Soil Biology & Biochemistry 63 (2013) 154–162

Contents lists available at SciVerse ScienceDirect

Soil Biology & Biochemistry

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

Tree identity surpasses tree diversity in affecting the community structure of oribatid mites (Oribatida) of deciduous temperate forests

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ARTICLE INFO

Article history:
Received 13 December 2012
Received in revised form
20 March 2013
Accepted 22 March 2013
Available online 13 April 2013

Keywords:
Temperate broadleaved forests
Beech
Ash
Lime
Litter quality
Fine roots
Fungi
Litter layer
Microhabitat heterogeneity
Feeding biology

ABSTRACT

The role of tree diversity and identity as determinants of soil animal community structure is little understood. In a mature deciduous forest dominated by beech we identified clusters of one, two and three tree species of beech, ash and lime allowing to investigate the role of tree species diversity and identity on the density and community structure of oribatid mites. To relate oribatid mite community structure to environmental factors we measured leaf litter input, fine root biomass, mass of organic layers, topsoil pH and C and N content. We expected oribatid mite density to increase with increasing tree diversity, but we expected the effects of tree species identity to override effects of tree diversity. Further, we hypothesized the density of oribatid mites to be reduced by the presence of beech but increased by the presence of lime and ash. As expected tree diversity little affected oribatid mite communities, whereas tree species identity strongly altered density and community structure of oribatid mites. However, in contrast to our expectations the density of oribatid mites was highest in presence of beech indicating that many oribatid mite species benefit from the presence of recalcitrant litter forming thick organic layers. Especially Oppioidea benefited from the presence of beech presumably due to an increased availability of food resources such as fungi and nematodes. Lower density of oribatid mites in monospecific clusters of lime and ash suggests that oribatid mites did not benefit from high quality litter of these species. Notably, large and strongly sclerotized oribatid mite species, such as *Steganacarus magnus* and *Chamobates voigtsi*, benefited from the presence of ash and lime. Presumably, these large species better resist harsh microclimatic conditions in shallow organic layers.

1. Introduction

Forest soils are colonized by animal communities of exceptional diversity (Scheu, 2005) which contribute to important ecosystem processes, such as decomposition and nutrient cycling (Gessner et al., 2010). Numerous field studies explored the effect of plant species diversity on ecosystem processes, but most studies were performed in systems dominated by short lived species, such as grasslands (Tilman et al., 1997; Hector et al., 1999). Results from such simple ecosystems may not apply to complex forest systems and research on the functions of biodiversity in forests is challenging. Studies in species rich complex forests are rare (Vilà et al., 2005) and the role of tree species diversity as structuring force of soil animal food webs is little understood. Recently, large-scale biodiversity experiments with trees have been initiated in different climatic regions, i.e. the tropics, the temperate and the boreal climate zones, to investigate the effects of increasing tree species richness on ecosystem functions (Scherer-Lorenzen et al., 2005). Observational studies on natural forests are needed to complement such experiments with planted trees since results from experiments with young even-aged stands may not be representative for mature forests (Leuschner et al., 2009).

The soil food web relies on energy and nutrients provided by primary producers which enter the soil via different pathways, i.e. leaf litter and root derived resources (Scheu, 2005; Högberg and Read, 2006). There is increasing evidence that resources provided via the root pathway exceed those entering the soil with leaf litter in fuelling the soil food web (Ruf et al., 2006; Pollierer et al., 2007; Eisenhauer and Reich, 2012). In contrast to leaf litter comprising predominantly structural carbon compounds, carbon entering the soil via root exudates is more easily available for soil organisms as it comprises mainly labile substances, such as sugars and amino acids

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http://dx.doi.org/10.1016/j.soilbio.2013.03.024

(Bardgett et al., 2005). Trees of temperate forests differ markedly in fine root architecture and host different microbial communities, i.e. rhizosphere associated bacteria and mycorrhizal fungi (Meinen et al., 2009; Lang et al., 2011; Jacob et al., 2013). Beech fine roots are finely branched and end in rootlets covered by ectomycorrhizal fungi. Roots of lime trees also form a fine network and are colonized by ectomycorrhizal fungi, whereas ash fine roots have rootlets of greater diameter that typically are colonized by arbuscular mycorrhizal fungi (Hölscher et al., 2002; Lang et al., 2011).

A large fraction of plant products enters the decomposer system as leaf litter (Gessner et al., 2010). Plant litter decomposition is an important ecosystem process ensuring organic matter turnover and nutrient cycling driven by microorganisms and soil animals (Swift et al., 1979; Hättenschwiler and Gasser, 2005; Berg and McClaugherty, 2008). The role of litter for soil animal nutrition is known to vary strongly with its chemical composition and this differs markedly between tree species (Cornwell et al., 2008). In European deciduous forests, litter quality ranges from beech (*Fagus sylvatica* L.), low in nutrients and high in structural compounds, to ash (*Fraxinus excelsior* L.), high in nutrients and low in structural compounds, with species, such as lime (*Tilia* sp.), being intermediate (Jacob et al., 2009, 2010).

Especially nitrogen limits the growth of plants, soil microorganisms and soil animals. Most nitrogen in plant litter is embedded in polymers, such as proteins or nucleic acids, or in recalcitrant compounds, such as lignin (Vitousek et al., 2002), with the latter being indigestible for soil animals (Neuhauser et al., 1978; Swift et al., 1979). Recalcitrant litter, such as beech, is decomposed slowly by saprotrophic fungi with readily biodegradable compounds being quickly digested, while structural components, such as lignin, remain (Sydes and Grime, 1981a, b; Osono, 2007). These remains can accumulate and form pronounced humus layers. Additionally, beech litter enhances soil acidification and thereby further reduces litter decomposition (Guckland et al., 2009; Langenbruch et al., 2012). In contrast, ash and lime litter decompose quickly with macro-detritivores, such as isopods, diplopods and earthworms, contributing significantly to the decomposition process (Cotrufo et al., 1998; Hobbie et al., 2006). Typically, only shallow organic layers are present in ash and lime forests due to the incorporation of litter into the mineral soil by detritivores, in particular earthworms (Muys et al., 2003; Jacob et al., 2010).

Mixing of different types of litter may result in non-additive changes in litter decomposition (Hättenschwiler et al., 2005; Ball et al., 2009). Especially recalcitrant litter decomposes faster in mixtures than in monocultures. Fungal hyphae actively transport nutrients needed for decomposing recalcitrant litter compounds from litter high in nitrogen to patches low in nitrogen (Lummer et al., 2012). However, decomposition of recalcitrant litter material still remains slower than that of high quality litter material. Ball et al. (2009) therefore concluded that recalcitrant litter functions as an organic matter pool that releases nutrients slowly but steadily.

The soil animal food web relies on resources of different energy channels (Moore and Hunt, 1988). Two channels are most important, i.e. the bacterial and the fungal energy channel (Coleman et al., 1983; Wardle, 2002). Saprotrophic fungi dominate in decomposition processes in forests with low quality litter (Coleman et al., 1983), and soil mesofauna species graze on fungal hyphae associated with decomposing litter materials (Berg and McClaugherty, 2008; Pollierer et al., 2009). Of litter mesofauna taxa oribatid mites typically are among the most important fungal feeders, but it is increasingly recognized that they feed on a wide variety of diets including animals, such as nematodes (Schneider et al., 2005; Heidemann et al., 2011; Perdomo et al., 2012).

We investigated the role of diversity and identity of tree species producing litter of contrasting quality, i.e. beech, ash and lime, on the density and community structure of oribatid mites. The study was carried out in the Hainich National Park, a diverse temperate deciduous old-growth forest. Tree triangles, i.e. one-, two- or three-species clusters of three trees consisting of beech, lime and/or ash were selected in the field and replicated four times. In order to relate oribatid mite community structure to environmental factors, leaf litter input, fine root biomass, mass of humus layer and topsoil pH, and C and N content were measured.

We expected both tree species diversity and identity to affect the density and community structure of oribatid mites. Specifically, we hypothesized (1) oribatid mite density to increase with increasing tree species diversity due to the availability of complementary resources, (2) the presence of beech to reduce the density of oribatid mites due to the production of recalcitrant leaf litter, and (3) the presences of lime and ash to increase the density of oribatid mites due to the production of high quality leaf litter.

2. Material and methods

2.1. Study site

The study was conducted in the Hainich National Park, the largest cohesive broadleaved forest in Germany (51°06′N, 10°31′E; 350 m a.s.l). The Hainich is a limestone mountain range of maximum altitude of 494 m a.s.l. Mean annual temperature is 7.5 °C, and mean annual precipitation is 670 mm. The predominant soil type is Luvisol developed from loess overlying Triassic limestone; the soil pH ranges between 4.5 and 5.8 (H_2O; Guckland et al., 2009). With up to 14 tree species per hectare the Hainich is among the most diverse broadleaved forest in Central Europe. Dominant tree species are European beech (*F. sylvatica*), European ash (*F. excelsior*) and lime (*Tilia platyphyllos* Scop. and *Tilia cordata* Mill.; Leuschner et al., 2009; Vockenhuber et al., 2011).

2.2. Experimental setup

In spring 2008, 14 sites were selected in each of two blocks separated by approximately 1.5 km. At each site a cluster of three tree individuals was identified comprising of only beech, ash or lime trees, or each of the two or three species combinations (Fig. 1). Each of the seven cluster types, i.e. beech, ash, lime, beech–ash, beech–lime, ash–lime, beech–ash–lime, was replicated four times, i.e. twice at each of the blocks. Mean cluster area was 20.0 ± 14.9 m^2. No other trees or shrubs were present inside the clusters. Cluster trees were mature with similar diameter at breast height (average 41.1 ± 8.6 cm). Canopy closure in the clusters was on average 90.4 ± 4.1% (Seidel, 2011).

2.3. Sampling and processing of oribatid mites

In May 2008, soil cores of a diameter of 5 cm were taken close to the centre of the clusters (Fig. 1). Soil animals were extracted by heat (Macfadyen, 1961) from the litter and upper 5 cm of the mineral soil. Animals were stored in 70% ethanol until determination. Adult oribatid mites were determined using Weigmann (2006). For Brachychthoniidae, Phthiracaridae, Desmonomata and Suctobelbidae only common species were determined to species level. Individuals of Damaeidae and Galumnidae were counted (see Appendix for list of species). Juvenile oribatid mites occurred at low density and were not considered in this study.

Oribatid mites were aggregated to taxonomic groups. Six groups of different taxonomic affiliation and life-history traits were separated: Oppiidae (including Quadroppiidae), Suctobelbidae, Enarthronota, Phthiracaridae, Poronota and Damaeidae (Maraun and