant growth and soil animal movement from the surrounding meadow. All vegetation was first removed from the plant-removal and replant plots. Plant roots were pulled out of the soil and at this point, the soil was disturbed by mixing the topsoil with the deeper layers. In August 1999, the replant plots were re-vegetated by planting one hundred mature *S. virgaurea* individuals into each plot. *S. virgaurea* is a very common, herbaceous perennial plant in the low-arctic meadows. It has a broad distribution in the northern hemisphere (Hultén and Fries, 1986) and can occur in many habitats, ranging from early successional sand dunes to late successional forests. It also sustains an intensive (typically 80–90% of root length colonized) and stable mycorrhizal colonization (Kytöviita et al., 2011). The plant material for replanting was collected from the surrounding undisturbed meadow. Seed rain on the plots was prevented by covering the plots (including the control plots) with a thin transparent cloth from mid-August to early June. The cloths were laid at the onset of the seed rain and remained in place until the soil was defrosted enough to remove them. To know whether this covering per se had effects on soil organisms, additional control samples were taken for microbes and nematodes at each replicate block from non-manipulated non-covered areas using the same procedures as for other samples. These plots are hereafter called as ‘additional controls’. The plant-removal and monoculture plots were weeded at every growing season (few seedlings emerged after the first season) and the plots were fenced to exclude reindeer. During the warmest summer months, July and August, the average (2000–2005) soil temperature at 3–5 cm depth was 10.6 °C, 10.6 °C, 11.9 °C and 12.0 °C in the control, additional control, monoculture and plant-removal plots, respectively.

2.2. Sampling and analyses

For evaluating the response of soil microbes, nematodes and collembolans to the treatments, the plots were sampled twice in 2005: at early growing season after the snow melt (middle June) and at late season (middle August). Six soil cores (diameter 3 cm, depth 6 cm) were first taken to estimate the biomass and community structure of microbes. The soil cores were sieved (4 mm) within 24 h, pooled and stored frozen until the phospholipid fatty acid (PLFA) analysis. For the analysis, 3.0 g sub-samples (fresh weight) of soil were first extracted with one-phase mixture of chloroform, methanol and phosphate-buffer (0.05 M K_2HPO_4, pH 4.0, 1:2:0.8 v/v/v). The phases were separated using water and chloroform, and the lower phase was collected and fractionated in silic acid columns (Bond Elut Extraction Cartridges, Varian US). Neutral lipids were extracted with 5 ml chloroform, glycolipids with 10 ml acetone and phospholipids with 5 ml methanol. The phospholipid fraction was collected and methyl nonadecanoate was added to the fraction as an internal standard. The fraction was