



Tree species diversity versus tree species identity: Driving forces in structuring forest food webs as indicated by soil nematodes

Simone Cesarz^{a,b,*}, Liliane Ruess^c, Mascha Jacob^d, Andreas Jacob^d, Matthias Schaefer^a, Stefan Scheu^a

^aJ.F. Blumenbach Institute of Zoology and Anthropology, Georg August University Göttingen, Berliner Straße 28, 37073 Göttingen, Germany

^bInstitute of Ecology, University of Jena, Dornburger Str. 159, 07743 Jena, Germany

^cInstitute of Biology, Humboldt University Berlin, Philippstraße 13, 10115 Berlin, Germany

^dAlbrecht-von-Haller-Institute of Plant Sciences, Georg August University Göttingen, Untere Karspüle 2, 37073 Göttingen, Germany

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ABSTRACT

Positive relationships between biodiversity and ecosystem functioning are reported in many studies. The underlying mechanisms are, however, only little understood, likely due to the focus on the aboveground system and neglecting species-specific traits. We used different clusters of tree species composition to investigate how tree species diversity and tree species identity affect belowground nematode communities. Since soil nematodes comprise different trophic groups and are strongly linked to the microbial community, results can provide insight on how soil food webs are structured. In addition, data on leaf litter and fine root biomass were included to account for different effects of aboveground and belowground resources. Clusters of three trees of one, two and three species were identified within a temperate deciduous forest. Target tree species were European beech (*Fagus sylvatica*), common ash (*Fraxinus excelsior*) and lime (*Tilia cordata*, *T. platyphyllos*) differing in physiology, leaf litter quality and type of mycorrhiza. Tree species identity strongly affected nematode trophic structure, whereas tree species diversity had no impact. Ash beneficially affected bacterial-feeding nematodes, whereas fungal feeders were suppressed, likely caused by ash litter increasing soil pH. Fostering of the bacterial food chain by ash additionally could be related to rhizodeposition gaining importance after disappearance of high quality ash litter in spring, highlighting seasonal shifts in root and leaf litter-derived resources. The negative effect of ash on fungal-feeding nematodes is suggested to be due to the lack of ectomycorrhizal fungi as ash roots only form arbuscular mycorrhiza. In contrast, beech benefited fungal feeders and detrimentally affected bacterial feeders due to more acidic soil conditions that increase the competitive strength of fungi. Lime tended to negatively impact total nematode density but positively influenced plant-feeding nematodes. Generally, beech and ash strongly but oppositely influenced the trophic structure of nematode communities suggesting that changes in tree species identity result in major shifts in the channeling of energy through decomposer food webs. The results indicate that the structure of soil food webs varies markedly with tree species and point to the importance of basal resources, i.e., leaf litter and rhizodeposits. This suggests bottom-up forces mediated by individual tree species to control major decomposition pathways rather than tree diversity.

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1. Introduction

The relationship between biodiversity and ecosystem functioning has been mainly investigated considering aboveground systems. However, aboveground and belowground systems are intimately linked and a combined approach is of significant importance when aiming to understand ecosystem functioning

* Corresponding author. Institute of Ecology, University of Jena, Dornburger Str. 159, 07743 Jena, Germany. Tel.: +49 3641 949407.

E-mail addresses: Simone.Cesarz@uni-jena.de, simone.cesarz@gmx.de (S. Cesarz).

(Wardle et al., 2004). Recently, above- and belowground systems were studied together in grasslands showing significant effects of biodiversity on the decomposer fauna (Scherber et al., 2010; Eisenhauer et al., 2012) being the driver of important ecosystem functions such as decomposition and nutrient mineralization. Grasslands, however, comprise short-lived plant species, therefore results are unlikely to be conferrable to forest systems, which, however, store about 60% of terrestrial carbon and are important for global carbon cycling (McKinley et al., 2011).

There is evidence that an increase in tree species diversity fosters ecosystem functions such as mineralization and decomposition

(Morin et al., 2011). However, an increasing number of studies also report identity effects of single tree species to be stronger than tree species diversity (De Deyn et al., 2004; Nadrowski et al., 2010). It is therefore important to identify the species-specific mechanisms responsible for biodiversity effects. Thus, is the observed positive biodiversity effect due to an increase in species number (true biodiversity effect) or to individual tree species in mixtures (identity effect)? Regarding soil decomposer systems, differences between tree species result in differences in the resources provided, mainly leaf litter and root exudates. Traditionally, effects of biodiversity on the decomposer system were investigated focusing on leaf litter residues regarded as the main driving factor for soil processes (Reich et al., 2005; Ball et al., 2009; Langenbruch et al., 2012) as they influence soil pH, microbial activity and biomass (Swift et al., 1979; Wardle et al., 1998). Recently, the importance of root-derived resources for soil food webs has been stressed (Albers et al., 2006; Pollierer et al., 2007; Endlweber et al., 2009; Keith et al., 2009). Rhizodeposits influence the soil system significantly by supplying labile resources to the food web and priming soil organic matter decomposition (Kuzakov, 2010; Bird et al., 2011). In forest soils the fungal energy channel is of predominant importance as litter resources entering the soil are low in nitrogen and rich in lignin as compared to e.g., grassland soils (Wardle, 2002).

The quality of leaf litter and rhizodeposits (e.g., sugars, amino acids, organic acids) varies strongly between plant species (Grayston et al., 1996; Jones et al., 2004, 2009) and this likely differentially affects decomposers. High quality leaf litter is characterized by low carbon-to-nitrogen ratio, high quantities of soluble nutrients and high calcium and magnesium concentrations resulting in fast decomposition, whereas high carbon-to-nitrogen ratio and high lignin content is regarded as low quality decreasing decomposition rates (Coûteaux et al., 1995; Cadish and Giller, 1997; Jacob et al., 2009). Rhizodeposits comprise mainly labile compounds so that quality differences may arise in specific compounds and the amount exudated (Grayston et al., 1996). Likely due to methodological limitation only few data are available on rhizodeposition of different tree species (but see Scandellari et al., 2010; Fender et al., 2013) and no published work provide data on the effect of tree diversity on rhizodeposition.

We investigated the effect of tree species identity and tree species diversity in a diverse old-growth deciduous forest in Central Germany by identifying tree clusters of three individuals varying in tree species composition, comprising one, two or three species. Target tree species were European beech (*Fagus sylvatica* L.), common ash (*Fraxinus excelsior* L.) and lime (*Tilia cordata* P. Mill., *T. platyphyllos* Scop). Leaf litter of beech has high carbon-to-nitrogen ratio and high lignin content while the opposite applies to leaf litter of ash and lime leaf litter, therefore spanning a wide range of litter quality (Jacob et al., 2009). Roots of beech and lime are colonized by ectomycorrhizal (EM) fungi, whereas ash roots are associated with arbuscular mycorrhizal (AM) fungi (Lang et al., 2011). Differences in rhizodeposition between the three tree species are little known. Fender et al. (2013) showed the amount of organic acids exudated by roots to be higher in beech as compared to ash, and Cesarz et al. (2013) suggested beech but not ash root exudates to acidify rhizosphere soil and to stimulate soil organic matter decomposition.

We used soil nematodes as representatives of soil invertebrates since they are highly abundant in soil, drive important ecosystem functions and comprise a wide range of trophic groups including bacteria, fungi and plant feeders as well as predators and omnivores (Yeates et al., 1993), therefore providing important information on how tree species structure soil food webs. There is a strong linkage between nematodes and their microbial diet, and the coincidence of functional groups of bacteria, fungi and their

nematode grazers during succession provides the opportunity to monitor the abundance of available resources (Ruess and Ferris, 2004). The occurrence of nematode functional guilds provides information on general soil food web conditions such as enrichment and structure (Ferris et al., 2001; Ruess and Ferris, 2004). Thus, nematodes are likely to respond to variations in resource diversity and due to their position in the soil food web, plant-feeding nematodes show the most pronounced association to plant communities (Yeates, 1999).

We hypothesized tree diversity to positively affect the abundance of soil nematodes due to an increase in resource partitioning and availability. Further we hypothesized tree species identity to affect specific nematode groups due to differences in litter and root quality, i.e., bacterial-feeding nematodes to increase in ash and lime clusters due to high quality litter by favoring bacteria, whereas fungal-feeding nematodes to benefit from recalcitrant beech litter and acid rhizodeposits of beech roots favoring fungi.

2. Materials and methods

2.1. Site description

The study site is located in the Hainich National Park, the largest cohesive deciduous forest in Central Germany (51°06'N, 10°31'E; 350 m a.s.l.). For the past four decades silvicultural management has been abandoned. Today large parts of the forest resemble semi-natural forest. Parent rock is Triassic Limestone covered by Pleistocene loess (Guckland et al., 2009). The soil is characterized as Stagnic Luvisol with pH values ranging from 4.5 ± 0.5 to 5.8 ± 0.6 . The mean annual temperature is $7.5 \text{ }^\circ\text{C}$ and precipitation averages 590 mm year^{-1} .

The three dominant tree species in the Hainich National Park are European beech (*F. sylvatica*), common ash (*F. excelsior*) and lime (*T. spp.*). To differentiate between tree species identity and diversity effects 28 tree clusters were established in areas with similar soil type. Individual clusters comprised three mature tree individuals of the canopy layer forming a triangle with the trees ranging 2.0–5.5 m from the center of the cluster (Fig. 1). Clusters were selected randomly and were spaced by at least 20–30 m (mean distance between clusters was 99 m). This distance was accepted because earlier studies on tree fine root dynamics in this forest (e.g., Meinen et al., 2009a) had shown a maximum horizontal extension of tree fine roots of <15 m, therefore water and nutrient fluxes between

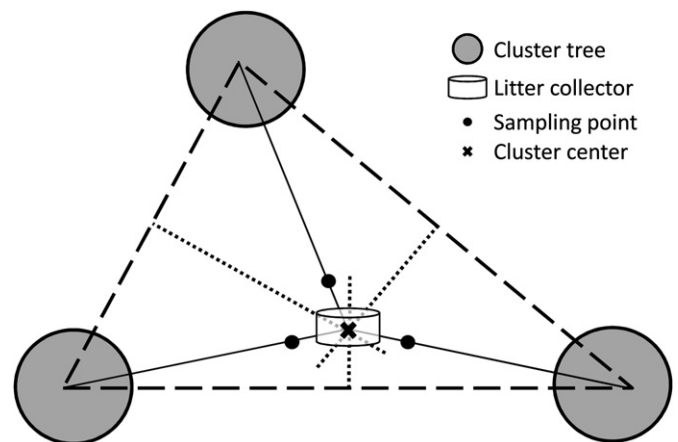


Fig. 1. Scheme of a tree cluster. Soil and fine root samples were taken 50 cm from the cluster center in direction to the cluster trees. Litter was collected with a litter collector in the cluster center.

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