



Effects of tree identity dominate over tree diversity on the soil microbial community structure



Andrea Scheibe ^a, Christina Steffens ^{b,1}, Jasmin Seven ^c, Andreas Jacob ^d, Dietrich Hertel ^d, Christoph Leuschner ^d, Gerd Gleixner ^{a,*}

^a Max Planck Institute for Biogeochemistry, Hans-Knöll-Straße 10, P.O.B. 100164, 07701 Jena, Germany

^b Georg-August-University Göttingen, Soil Science of Temperate and Boreal Ecosystems, Büsgen Institute, Büsgenweg 2, 37077 Göttingen, Germany

^c Georg-August-University Göttingen, Department of Forest Botany and Tree Physiology, Büsgen Institute, Büsgenweg 2, 37077 Göttingen, Germany

^d Georg-August-University Göttingen, Plant Ecology and Ecosystem Research, Albrecht-von-Haller Institute for Plant Sciences, Untere Karspüle 2, 37073 Göttingen, Germany

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ABSTRACT

This study investigated the possible effects of tree species diversity and identity on the soil microbial community in a species-rich temperate broad-leaved forest. For the first time, we separated the effects of tree identity and tree species diversity on the link between above and belowground communities in a near-natural forest. We established 100 tree clusters consisting of each three tree individuals represented by beech (*Fagus sylvatica* L.), ash (*Fraxinus excelsior* L.), hornbeam (*Carpinus betulus* L.), maple (*Acer pseudoplatanus* L.), or lime (*Tilia spec.*) at two different sites in the Hainich National Park (Thuringia, Germany). The tree clusters included one, two or three species forming a diversity gradient. We investigated the microbial community structure, using phospholipid fatty acid (PLFA) profiles, in mineral soil samples (0–10 cm) collected in the centre of each cluster.

The lowest total PLFA amounts were found in the pure beech clusters (79.0 ± 23.5 nmol g⁻¹ soil dw), the highest PLFA amounts existed in the pure ash clusters (287.3 ± 211.3 nmol g⁻¹ soil dw). Using principle components analyses (PCA) and redundancy analyses (RDA), we found only for the variables 'relative proportion of beech trees' and 'living lime fine root tips associated with ectomycorrhiza' a significant effect on the PLFA composition. The microbial community structure was mainly determined by abiotic environmental parameters such as soil pH or clay content. The different species richness levels in the clusters did not significantly differ in their total PLFA amounts and their PLFA composition. We observed a tendency that the PLFA profiles of the microbial communities in more tree species-rich clusters were less influenced by individual PLFAs (more homogenous) than those from species-poor clusters.

We concluded that tree species identity and site conditions were more important factors determining the soil microbial community structure than tree species diversity *per se*.

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1. Introduction

In recent years, the interest in investigating the linkages between above- and belowground biodiversity has steadily increased (Wardle, 2006; Cardinale et al., 2011). However, we still poorly

understand, whether the soil microbial communities of mixed forests are influenced to a larger extent by tree species identity or by tree species diversity (Scherer-Lorenzen et al., 2005; Prescott and Grayston, 2013).

The microbial communities are influenced by the microhabitat conditions in the soil (Ranjard and Richaume, 2001; Neumann et al., 2013). Individual tree species, with their litter inputs or root activities, are able to directly or indirectly influence microbial communities through changes of the abiotic environmental variables, e.g. such as the soil pH (Eviner and Chapin, 2003). In the

* Corresponding author. Tel.: +49 (0) 3641 576172; fax: +49 (0)3641 5770.

E-mail address: gerd.gleixner@bgc-jena.mpg.de (G. Gleixner).

¹ Present address: Universität Hamburg, Institute of Soil Science/Center for Earth System Research and Sustainability, Allende-Platz 2, D-20146 Hamburg, Germany.

upper soil horizons, the microbial communities depend on the decomposition of dead plant material (leaf or root litter) and/or the availability of rhizodepositions (Hättenschwiler et al., 2005; Bais et al., 2006; Kramer and Gleixner, 2006; Herman et al., 2012). Tree species differ in their litter quality (e.g. C/N) and may also produce different root exudates, thereby influencing the nutrient availability (Jacob et al., 2009; Vesterdal et al., 2012; Mitchell et al., 2012a; Fender et al., 2013). Generally, the variability in litter quality and often also in nutrient availability in mixed stands due to patches of different tree species can significantly influence decomposition processes. In these stands, decay rates of individual litter types in litter-mixtures are non-additive in most cases (Wardle et al., 1997; Gartner and Cardon, 2004; Hättenschwiler et al., 2005). Therefore, results from pure stands cannot simply be transferred to mixed stands. However, to which extent the microbial communities depend on the different environmental parameters (biotic and abiotic), is still under discussion (Merilä et al., 2010; Mitchell et al., 2012b).

In sown grassland mixtures, higher plant diversity was found to positively influence the microbial biomass (Zak et al., 2003; Eisenhauer et al., 2010; Lange et al., 2014). These positive influences can in some cases even cause a higher microbial biomass with higher plant diversity than in the weighted average of the respective monocultures (overyielding effect), which is explained by plant complementary resource use (Eisenhauer et al., 2012; Guenay et al., 2013; Lange et al., 2014). However, from studies in grasslands, it was also suggested that soil microbial communities depend more on the presence/absence or abundance of individual plant species (“singular hypothesis”), which influence the functioning of the microbial community through specific traits, than on plant diversity *per se* (Porazinska et al., 2003; Eisenhauer et al., 2010). So far, it is poorly investigated, if plant species identity is also a dominant factor for the microbial community composition in forest ecosystems, as it is in synthetic grasslands.

The linkages between above- and belowground biodiversity were investigated in a wide range of grassland and forest systems (Bardgett and Wardle, 2010). In a near-natural forest, Thoms et al. (2010) recently observed an increase in the microbial biomass and a shift in the microbial community structure with increasing tree diversity. However, it was not possible to clearly differentiate if the observed changes in the microbial community were caused by higher tree species diversity or by decreasing abundance of one important tree species, European beech.

We designed a comparative field study as a follow-up of the study of Thoms et al. (2010) aimed to answering the question, whether tree species diversity or rather tree species identity had a more important effect on microbial community structure. We further wanted to elucidate, which environmental (biotic and/or abiotic) variables are the most important drivers of the microbial community composition. We applied a tree cluster approach to investigate the effect of tree species identity and diversity on the soil microbial community structure in a near-natural deciduous forest (Hainich National Park, Germany). We selected 100 tree clusters consisting of each three mature trees of variable species identity (Leuschner et al., 2009). The trees belonged to the six most common tree species in this forest (*Fagus sylvatica* L., *Fraxinus excelsior* L., *Carpinus betulus* L., *Acer pseudoplatanus* L. and *Tilia cordata* Mill. or *T. platyphyllos* Scop.), which are known to differ in litter quality (Jacob et al., 2009, 2010a). The clusters were divided into three species richness levels (SR) with clusters consisting of one (SR 1), two (SR 2) or three (SR 3) tree species. The soil microbial community structure was investigated using phospholipid fatty acid (PLFA) profiles.

We hypothesized that the microbial biomass increases with increasing a) tree species diversity and b) litter quality.

Furthermore we hypothesized that c) the microbial community structure changes with increasing tree species diversity and d) the microbial community in the upper mineral soil horizon (0–10 cm) is mainly determined by biotic factors (e.g. tree species composition or litter C/N ratio).

2. Material and methods

2.1. Sampling site

The study was performed in the Hainich National Park (Thuringia, Germany). The National Park protects the largest continuous temperate mixed broad-leaved forest in central Germany (ca. 7500 ha). Due to historical forest utilization regimes, a small-scale mosaic of forest patches developed in which a maximum tree species diversity is as high as 14 tree species per ha (Mölder et al., 2006; Leuschner et al., 2009). The forest at the study sites is an old-growth forest, which has existed for over 200 years (Mund, 2004). Large parts of the Hainich forest were used as military training area since 1960, until the southern part of the Hainich became a National Park in 1997. Over these last 50 years, the forest was able to grow nearly undisturbed and is now very close to the original deciduous forests of Central Europe (Mund, 2004; Gleixner et al., 2009). The stem density (>7 cm dbh ha⁻¹) ranged from 291 ± 69 to 581 ± 101 in the study area (Jacob et al., 2010b). The mean annual temperature is 7.7 °C and the mean annual precipitation is 590 mm (period 1973–2004, station Weberstedt/Hainich; 51°06'N, 10°31'E, 270 m a.s.l., Deutscher Wetterdienst 2005). The forest grows on a Luvisol developed on loess over Triassic limestone (Guckland et al., 2009).

2.2. Experimental setup

For this study, 100 tree clusters were randomly selected in the study area. The clusters consisted of three individual trees standing in a triangle. Each tree was represented by one of the six main tree species of the National Park: beech (*Fagus sylvatica* L.), ash (*Fraxinus excelsior* L.), hornbeam (*Carpinus betulus* L.), maple (*Acer pseudoplatanus* L.) and lime (*Tilia cordata* Mill. and/or *T. platyphyllos* Scop.), whereby we considered the two *Tilia* species collectively in the further data analyses (Leuschner et al., 2009). All five tree genera not only differ in their leaf litter quality (see Table A1 in the Supplementary Material), but also in their mycorrhizal symbiont association type (ecto-vs. arbuscular mycorrhizal). Trees of beech and hornbeam are associated with ectomycorrhizal symbionts, whereas trees of ash and maple are associated with arbuscular mycorrhizal symbionts. Lime trees belong to the few tree genera, which can be associated by both ecto- and arbuscular mycorrhizal fungi (Pigott, 1991; Timonen and Kauppinen, 2008).

We established three species richness levels (SR) in this field study. The SR 1 clusters consisted of only one tree species, SR 2 clusters of two (2:1 or 1:2) and SR 3 clusters of three different tree species. We randomly chose 25 variants of tree combinations with four replicates of each combination. Two replicates were localized at the Thiemsburg ($n = 50$) and two at the Lindig site ($n = 50$). The cluster trees were mature trees with a mean breast height diameter of 0.43–0.46 m and of 80–160 years of age, which formed a closed canopy (Jacob et al., 2013, 2014). No significant differences between the three SR level of the clusters were found for mineral soil (0–10 cm) parameters, such as pH, C/N ratio or clay content (see Table A2 in the Supplementary Material). The soil texture of the mineral soil varied between a silty loam to silty clayey loam characterized by a high (~74%) silt content and low (<5%) sand content (Guckland et al., 2009).

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