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Contamination-induced transformation of bacterial and fungal communities in spruce-fir and birch forest litter

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ABSTRACT

This study examines the diversity and community structure of Acidobacteria, Actinobacteria, Eumycota, and Glomeromycota, as well as the microbial catabolic profile of spruce-fir and birch forest litter from control and industrially contaminated sites in the Middle and Southern Urals. Rare and dominant operational taxonomic units' (OTU) role in contamination-induced community transformation was assessed using Hill profiles and abundance-weighted multivariate analysis of variance. In contaminated sites, OTU loss represented 3–19% of each group, with Acidobacteria exhibiting the lowest amount of OTU loss. Acidobacteria in spruce-fir forests, along with Actinobacteria and Eumycota in both forest types, exhibited a significant alpha-diversity decrease. Two taxon- and forest type-specific patterns in the spatial distribution transformation were observed in the contaminated sites: increased beta-diversity, which is attributable to differences in the number of OTUs between local assemblages; and decreased spatial variation of dominants. Despite a high proportion of shared OTUs (54–76%), community differentiation between contaminated and control sites was significant in all groups, primarily due to dominant OTUs in Actinobacteria and rare OTUs in the other target groups. Despite a lack of herbaceous vegetation in the contaminated sites, the least effect of contamination on community diversity and structure was evident in Glomeromycota. Microbial biomass in contaminated forest litter was three to five times lower than in the control areas, though only slight catabolic profile differences were found based on the relative consumption intensity of simple organic compounds in the multiple-substrate-induced respiration test.

1. Introduction

Terrestrial ecosystem functioning depends on the rate of soil microbiota-mediated organic matter turnover. The imbalance between organic matter's input and decomposition, usually registered in industrially contaminated areas, was supposedly a result of heavy metal excess decreasing soil microbial diversity, biomass, and activity (Giller et al., 2009; Smorkalov and Vorobeichik, 2016; Vorobeichik and Pishchulin, 2016; Wang et al., 2007). However, the data on long-term heavy metal contamination's effect on microbial diversity, which was gathered using genetic fingerprinting, is far from generalizable. For example, contradicting responses to heavy metal soil pollution were demonstrated in different works for communities of Actinobacteria (see detailed overview in Větrovský and Baldrian, 2015), Acidobacteria (Berg et al., 2012; Chen et al., 2014), and other bacterial groups (see overview in Berg et al., 2012). There is a great deal of evidence indicating heavy metal excess's low effect on the diversity of ectomycorrhizal fungi (Krpata et al., 2008; Hui et al., 2012), while the response of saprotrophic and arbuscular mycorrhizal fungal communities to contamination is less uniform (Meharg, 2003; Baldrian, 2010; Zarei et al., 2010; Mikryukov et al., 2015).

Historically, the relationship between ecosystem disturbance and the diversity of soil bacteria and fungi has typically been explored in terms of gamma- and alpha-diversity (e.g., Rühling and Söderström, 1990; Hui et al., 2011; Berg et al., 2012; Větrovský and Baldrian, 2015). By contrast, beta-diversity – i.e., the community composition's spatial variation within a single biotope – has typically been regarded as random noise (Krpata et al., 2008; Frey, 2015). However, assessing microscale spatial variation and its drivers is important for determining community transformation patterns in changing environments (Vorobeichik and Pishchulin, 2016). Moreover, abundance-sensitive measures of communities' diversity or dissimilarity, such as Hill profiles (Hill, 1973; Jost, 2006), abundance-weighted multivariate analysis of variance

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(Anderson et al., 2011), and dissimilarity partitioning (Baselga, 2013), are rarely applied in soil microbial ecology. However, they do provide useful insights into the specific nature of community-level changes (Lucas et al., 2016).

The range and evenness of functions, expressed by soil biota, i.e., the microbial functional diversity in the soil (Zak et al., 1994), is an even more ecologically meaningful parameter, as it directly determines the nutrient cycling rate, and thereby the ecosystem functioning and disturbance resistance. Functional diversity is currently less precisely measured than taxonomic diversity. To some extent, many soil microbiota functions can be described with catabolic profiles, which are commonly obtained through the multiple-substrate-induced respiration (MSIR) technique, which provides short-term soil respiration responses to the addition of a range of simple organic compounds. Despite this method being utilized in many studies to determine microbial functional diversity in clean and heavy-metal-contaminated soils, the general patterns observed in such studies are merely beginning to outline the underlying mechanisms (Banning et al., 2012; Bérard et al., 2016, 2014; Boivin et al., 2006; Campbell et al., 2003; Kools et al., 2009; Liao and Xie, 2007).

The present study aims to assess four bacterial and fungal groups' diversity and community structure in a litter of spruce-fir and birch forests exposed to long-term severe contamination from large copper smelters in the Middle and Southern Urals. For 75 and 100 years of manufacturing, copper smelters' emissions have caused soil leaching, acidification, and heavy metal accumulation in the adjacent territories (Vorobeichik et al., 2014). We chose target microbial groups that play a vital role in ecosystem functioning. Specifically, Eumycota, Actinobacteria, and Acidobacteria present the most abundant and active organic matter decomposers in boreal and temperate forest soils with the highest abundance in O-horizon (Janssen, 2006; Lindahl et al., 2007; Zhang et al., 2014). Glomeromycota, on the other hand, are essential symbionts in a large majority of temperate herbaceous species, and they are therefore considered important drivers of terrestrial ecosystems' diversity, productivity, and succession following disturbances (Öpik et al., 2008). In the present study, we expect that forest litter microbiota's catabolic profiles differ significantly between contaminated and control sites. We also hypothesize that long-term industrial contamination decreased the target groups' gamma- and alpha-diversity, and significantly altered their assemblages' composition and structure. Finally, we expect to find taxon-specific differences in contamination-induced community transformation mechanisms.

2. Material and methods

2.1. Study area

The study sites were located in areas surrounding two large copper enterprises: 1) the Middle Ural Copper Smelter (MUCS), located in Revda in the Sverdlovsk region, 50 km from Ekaterinburg and operating since 1940; and 2) the Karabash Copper Smelter (KCS), located in Karabash in the Chelyabinsk region, 90 km northwest from Chelaybinsk and operating since 1910. Total emissions from the MUCS exceeded 140,000 tons/year in 1990–2000 and decreased to 3000–5000 tons/year in 2013 (Vorobeichik et al., 2014). KCS emitted more than 370,000 tons/year in 1970 and decreased to less than 41,000 tons/year in 2005 (Kozlov et al., 2009). The main component of the emissions from these smelters is gas, which includes SO_2, HF, and NO_x, with dust particles with sorbed heavy metals (mainly Cu, Fe, Zn, Pb, and Cd) and As. The smelters' emissions formed pronounced 20–30 km contamination gradients and transformed various ecosystem parameters (Vorobeichik et al., 2014). Despite the reduction in emissions beginning in 1990s, heavy metals did not leach from the soil as a result of the slight reduction in acidity due to a reduction in acid fallout (Kaigorodova, 2012; Trubina et al., 2014).

Within each region, two sites were chosen with contrasting degrees of ecosystem damage, namely control sites (Fig. S1a and b) situated 30 km west of MUCS (56° 47.92′ N, 59° 25.60′ E) and 32 km north of KCS (55° 42.80′ N, 60° 27.99′ E), and contaminated sites (Fig. S1c and d), 2.5 km west of MUCS (56° 50.24′ N, 59° 52.38′ E) and 5 km north of KCS (55° 29.90′ N, 60° 15.59′ E). In each area, study sites were located in similar biotopes with similar soil groups (i.e., in the MUCS region, spruce-fir forests with an admixture of pine, birch, and aspen on umbric- and umbric-gleyic albeluvisols, and in the KSC region, pine–birch forest on haplic cambisols) (Kaigorodova, 2012).

2.2. Sampling

In 2013, forest litter samples were taken from 23 to 25 sampling plots ($0.5 \times 0.5\ m^2$) 1–168 m apart within each area on July 18 in the KCS region and on August 8 in the MUCS region. The geographical position of each sampling plot was determined using a GPS receiver (Etrex C20, Garmin, USA), measuring tape, and compass. In each sampling plot, five litter subsamples were taken and combined into a bulk sample. Since topsoil profile differed substantially in the thickness of organic horizons between control and contaminated sites (Korkina and Vorobeichik, 2016), samples were collected based on the structural similarity of degraded material. Therefore, sampling layers included OF-horizon and the upper part of OH-horizon, which corresponds to "Fragmented litter" and "Humus 1", as illustrated by Lindahl et al. (2007). Fresh plant litter and debris were removed, and a small pit was excavated in each plot. For molecular analysis, the material was cored from the pit at an appropriate depth with sterile 60 ml plastic containers (4 cm in diameter), and was stored at −20 °C. Further, two 500 g samples were taken by shovel and kept at −20 °C for catabolic profiling, and air-dried for chemical analyses. Root fragments greater than 0.5 mm in diameter were removed from the samples prior to storage. Finally, the following parameters were obtained for each sampling plot: the diversity of each target group, catabolic profile, O-horizon thickness, mass water content, pH, heavy metal concentrations in the litter, and the coverage of each herbaceous species. Authors possessed all permits and approvals necessary for the conducted field work. Sampling procedures were designed to minimize the impact on study sites.

2.3. Chemical analysis

The mass water content in litter samples was measured using a UW2200H laboratory balance (Shimadzu, Japan). Air-dried samples were ground into 1–2-mm powder (MF 10 basic IKA, Germany). The extraction was performed following modified methodology of Rodrigues et al. (2010) using 5% HNO_3 (litter:acid ratio of 1:10 and an extraction period of 24 h after 1 h of shaking). After filtration through paper filter with pore size 8–12 μm (Melior XXI, Russia) extracts were analyzed for Cu, Cd, Pb, Zn, and Fe concentrations using an AAS Vario 6 atomic-absorption spectrometer (Analytic Jena AG, Germany) following USEPA Method 7000B (USEPA, 2007). The pH of the litter in deionized water extract (1:10) was measured using an inoLab 740 ionometer (WTW, Germany). The analytical laboratory is technically certified (certificate ROSS.RU0001.515630).

2.4. Catabolic profiling

For catabolic profiling, the MSIR technique was utilized using whole soil. This approach has advantages over the use of soil