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Tree species as determinants of the structure of oribatid mite communities (Oribatida) and the incorporation of plant carbon and nitrogen into the soil animal food web

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vorgelegt von

Diplom Biologin

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Contents

Summary

In this dissertation I investigated the role of tree species for the structure and functioning of soil animal food webs in temperate forests. In the field, the role of tree species diversity as compared to tree species identity for the structure of oribatid mite communities was investigated. Two laboratory studies focused on the role of two important tree species of deciduous forests (beech and ash) as determinants of the flux of C and N through the soil animal food web.

In Chapter 2 results of a field experiment investigating the density, community structure and diversity of oribatid mites (Oribatida) conducted in Hainich National Park are presented. Due to the small scale approach with beech, ash and lime stands (clusters) effects of tree diversity were separated from effects of tree identity. While tree diversity effects on oribatid mites were of minor importance, tree identity effects were strong. Oribatid mite densities were highest in beech clusters, highlighting the importance of thick organic layers formed by recalcitrant beech litter providing habitable space and food resources. The results underline the dominance of fungal feeders and high importance of animal prey for abundant oribatid mite groups such as Oppioidea. The results supported the view that oribatid mite communities are fuelled predominantly by belowground rather than aboveground resources. Ash and lime stands were colonized by few mainly large and strongly sclerotized oribatid mite species able to withstand harsh environmental conditions in shallow humus layers.

In the dual labeling experiment presented in Chapter 3, the incorporation of carbon from beech and ash seedlings exposed to $^{13}CO_2$ enriched atmosphere into the soil animal food web was investigated. In parallel, the incorporation of nitrogen from ^{15}N enriched nutrient solution into the soil animal food web via fungi was studied. ^{13}C and ^{15}N signals were similar in beech and ash rhizosphere suggesting that belowground tree species traits, such as fine root architecture and mycorrhiza type (ectomycorrhiza in beech vs. arbuscular mycorrhiza in ash), had minor effects on the channeling of C and N into the soil animal food web. Incorporation of labelled C and N into secondary decomposers exceeded that of primary decomposers suggesting that fungi are of major importance for C and N fluxes into the soil animal food web. Notably, incorporation of labelled C and N was highest in predators suggesting that they heavily rely on rhizosphere associated prey, such as Collembola, but likely also on Nematoda, Enchytraeidae and Lumbricidae.

The experiment presented in Chapter 4 investigated the role of structural compounds for incorporation of litter C and N into the soil animal food web. Dual labeled leaf litter of beech and ash, similar in N concentrations but differing in structural compounds, was used. Soil animals preferentially incorporated C from litter low in structural compound highlighting the importance of litter low in structural compounds, such as ash, for fuelling soil animal food

webs. Soil animals incorporated similar amounts of N from both ash and beech indicating that structural compounds of litter little affect the availability of litter N. Incorporation of litter C and N into secondary decomposers exceeded that of primary decomposers. Further, mixing of litter differing in concentrations of structural compounds was of minor importance for incorporation of litter resources into the soil animal food web. Both results stress the importance of the fungal energy channel for incorporation of litter resources into the soil animal food web.

1 General Introduction

General Introduction

1. Processing of C and N in forest soils

The functioning of forest ecosystems relies on a wide range of processes, i.e. decomposition of organic matter and cycling of carbon (C) and nutrients, most important nitrogen (N) (Swift, 1979; Bengtsson et al., 2000; Hättenschwiler et al., 2005). Many ecosystem processes involve aboveground-belowground interactions and the fundamental importance of soils for ecosystem functioning is increasingly recognized (Wardle, 2002; Wardle et al., 2004; Ball et al., 2009a; Aubert et al., 2010). However, most studies investigating such aboveground-belowground interactions were conducted in systems dominated by herbaceous plants such as grasslands whereas few studies investigated ecosystems comprising long-lived species such as forests (Scherer-Lorenzen, 2005; Leuschner et al., 2009).

Forest soils are colonized by an outstandingly diverse community of fungi, bacteria and soil animals, and soil biodiversity has been recognized as major determinant for ecosystem functioning (Hooper et al., 2005; Wardle, 2006; Kardol et al., 2009). Soil animals contribute to ecosystem processes, such as decomposition and C and N cycling, and are interlinked in complex food webs (Moore et al., 1988; Scheu, 2005; Osler and Sommerkorn, 2007). There is increasing interest in mechanistic understanding of the role of soil fauna for aboveground-belowground interactions and their contribution to ecosystem functioning. There is incomplete knowledge how tree species diversity and traits of tree species influence belowground animal communities, and how this may feed back to trees.

Soil animal communities rely on energy derived from aboveground primary producers, i.e. C and nutrients, most importantly N. Plant resources enter the belowground system via two different pathways, i.e. litter and root derived resources (Scheu, 2005; Högberg and Read, 2006). C and N inputs entering the soil animal food web via both pathways may vary considerably with tree diversity, but also with traits of tree species, e.g. leaf litter quality or rhizosphere architecture. The activity of soil animals may in turn feedback to the aboveground part of the ecosystem, e.g. may impact plant growth and community structure (Scheu and Setälä, 2002; Wardle, 2002; Bardgett et al., 2005).

Up to 90% of what is produced by plants enters the decomposer system as detritus (Gessner et al., 2010). Litter decomposition contributes fundamentally to ecosystem functioning since it ensures organic matter turnover and cycling of C and N (Polis and Strong, 1996; Meier and Bowman, 2008; Swan and Kominowski, 2012). In fact, C and N in plant litter are assumed to be the main sources of energy and nutrients for soil microbes (Swift et al., 1979; Berg and McClauthery, 2008) and decomposer animals (Hättenschwiler and Gasser, 2005; Scheu, 2005). The effect of soil animals on litter decomposition depends on the nutritional quality of the litter and this varies strongly between tree species (Hättenschwiler and Gasser, 2005). From the perspective of detritivores the quality of litter as food resource is determined mainly by its chemical composition (Pérez-Harguindeguy et al., 2000; Cornwell et al., 2008). Concentrations of C and N and of structural and secondary compounds are major determinants of the food quality of litter for detritivores (Wardle et al., 2006). Further, accessibility of litter C and N is an important factor altering food quality of litter for detritivores and this is related to the complexity of structural litter compounds (Gessner et al., 2010; Hättenschwiler and Bracht-Joergensen, 2010). Among the tree species investigated in this dissertation litter quality ranges from beech (*Fagus sylvatica* L.) low in nutrients and high in structural compounds to lime (*Tilia* sp.) as intermediate species to ash (*Fraxinus excelsior* L.) with high nutrients contents and low in structural compounds (Jacob et al., 2009, 2010).

Nitrogen limits the growth of plants, soil microorganisms and soil animals. Nitrogen in litter is mainly embedded in insoluble polymers, such as proteins or nucleic acids, or in recalcitrant compounds such as lignin (Swift et al., 1979; Vitousek et al., 2002) with the latter being indigestible for soil animals (Neuhauser et al., 1978). Thus, the release of N from decomposing litter is mainly driven by the activity of microorganisms (Schimel and Hättenschwiler, 2007). In temperate forests decomposition of recalcitrant litter such as beech litter is dominated by saprotrophic fungi (Osono, 2007). Recalcitrant litter is decomposed slowly and the residues accumulate thereby forming pronounced humus layers (Sydes and Grime, 1981a, b). In contrast, high quality litter of ash and lime is quickly processed by macro-detritivores (Hobbie et al., 2006) and incorporated into upper soil layers by the activity of earthworms; thus, in ash and lime forest stands typically only shallow organic layers are present (Weland, 2009).

Mixing of different litter types may result in non-additive decomposition rates (Gartner and Cardon, 2004; Ball et al., 2009b). Especially recalcitrant litter decomposes faster in mixtures than in monocultures which mainly is attributed to the activity of fungi that acquire nitrogen needed for the decomposition of recalcitrant litter from litter with high nitrogen concentrations (Frey et al., 2000; Lummer et al., 2011). Additionally, detritivores feeding on litter mixtures are likely to accelerate decomposition rates of recalcitrant litter in mixtures (Hättenschwiler and Gasser, 2005). Notably, saprotrophic microorganisms immobilize much of the N derived from decomposing leaf litter and thereby, plants compete with microorganisms for N resources (Chapman et al., 2006; Geissler et al., 2010). Tree roots are capable to take up nitrogen directly from soil, but in temperate forests most of the nitrogen is channeled to plants via mycorrhizal fungi (Hobbie and Hobbie, 2006; van der Heijden et al., 2008; van der Heijden and Horton, 2009).

There is increasing evidence that the soil animal food web is mainly fuelled by C and N resources provided via the root pathway rather than by resources derived via decomposition of aboveground litter material (Ruf et al., 2006; Pollierer et al., 2007; Strickland et al., 2012). Large fractions of the photosynthates of plants are translocated to plant roots and into the rhizosphere (Bardgett et al., 2005; Högberg et al., 2008). Root exudates are known to be easily available for soil organisms since they comprise predominantly labile C substances, such as amino acids, sugars and peptides (Dennis et al., 2010). However, the availability of root C and N for soil animal nutrition likely differs between tree species, such as the ones investigated in this dissertation. It is known that beech and ash differ in fine root architectures and the compositions of rhizosphere microbial communities, i.e. bacteria, and endo- and ectomycorrhizal fungi (Lang et al., 2011; Lang and Polle, 2011). Fine roots of beech are finely branched and end in rootlets covered by ectomycorrhizal fungi, whereas ash fine roots have rootlets of greater diameter that typically are colonized by arbuscular mycorrhizal (AM) fungi (Hölscher et al, 2002; Lang et al., 2011). Ectomycorrhizal fungi form a well-dispersed extramatrical mycelium which effectively transfers C from the plant to the outer rhizosphere thereby making it available for fungal feeding soil animals (Högberg et al., 2008; Cairney, 2012, Pollierer et al., 2012). In contrast, with fine roots colonized by (AM) fungi the outer rhizosphere of ash presumably receives less root-derived C (Smith and Read, 1997).

From a trophic level point of view the soil food web can be separated into primary decomposers, secondary decomposers and predators (Scheu, 2002). There is increasing evidence that only few animal species, such as Diplopoda and certain species of Oribatida and Lumbricidae, are able to utilize resources directly from decomposing litter material, i.e. function as primary decomposers (Pollierer et al., 2009). The soil fauna food web comprises a large fraction of secondary decomposers, i.e. species that rely on diets predominantly based on fungi and/or microbial residues, such as most Oribatida, Collembola and certain species of Isopoda and Lumbricidae (Maraun et al., 1998, 2003; Scheu and Falca, 2000). A large fraction of soil mesofauna species have been shown to graze on microbial mats or fungal hyphae associated with decomposing litter materials (Berg and McClaughtery, 2008; Pollierer et al., 2009), but some species have also been shown to rely on rhizosphere associated microbial communities and/or on mycorrhizal fungi (Moore et al., 1985; Schneider et al., 2005; Pollierer et al., 2012). Soil and litter predators, such as Lithobiidae, Araneida and Mesostigmata, may rely mainly on secondary decomposers as prey (Oelbermann and Scheu, 2008; Schneider et al., 2012; Ferlian et al., 2012; Klarner et al., 2013) since most primary decomposers form unsuitable prey due to strong sclerotization, high mobility or large body size (Scheu, 2002; Peschel et al., 2006; Pollierer et al., 2009).

Resources fuelling the soil animal food web have been described to be processed along different energy channels (Moore and Hunt, 1988; Moore et al., 2005). Among these channels, the bacterial and the fungal energy channel are most important and serve distinct functions, i.e. are associated with fast and slow cycling of C and N (Coleman et al., 1983; Wardle et al., 2002). In ecosystems with acidic soils, pronounced organic layers and/or low litter quality, such boreal and in part temperate forests, energy and nutrients predominantly are processed via the fungal energy channel by the activity of saprotrophic fungi (Coleman et al., 1983; Wardle et al., 2004). However, there is increasing evidence that energy and nutrients entering soil animal food webs via the fungal energy channel are incorporated through both feeding on saprotrophic and ectomycorrhizal fungi (Moore-Kucera and Dick, 2008; Pollierer et al., 2012). In contrast to the fungal energy channel, the bacterial energy channel predominantly processes C and N resources provided by roots via exudates (Crotty et al., 2011).

2. Study site: Hainich National Park

The field studies of this PhD thesis were conducted in the Hainich forest which is located along the western part of the Thuringian basin in central Germany. The Hainich covers ~15,000 ha and represents the largest coherent area covered by deciduous forests in Central Europe. The studies were conducted in the south eastern part of the Hainich near the village of Weberstedt (51°05'28''N, 10°31'24''O). This old part of the Hainich was covered by forests since the mid 18th century. Due to differences in historic land ownership and management practices, the forests comprise of a mosaic of at least 200 years old stands differing in tree diversity, ranging from monospecific beech stands (Müllverstädter Chausse) to species rich stands with up to 14 tree species per hectare (Schmidt et al., 2009; Leuschner et al., 2009). Dominant tree species include beech (*Fagus sylvatica* L.), ash (*Fraxinus excelsior* L.), lime (*Tilia platyphyllos* Scop. and *Tilia cordata* P. Mill.) and maple (*Acer pseudplatanus* L.; Leuschner et al., 2009; Vockenhuber et al., 2011). The southern part of the Hainich forest was declared National Park in 1997 and in 2011 part of it was included into old-growth beech forests of the UNESCO World Natural Heritage Sites. The herb layer is dominated by *Allium ursinum* (L.), *Anemone nemorosa* (L.) and *Galium odoratum* (L.; Vockenhuber et al., 2011). The mean annual temperature ranges from 7.5 to 8.0^{o}C and the mean annual precipitation varies between 590 to 700 mm (Meteomedia station Weberstedt). The area represents a slightly sloping limestone plateau from the Triassic Upper Limestone formation covered by Pleistocene loess (60-120 cm; Guckland et al., 2009).

3. Labeling studies with stable isotopes (^{13}C and ^{15}N) for food web analyses

Natural variations in stable isotope ratios of carbon (^{13}C/^{12}C) and nitrogen (^{15}N/^{14}N) have been shown to be a powerful tool for the investigation of nutrient fluxes and trophic interactions in soil food webs (Scheu and Falca, 2000; Post, 2002; Tiunov, 2007). δ^{15}N signatures have been used to assign soil animals to trophic levels, i.e. primary decomposers, secondary decomposers and predators (Scheu and Falca, 2000; Oelbermann and Scheu, 2010). In these studies it has been shown that detritivorous soil animal species, i.e. primary and secondary decomposers form a continuum rather than representing distinct trophic levels with

species feeding exclusively on litter or on microbial based diets (Scheu, 2002). Further, differences in $\delta^{15}N$ signatures in mesofauna species, such as oribatid mites (Oribatida, Acari), suggest that they feed on a wide spectrum of diets (Schneider et al., 2004; Maraun et al., 2011). Presumably, only few oribatid mite species rely on litter based diets, rather, most species rely on fungi as major food resource (Pollierer et al., 2009). Further, it is increasingly recognized that oribatid mites include species living as predators or scavengers, presumably feeding predominantly on nematodes (Rockett and Woodring, 1966; Schneider et al., 2005; Heidemann et al., 2011). In contrast to $\delta^{15}N$ signatures, $\delta^{13}C$ signatures of soil animals are only slightly enriched per trophic level, thereby allowing to identify basal resources of animal food webs (Oelbermann et al., 2008; Scheunemann et al., 2010).

Major progress has been achieved by analyzing natural variations in stable isotope signatures of soil animal species. However, for tracing C and N fluxes through decomposer systems labeling experiments with enriched ^{13}C and ^{15}N compounds are indispensible (Ruf et al., 2006; Pollierer et al., 2007). Labeling experiments with $^{13}CO_2$ have been conducted to trace the flux of C in photosynthates into roots, the rhizosphere, root associated microorganisms including mycorrhizal fungi (Johnson et al., 2002; Olsson and Johnson, 2005; Leake et al., 2006) and into soil arthropods (Sticht et al., 2008; Högberg et al., 2010; Pollierer et al., 2012). Labeling experiments with litter material enriched in ^{13}C and ^{15}N were conducted for tracing the flux of C and N from decomposing litter into saprotrophic microorganisms (Zeller et al., 2000; Fahey et al., 2011) and into the soil animal food web (Elfstrand et al., 2008; Lummer et al., 2012). In this study labeling experiments with ^{13}C and ^{15}N were used to trace on one side the incorporation of photosynthates into the rhizosphere food web and on the other the incorporation of litter C and N into the decomposer system.

4. Study objectives and hypotheses

My research work was conducted as part of the Research Training Group (RTG 1086) “The role of biodiversity for biogeochemical cycles and biotic interactions in temperate deciduous forests”. In this interdisciplinary program, 14 PhD were working together in three project groups: (A) Biodiversity analyses and biotic interactions, (B) biogeochemical cycles, and (C) syntheses, with my project being

integrated into project group A. For further information on the RTG 1086 see: http://www.uni-goettingen.de/en/82664.html.

The main focus of this dissertation was to investigate the role of trees as primary producers of forest ecosystems for the structure and functioning of soil animal food webs. I focused on two aspects: (1) Separating effects of tree diversity from effects of tree species identity, and (2) effects of tree species on the flux of C and N through the soil animal food web. Two tree species were selected for setting up two experiments, i.e. beech and ash that differ strongly in important traits such as root architecture, colonization by mycorrhiza and litter quality. For separating effects of tree diversity from those of tree identity a small scale experiment including one, two and three species combinations of beech, ash and lime trees was conducted in the field. Here, we focused on oribatid mites as major decomposer soil mesofauna group (Chapter 2). For testing the role of beech and ash for the flux of C and N through the soil animal food web two experiments with plant materials labeled with both ^{13}C and ^{15}N were conducted. I aimed at tracing the flux of C and N via the root pathway into the soil animal food web (Chapter 3), and the flux of C and N derived from decomposing litter material into the soil animal food web (Chapter 4). For tracing the flux of freshly assimilated rhizosphere derived C and mineral N into the soil animal food web a labeling study was conducted by exposing tree saplings to $^{13}CO_2$ atmosphere and by using ^{15}N enriched nutrient solution. Beech and ash seedlings were investigated representing tree species with markedly different root traits and different mycorrhizal communities. For tracing litter derived C and N into the soil animal food web ^{13}C and ^{15}N labeled leaf litter was used and the incorporation of the label into soil animals was followed in a field microcosm study. Here, I focused on the role of structural compounds of litter as determinant of the flux of litter resources into the decomposer systems. Beech and ash leaves differing in structural compounds but containing very similar concentrations of N were used in this study. Similar N concentrations were obtained by fertilizing beech and ash seedlings with the same nutrient solution.

The following main hypotheses were investigated:

(1) Tree diversity beneficially affects the abundance and alters community structure of soil mesofauna, i.e. oribatid mites, but tree identity effects surpass effects of tree diversity. Tree identity effects are mainly due to differences in nutrient quality of litter material, i.e. effects of ash being more beneficial than those of beech (Chapter 2).

(2) The flux of plant ^{13}C and mineral ^{15}N can be traced into the soil animal food web, and incorporation is highest in primary decomposers and diluted towards higher trophic levels, i.e. secondary decomposers and predators. The flux of ^{13}C from beech roots associated with ectomycorrhizal fungi into the soil animal food web exceeds that from ash roots associated with arbuscular mycorrhizal fungi. In contrast, incorporation of ^{15}N into the soil animal food web mainly occurs via saprotrophic fungi and differs little between beech and ash treatments (Chapter 3).

(3) Incorporation of litter resources into the soil animal food web is mainly driven by litter structural compounds; less litter resources are incorporated from litter high in structural compounds, such as beech, as compared to litter low in structural compounds, such as ash. Differences in incorporation of litter resources are most pronounced in primary decomposers, less in secondary decomposers and lowest in predators (Chapter 4).

Outlines of the chapters are presented below:

CHAPTER 2 Tree diversity little affected oribatid mite density and community structure, whereas effects of tree species identity were strong. Abundant oribatid mite groups, such as fungivorous and/or zoophagous Oppioidea, benefitted from the presence of beech, presumably due to thick organic layers formed by recalcitrant beech litter providing habitable space and food resources, such as fungi and nematodes. Oribatid mite density was low in stands with ash and lime and oribatid mite species comprised mainly large and strongly sclerotized species able to withstand harsh microclimatic conditions in shallow humus layers of these tree species.

CHAPTER 3 Carbon from beech and ash seedlings exposed to $^{13}CO_2$ enriched atmosphere in the greenhouse was incorporated into the soil animal food web. In parallel, nitrogen from ^{15}N enriched nutrient solution was channeled into the soil animal food web via fungi. ^{13}C and ^{15}N signals were similar in beech and ash rhizosphere suggesting that channeling of C and N was little affected by tree species and species specific root traits including differences in root colonization by mycorrhiza. Incorporation of labelled C and N into secondary decomposers exceeded that into primary decomposers suggesting that fungi form a major control point in the flux of C and N into the soil animal food web. Notably, incorporation of labelled C and N was highest in predators suggesting that they heavily rely on fungal feeding prey, such as Collembola, but also on other prey species high in labelled C and N, potentially Nematoda and Lumbricidae.

CHAPTER 4 As indicated by the use of beech and ash litter similar in N concentrations but differing in structural compounds soil animals preferentially incorporate C from litter low in structural compound. The results highlight the importance of litter low in structural compounds, such as ash, for fuelling soil animal food webs. Soil animals incorporated similar amounts of N from both ash and beech indicating that structural compounds of litter little affect the availability of litter N. Incorporation of litter C and N into secondary decomposers exceeded that into primary decomposers indicating that litter resources are incorporated into the soil animal food web predominantly via the fungal energy channel. Mixing of litter differing in concentrations of structural compounds affected the incorporation of litter resources into the soil animal food web only little suggesting that channeling of litter resources via the fungal energy channel into higher trophic levels varies little with concentrations of litter structural compounds.

References

Aubert, A., Margerie, P., Trap, J., Bureau, F., 2010. Aboveground-belowground relationships in temperate forests: Plant litter composes and microbiota orchestrates. Forest Ecology and Management 259, 563-572.

Ball, B.A., Bradford, M.A., Coleman D.C., Hunter M.D., 2009a. Linkages between below and aboveground communities: Decomposer responses to simulated tree species loss are largely additive. Soil Biology and Biochemistry 41, 1155-1163.

Ball, B.A., Bradford, M.A., Hunter, M.D., 2009b. Nitrogen and phosphorous release from mixed litter layers is lower than predicted from single species decay. Ecosystems, 12, 87-100.

Bardgett, R.D., Bowman, W.D., Kaufmann, R., Schmidt, S.K., 2005. A temporal approach to linking aboveground and belowground ecology. Trends in Ecology and Evolution 20, 634–641.

Bengtsson J., Nilsson, S.G., Franc, A., Menozzi, P., 2000. Biodiversity, disturbances, ecosystem function and mamagement of European forests. Forest Ecology and Management 132, 39-50.

Berg, B., McClaugherty, C., 2008. Plant Litter - Decomposition, Humus Formation, Carbon Sequestration. Springer, Berlin, Germany.

Cairney, J.W.G., 2012. Extramatrical mycelia of ectomycorrhizal fungi as moderators of carbon dynamics in forest soil. Soil Biology & Biochemistry 147, 198-208.

Chapman, S.K., Langely, J.A., Hart, S.C., Koch, G.W., 2006. Plants actively control nitrogen cycling: uncorking the microbial bottleneck. New Phytologist 169, 27-34.

Coleman, D.C., Reid, C.P.P., Cole, C.V., 1983. Biological strategies of nutrient cycling in soil systems. Advances in Ecological Research 13, 1-55.

Cornwell, W.K., Cornelissen, J.H.C., Amatangelo, K., et al., 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. Ecology Letters 11, 1065-1071.

Crotty, F.V., Blackshaw, R.P., Murray, P.J., 2011. Tracking the flow of bacterially derived ^{13}C and ^{15}N through soil faunal feeding channels. Rapid Communications in Mass Spectrometry 25, 1503-1513.

Dennis, P.G., Miller, A.J., Hirsch, P.R., 2010. Are root exudates more important than other sources of rhizodeposits in structuring rhizosphere bacterial communities? FEMS Microbiology Ecology 72, 313-327.

Elfstrand, S., Lagerlöf, J., Hedlund, K., Martensson, A., 2008. Carbon routes from decomposing plant residues and living roots into soil food webs assessed with ^{13}C labeling. Soil Biology and Biochemistry 40, 2530-2539.

Fahey, T.J., Yavitt, J.B., Sherman, R.E., Groffman, P.M., Fisk, M.C., Maerz, J.C., 2011. Transport of carbon and nitrogen between litter and soil organic matter in a northern hardwood forest. Ecosystems 14, 326-340.

Ferlian, O., Scheu, S., Pollierer, M.M., 2012. Trophic interactions in centipeds (Chilopoda, Myriapoda) as indicated by fatty acid patterns: Variations with life stage, forest age and season. Soil Biology and Biochemistry 52, 33-42.

Frey, S.D., Elliott, E.T., Paustian, K., Peterson, G.A., 2000. Fungal translocation as a mechanism for soil nitrogen inputs to surface residue decomposition in a no-tillage agroecosystem. Soil Biology and Biochemistry 32, 1001-1004.

Gartner, T.B., Cardon Z.G., 2004. Decomposition dynamics in mixed species leaf litter. Oikos 104, 230-246.

Geissler, D., Horwath, W.R., Joergensen, R.G., 2010. Pathways of nitrogen utilization by soil microorganisms - A review. Soil Biology and Biochemistry 42, 2058-2067.

Gessner, M.O., Swan, M.S., Dang, C.K., McKie, B.G., Bardgett, R.D., Wall, D.H., Hättenschwiler S., 2010. Diversity meets decomposition. Trends in Ecology and Evolution 25, 372-380.

Guckland, A., Flessa, H., Prenzel, J., 2009. Controls of temporal and spatial variability of methane uptake in soils of a temperate deciduous forest with different abundance of European beech (*Fagus sylvatica* L.). Soil Biology and Biochemistry 41, 1659-1667.

Hättenschwiler, S., Bracht-Joergensen, H., 2010. Carbon quality rather than stoichiometry controls litter decomposition in a tropical rain forest. Journal of Ecology 98, 754-763.

Hättenschwiler, S., Gasser, P., 2005. Soil animals alter plant litter diversity effects on decomposition. Proceedings of the National Academy of Science of the USA 102, 1519-1524.

Hättenschwiler, S., Tiunov, A.V., Scheu S., 2005. Biodiversity and litter decomposition in terrestrial ecosystems. Annual Reviews of Ecology, Evolution and Systematics 36, 191-218.

Heidemann, K., Scheu, S., Ruess, L., Maraun, M., 2011. Molecular detection of nematodes predation and scavenging in oribatid mites: Laboratory and field experiments. Soil Biology & Biochemistry 43, 2229–2236.

Hobbie, J.E., Hobbie, E.A., 2006. ^{15}N in symbiotic fungi and plants estimates nitrogen and carbon flux rates in arctic tundra. Ecology 87, 816–822.

Hobbie, S.E., Reich, P.B., Oleksyn, J., Ogdahl, M., Zytkowiak, R., Hale, C., Karolewski, P., 2006. Tree species effects on decomposition and forest floor dynamics in a common garden. Ecology 87, 2288-2297.

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchaustl, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J., Wardle, D.A., 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological Monographs 75, 3–35.

Högberg, P., Read, D.J., 2006. Towards a more plant physiological perspective on soil ecology. Trends in Ecology and Evolution 21, 548-554.

Högberg, P., Högberg, M.N., Göttlicher, S.G., Betson, N.R., Keel, S.G., Metcalfe, D.B., Campbell, C., Schindlbacher, A., Hurry, V., Lundmark, T., Linder, S., Näsholm, T., 2008. High temporal resolution tracing of photosynthate carbon from tree canopy to forest soil microorganisms. New Phytologist 177, 220-228.

Högberg, M.N., Briones, M.J.I., Keel, S.G., Metcalfe, D.B., Campbell, C., Midwood, A.J., Thornton, B., Hurry, V., Linder, S., Näsholm, T. and Högberg, P., 2010. Quantification of effects of season and nitrogen supply on tree below-ground carbon transfer to ectomycorrhizal fungi and other soil organisms in a boreal pine forest. New Phytologist 154, 791-795.

Hölscher, D., Hertel D., Leuschner C., Hottkowitz M., 2002. Tree species diversity and soil patchiness in a temperate broad-leaved forest with limited rooting space. Flora 197, 118–125.

Jacob, M., Weland, N., Platner, C., Schaefer, M., Leuschner, C., Thomas, F.M., 2009. Nutrient release from decomposing leaf litter of temperate deciduous forest trees along a gradient of increasing tree species diversity. Soil Biology and Biochemistry 41, 2122-2130.

Jacob, M., Viedenz, K., Polle, A., Thomas, F.M., 2010. Leaf litter decomposition in temperate deciduous forest stands with a decreasing fraction of beech (*Fagus sylvatica*). Oecologia 164, 1083-1094.

Johnson, D., Leake, J.R., Ostle, N., Ineson, P., Read, D.J., 2002. *In situ* $^{13}CO_2$ pulse-labelling of upland grassland demonstrates a rapid pathway of carbon flux from arbuscular mycorrhizal mycelia to the soil. New Phytologist 153, 327-334.

Kardol, P., Newton, J.S., Bezemer, T.M., Maraun, M., van der Putten, W.H., 2009. Contrasting diversity patterns of soil mites and nematodes in secondary succession. Acta Oecologica 35, 603-609.

Klarner, B., Maraun, M., Scheu, S., 2013. Trophic diversity and niche partitioning in a species rich predator guild - Natural variations in stable isotope ratios ($^{13}C/^{12}C$, $^{15}N/^{14}N$) of mesostigmatid mites (Acari, Meesostigmata) from Central European beech forests. Soil Biology and Biochemistry 57, 327-333.

Lang, C., Polle, A., 2011. Ectomycorrhizal fungal diversity, tree diversity and nutrient relations in a mixed Central European forest. Tree Physiology 31, 531-538.

Lang, C., Seven, J., Polle, A., 2011. Host preferences and differential contributions of deciduous tree species shape mycorrhizal species richness in a mixed Central European forest. Mycorrhiza 21, 297-308.

Leake, J.R., Ostle, N.J., Rangel-Castro, J.I., Johnson D., 2006. Carbon fluxes from plants through soil organisms determined by filed $^{13}CO_2$ pulse-labelling in an upland grassland. Applied Soil Ecology 33, 152-175.

Leuschner C, Jungkunst HF, Fleck S., 2009. Functional role of forest diversity: Pros and cons of synthetic stands and across-site comparisons in established forests. Basic and Applied Ecology 10: 1-9.

Lummer, D., Scheu, S., Butenschoen, O., 2012. Nitrogen transfer between decomposing litter species is an important but not the only factor responsible for synergistic mixture effects on litter decomposition. Oikos, 121, 1649-1655.

Maraun, M., Alphei, J., Bonkowski, M., Buryn, R., Migge, S., Pter, M., Schaefer, M., Scheu, S., 1999. Middens of the earthworm *Lumbricus terrestris* (Lumbricidae): microhabitats for micro- and mesofauna in forest soil. Pedobiologica 43, 276-287.

Maraun, M., Martens, H., Migge, S., Theenhaus A., Scheu, S., 2003. Adding to „the enigma of soil animal diversity“: fungal feeders and saprophagous soil invertebrates prefer similar food substrates. European Journal of Soil Biology 39, 85-95.

Maraun, M., Erdmann, G., Fischer, B.M., Pollierer, M.M., Norton, R.A., Schneider, K., Scheu, S., 2011. Stable isotopes revisited: their use and limits for oribatid mite trophic ecology. Soil Biology and Biochemistry 43, 877–882.

Meier, C.L., Bowman, W.D., 2008. Linke between plant litter chemistry, species diversity, and belowground ecosystem function. Proceedings of the National Academy of Sciences 105, 19780-19785.

Moore, J.C., Hunt, H.W., 1988. Resource compartmentation and the stability of real ecosystems. Nature 333, 261-263.

Moore, J.C., St. John, T.V., Coleman, D.C., 1985. Ingestion of vesicular-arbuscular mycorrhizal hyphae and spores by soil microarthropds. Ecology 66, 1979-1981.

Moore, J.C., McCann, K., de Ruiter P.C., 2005. Modeling trophic pathways, nutrient cycling, and dynamic stability in soils. Pedobiologia 49, 499-510.

Moore-Kucera, J., Dick, R.P., 2008. Application of ^{13}C-labeled litter and root materials for in situ decomposition studies using phospholipids fatty acids. Soil Biology & Biochemistry 40, 2485-2493.

Neuhauser, E.F., Hartenstein, R., Connors, J., 1978. The role of soil macroinvertebrates in the degradation of vanillin, cinnamic acid, and lignins. Soil Biology and Biochemistry 10, 431-435.

Oelbermann, K., Langel, R., Scheu, S., 2008. The role of prey out of the decomposer system for generalist predators of grassland. Oecologia 155, 605-617.

Oelbermann, K. and Scheu, S., 2010. Trophic guilds of generalist feeders in soil animal communities as indicated by stable isotope analysis (^{15}N/^{14}N). Bulletin of Entomological Research 100, 511-520.

Olsen, P.A., Johnson, N.C., 2005. Tracking carbon from the atmosphere to the rhizosphere. Ecology Letters 8, 1264-1270.

Osler, G.H.R., Sommerkorn M., 2007. Toward a complete soil C and N cycle: incorporating the soil fauna. Ecology 88, 1611-1621.

Osono, T., 2007. Ecology of lignolytic fungi associated with leaf litter decomposition. Ecology Research 22, 955-974.

Pérez-Harguindeguy, N., Díaz, S., Cornelissen, J.H.C., Vendramini, F., Cabido M., and Castellanos, A., 2000. Chemistry and toughness predict litter decomposition rates over a wide spectrum of functional types and taxa in central Argentinia. Plant and Soil 218, 21-30.

Peschel, K., Norton, R.A., Scheu, S., Maraun, M., 2006. Do oribatid mites live in enemy-free space? Evidence from feeding experiments with the predatory mite *Pergamasus septentrionalis*. Soil Biology & Biochemistry 38, 2985-2989.

Pollierer, M.M., Langel, R., Korner, C,.Maraun, M., Scheu, S., 2007. The underestimated importance of belowground carbon input for forest soil animal food webs. Ecology Letters 10, 729-736.

Pollierer, M.M., Langel, R., Scheu, S., Maraun, M., 2009. Compartmentalization of the soil animal food web as indicated by dual analysis of stable isotope ratios ($^{15}N/^{14}N$ and $^{13}C/^{12}C$). Soil Biology & Biochemistry 41, 1221–1226.

Pollierer, M.M., Dykmans, J., Scheu, S., Haubert, D., 2012. Carbon fluxes through fungi and bacteria into the forest soil animal food web as indicated by compound-specific 13C fatty acid analysis. Functional Ecology, doi: 10.1111/j.1365-2435.2012.02005.x.

Polis, G.A., Strong D.R., 1996. Food web complexity and community dynamics. American Naturalist 147, 813-846.

Post, D.M., 2002. Using stable isotopes to estimate trophic position: models, methods and assumptions. Ecology 83, 703-718.

Rockett, C.L., Woodring, J.P., 1966. Oribatid mites as predators of soil nematodes. Annales of the Entomological Society of America 59, 669-671.

Ruf, A., Kuzyakov, Y., Lopatovskaya, O., 2006. Carbon fluxes in soil food webs of increasing complexity revealed by ^{14}C labeling and ^{13}C natural abundance. Soil Biology & Biochemistry 38, 2390-2400.

Scherer-Lorenzen, M., Potvin, C., Koricheva, J., Schmid, B., Hector, A., Bornik, Z., Reynolds, G., Schulze, E.-D., 2005. The design of experimental tree plantations for functional biodiversity research. In: Scherer-Lorenzen, M., Körner, C., Schulze, E.-D. (eds), Forest Diversity and Function: Temperate and Boreal Systems, Ecological Studies, 176, Springer, Berlin, 347–376.

Scheu, S., Falca, M., 2000. The soil food web of two beech forests (*Fagus sylvatica*) of contrasting humus type: stable isotope analysis of a macro- and a mesofauna-dominated community. Oecologia 123, 285–286.

Scheu, S., 2002. The soil food web: structure and perspectives. European Journal of Soil Biology 38, 11−20.

Scheu, S., Setälä, H., 2002. Multitrophic interactions in decomposer food webs. In: Hawkins, B.A., Tscharntke, T. (eds.) Multitrophic level interactions. Cambridge University Press, Cambridge, pp. 223-264.

Scheu, S., 2005. Linkages between tree diversity, soil fauna and ecosystem processes. In: Scherer-Lorenzen, M., Köhler, C., Schulze, E.-D., (Eds.) Forest Diversity and Function: Temperate and Boreal Systems, Ecological Studies 176, Springer, Berlin, Germany, 211-233.

Scheunemann, N., Scheu, S., Butenschoen, O., 2010. Incorporation of decade old soil carbon into the soil animal food web of an arable system. Applied Soil Ecology 46, 59-63.

Schmidt, I., Leuschner, C., Mölder, A., Schmidt, W., 2009. Structure and composition of the seed bank in monospecific and tree species-rich temperate broad-leaved forests. Forest Ecology and Management 257, 695–702.

Schneider, K., Migge, S., Norton, R.A., Scheu, S., Langel, R., Reineking, A., Maraun, M., 2004. Trophic niche differentiation in soil microarthropods (Oribatida, Acari): evidence from stable isotope ratios ($^{15}N/^{14}N$). Soil Biology and Biochemistry 36, 1769–1774.

Schneider, K., Renker, C., Maraun, M., 2005. Oribatid mite (Acari, Oribatida) feeding on ectomycorrhizal fungi. Mycorrhiza 16, 67-72.

Schneider, F.D., Scheu, S., Brose, U., 2012. Body mass constraints on feeding rates determine the consequences of predator loss. Ecology Letters 15, 436-443.

Schimel J.P., Hättenschwiler, S., 2007. Nitrogen transfer between decomposing leaves of different N status. Soil Biology and Biochemistry 39, 1428-1436.

Smith, S.E., Read, D.J., 1997. Mycorrhizal Symbiosis, 3rd ed. Elsevier, Oxford, UK.

Sticht, C., Schrader, S., Giesemann, A., Weigel, H.J., 2008. Effects of elevated atmospheric CO_2 and N fertilization on abundance, diversity and C-isotopic signature of collembolan communities in arable soil. Applied soil Ecology 34, 219-229.

Strickland, M.S., Wickings, K., Bradford, M.A., 2012. The fate of glucose, a low molecular weight compound of root exudates, in the belowground foodweb of forests and pastures. Soil Biology and Biochemistry 49, 23-29.

Swan, C.M., Kominoski, J.S., 2012. Biodiversity and Ecosystem Function of Decomposition. In: eLS. John Wiley & Sons, Ltd: Chichester. doi: 10.1002/9780470015902.a0023601.

Swift, M.J., Heal, O.W., Anderson, J.M., 1979. Decomposition in terrestrial ecosystems. Blackwell, Oxford, UK.

Sydes, C., Grime, J.P., 1981a. Effects of tree leaf litter on herbaceous vegetation in deciduous woodland. I. Field investigations. Journal of Ecology 69, 237-248.

Sydes, C., Grime, J.P., 1981b. Effects of tree leaf litter on herbaceous vegetation in deciduous woodland. II. An experimental investigation. Journal of Ecology 69, 249-262.

Tiunov, A.V., 2007. Stable isotopes of carbon and nitrogen in soil ecological studies. Biology Bulletin 34, 395-407.

Van der Heijden, M.G.A., Bardgett, R.D., van Straalen N.M., 2008. The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. Ecology Letters 11, 296-310.

Van der Hejden, M.G.A., Horton, T.R., 2009. Socialism in soil? The importance of mycorrhizal fungal networks for facilitation in natural ecosystems, Jounal of Ecology 97, 1139-1150.

Vockenhuber, E., Scherber, C., Langenbruch, C., Meißner, M., Seidel, D., Tscharntke, T., 2011. Tree diversity and environmental context predict herb species richness cover in Germany´s largest connected deciduous forest. Perspectives in Plant ecology, Evolution and Systematics, 13, 111-119.

Vitousek, P.M., Hättenschwiler, S., Olander, L., Allison S., 2002. Nitrogen and Nature. Ambio 31, 97-101.

Wardle, D.A., 2002. Communities and Ecosystems: Linking the Aboveground and Belowground Components. Monographs in Population Biology. Princeton University Press, Princeton, USA.

Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setälä, H., van der Putten, W.H., Wall, D.H., 2004. Ecological linkages between aboveground and belowground biota. Science 304, 1629-1633.

Wardle, D.A., 2006. The influence of biotic interactions on soil biodiversity. Ecology Letters 9, 870-886.

Weland, N., 2009. Diversity and trophic structure of the soil fauna and its influence on litter decomposition in deciduous forests with increasing tree diversity. Dissertation, University of Göttingen, Göttingen, 110 pp.

Zeller, B., Coiln-Belgrand, M., Dambrine, E., Martin, F., Bottner, P., 2000. Decomposition of ^{15}N-labeled beech litter and fate of nitrogen derived from litter in a beech forest. Oecologia, 550-559.

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

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submitted

Abstract

The role of tree diversity and identity as determinants of soil animal community structure is little understood. By using three tree species (beech, ash and lime) positioned in a triangle we aimed at investigating the role of tree species diversity and identity on the density and community structure of oribatid mites. One, two and three tree species study plot combinations were selected in the field and each replicated four times. 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. In detail, we hypothesized that the presence of beech reduces the density of oribatid mites due to recalcitrant litter, whereas the presence of lime and ash increases the density of oribatid mites due to high quality litter. 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 pure clusters of lime and ash with shallow organic layer suggests that high quality litter cannot compensate the lack of pronounced organic layers. 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.

Keywords

Temperate broadleaved forests, beech, ash, lime, litter quality, fine roots, fungi, litter layer, microhabitat heterogeneity, feeding biology

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, 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, 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 (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., 2012). 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 McClaughtery et al., 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 insoluble 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 fastly 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; Weland, 2009; 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., 2011). 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 et al., 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 McClaughtery, 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 forests 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 m². 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, Galumnidae oribatid mites 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: Enarthronota, Phthiracaridae, Damaeidae, Oppioidea (Oppiidae and Quadroppiidae), Suctobelbidae and Poronota (Maraun and Scheu, 2000). Other species and genera comprising less than 2% of total oribatid mite density were grouped as „others“.

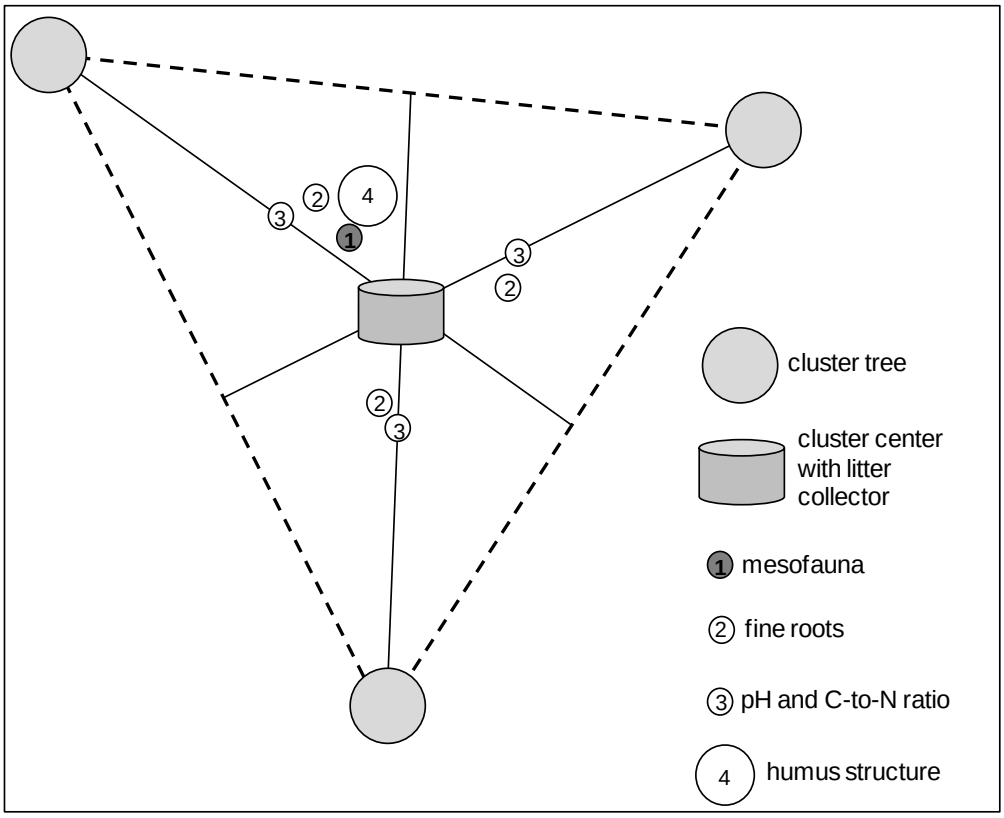

Fig. 1: Clusters of three trees with locations of litter collectors (centre of cluster) and sampling sites for soil mesofauna and structure of the humus layer (ca. 0.5 m from centre), and for fine roots, pH and C-to-N ratio of upper mineral soil (ca. 1 m from centre).

2.4. Environmental factors

In the centre of each cluster, the leaf litter was collected using 35 l buckets with an aperture of 0.29 m² (Fig. 1). Water could drain from the buckets through 8 mm holes in the bottom. Leaf litter was sampled at four sampling dates from autumn 2008 to spring 2009 and sorted by species, dried at 70°C for three days and weighed (for details see Langenbruch et al., 2012).

Fine roots were sampled in each of the clusters in May 2008 (Fig. 1). Soil cores were taken from the upper 0-20 cm of the mineral soil and organic layer using a steel corer of a diameter of 35 mm. Samples were transferred into polyethylene bags and stored in darkness at 4°C until determination within three weeks. Living fine root fragments (<2 mm in diameter) longer than 1 cm were collected with a pair of tweezers and ascribed to species (for details see Jacob et al., 2012). Species specific fine root biomass was determined after drying at 70°C for 48h and was expressed as dry mass per square meter of soil surface area.

Humus type was determined close to the centre of the clusters; dominating humus types were L- and F-mull. Soil samples (0-10 cm and 10-20 cm) were taken in triplicate using an auger (Fig. 1). Soil samples were dried at 40°C until constant weight and then passed through a 2 mm sieve. Soil pH was measured in 1 *M* KCl solution (soil-to-KCl solution ratio of 1.0:2.5). A subsample of the soil was ground using a planetary ball mill (Retsch PM 4000, Haan, Germany), and the contents of organic carbon and total nitrogen were measured using an elemental analyzer (Heraeus Elementar Vario EL, Hanau, Germany).

2.5. Statistical analyses

Densities of adult oribatid mites, the six oribatid mite groups, oribatid mite species numbers and data on environmental factors, i.e. leaf litter input, fine root biomass and mass of humus layers were analyzed using hierarchical ANOVAs (type I sum of squares; Schmid et al., 2002). First, the diversity of the clusters (1-3) was fitted followed by tree species identity (beech, ash, lime). F-values for tree identity given in text and tables refer to those fitted first. Differences between means were inspected using Tukey´s HSD test. The two sampling locations were coded as blocks, but as differences between blocks generally were not significant block was excluded from the final model. To improve homogeneity of variances data were log-transformed if necessary. Statistical analyses were conducted using SAS 9.2 (SAS Institute; Cary, NC, USA). Data given in text and figures represent means and standard errors calculated from the untransformed data.

Canonical Correspondence Analyses (CCA) was used to relate species to environmental variables. In addition to the environmental variables measured in this study, the bacterial-to-fungal PLFA ratio (A. Scheibe, pers. comm.) and the density of nematodes (Cesarz et al., 2012) were included. Only oribatid mite species that were present in at least three independent samples were included; the seven cluster types were coded as supplementary variables. CCA was performed using CANOCO 4.5 (Jongman et al., 1995; ter Braak and Smilauer, 2002).

3. Results

3.1. Litter input, root biomass and mass of humus layers

On average 102.5 ± 11.2 g/m² of leaf litter entered the clusters (Fig. 2a). The amount of litter varied significantly with cluster diversity ($F_{2,20}$ = 4.77; p = 0.0202); i.e. it was significantly lower in monospecific clusters (87.9 ± 9.3 g/m²) than in clusters with two species (117.9 ± 13.6 g/m²), with three-species-clusters being intermediate (100.1 ± 9.9 g/m²). Tree species identity did not significantly affect the amount of litter entering the clusters. Each of the clusters including monospecific clusters received litter from each of the three tree species, but the dominant litter type entering the clusters reflected the composition of cluster tree species. Monospecific beech clusters received 86% beech litter, ash clusters received 68% ash litter and lime clusters received 61% lime litter. Beech litter contributed ~20% to total leaf litter input in pure lime and ash clusters, whereas in mixed clusters with beech, i.e. beech-lime, beech-ash, beech-ash-lime, but also ash-lime clusters ~40% of litter comprised beech litter.

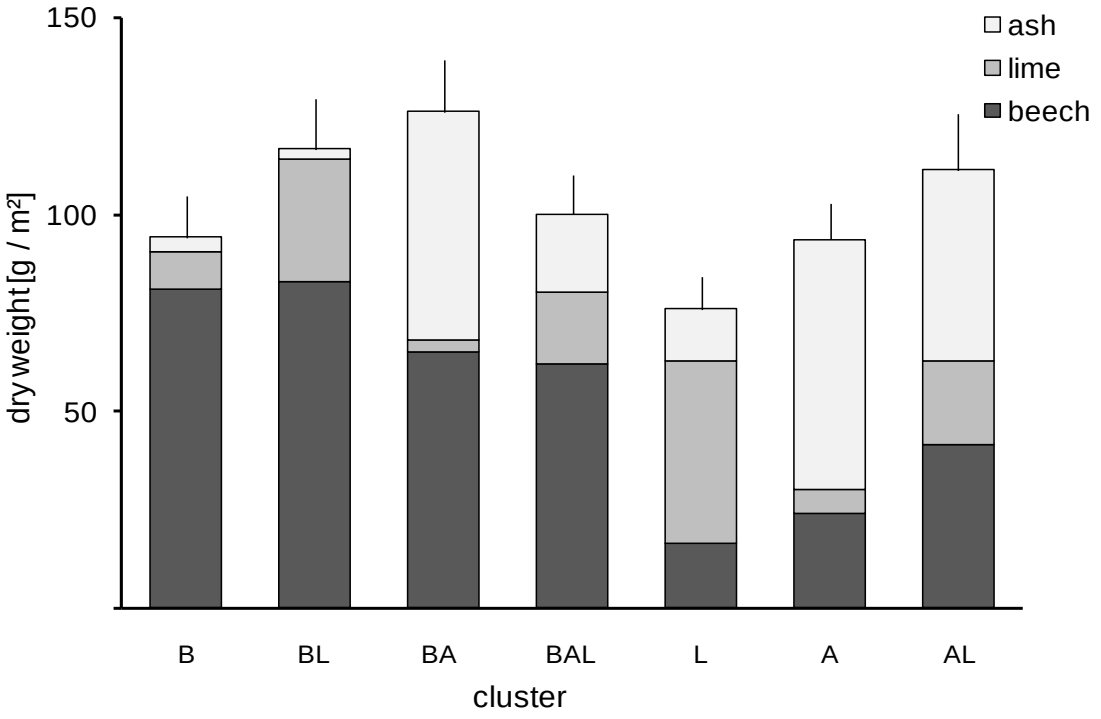

Fig. 2: (a) Dry weight of leaf litter (annual means ± SE) of beech, lime and ash entering clusters of pure and mixed stands of beech (B), lime (L) and ash (A) (for details see Materials and Methods and Fig. 1).

Mean fine root biomass was 253.2 ± 20.5 g/m²; it neither varied with tree diversity nor with tree identity of the clusters (Fig. 2b). However, similar to leaf litter the presence of species specific fine root biomass reflected the tree species composition of the clusters. Roots in monospecific clusters comprised almost exclusively of fine roots of the respective tree species. In mixed clusters, only roots of the respective tree species of the clusters were present, but in two species mixtures with ash roots ash predominated, i.e. 49.6% and 72.2% of the roots comprised ash roots in ash-beech and ash-lime clusters, respectively.

The mass of humus layers was 68.1 ± 17.2 g/m². It did not vary with tree diversity but markedly with tree species identity (Fig. 3). Generally, it declined from pure beech clusters over two- and three-species clusters with beech to clusters without beech (significant three way interaction of beech, ash and lime; $F_{4,20} = 6.28$, $p = 0.0019$). The mass of humus layers in pure ash was only 29% of that in pure beech clusters (114.5 ± 10.4 g/m²).

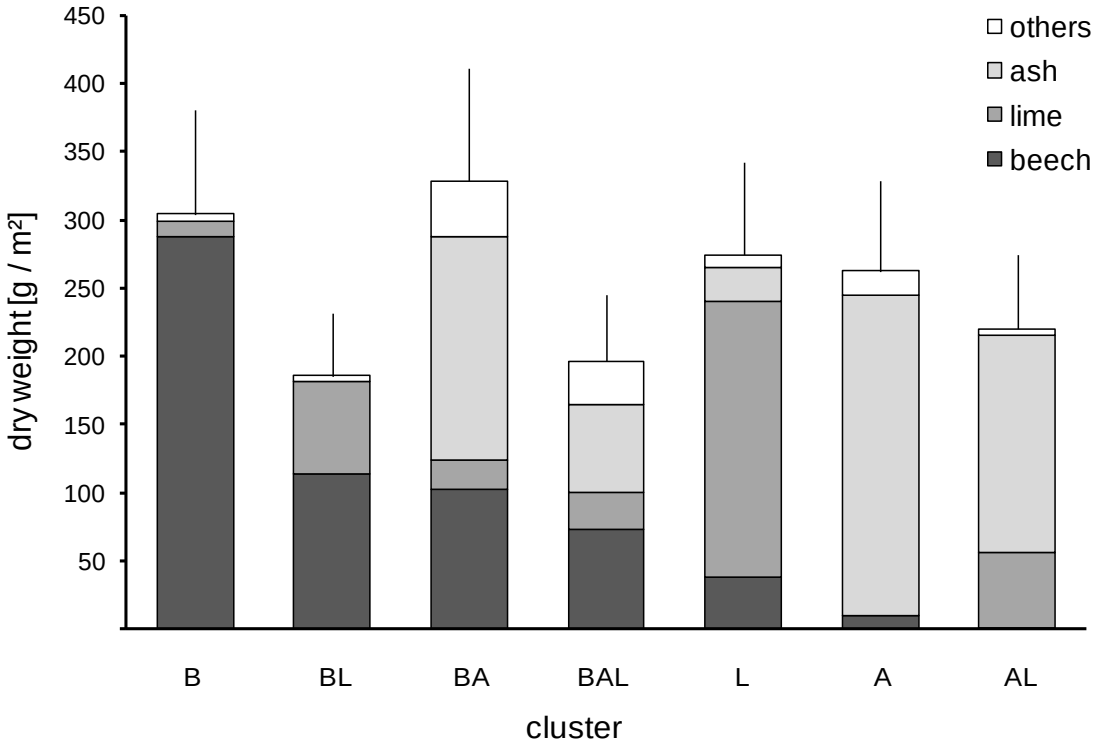

Fig. 2: (b) Dry weight of fine roots of beech, lime, ash and other tree fine roots ("others") in the clusters (May 2008; for details see Materials and Methods and Fig. 1).

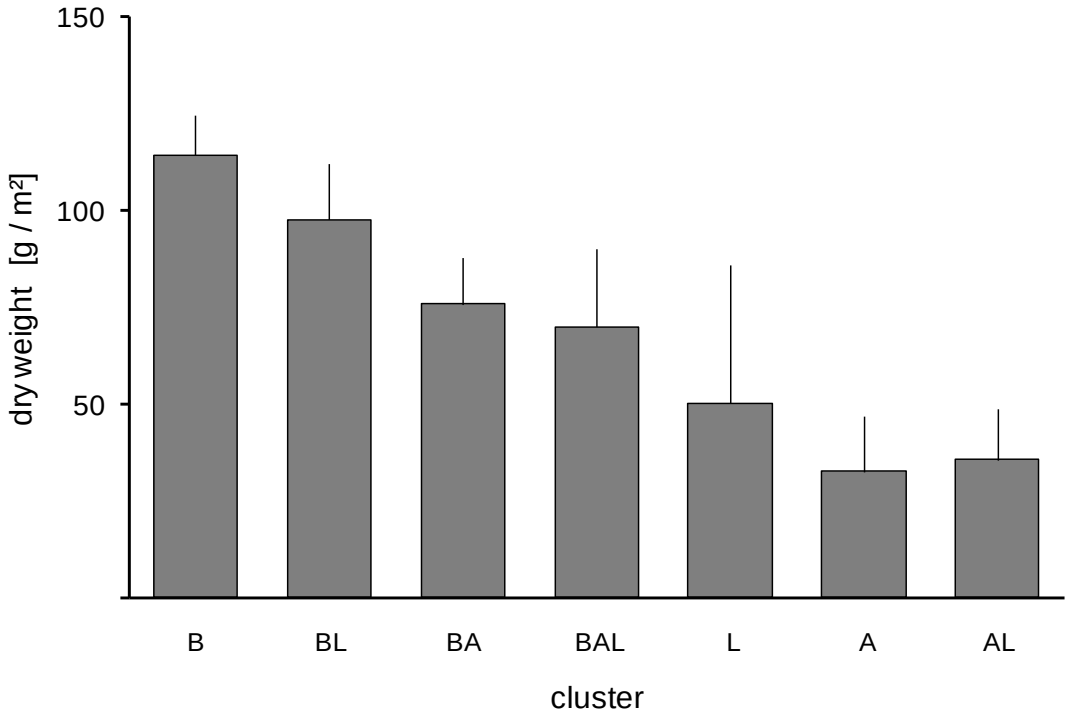

Fig. 3: Weight of organic layers (means ± SE) in clusters of pure and mixed stands of beech (B), lime (L) and ash (A).

3.2. Oribatid mite density

Mean oribatid mite density was 20,469 ± 7,168 ind./m²; it did not vary with tree diversity but tree species identity significantly influenced the density of oribatid mites (Table 1, Fig. 4). Presence of beech significantly increased oribatid mite density; it declined from a maximum in pure beech clusters over mixed clusters with beech (ca. 50% of that of pure beech clusters) to pure ash and lime clusters (26% and 18% of that in pure beech clusters, respectively).

Tree diversity did not affect the density of oribatid mite groups, except for Enarthronota, with their density declining from one (2,927 ± 1,086 ind./m²) over two (1,103 ± 252 ind./m²) to three species clusters (509 ± 208 ind./m²; Table 1). In contrast, tree species identity strongly affected the density of oribatid mite groups but the influence of individual tree species on oribatid mites varied between the different groups (Fig. 4 and 5, Table 1). The two most abundant groups, i.e. Oppioidea and Suctobelbidae, benefited from the presence of beech but were detrimentally affected by lime and ash, reaching very low densities in monospecific stands of these species. In pure lime and pure ash clusters densities of Oppioidea were 48% and 19% of those in pure beech clusters, respectively. Densities of

Suctobelbidae in pure lime and pure ash clusters were only 15% and 6% of the densities in pure beech clusters (Fig. 4 and 5, Table 1). Damaeidae also benefited from beech but their density was generally low with an overall mean of 618 ± 132 ind./m^2. Poronota were detrimentally affected by ash and lime but only in monocultures. In contrast, Enarthronota were beneficially affected by ash but the response was modified by each of the other two tree species; their density was high in ash and ash-lime clusters but at a maximum in mono-species beech clusters. Phthiracaridae was the only group that was not affected by tree identity; on average their density was 1,727 ± 262 ind./m^2.

3.3. Oribatid mite diversity and community structure

A total of 83 species of 31 families of Oribatida were recorded; 46% of the individuals comprised Oppioidea, 14% Suctobelbidae, 10% “others”, 9.8% Enarthronota, 8.3% Phthiracaridae, 8.2% Poronota and 3.5% Damaeidae. As was also observed for density, tree diversity did not significantly affect oribatid mite species diversity, whereas oribatid mite diversity varied markedly with tree identity. The presence of beech beneficially affected species numbers which were highest in pure beech clusters (45), intermediate in beech-lime (33), beech-ash (29), ash-lime (24) and beech-ash-lime clusters (24) and lowest in monospecies clusters of lime (20) and ash (19). In accordance to total species numbers, species numbers per sample differed significantly between cluster types ($F_{4,20}$ = 2.76, p = 0.0389 for the three factor interaction of beech, lime and ash), i.e. they were highest in beech only clusters (18.5 ± 3.7) and lowest in clusters with ash and lime only (6.5 ± 1.7 and 6.0 ± 1.9, respectively).

Table 1: Means (± standard error) and ANOVA table of F-values on the effect of tree species diversity and identity in pure and mixed clusters of beech, ash and lime on the density of total oribatid mites (Oribatida) and oribatid mite groups (Oppioidea, Suctobelbidae, Enarthronota, Phthiracaridae, Poronota and Damaeidae). F-values refer to those when fitted first in hierarchical ANOVAs (SS1; see Materials and Methods); *, P < 0.05; **, P < 0.01

	mean	**SE**	**diversity**	**beech**	**ash**	**lime**	**beech × ash**	**beech × lime**	**ash × lime**	**beech × ash × lime**
			$F_{2,20}$	$F_{1,20}$	$F_{1,20}$	$F_{1,20}$	$F_{3,20}$	$F_{3,20}$	$F_{3,20}$	$F_{4,20}$
Oribatida	20,469.1	7,168.3	0.58	**4.38***	0.82	1.41	2.48	1.53	3.07	2.44
Oppioidea	8,125.8	2,591.3	0.51	**5.67***	**5.49***	0	**3.55***	**2.84***	**4.34***	**3.38***
Suctobelbidae	2,290.5	926	0.24	**8,03***	1.95	2.06	3.03	**3.68***	**5.22****	**3.95***
Enarthronota	1,799.7	597.1	**5.97****	4.25	**9.17****	0.94	**5.78****	**3.23***	**6.47****	5.43
Phthiracaridae	1,727	261.8	0.42	0.02	0.15	0.06	0.25	0.12	0.08	0.19
Poronota	1,472.5	368.2	3.16	4.17	0.21	2.5	1.64	2.5	**3.29***	2.57
Damaeidae	618.1	320.8	1.33	5.79*	0.13	4.2	2.91	2.49	2.35	2.19

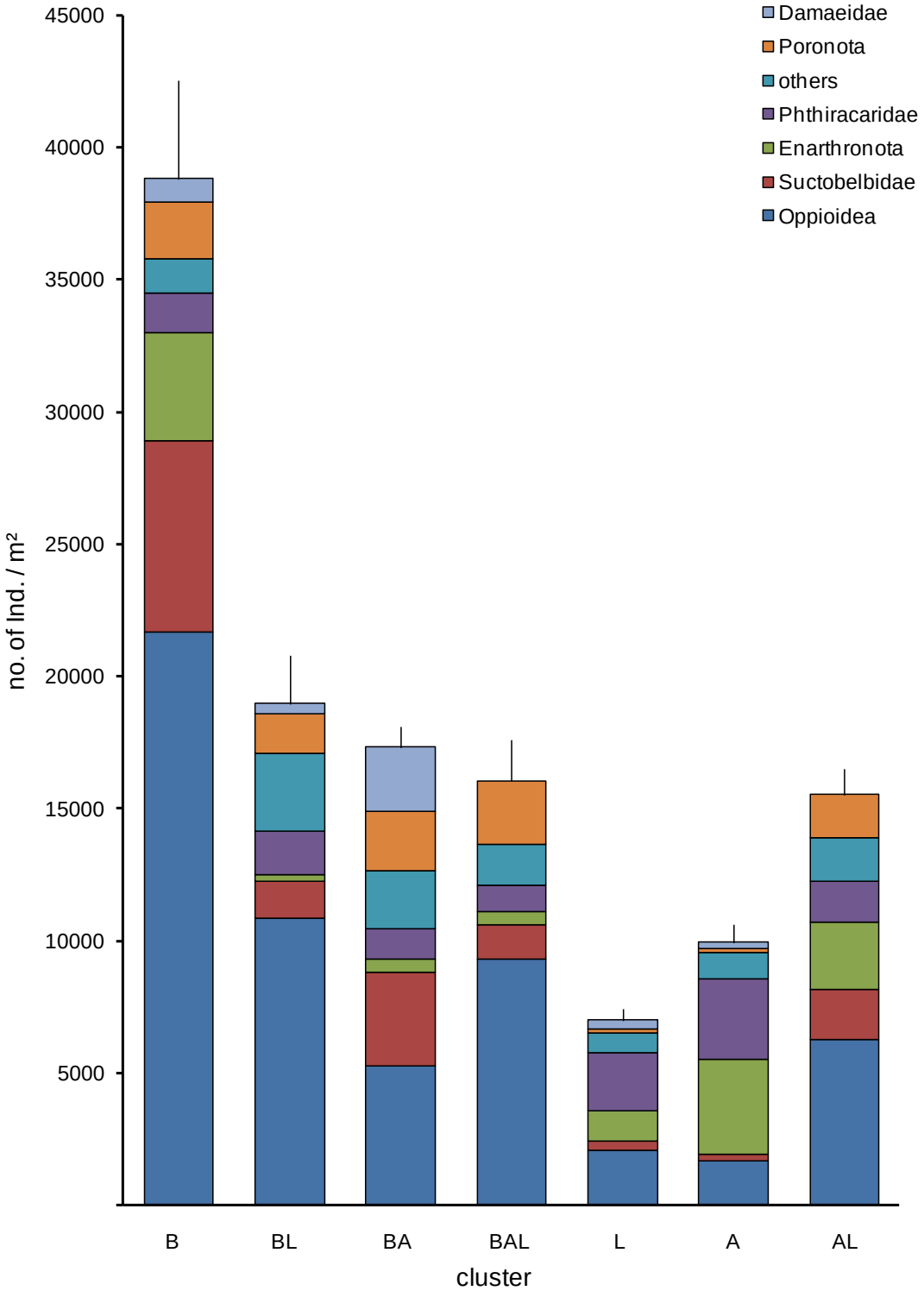

Fig. 4: Density of total oribatid mites (means ± SE) and contribution of Enarthronota, Phthiracaridae, Damaeidae, Oppioidea, Suctobelbidae Poronota and other oribatid mite taxa ("others"; see Materials and Methods) to total oribatid mite density in clusters of pure and mixed stands of beech (B), lime (L) and ash (A).

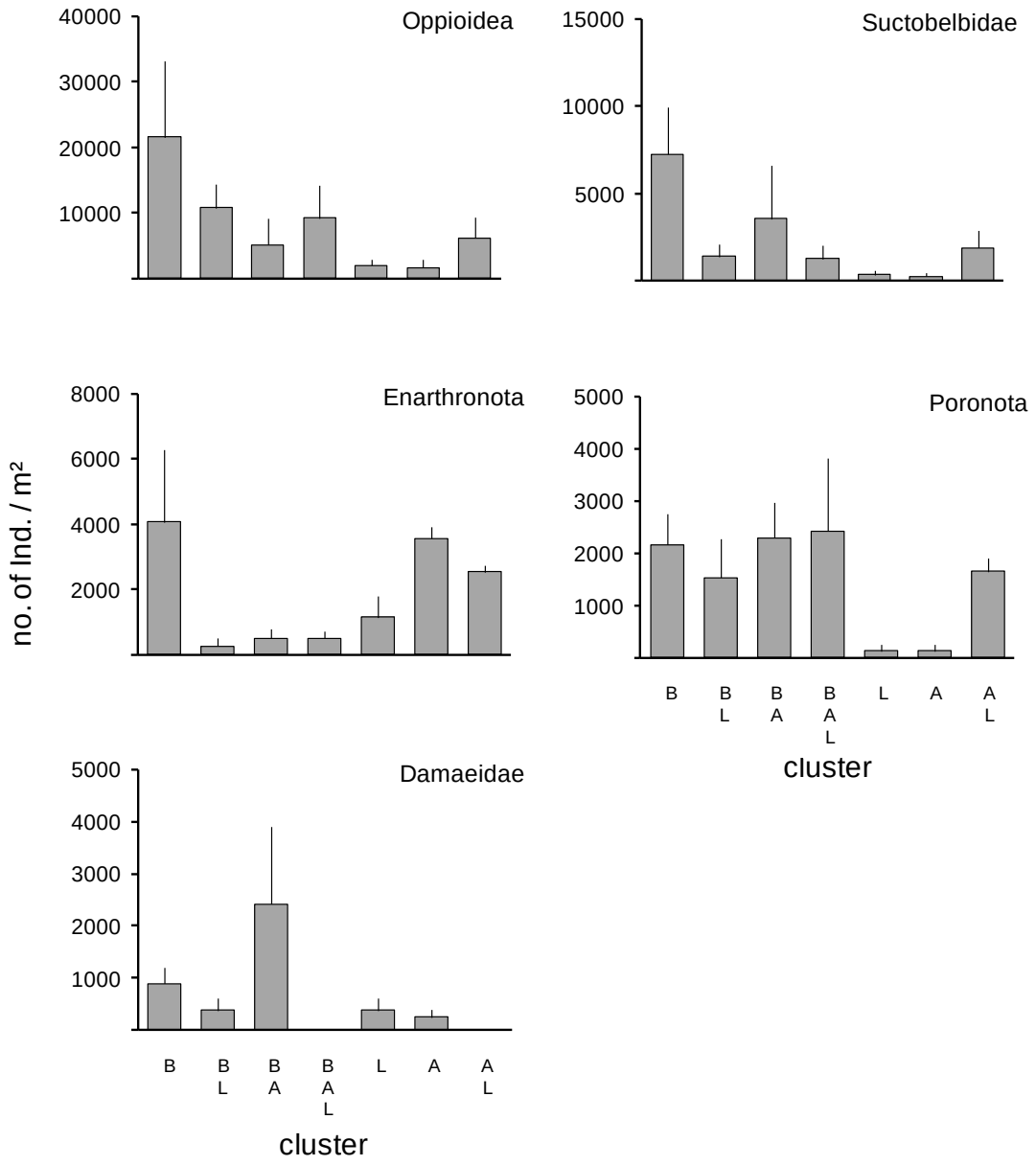

Fig. 5: Density of Oppioidea, Suctobelbidae, Enarthronota, Poronota and Damaeidae (means ± SE) in clusters of pure and mixed stands of beech (B), lime (L) and ash (A).

In accordance with the density and diversity of oribatid mites, CCA reflected that oribatid mite community structure varied with tree species identity (Fig. 6). Along the first CCA axis clusters beech, ash and lime were separated. Among the environmental factors, topsoil pH and the amount of lime litter entering the clusters correlated closest with the first axis; both were at a maximum in clusters with lime. Along the second axis oribatid mite communities of ash clusters were separated from those with beech and lime. The second axis correlated positively with the amount of ash and negatively with the amount of beech litter, with the latter being closely associated with the soil C-to-N ratio, the mass of the humus layer and beech fine roots. Notably, each of these beech associated variables correlated negatively with soil pH. Further, low pH was associated with high bacterial-to-fungal ratio (as measured by PLFAs) and high nematode density. Generally, most species of oribatid mites clustered with beech, which was most pronounced in Oppiidae, i.e. *Oppiella obsoleta*, *O. margidentata*, *O. nasuta*, *O. hauseri*, *O*. cf. *epilata*, *O. nova*, *O. subpectinata*, *O. falcata*, *Dissorhina ornata* and *Microppia minus*, but also in Suctobelbidae, i.e. *Suctobelbella* spp., *S. subcornigera* and *S. falcata*. In contrast, only few species clustered with lime including *Eupelops hirtus*, *Suctobelbella subtrigona* and *Tectocepheus velatus*. In clusters with ash, predominantly large and/or strongly sclerotized species were present, such as *Steganacarus magnus*, *S. striculus*, *Pantelozetes paolii*, *Hermannia gibba*, *Quadroppia hammerae*, *Chamobates voigtsi* and *Nothrus palustris*.

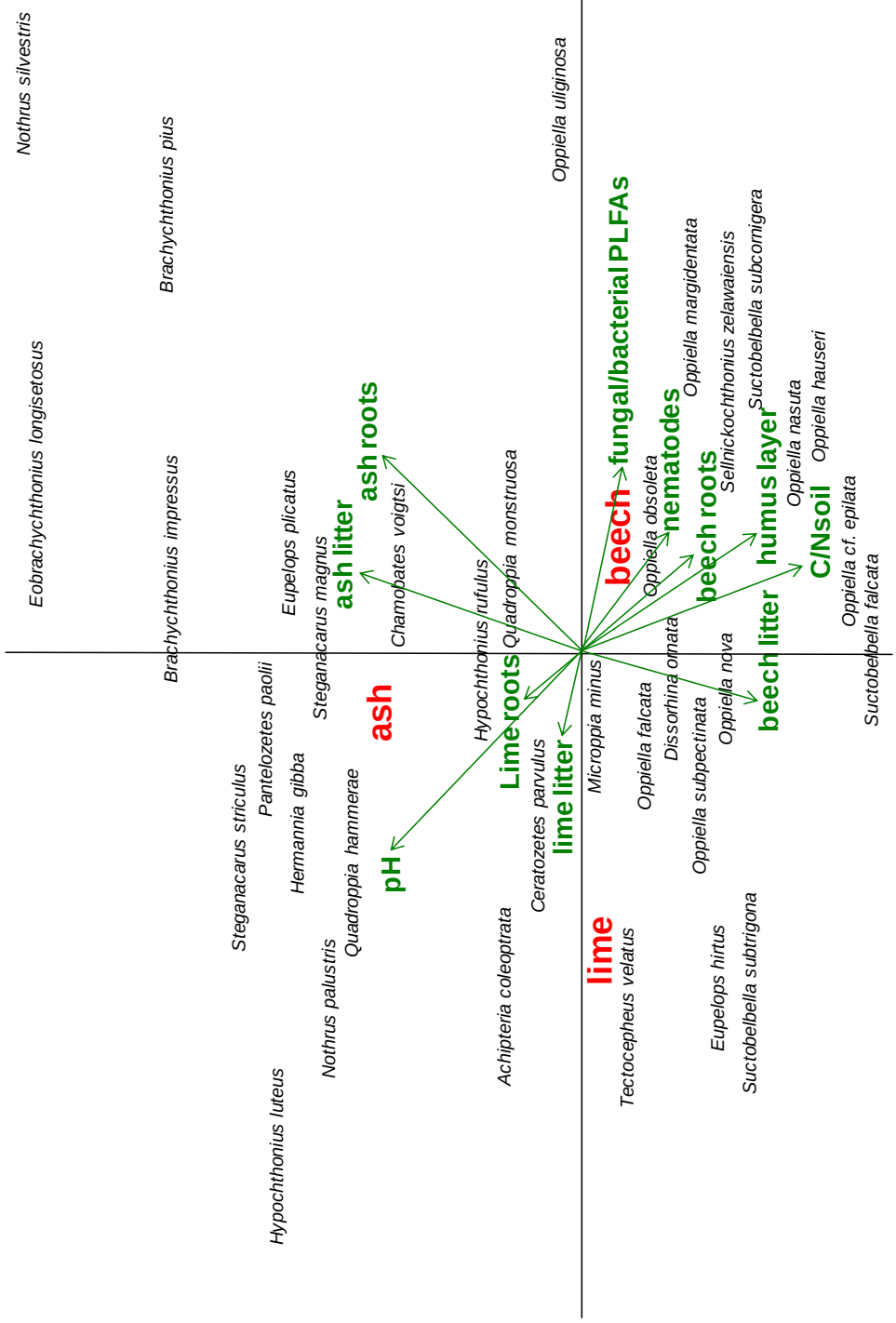

Fig. 6: Canonical Correspondence Analysis of oribatid mite species in clusters of pure and mixed stands of beech, ash and lime with environmental factors given as arrows. Centroids of tree species are given in red; environmental factors are given in green (humus layer = dry weight of humus layer; beech litter, ash litter and lime litter = annual amount of leaf litter of beech, ash and lime; beech roots, ash roots and lime roots = biomass of beech, ash and lime fine roots; C/N soil = C-to-N ratio of upper mineral soil; fungal/bacterial PLFAs = fungal-to-bacterial PLFA ratio; nematodes = density of nematodes; for details see Materials and Methods, for locations of sampling sites see Fig. 1). Eigenvalues of the first and second axis were 0.31 and 0.24, respectively.

4. Discussion

4.1. Oribatid mite density

Mean oribatid mite densities were ~20,500 ind./m² which is low compared to other temperate deciduous forests (Maraun and Scheu, 2000; Zaitsev and Wolters, 2006), but similar to previous studies in the Hainich National Park (Erdmann et al., 2012). Results of the study suggest that our first hypothesis needs to be rejected since oribatid mite densities did not increase with increasing tree diversity. This indicates that neither higher diversity of leaf litter nor higher diversity of fine roots affects oribatid mite density. This is in line with results of the study of Kaneko et al. (2005) who found oribatid mite density to vary little with tree diversity in broadleaved forests in Japan. However, the results contrast those of the study of Hansen et al. (2000) who found oribatid mite density to increase with increasing leaf litter diversity in North American broadleaved forests. They concluded that oribatid mites benefit from increased numbers of microhabitats in litter mixtures. Further, they assumed different litter types to serve complementary functions with recalcitrant leaf litter providing habitable space due to slow decomposition and high quality leaf litter adding additional spatial niches but also resources. Although our results are not conform to these conclusions in respect to oribatid mite density they are in line with these conclusions in respect to oribatid mite diversity (see below).

Conform to our expectation oribatid mite density was strongly affected by tree species identity. However, in contrast to our second hypothesis total density and the density of several of the studied oribatid mite groups benefited from the presence of beech. Notably, the density of oribatid mites were highest in pure beech clusters with ~47,000 ind./m². This indicates that oribatid mites indirectly benefit from low quality beech litter presumably because low quality litter decomposes slowly thereby providing habitably space in organic layers. Indeed, beech and coniferous forests with thick humus layers harbor high densities of oribatid mites (Migge et al., 1998; Maraun and Scheu, 2000; Osler, 2006). In addition to habitable space, organic layers provide stable environmental conditions and a wide range of food resources (Ponge, 1991; Schneider et al., 2004). Decomposing recalcitrant litter is predominantly colonized by fungi providing food for fungivorous microarthropods (Maraun et al., 2003). Further, oribatid mites likely benefited from fine roots in beech clusters and associated ectomycorrhizal fungal hyphae as oribatid mites feed on both saprotrophic and mycorrhizal fungi (Maraun

et al., 2003; Schneider et al., 2005; Pollierer et al., 2007; Rémen et al., 2008). Further, in pure beech clusters nematodes were most abundant (S. Cesarz, unpubl. data) providing additional food for oribatid mites. It is increasingly recognized that a number of oribatid mite species feed on nematodes (Muraoka and Ishibashi, 1976; Maraun et al., 2011; Heidemann et al., 2011).

In contrast to beech clusters, oribatid mite densities were low in monospecific clusters of ash and lime with ~11,000 ind./m² and ~7,500 ind./m², respectively, and these densities resemble those in fallows and arable land (Hoffmann et al., 1991; Scheu and Schulz, 1996; Maraun and Scheu, 2000). In contrast to our third hypothesis this indicates that oribatid mites do not benefit from high quality leaf litter. Rather, the results suggest that they suffer from the lack of a pronounced humus layers in ash and lime clusters. Presumably, thin organic layers are associated with strong seasonal changes in microclimatic conditions; in particular desiccation in summer may detrimentally affect oribatid mites and small species such as Oppioidea may suffer most (Taylor and Wolters, 2005).

Increasing tree diversity in Hainich National Park, i.e. the rising admixture of ash and lime trees to beech stands, beneficially impacts saprophagous macrofauna such as isopods, diplopods and earthworms (Weland, 2009; Cesarz et al., 2007). The input of high quality litter leads to a pulse of easily accessible C and nutrients, and this is accompanied by a peak of macrofauna activity resulting in rapid processing of litter thereby disturbing the habitat of oribatid mites. Oribatid mites are known to be sensitive to disturbances and to be detrimentally affected by macrofauna, in particular earthworms (Norton and Palmer, 1991; Maraun et al., 2003, Salamon et al., 2006; Eisenhauer, 2010). Further, ash clusters comprised exclusively ash fine roots which provide little resources for soil biota presumably because they are comparatively thick and form arbuscular mycorrhiza (S. Cesarz, submitted).

4.2. Oribatid mite community structure

Overall, approximately 50% of all oribatid mite individuals comprised Oppioidea; Enarthronota, Phthiracaridae and Suctobelbidae each contributed ~10% and Damaeidae contributed only 3.5% to oribatid community. Recent advances in trophic ecology of soil animal communities suggest that many species of oribatid mites occupy higher trophic levels and include a number of species living on an

animal diet, i.e. are predators or scavengers (Schneider et al., 2004; Maraun et al., 2011). Assuming that Oppioidea, Hypochthoniidae, Damaeidae, Suctobelbidae feed on fungi or live on an animal diet about 65% of the oribatid mite species of the Hainich National Park comprise secondary decomposers, predators or scavengers. This supports earlier findings that only a minor fraction of oribatid mite species in deciduous forests function as primary decomposers (Pollierer et al., 2009; Maraun et al., 2011).

Similar to oribatid mite density, community structure of oribatid mites did not vary significantly with tree diversity but markedly with tree identity. However, oribatid mite groups differentially responded to tree species. In particular Oppioidea and Suctobelbidae benefited from the presence of beech where they contributed ~50% to the numbers of oribatid mites. Oppioidea recently have been suggested to at least in part live on an animal diet (Maraun et al., 2011; Perdomo et al., 2012) suggesting that they benefited from high nematode densities in beech clusters. This is supported by CCA since most species of Oppiidae, i.e *Oppiella obsoleta*, *O. margidentata*, *O. nasuta*, *O. hauseri*, *O*. cf. *epilata*, *O. nova*, *O. subpectinata*, *O. falcata*, *Dissorhina ornata* and *Microppia minus,* were associated with high density of nematodes in beech clusters.

Oribatid mite community structure in monospecies ash and lime clusters differed strongly from those in beech clusters. In contrast to beech clusters, oribatid mites in ash clusters comprised few Oppioidea and Suctobelbidae but rather mainly Phthiracaridae, and Enarthronota (ash only). This indicates that Phthiracaridae and Enarthronota are rather insensitive to disturbances and harsh environmental conditions in the shallow humus layer of ash and lime forests. Brachychthoniidae (the main group of Enarthronota) live in upper mineral soil (Schulz, 1991) and therefore are likely to be insensitive to changes in the litter layer. Further, Brachychthoniidae likely take advantage of high density of microorganisms in these layers in ash forests (Thoms et al., 2010). Lower density of Enarthronota in lime than in ash clusters is probably due to a lower microbial biomass in the mineral soil in lime as compared to ash clusters. Phthiracaridae comprise large strongly sclerotized species that are likely unaffected by harsh microclimatic conditions in shallow humus layers and therefore might take advantage of high quality litter input in ash and lime clusters. Most oribatid mite species that predominated in ash clusters, i.e. *Eupelops plicatus, Chamobates voigtsi, Pantelozetes paolii*, *Hermannia gibba*, *Quadroppia hammerae*, *Chamobates voigtsi* and *Nothrus*

palustris, are also well protected against harsh environmental conditions due to thick exoskeletons. Further, *Steganacarus magnus* has been described to be insensitive to disturbances caused by bioturbation of earthworms (Maraun et al. 1999, 2003). Few species preferentially colonized lime clusters, i.e. *E. hirtus*, *Suctobelbella subtrigona* and *Tectocepheus velatus*. *E. hirtus* is large and strongly sclerotized and Suctobelbidae predominantly live in upper soil layers and for these species similar arguments as proposed for species preferentially colonizing ash clusters apply. *T. velatus* typically colonizes disturbed habitats and as parthenogenetic species it is well adapted to changes in habitat conditions (Skubala and Gulvik, 2005).

4.3. Oribatid mite diversity

In total, 83 species of oribatid mites were found which is in the range of earlier studies on oribatid mites in the Hainich National Park (Erdmann et al., 2012; S. Beyer, unpubl. data). Similar to oribatid mite density and community structure tree diversity did not affect oribatid mite diversity but strongly varied with tree identity. This contradicts earlier suggestions that oribatid mite diversity increases with the diversity of litter materials (Anderson et al., 1978; Hansen et al., 2000).

In contrast to tree diversity, the identity of tree species strongly affected the diversity of oribatid mites reaching a maximum in monospecific beech clusters and a minimum in monospecific ash and lime clusters. As in density this indicates that the litter layer functioning as habitat space is of major importance for oribatid mite diversity. This supports our conclusion that only few species of oribatid mites are able to withstand disturbances and harsh environmental microclimatic conditions in soils devoid of organic layers. Conform to these findings oribatid mite diversity was found to be high in beech and conifer forests with recalcitrant litter and low in maple and mixed forests with high quality litter (Sylvain and Buddle, 2010). Further, it has been documented that oribatid mite diversity increases markedly during secondary succession from arable and grassland systems over ash dominated forest with high quality litter to beech forests with recalcitrant litter (Scheu and Schulz, 1996).

4.4. Conclusions

Oribatid mite density, community structure and diversity varied little with tree species diversity but were significantly affected by tree species identity. Notably, both oribatid mite density and diversity reached a maximum in monospecific beech clusters suggesting that oribatid mites benefit from tree species producing recalcitrant litter. In contrast, in ash and lime clusters both oribatid mite density and diversity were low indicating that litter of high quality is of little importance as driving factor for oribatid mite density and diversity. The results highlight the importance of organic layers for oribatid mite communities and support the view that oribatid mite communities are fuelled predominantly by belowground rather than aboveground resources. Further, the results indicate that in forests lacking organic layers large and strongly sclerotized oribatid mite species gain importance presumably as they are insensitive to environmental fluctuations. CCA ordination suggested that in addition to pronounced organic layers various factors contributed to favorable conditions in beech clusters including soil pH as well as high densities of fungi and nematodes, reflecting the dominance of fungal feeders but also the importance of animal prey for oribatid mites.

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References

Anderson, J.M., 1975. Succession, diversity and trophic relationships of some soil animals in decomposing leaf litter. Journal of Animal Ecology 44, 475-495.

Anderson, J.M., 1978. Inter- and intra- habitat relationships between woodland Cryptostigmata species diversity and the diversity of the soil and litter microhabitats. Oecologia 32, 341-8.

Ball, B.A., Bradford, M.A., Coleman D.C., Hunter M.D., 2009. Linkages between below and aboveground communities: Decomposer responses to simunlated tree species loss are largely additive. Soil Biology and Biochemistry 41, 1155-1163.

Bardgett, R.D., Bowman, W.D., Kaufmann, R., Schmidt, S.K., 2005. A temporal approach to linking aboveground and belowground ecology. Trends in Ecology and Evolution 20, 634–641.

Berg, B., McClaugherty, C., 2008. Plant Litter - Decomposition, Humus Formation, Carbon Sequestration. Springer, Berlin, Germany.

Beyer, S., 2008. Einfluss unterschiedlicher Baumartendiversitäten auf die Gemeinschaftsstruktur der saprophagen Bodenfauna: ein Streuaustausch-experiment im Laubmischwald. Diploma Theses, University of Göttingen, Göttingen. 115 pp.

Cannell, M.G.R., Malcolm, D.C., Robertson, P.A. (eds.), 1992. The ecology of mixed-species stands of trees. Blackwell Scientific Publications, Oxford.

Cesarz S., Fahrenholz, N., Migge-Kleian, S., Platner, C., Schaefer M., 2007. Earthworm communities in relation to tree diversity in a deciduous forest. European Journal of Soil Biology 43, 61-67.

Cesarz S., 2012. Plant species and global change agents as driving factors of rhizosphere processes and soil nematode communities. Dissertation, University of Göttingen, Göttigen, 162 pp.

Cesarz, S., Ruess, L., Jacob, M., Jacob, A., Schaefer, M., Scheu, S. Soil energy channels of forests differing in tree species identity and diversity as indicated by nematode communities. Unpublished.

Coleman et al., 1983; Coleman, D.C., Reid, C.P.P., Cole, C.V., 1983. Biological strategies of nutrient cycling in soil systems. Advances in Ecological Research 13, 1-55.

Cornwell, W.K., Cornelissen, J.H.C., Amatangelo, K., et al., 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. Ecology Letters 11, 1065-1071.

Cotrufo, M.F., Briones, M.J.I., Ineson, P., 1998. Elevated CO_2 affects field decomposition rate and palatability of tree leaf litter - importance of changes in substrate quality. Soil Biology and Biochemistry 30, 1565-1571.

De Ruiter, P.C., Griffiths, B., Moore, J.C., 2002. Biodiversity and stability in soil ecosystems: patterns, processes and the effects of disturbance. In: Loreau M, Naeem S, Inchausti P (eds) Biodiversity and ecosystem functioning. Synthesis and perspectives. Oxford University Press, Oxford, 102–113.

Erdmann, G., Scheu S., Maraun, M., 2012. Regional factors rather than forest type drive the community structure of soil living oribatid mites (Acari, Oribatida). Experimental and Applied Ecology 57, 157-169.

Eisenhauer, N., 2010. The action of an animal ecosystem engineer: Identification of the main mechanisms of earthworm impacts on soil microarthropods. Pedobiologica 53, 343-352.

Eisenhauer, N., Reich, P.B., 2012. Above- and below-ground plant inputs both fuel soil food webs. Soil Biology and Biochemistry 45, 156-160.

Gessner, M.O., Swan, M.S., Dang, C.K., McKie, B.G., Bardgett, R.D., Wall, D.H., Hättenschwiler, S., Gasser, P., 2005. Soil animals alter plant litter diversity effects on decomposition. Proceedings of the National Academy of Science of the USA 102, 1519-1524.

Guckland, A., Flessa, H., Prenzel, J., 2009. Controls of temporal and spatial variability of methane uptake in soils of a temperate deciduous forest with different abundance of European beech (*Fagus sylvatica* L.). Soil Biology and Biochemistry 41, 1659-1667.

Hansen, R.A., 2000. Effects of habitat complexity and composition on a diverse litter microarthropod assemblage. Ecology 81, 1120-1132.

Hättenschwiler, S., Gasser, P., 2005. Soil animals alter plant litter diversity effects on decomposition. Proceedings of the National Academy of Science of the USA 102, 1519-1524.

Hättenschwiler, S., Tiunov, A.V., Scheu S., 2005. Biodiversity and litter decomposition in terrestrial ecosystems. Annual Reviews of Ecology, Evolution and Systematics 36, 191-218.

Hättenschwiler, S., Bracht-Joergensen, H., 2010. Carbon quality rather than stoichiometry controls litter decomposition in a tropical rain forest. Journal of Ecology 98, 754-763.

Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M.C., Diemer, M., Dimitrakopoulos, P.G., Finn, J., Freitas, H., Giller, P.S., Good, J., Harris, R., Högberg, P., Huss-Danell, K., Joshi, J., Jumpponen, A., Körner, C., Leadley, PW., Loreau, M., Minns, A., Mulder, C.P.H., O'Donovan, G., Otway, S.J., Pereira, J.S., Prinz, A., Read, D.J., Scherer-Lorenzen, M., Schulze, E.-D., Siamantziouras, A.-S.D., Spehn, E.M., Terry, A.C., Troumbis, A.Y., Woodward, F.I., Yachi, S., Lawton, J.H., 1999. Plant diversity and productivity experiments in European grasslands. Science 286: 1123–1127.

Heidemann, K., Scheu, S., Ruess, L., Maraun, M., 2011. Molecular detection of nematodes predation and scavenging in oribatid mites: Laboratory and field experiments. Soil Biology & Biochemistry 43, 2229–2236.

Hobbie, S.E., Reich, P.B., Oleksyn, J., Ogdahl, M., Zytkowiak, R., Hale, C., Karolewski, P., 2006. Tree species effects on decomposition and forest floor dynamics in a common garden. Ecology 87, 2288-2297.

Hoffmann K., 1991. Ökologische Untersuchungen an ausgewählten Milbengruppen von verschiedenen bewirtschafteten landwirtschaftlichen Nutzflächen (Acari: Gamasida, Oribatei). Dissertation, Universität Bonn.

Högberg, P., Read, D.J., 2006. Towards a more plant physiological perspective on soil ecology. Trends in Ecology and Evolution 21, 548-554.

Hölscher, D., Hertel D., Leuschner C., Hottkowitz M., 2002. Tree species diversity and soil patchiness in a temperate broad-leaved forest with limited rooting space. Flora 197, 118–125.

Jacob, M., Weland, N., Platner, C., Schaefer, M., Leuschner, C., Thomas, F.M., 2009. Nutrient release from decomposing leaf litter of temperate deciduous forest trees along a gradient of increasing tree species diversity. Soil Biology and Biochemistry 41, 2122-2130.

Jacob, M., Viedenz, K., Polle, A., Thomas, F.M., 2010. Leaf litter decomposition in temperate deciduous forest stands with a decreasing fraction of beech (*Fagus sylvatica*). Oecologia 164, 1083-1094.

Jacob A., Hertel D., Leuschner C., 2012. On the significance of belowground overyielding in temperate mixed forests: separating species identity and species diversity effects. OIKOS, in press.

Jongman, R.H.G., ter Braak, C.J.F., van Tongeren, O.F.R., 1995. Data analysis in community and landscape ecology. Cambridge University Press, Cambridge.

Kaneko, N., Yasunori, S., Miyamoto, T., Hasegawa, M., Hiura, T., Oribatid mite community structure and tree species diversity: A link?. Pedobiologica 49, 521-528.

Lang, C., Polle, A., 2011. Ectomycorrhizal fungal diversity, tree diversity and nutrient relations in a mixed Central European forest. Tree Physiology 31, 531-538.

Lang C., Seven S., Polle A., 2011. Host preferences and differential contributions of deciduous tree species shape mycorrhizal species richness in a mixed Central European forest. Mycorrhiza, 21, 297-308.

Langenbruch, C., Helfrich, M., Flessa, H., 2012. Effects of beech (*Fagus sylvatica*), ash (*Fraxinus excelsior*) and lime (*Tilia* spec.) on soil chemical properties in a mixed deciduous forest. Plant and Soil, 352, 389-403.

Leuschner C, Jungkunst HF, Fleck S., 2009. Functional role of forest diversity: Pros and cons of synthetic stands and across-site comparisons in established forests. Basic and Applied Ecology 10: 1-9.

Lummer, D., Scheu, S., Butenschoen, O., 2012. Nitrogen transfer between decomposing litter species is an important but not the only factor responsible for synergistic mixture effects on litter decomposition. Oikos, 121, 1649-1655.

Macfadyen, A., 1961. Improved funnel-type extractors for soil arthropods. Journal of Animal Ecology 30, 171–184.

Maraun, M., Alphei, J., Bonkowski, M., Buryn, R., Migge, S., Pter, M., Schaefer, M., Scheu, S., 1999. Middens of the earthworm *Lumbricus terrestris* (Lumbricidae): microhabitats for micro- and mesofauna in forest soil. Pedobiologica 43, 276-287.

Maraun, M., Scheu, S., 2000. The structure of oribatid mite communities (Acari Oribatida): patterns mechanisms and implications for future research. Ecography 23, 374–383.

Maraun, M., Martens, H., Migge, S., Theenhaus A., Scheu, S., 2003. Adding to „the enigma of soil animal diversity“: fungal feeders and saprophagous soil invertebrates prefer similar food substrates. European Journal of Soil Biology 39, 85-95.

Maraun, M., Erdmann, G., Fischer, B.M., Pollierer, M.M., Norton, R.A., Schneider, K., Scheu, S., 2011. Stable isotopes revisited: their use and limits for oribatid mite trophic ecology. Soil Biology and Biochemistry 43, 877–882.

Meinen, C., Hertel, D., Leuschner, C., 2009. Biomass and morphology of fine roots in temperate broad-leaved forests differing in tree species diversity: is there evidence of below-ground overyielding? Oecologia, 161, 99-111.

Muraoka, M., Ishibashi, N., 1976. Nematode-feeding mites and their feeding behaviour. Applied Entomology and Zoology 11, 1–7.

Migge, S., Maraun, M., Scheu, S., Schaefer, M., 1998. The oribatid mite community (Acarina: Oribatida) of pure and mixed stands of beech (*Fagus sylvatica*) and spruce (*Picea abies*) of different age. Applied Soil Ecology 9, 115-121.

Moore and Hunt, 1988 Moore, J.C., Hunt, H.W., 1988. Resource compartmentation and the stability of real ecosystems. Nature 333, 261-263.

Muys, B., Beckers, G., Nachtergale, L., Lust, N., Merckx, R., Granval, P., 2003. Medium-term evaluation of a forest soil restoration trial combining tree species change, fertilisation and earthworm introduction. Pedobiologia 47, 772-781.

Neuhauser, E.F., Hartenstein, R., Connors, J., 1978. The role of soil macroinvertebrates in the degradation of vanillin, cinnamic acid, and lignins. Soil Biology and Biochemistry 10, 431-435.

Norton, R.A., Palmer, S.C., 1991. The distribution, mechanisms and evolutionary significance of parthenogenesis in oribatid mites. In: Schuster, R., Murphy, P.W. (eds) The Acari: Reproduction, development and life- history traits. Chapman and Hall, London, pp. 107-136.

Osono, T., 2007. Ecology of lignolytic fungi associated with leaf litter decomposition. Ecology Research 22, 955-974.

Perdomo, G., Evans, A., Maraun, M., Sunnucks, P., Thompson R., 2012. Mouthpart morphology and trophic postion of microarthropods from soils and mosses are strongly correlated. Soil Biology and Biochemistry, in press.

Pollierer, M.M., Langel, R., Korner, C,.Maraun, M., Scheu, S., 2007. The underestimated importance of belowground carbon input for forest soil animal food webs. Ecology Letters 10, 729-736.

Pollierer, M.M., Langel, R., Scheu, S., Maraun, M., 2009. Compartmentalization of the soil animal food web as indicated by dual analysis of stable isotope ratios ($^{15}N/^{14}N$ and $^{13}C/^{12}C$). Soil Biology & Biochemistry 41, 1221–1226.

Pollierer, M.M., Dykmans, J., Scheu, S., Haubert, D., 2012. Carbon fluxes through fungi and bacteria into the forest soil animal food web as indicated by compound-specific 13C fatty acid analysis. Functional Ecology, doi: 10.1111/j.1365-2435.2012.02005.x.

Ponge, J.F., 1991a. Food resources and diets of soil animals in a small area of Scots pine litter. Geoderma 49, 33-62.

Pretzsch, H., 2005. Diversity and productivity in forests: evidence from long-term experimental plots. In: Scherer- Lorenzen, M., Körner, C., Schulze, E.-D. (eds). Forest Diversity and Function: Temperate and Boreal Systems, Ecological Studies, 176. Springer, Berlin, pp. 41–64.

Rémen C., Tryggve, P., Finlay, R., Ahlström K., 2008. Responses of oribatid mites to tree gridling and nutrient addition in boreal coniferous forests. Soil Biology and Biochemistry 40, 2881-2890.

Ruf, A., Kuzyakov, Y., Lopatovskaya, O., 2006. Carbon fluxes in soil food webs of increasing complexity revealed by ^{14}C labeling and ^{13}C natural abundance. Soil Biology and Biochemistry 38, 2390-2400.

Salamon, J., Alphei, J., Ruf, A., Schaefer, M., Scheu, S., Schneider, K., Sührig, A., Maraun, M., 2006. Transitory dynamic effects in the soil invertebrate community in a temperate deciduous forest: effects of resource quality. Soil Biology and Biochemistry 38, 209-221.

Scherer-Lorenzen, M., Potvin, C., Koricheva, J., Schmid, B., Hector, A., Bornik, Z., Reynolds, G., Schulze, E.-D., 2005. The design of experimental tree plantations for functional biodiversity research. In: Scherer-Lorenzen, M., Körner, C., Schulze, E.-D. (eds), Forest Diversity and Function: Temperate and Boreal Systems, Ecological Studies, 176, Springer, Berlin, 347–376.

Scheu, S., Schulz, E., 1996. Secondary succession, soil formation and development of a diverse community of saprophagous soil macro-invertebrates and oribatids. Biodiversity and Conservation 5, 235-250.

Scheu, S., Falca, M., 2000. The soil food web of two beech forests (*Fagus sylvatica*) of contrasting humus type: stable isotope analysis of a macro- and a mesofauna-dominated community. Oecologia 123, 285–286.

Scheu, S., 2005. Linkages between tree diversity, soil fauna and ecosystem processes. In: Scherer-Lorenzen, M., Köhler, C., Schulze, E.-D., (Eds.) Forest Diversity and Function: Temperate and Boreal Systems, Ecological Studies 176, Springer, Berlin, Germany, 211-233.

Schmid, B., Hector, A., Huston, M.A., Inchausti, P., Nijs, I., Leadley, P.W., Tilman, D., 2002. The design and analysis of biodiversity experiments. Biodiversity and Ecosystem Functioning (eds M. Loreau, S. Naeem and P. Inchausti), pp. 61–75, Oxford University Press, Oxford.

Schneider, K., Migge, S., Norton, R.A., Scheu, S., Langel, R., Reineking, A., Maraun, M., 2004. Trophic niche differentiation in soil microarthropods (Oribatida, Acari): evidence from stable isotope ratios ($^{15}N/^{14}N$). Soil Biology and Biochemistry 36, 1769–1774.

Schneider, K., Renker, C., Maraun, M., 2005. Oribatid mite (Acari, Oribatida) feeding on ectomycorrhizal fungi. Mycorrhiza 16, 67-72.

Schulz E., 1991. Die Milbenfauna (Acari: Mesostigmata und Cryptostigmata) in Lebensräumen auf Kalkstein: Populationsökologie, Sukzession and Beziehungen von Lebensraum. University of Göttingen, Dissertation, Göttingen. Forschungszentrum Waldökosysteme 91, 245 pp.

Seidel, D., 2011. Terrestrial laser scanning- Applications in forest ecological research. University of Göttingen, Dissertation, Göttingen, Biodiversity and Ecology series B, 136 pp.

Skubala, P., Gulvik, M., 2005. Pioneer oribatid mite communities (Acari, Oribatida) in newly exposed natural (glacier forelands) and anthropogenic (post-industrial dump) habitats. Polish Journal of Ecology 53, 395-407.

Smrz, J., 1998. Interactions between oribatids and microorganisms: A complex method of study. Applied Soil Ecology 9, 109-110.

Swift, M.J., Heal, O.W., Anderson, J.M., 1979. Decomposition in terrestrial ecosystems. Blackwell, Oxford, UK.

Sydes, C., Grime, J.P., 1981a. Effects of tree leaf litter on herbaceous vegetation in deciduous woodland. I. Field investigations. Journal of Ecology 69, 237-248.

Sydes, C., Grime, J.P., 1981b. Effects of tree leaf litter on herbaceous vegetation in deciduous woodland. II. An experimental investigation. Journal of Ecology 69, 249-262.

Sylvain, Z.A., Buddle, C.M., 2010. Effects of forest stand type on oribatid mites (Acari, Oribatida) assemblages in a southwestern Quebec forest. Pedobiologica, 53, 321-325.

Taylor A.R., Wolters V., 2005. Responses of oribatid mite communities to summer drought: The influence of litter type and quality. Soil Biology and Biochemistry 37, 2117-2130.

ter Braak, C.J.F., Similauer, P., 2002. CANOCO reference manual and CanoDraw for windows user's guide: software for canonical community ordination (version 4.5). Microcomputer Power Ithaca, New York.

Thoms, C., Gattinger, A., Jacob, M., Thomas, F.M., Gleixner G., 2010. Direct and indirect effects of tree diversity drive soil microbial diversity in a temperate deciduous forest. Soil Biology and Biochemistry 42, 1558-1565.

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., Siemann, E., 1997. The Influence of Functional Diversity and Composition on Ecosystem Processes. Science 277: 1300-1302.

Vilà, M., Inchausti, P., Vayreda, J., Barrantes, O., Gracia, C., Ibanez, J.J., Mata, T., 2005. Confounding factors in the observational productivity-diversity relationship in forests. In: Scherer-Lorenzen M, Körner C, Schulze E-D (eds) Forest Diversity and Function: Temperate and Boreal Systems, Springer, Berlin, 65–81.

Vitousek, P.M., Hättenschwiler, S., Olander, L., Allison S., 2002. Nitrogen and Nature. Ambio 31, 97-101.

Vockenhuber, E., Scherber, C., Langenbruch, C., Meißner, M., Seidel, D., Tscharntke, T., 2011. Tree diversity and environmental context predict herb species richness cover in Germany´s largest connected deciduous forest. Perspectives in Plant ecology, Evolution and Systematics, 13, 111-119.

Wardle, D.A., 2002. Communities and Ecosystems: Linking the Aboveground and Belowground Components. Monographs in Population Biology. Princeton University Press, Princeton, USA.

Weland, N., 2009. Diversity and trophic structure of the soil fauna and its influence on litter decomposition in deciduous forests with increasing tree diversity. Dissertation, University of Göttingen, Göttingen, 110 pp.

Weigmann, G., 2006. Hornmilben (Oribatida). Goecke und Evers, Keltern.

Zaitsev, A.S., Wolters, V., 2006. Geographic determinants of oribatid mite community structure and diversity across Europe: longitudinal perspective. European Journal of Soil Biology 42, 358-361

Supplementary material

Appendix List of species of oribatid mites (Oribatida) in clusters of pure and mixed stands of beech, ash and lime in the Hainich National Park (Thuringia, Germany). For Brachychthoniidae, Phthiracaridae, Desmonomata and Suctobelbidae only common species were identified. Species of Damaeidae and Galumnidae were not identified.

Enarthronota

Hypochthoniidae

Hypochthonius luteus Oudeman, 1917
Hypochthonius rufulus C.L. Koch, 1841

Brachychthoniidae

Eobrachychthonius longisetosus Csiszar, 1961
Eobrachychthonius latior (Berlese, 1910)
Brachychthonius impressus Moritz, 1976
Brachychthonius pius (Moritz, 1976)
Brachychthonius bimaculatus (Willmann, 1936)
Brachychthonius berlesei Willmann, 1928
Sellnickochthonius hungaricus (Balough, 1943)
Sellnickochthonius zelawaiensis (Sellnick, 1928)
Sellnickochthonius immaculatus (Forsslund, 1942)
Sellnickochthonius suecicus (Forsslund, 1942)
Liochthonius leptaleus Moritz, 1976
Liochthonius strenzkei Forsslund, 1963
Neoliochthonius globuliferus (Strenzke, 1951)

Holonota

Eulohmaniidae

Eulohmannia ribagai (Berlese, 1910)

Mixonomata

Phthiracaridae

Steganacarus (Atropacarus) striculus (C.L. Koch, 1835)
Steganacarus (Atropacarus) magnus (Nicolet, 1855)

Holosomata

Nothridae

Nothrus palustris C.L. Koch, 1839

Nothrus silvestris (Nicolet, 1855)

Plathynothrus peltifer (C.L. Koch, 1839)

Hermanniidae

Hermannia gibba (C.L. Koch, 1839)

Circumdehiscentiae

"Pycnonota"

Hermannellidae

Hermanniella punctulata (Berlese, 1908)

Cepheidae

Tritegeus bisulcatus (Grandjean, 1953)

Damaeolidae

Fosseremus laciniatus (Berlese, 1905)

Microzetidae

Microzetes septentrionalis (Kunst, 1963)

Tenuialidae

Hafenrefferia gilvipes (Oudemans, 1906)

Astegistidae

Cultroribula bicultrata (Berlese, 1905)

Liacaridae

Xenillus tegeocranus (Hermann, 1804)

Carabodidae

Carabodes femoralis (Nicolet, 1855)

Carabodes reticulatus (Berlese, 1913)

Haplozetes tenuifusus (Berlese, 1916)

Tectocepheidae

Tectocepheus velatus (sarekensis) - group

Tectocepheus minor Berlese, 1903

Oppioidea

Quadroppiidae

Quadroppia michaeli Mahunka 1967

Quadroppia quadricarinata (Michael, 1885)

Quadroppia hammerae Minguez et al., 1985

Quadroppia monstruosa (Minguez et al., 1985)

Oppiidae

Dissorhina ornata (Oudemans, 1900)

Berniniella conjuncta (Strenzke, 1951)

Microppia minus (Paoli, 1908)

Oppiella (Oppiella) nova (Oudemans, 1902)

Oppiella (Oppiella) falcata (Paoli, 1908)

Oppiella (Rhinoppia) obsoleta (Paoli, 1908)

Oppiella (Oppiella) maritima (Willmann, 1929)

Oppiella (Oppiella) uliginosa (Willmann, 1919)

Oppiella (Rhinoppia) cf. *epilata* (Miko, nov. spec.)

Oppiella (Oppiella) margidentata (Strenzke, 1951)

Oppiella (Rhinoppia) hauseri (Mahunka and Mahunka-Papp, 2000)

Oppiellla (RHINOPPIA) similifax (Subias and Minguez, 1986)

Oppiella (Rhinoppia) nasuta (Moritz, 1956)

Oppiella (Rhinoppia) fallax (Paoli, 1908)

Oppiella (Rhinoppia) subpectinata (Oudemans, 1900)

Suctobelbidae

Suctobelbella falcata (Forsslund, 1941)

Suctobelbella subcornigera (Forsslund, 1941)

Suctobelbella sarekensis (Forsslund, 1941)

Suctobelbella duplex (Strenzke, 1950)

Suctobelbella subtrigona (Oudemans, 1916)

Suctobelbella nasalis (Forsslund, 1941)

Suctobelbella falcata (Forsslund, 1941)

Suctobelbella reticulata Moritz, 1917

Thyrisomidae

Pantelozetes paolii (Oudemans, 1913)

Cymbaeremaeidae

Scapheremaeus cf. *palustris* (Sellnick, 1924)

Poronota

Phenopelopidae

Eupelops plicatus (C.L.Koch, 1836)

Eupelops occuluts (C.L.Koch, 1935)

Eupelops hirtus (Berlese, 1916)

Achipteriidae

Achipteria coleoptrata (Linné, 1758)

Oribatellidae

Oribatella calcarata (C.L.Koch, 1835)

Oribatella quadricornuta Michael, 1880

Ceratozetidae

Ceratozetes minimus (Sellnick, 1928)

Ceratozetes gracilis (Michael, 1884)

Ceratozetes psammophilus (Horak, 2000)

Ceratozetes parvulus (Sellnick, 1922)

Ceratozetes mediocris (Berlese, 1908)

Ceratozetoides maximus (Berlese, 1908)

Sphaerozetes piriformis (Nicolet, 1855)

Chamobatidae

Chamobates cuspidatus (Michael, 1884)

Chamobates voigtsi (Oudemans, 1902)

Euzetidae

Euzetes globulosus (Nicolet, 1855)

Haplozetidae

Protoribates dentatus (Berlese, 1883)

Scheloribatidae

Scheloribates (Scheloribates) quintus Wunderle, Beck and Woas, 1990

Liebstadia similis (Michael, 1888)

Liebstadia longior (Berlese, 1908)

Oribatulidae

Oribatula tibialis (Nicolet, 1855)

3 Incorporation of plant carbon and microbial nitrogen into the rhizosphere food web of beech and ash

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submitted

Abstract

We performed a dual labeling experiment with tree saplings of beech and ash using ^{15}N and ^{13}C as tracers in a greenhouse experiment. Carbon (C) was applied as $^{13}CO_2$ to plants and nitrogen (N) was added as $^{15}NH_4{}^{15}NO_3$ to the soil. We hypothesized that C will be transferred from plants to the rhizosphere, subsequently in beech to ectomycorrhiza (EM), in ash to arbuscular mycorrhiza (AM) and finally to soil animals. We expected the C signal to be more effectively transferred to soil animals in EM as compared to AM systems since fungal feeders prefer EM over AM fungi. For ^{15}N we hypothesized that it will be taken up by both saprotrophic microorganisms and mycorrhizal fungi and then channeled to soil animals. After five month, $\delta^{13}C$ and $\delta^{15}N$ signatures of soil animals, EM and fine roots of beech and ash were measured. Litter and soil were hardly enriched in ^{15}N whereas fine roots of beech and ash were highly enriched suggesting that nitrogen in $^{15}NH_4{}^{15}NO_3$ was predominantly taken up by plants and mycorrhizal fungi but little by saprotrophic microorganisms. Roots of beech and ash were highly enriched in ^{13}C with maximum values in EM proving that ^{13}C was translocated into roots and mycorrhizal fungi. Soil animals were a priori assigned to primary decomposers, secondary decomposers and predators. Generally, signatures of soil animals did not significantly vary between beech and ash and therefore were pooled. Primary decomposers had low $\delta^{13}C$ and $\delta^{15}N$ signatures similar to litter and soil confirming that rhizosphere C and microbial N are of limited importance for primary decomposer taxa. $\delta^{13}C$ and $\delta^{15}N$ signatures of secondary decomposers were higher than those of primary decomposers and spanned a large gradient indicating that certain secondary decomposers rely on root derived C and microbial N, however, none of the secondary decomposers had signatures pointing to exclusive feeding on EM. Unexpectedly, $\delta^{13}C$ and $\delta^{15}N$ signatures were highest in predators suggesting that they heavily preyed on individual species of secondary decomposers such as the litter dwelling Collembola species *Lepidocyrtus cyaneus* and species not captured by the heat extraction procedure used for capturing prey taxa, presumably predominantly root associated nematodes. Overall, the results highlight that in particular higher trophic levels rely on carbon originating from other resources than litter with these resources channeled to dominant predators via litter dwelling Collembola species.

Keywords

Soil food web, labeling experiment, fine roots, mycorrhizal fungi, fungal energy channel, bacterial energy channel

1. Introduction

In forest ecosystems most of the net primary production enters the decomposer community as detritus. This dead organic material usually is assumed to be the main source of nutrients for soil microbes (Swift et al., 1979; Berg and McClauthery, 2008) and decomposer animals (Hättenschwiler and Gasser, 2005; Scheu, 2005). However, this view has been challenged recently by documenting that soil animals strongly rely on root-derived carbon (Ruf et al., 2006; Albers et al., 2006; Pollierer et al., 2007, 2012). In fact, a large fraction of plant fixed carbon enters the belowground system via roots and root exudates (Bardgett et al., 2005; Leake et al., 2006) and this carbon is more easily available for soil organisms than the recalcitrant carbon in plant litter since it comprises predominantly amino acids, sugars and peptides (Bais et al., 2006; Dennis et al., 2010).

Most plant roots are closely associated with mycorrhizal fungi and therefore carbon enters the outer rhizosphere region via mycorrhizal fungi (Smith and Read, 1997; Wallander et al., 2009). However, there are different types of mycorrhizal fungi, such as ectomycorrhizal fungi (EMF) and arbuscular mycorrhizal fungi (AMF). In temperate forest ecosystems, ectomycorrhizal fungi dominate (e.g., in beech, oak, lime and hornbeam), but some tree species are associated with AMF (e.g., ash and acer; Lang and Polle, 2011; Lang et al. 2011). The transfer of carbon from the plant to the rhizosphere likely is more effective in the well-dispersed extramatrical mycelium of the EMF (Högberg et al., 2008; Cairney et al., 2012) than in AMF which do not form intensive extramatrical mycelia (Smith and Read, 1997).

Nitrogen is of crucial importance for soil microorganisms and plants. During decomposition of litter material and for microbial growth in general microorganisms immobilize mineral nutrients in soil and thereby may compete with plants for these resources (Chapman et al., 2006; Geissler et al., 2010). Tree roots take up nitrogen from soil, but in temperate forests most nitrogen is channeled to plants via EMF (Hobbie and Hobbie, 2006; van der Heijden et al., 2008). In soil food webs carbon is channeled along two main energy pathways, the fungal and bacterial energy channel (Moore and Hunt, 1988; Moore et al., 2005; Crotty et al., 2011). In

temperate forests litter quality typically is low and litter is mainly processed by saprotrophic fungi (Wardle et al., 2004). Together with EMF saprotrophic fungi form the main source of N for the fungal energy channel of soil food webs (Moore-Kucera and Dick, 2008). In contrast, bacteria predominantly consume root exudates and serve as source for N (and other elements) for the bacterial energy channel (Crotty et al., 2011).

From a trophic level point of view the soil food web might be separated into primary decomposers, secondary decomposers and predators with the latter relying predominantly on secondary decomposers (Scheu, 2002). Primary decomposers, such as Diplopoda, and certain species of Oribatida and Lumbricidae, are assumed to feed mainly on litter material (Pollierer et al., 2009). Secondary decomposers, such as most Oribatida, Collembola and certain species of Isopoda and Lumbricidae, are assumed to feed predominantly on fungi and microbial residues (Maraun et al., 1998; Scheu and Falca, 2000). Predators, such as Lithobiidae or Araneida, have been assumed to rely predominantly on secondary decomposers as food (Pollierer et al., 2012; Ferlian et al., 2012).

Natural variations in stable isotope ratios of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) have been shown to be a powerful tool for investigating nutrient fluxes and trophic interactions in soil food webs (Scheu and Falca, 2000; Illig et al., 2005; Tiunov, 2007; Pollierer et al., 2009). However, labeling experiments with enriched ^{13}C and ^{15}N compounds are indispensable for tracing carbon and nitrogen fluxes through decomposer systems (Ruf et al., 2006; Pollierer et al., 2007; Sticht et al., 2008; Högberg et al., 2010).

We conducted a $^{13}CO_2$ labeling experiment in the greenhouse to follow the flux of carbon from plant shoots to the rhizosphere and into the soil animal food web. In parallel, we used^{15}N labeled mineral nitrogen (NH_4NO_3) to follow the flux of nitrogen via saprotrophic microorganisms and mycorrhiza into the soil animal food web. Saplings of European beech and European ash were excavated in the field, potted into mesocosms including rhizosphere soil and the associated soil animal community. After five months of labeling i.e., after one vegetation period, $\delta^{13}C$ and $\delta^{15}N$ signatures of beech and ash roots, ectomycorrhiza and soil animals were measured.

We hypothesized that (1) plant carbon will be translocated via roots and mycorrhiza into fungal feeding soil invertebrates. Furthermore, we hypothesized that (2) carbon as well as nitrogen will be transferred mainly to lower trophic levels

and will be diluted towards higher trophic levels due to predators incorporating prey relying in part on root and in part on litter carbon. We expected the transfer of carbon and nitrogen into soil animals to be more pronounced in beech with ectomycorrhiza (EM) than in ash with arbuscular mycorrhiza (AM). Finally, we assumed that (3) mineral nitrogen will be translocated to higher trophic levels via both saprotrophic microorganisms and mycorrhizal fungi and subsequently into soil animals.

2. Material and methods

2.1. Study site and experimental setup

Tree saplings were collected at two locations (Thiemsburg and Lindig) in the south east of the Hainich National Park, Thuringia, Germany (51°05′28″N, 10°31′24″E). The Hainich is the largest cohesive deciduous forest in Germany and was declared National Park in 1997. In the sampling area, forest cover was present since the mid 18th century. In the last four decades, the area was used for military training and has been managed extensively (Schmidt et al., 2009). The dominating tree species at the study sites is beech (*Fagus sylvatica* L.) but ash (*Fraxinus excelsior* L.), maple (*Acer pseudplatanus* L.) and lime (*Tilia platyphyllos* Scop. and *Tilia cordata* P. Mill.) are interspersed. The herb layer of the Hainich is dominated by *Allium ursinum* (L.), *Anemone nemorosa* (L.) and *Galium odoratum* (L.) (Vockenhuber et al., 2011). The mean annual temperature ranges from 7.5 to 8.0^{o}C and the mean annual precipitation is 600 mm (Leuschner et al., 2009). The area represents a slightly sloping limestone plateau from the Triassic Upper Muschelkalk formation covered by Pleistocene loess (Leuschner et al., 2009).

At the study sites 15 saplings of *F. sylvatica* and 14 saplings of *F. excelsior* (height ca. 60 cm) were excavated together with the surrounding intact soil (depth 25 cm and 2-3 cm litter layer) and placed into containers. The containers (diameter 25 cm, height 45 cm) were equipped with drainage at the bottom. For ^{13}C labeling tree saplings were exposed to $^{13}CO_2$ enriched atmosphere (maximum CO_2 concentration 1,200 ppm) in a greenhouse for five month at 23^{o}C and 70 % humidity. For ^{15}N labeling the mesocosms were irrigated daily with a Hoagland-based nutrient solution containing 0.1 mM $^{15}NO_3$ $^{15}NH_4$ and 0.6 mM $CaCl_2$, 0.4 mM $MgSO_4$, 0.01 mM $FeCl_3$, 0.4 mM K_3PO_4, 1.8 µM $MnSO_4$, 0.064 µM CuCl, 0.15 µM

$ZnCl_2$, 0.1 µM MoO_3, 0.01 mM H_3BO_3 and 5 mM NO_3NH_4 (Euriso-top, Saint-Aubin, Essonne, France). The soil was moistened at regular intervals by adding tap water.

2.2. Sampling of soil, litter, plants and ectomycorrhiza

The experiment was terminated after five month. The soil was divided into two horizons, 0-10 cm (A1 horizon, incl. litter) and 10-25 cm (A2 horizon). Aliquots of soil material for stable isotope analyses were collected from the A1 horizon, dried and stored in plastic bags until analysis. From the litter layer and A1 horizon large soil animals were picked by hand. From the A1 and A2 layer roots were washed, divided in coarse (> 2 mm) and fine roots (< 2 mm), dried (48 h, 70°C) and weighed. Aliquots of the litter were taken, dried and stored in plastic bags until stable isotope analysis. Mycorrhizal root tips were classified according to morphotypes (Agerer, 1987-2006) and collected for chemical analysis.

2.3. Sampling of soil animals

Animals of the litter and A1 layer were extracted by heat using a high-gradient canister method (Kempson et al., 1963). Soil animals were transferred into 70 % alcohol and sorted to groups. Individuals were counted and determined to family, genus or species level (see Appendix). Based on natural variations in stable isotope ratios ($^{13}C/^{12}C$; $^{15}N/^{14}N$), feeding experiments, analyses of fatty acids and gut content analyses soil animal species were classified into primary decomposers, secondary decomposers and predators (see Appendix). Primary decomposers included eleven species i.e., *Octolasion tyrtaeum* (Lumbricidae), two species of Diplopoda and nine taxa of Oribatida. Secondary decomposers comprised 16 taxa, i.e., four taxa of Lumbricidae, four taxa of Isopoda, *Craspedosoma* sp. (Diplopoda), four taxa of Oribatida, and *Sinella*/*Pseudosinella* spp. and *Lepidocyrtus cyaneus* (Collembola). Fourteen soil arthropod taxa were classified as predators including *Neobisium carcinoides* (Pseudoscorpionida), six taxa of Chilopoda, three taxa of Araneida, three taxa of Opilionida and *Acrogalumna longipluma* and *Hypochthonius rufuls* (Oribatida).

2.4. Stable isotope analyses

Dry plant tissues of leaves, stems, coarse roots and fine roots, aliquots of litter and of soil of the A1 horizon were dried and milled with a ball mill (Type MM 2, Retsch, Haan, Germany), dried again at 70°C for 24 h and kept in a desiccator until analysis. Aliquots of the samples were weighed into tin capsules and $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios were analyzed. Additionally, EM were weighed into tin capsules (ca. 1 mg) for analysis of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios. For stable isotope analyses of soil animals, individual or bulked specimens corresponding to a minimum of 5 µg N were weighed into tin capsules. Large species were dried, fragmented mechanically and a subsample was analyzed. The capsules were dried at 60°C for 24 h and stored in a desiccator prior to the analysis.

Stable isotope ratios were analyzed with a coupled system consisting of an elemental analyzer (NA 1500, Carlo Erba, Mailand) and a mass spectrometer (MAT 251, Finnigan, Bremen, Germany). Abundances of ^{13}C and ^{15}N are expressed using the δ notation with δ_{sample} [‰] = $[(R_{sample} - R_{standard}) / R_{standard}] \times 1000$. R_{sample} and $R_{Standard}$ represent the $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios of samples and standard, respectively. For ^{13}C PD Belemnite (PBD) and for ^{15}N atmospheric nitrogen served as the primary standard. Acetanilide (C_8H_9NO, Merck, Darmstadt) was used for internal calibration.

2.5. Statistical analyses

Differences in $\delta^{13}C$ and $\delta^{15}N$ signatures of the three groups of soil animal taxa, primary decomposers, secondary decomposers and predators, were analyzed with single factor analysis of variance (ANOVA) with the general linear model (GLM) procedure using SAS 9.13 (SAS Institute, Cary, NC, USA). Homogeneity of variances was inspected using Levene test. For post-hoc comparison of means, Scheffé test was used. Differences in $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios of soil animals between beech and ash trees were tested with single factor ANOVA. As data from beech and ash generally did not differ significantly animal taxa of the two tree species were pooled. Data given in text and figures represent means and standard errors.

3. Results

3.1. Soil, plants and ectomycorrhiza

$\delta^{13}C$ values in litter and soil (-20.1 ± 2.2 and -23.1 ± 0.5‰, respectively) were slightly increased compared to natural variations (respective values of -26.8 ± 0.1 and -27.8 ± 0.2‰). In contrast, $\delta^{15}N$ values of litter and soil (744.1 ± 164.8 and 230.3 ± 38.6‰, respectively) were markedly increased compared to natural variations (respective values of $\delta^{13}C$ and $\delta^{15}N$ were 0.1 ± 1.5 and -27.21 ± 3.6‰).

In saplings both, $\delta^{13}C$ and $\delta^{15}N$ signatures were markedly increased with $\delta^{13}C$ and $\delta^{15}N$ signatures increasing from stems (41.3 ± 3.6‰ and 5,434 ± 327.8‰) to leaves (80.4 ± 8.2‰ and 3,506 ± 322‰, respectively) to coarse roots (48.0 ± 6.6‰ and 6,152 ± 676.8‰) to fine roots (113.3 ± 7.7‰ and 9,328 ± 1,066‰) (Fig. 1).

On average 96.0 ± 3.5‰ of vital root tips of beech were colonized by EMF. Twenty samples of mycorrhiza were analyzed for stable isotope ratios. $\delta^{13}C$ and $\delta^{15}N$ values averaged 114.6 ± 8.2‰ and 13,484 ± 1,929‰, respectively (Fig. 1).

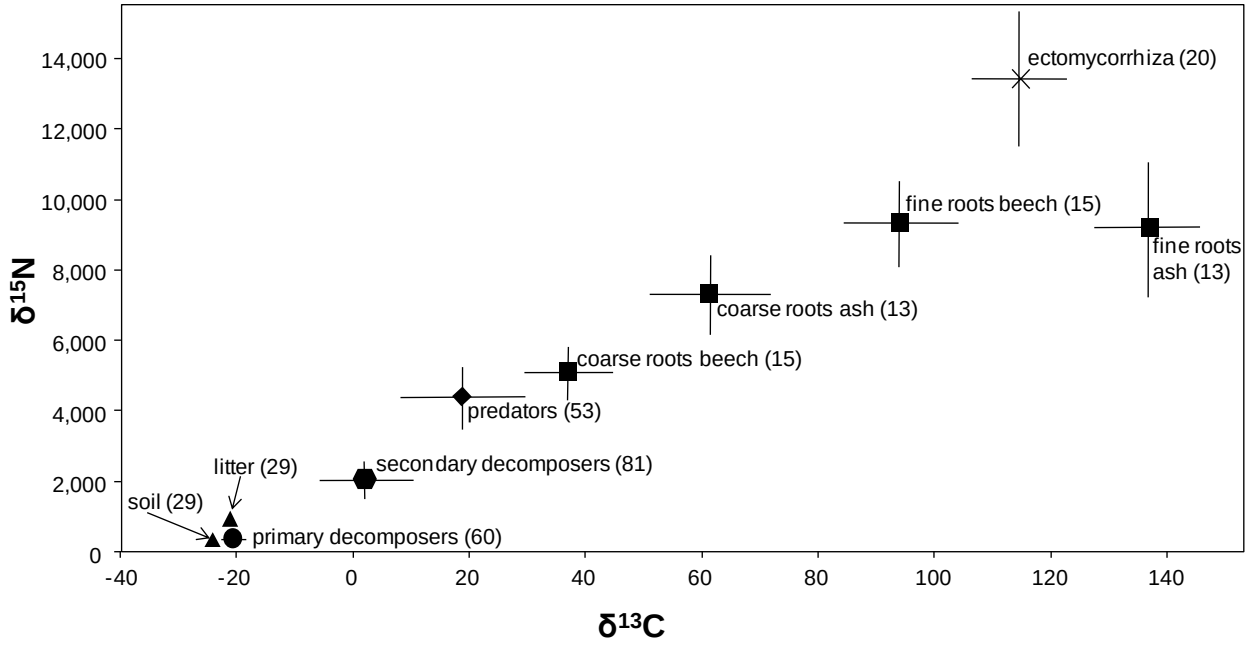

Fig. 1. Mean (± standard error) $\delta^{13}C$ and $\delta^{15}N$ value of primary decomposers (circle), secondary decomposers (hexagon) and predators (diamond). Means (± standard error) of $\delta^{13}C$ and $\delta^{15}N$ signatures of the soil and leaf litter (triangles) and coarse roots and fine roots of *Fagus sylvatica* and *Fraxinus excelsior* (squares) and of ectomycorrhiza (cross). Numbers of replicates are given in brackets.

3.2. Soil animals

In total 40 taxa of soil animals were analyzed (see Appendix). The overall mean $\delta^{13}C$ and $\delta^{15}N$ signatures of soil arthropods were -0.2 ± 6.6‰ and 2,282 ± 507.5‰, respectively, and markedly exceeded those of the soil and litter layer, but were lower than that of plant roots and in particular those of mycorrhiza (Fig. 1). Notably this was true for each of the three trophic groups of soil animals including predators with the highest stable isotope signatures. $\delta^{13}C$ and $\delta^{15}N$ signatures spanned from for *Eupelops plicatus* (-28.0 ± 0.7‰ and 82.9 ± 57.8‰, respectively) to *Clubiona compta* (76.0 ± 11.7‰ and 13,673 ± 1,522‰).

Primary decomposers included 11 taxa with mean $\delta^{13}C$ and $\delta^{15}N$ values of -21.6 ± 4.8‰ and 666.8 ± 584.9‰ (Appendix, Fig. 2). $\delta^{13}C$ and $\delta^{15}N$ values ranged from *E. plicatus* (-28.0 ± 0.7‰ and 82.9 ± 57.8‰, respectively) to *Glomeris undulata* (-11.2 ± 3.7‰ and 1,928 ± 465.1‰) (Fig. 2).

Secondary decomposers included 16 taxa with mean $\delta^{13}C$ and $\delta^{15}N$ values of 2.2 ± 8.0‰ and 2,105 ± 504.8‰, respectively, differing not significantly from respective values of primary decomposers. $\delta^{13}C$ and $\delta^{15}N$ values were lowest in *Nothrus palustris* with -23.8 ± 1.5‰ and 951.8 ± 285.4‰, respectively, and highest in *Craspedosoma* sp. with respective values of 38.8‰ and 7,383‰ (both single measurements; Fig. 2).

Predators included 13 taxa with mean $\delta^{13}C$ and $\delta^{15}N$ values of 18.8 ± 10.8‰ and 4,443 ± 876.8‰, respectively, differing significantly from respective values of primary and secondary decomposers ($F_{2,38} = 35.47$, $p < 0.0001$ and $F_{2,38} = 17.36$, $p < 0.0001$, respectively). $\delta^{13}C$ and $\delta^{15}N$ values were lowest in *Necrophleophagus longicornis* with -9.2 ± 3.6‰ and 1,331 ± 391.3‰, respectively, and highest in *C. compta* with respective values of 76.0 ± 11.7‰ and 13,673 ± 1,522‰.

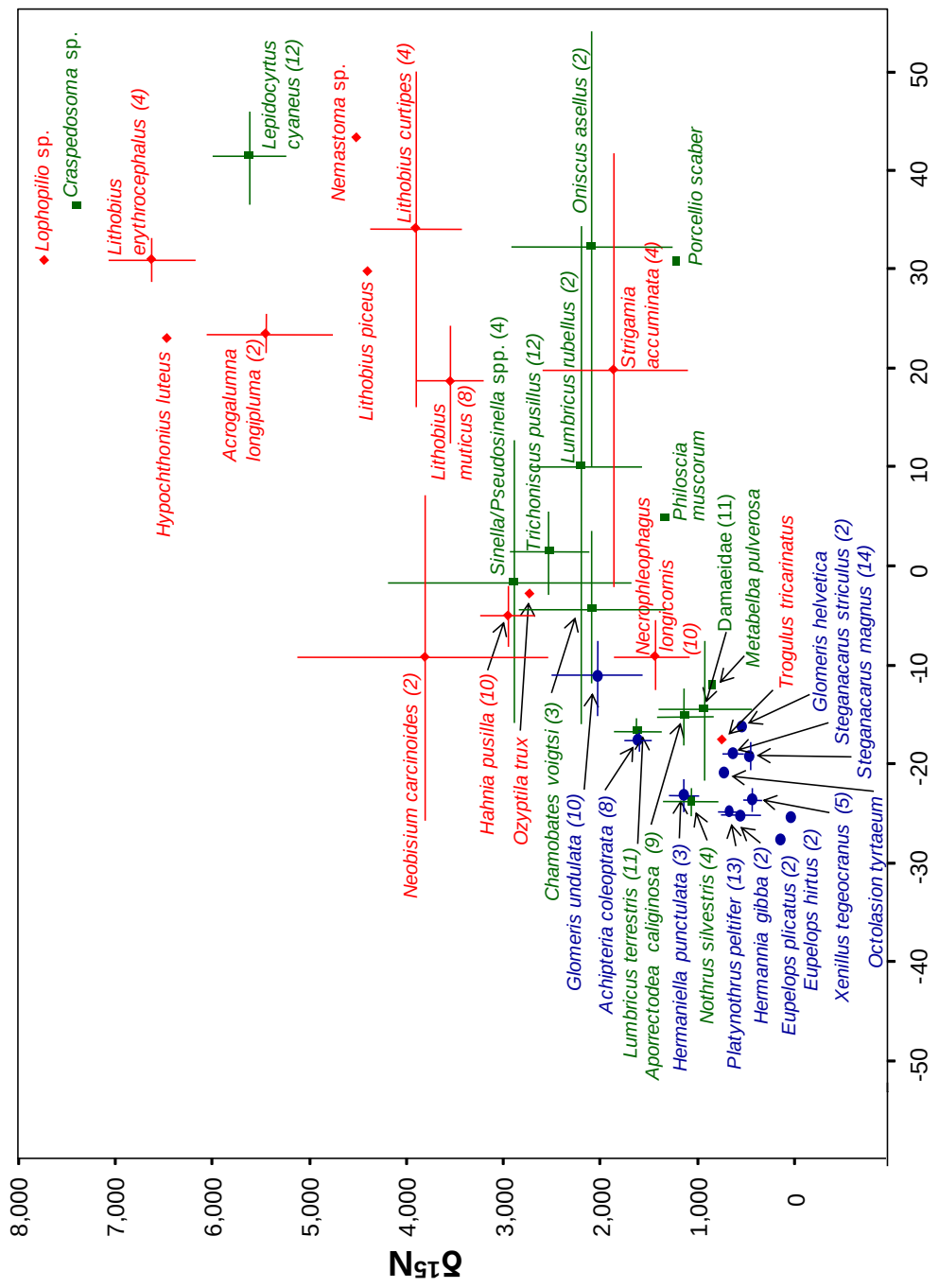

Fig. 2. Mean (± standard error) $\delta^{13}C$ and $\delta^{15}N$ signatures of primary decomposers (blue circles), secondary decomposers (green squares) and predators (red diamonds) (for details see Appendix). $\delta^{13}C$ and $\delta^{15}N$ values of *Clubiona compta* were 76.0 ± 11.7‰ and 13,673 ± 1,522‰, respectively (not shown). Numbers of replicates are given in brackets. Dots without standard error represent single measurements.

4. Discussion

The main objective of this study was to follow the flux of plant carbon and soil mineral nitrogen into the soil animal food web of temperate forests. Therefore, we labeled ash and beech tree saplings with $^{13}CO_2$ and added $^{15}NO_3{}^{15}NH_4$ to their rhizosphere. Ash and beech saplings were used for investigating of the food web in the rhizosphere of plants colonized by EMF (beech) as compared to AMF (ash). The plants assimilated the $^{13}CO_2$, translocated the label to roots and in beech transferred it to EM but little ^{13}C was transferred into soil and litter. Mineral nitrogen ($^{15}NO_3{}^{15}NH_4$) added to soil was transported via mycorrhizal fungi to plant roots as indicated by the signature of EM exceeding that of beech fine roots. Similar to plant carbon, mineral nitrogen was only little incorporated into the soil but to some extend into litter probably by unspecific soaking during irrigation but $\delta^{15}N$ values in fine roots exceeded those in litter by more than a factor of twelve indicating that $^{15}NO_3{}^{15}NH_4$ was primarily assimilated by mycorrhizal fungi and transported to plant roots rather than immobilized by saprotrophic microorganisms and incorporated into litter (Lummer et al., 2012). Incorporation of label into higher trophic levels therefore likely was mainly via animals feeding on roots and/or AMF or EMF. However, in part $^{15}NO_3{}^{15}NH_4$ may also have been assimilated by algae potentially contributing to increased litter $\delta^{15}N$ signatures.

In contrast to our expectations, $\delta^{13}C$ and $\delta^{15}N$ signatures of soil animal species did not differ significantly between beech and ash treatments. The similar stable isotope signatures of soil animal species suggest that morphological and structural differences between the EM rhizosphere of beech and the AM rhizosphere of ash little affected the incorporation of label into higher order consumers. Potentially, stronger incorporation of label into soil animals via EMF in beech treatments was compensated by stronger transfer of label into soil animals via rhizosphere bacteria in ash treatments (Cesarz et al., submitted).

4.1. Primary decomposers

As expected, plant C and microbial N were little incorporated into primary decomposers supporting the assumption that they almost exclusively rely on litter and soil organic matter resources rather than root derived C and microbial N. This is consistent with findings of Pollierer et al. (2007) who also suggested that *Steganacarus magnus* and *Glomeris* sp. function as primary decomposers.

However, primary decomposers were not trophically uniform but formed a gradient of taxa that incorporated virtually no plant C and microbial N [*E. hirtus*, *E. plicatus*, *S. magnus, S. striculus*, *Platynothrus peltifer*, *Hermannia gibba*, *Xenillus tegeocranus* (all Oribatid mites), *Glomeris helvetica* (Diplopoda) and *O. tyrtaeum* (Lumbricidae)] to those also incorporating plant C and microbial N [*Hermaniella punctulata*, *Achipteria coleoptrata* (both Oribatid mites) and *Glomeris undulata* (Diplopoda)], indicating that the latter in addition to dead organic matter to some extend also digest microorganisms that colonize these resources.

4.2. Secondary decomposers

Secondary decomposers incorporated significantly more ^{13}C and ^{15}N than primary decomposers supporting the hypothesis that secondary decomposers essentially rely on plant C and microbial N. However, ^{15}N and ^{13}C signatures of some secondary decomposer species overlapped with those of primary decomposers reflecting that in fact decomposer soil invertebrates form a gradient from species exclusively incorporating litter C to those exclusively feeding on microorganisms (Scheu and Falca, 2000). In fact, species rich taxa previously assumed to predominantly feed on fungi, such as Collembola and Oribatida, have been shown to partition resources ranging from plant litter to microorganisms to even higher order animal consumers (Schneider et al., 2004; Chahartaghi et al., 2005). In the present study, secondary decomposers of the lower end of this gradient included Damaeidae, *M. pulverosa*, *N. palustris* (Oribatida), *Aporrectodea caliginosa*, *Lumbricus terrestris* (Lumbricidae), *Philoscia muscorum* and *Porcellio scaber* (Isopoda) whereas those at the higher end included *Chamobates voigtsi* (Oribatida), *Sinella/Pseudosinella* spp. (Collembola), *Lumbricus rubellus* (Lumbricidae), *Trichonicus pusillus* and *Oniscus assellus* (Isopoda). $\delta^{15}N$ signatures of two secondary decomposers, i.e., *L. cyaneus* (Collembola) and *Craspedosoma* sp. (Diplopoda) were exceptionally high pointing to specific food resources. *L. cyaneus* is known to feed on algae (Scheunemann et al., 2010) and this may explain its high signature as algae on litter presumably directly incorporated ^{13}C and ^{15}N from the labeled atmospheric CO_2 and NH_4NO_3 in irrigation water. Unfortunately, measuring stable isotope signatures of algae growing on leaf litter is virtually impossible. For high stable isotope signatures of Craspedosomatidae the same as for *L. cyaneus* may apply. Notably, ^{13}C and ^{15}N signatures of secondary

decomposers were considerably lower than those of EM or roots indicating that none of them exclusively fed on mycorrhizal fungi; rather, the data suggest that they fed on a combined diet of mycorrhizal and saprotrophic fungi.

4.3. Predators

Contrary to our expectations, predators incorporated the highest amount of ^{13}C and ^{15}N. We hypothesized that predators predominantly feed on secondary decomposers, such as Collembola and Isopoda, as suggested earlier (Scheu, 2002). In part this hypothesis is supported as $\delta^{15}N$ and $\delta^{13}C$ signatures of e.g., *N. carcinoides* (Pseudoscorpionida), *Hahnia pusilla* and *Ozyptila trux* (both Araneida) were similar to secondary decomposers, indicating that these predators predominantly feed on secondary decomposers such as *Sinella/Pseudosinella* spp. (Collembola), *T. pusillus* (Isopoda) and *C. voigtsi* (Oribatida). However, the label of both ^{15}N and ^{13}C of most predator taxa including *Lithobius muticus*, *Lithobius curtipes*, *L. piceus*, *L. erythrocephalus* (all Chilopoda), *Lophopilio* sp., *Nemastoma* sp. (Opilionida) *Hypochthonius luteus* and *Acrogalumna longipluma* (Oribatida), considerably exceeded that of the great majority of secondary decomposers indicating that they fed on higher labeled prey species such as the two highly labelled secondary decomposers *L. cyaneus* (Collembola) and *Craspedosoma* sp. (Diplopoda) and potentially other species not measured in this study such as small Collembola, Nematoda and Enchytraeidae. Lithobiidae predominantly hunt in the litter layer (Poser, 1990) which is colonized by epigeic Collembola such as *L. cyaneus.* High $\delta^{13}C$ and $\delta^{15}N$ signatures of *Lophopilio* sp. and *Nemastoma* sp. presumably are related to the wide feeding strategies of many Opilionida including intraguild predation and cannibalism (Martens, 1978). Further, Lithobiidae and Opilionda likely also fed on as the highly labelled secondary decomposers *L. cyaneus* and *Craspedosoma* sp. The high $\delta^{13}C$ and $\delta^{15}N$ signatures of *H. luteus* and *A. longipluma* (Oribatida) likely are related due to feeding on prey closely connected to the rhizosphere and the high label of roots. Hypochthoniidae are known to rely on belowground carbon and presumably predominantly prey on nematodes (Pollierer et al. 2012) and this also applies to Galumnidae (Rockett and Woodring, 1966; Muraoka and Ishibashi, 1976). Therefore, high $\delta^{13}C$ and $\delta^{15}N$ signatures of *H. luteus* and *A. longipluma* likely resulted from feeding on nematodes which either directly fed on roots or on mycorrhizal fungi. High stable isotope

signature in predators therefore presumably resulted from incorporation of the label via two different pathways, the one via consumers of algae the other via root associated nematodes. Potentially, the first pathway was more pronounced as in the field since the canopies of the tree seedlings were rather open thereby allowing more light entering the soil surface resulting in more pronounced algal growth.

Two predator taxa, *Necrophloeophagus longicornis* and *Strigamia accuminata* (both Geophilomorpha), had rather low $\delta^{15}N$ signatures indicating that they fed on prey with low $\delta^{15}N$ signature, potentially a mixture of Lumbricidae and Isopoda. Indeed, Geophilomorpha are known to hunt for Lumbricidae by following them in large soil pores (Poser, 1990; Wolters and Ekschmitt, 1997). Low $\delta^{15}N$ signatures of *S. accuminata* may also be related to feeding on earthworms, however, high $\delta^{13}C$ signatures exceeding those of Lumbricidae suggest that they included also other prey, potentially Isopoda such as *O. asellus* and *P. scaber*.

4.4. Conclusions

Results of this study showed that primary and secondary decomposers comprise a gradient of species relying to different degrees on root C and microbial N. High stable isotope incorporation into EM and considerably lower signatures in soil animals suggest that the animal species studied do not exclusively feed on mycorrhizal fungi but long-term studies exceeding the life span of the animals are needed to prove this assumption. Surprisingly, predators were most intensively labeled with plant C and root N. Presumably, this high label was due to both feeding on algal consumers, such as the Collembola species *L. cyaneus*, and on plant rhizosphere associated root or mycorrhiza feeding nematodes. The results indicate that predators in soil animal food webs rely on very different carbon resources including algae, roots and microorganisms which are channeled to higher trophic levels predominantly via Collembola, Nematoda and Lumbricidae. Notably, dominant predators of temperate forests such as Lithobiidae appear to predominantly prey on individual species of litter dwelling Collembola such as *L. cyaneus.*

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References

Albers, D., Schaefer, M., Scheu, S., 2006. Incorporation of plant carbon into the soil animal food web of an arable system. Ecology 87, 235–245.

Agerer, R., 1987-2006. Colour Atlas of Ectomycorrhizae. Einhorn Verlag, Schwäbisch Gmünd, Germany.

Bardgett, R.D., Bowman, W.D., Kaufmann, R., Schmidt, S.K., 2005. A temporal approach to linking aboveground and belowground ecology. Trends in Ecology and Evolution 20, 634–641.

Bais, H.P., Weir, T.L., Perry, L.G., Gilroy, S., Vivanco, J.M., 2006. The role of root exudates in rhizosphere interactions with plants and other organisms. Annual Review of Plant Biology 57, 233-266.

Berg, B., McClaugherty, C., 2008. Plant Litter - Decomposition, Humus Formation, Carbon Sequestration. Springer, Berlin, Germany.

Cairney, J.W.G., 2012. Extramatrical mycelia of ectomycorrhizal fungi as moderators of carbon dynamics in forest soil. Soil Biology & Biochemistry 147, 198-208.

Bonkowski, M., Griffiths, B.S., Ritz, K., 2000. Food preferences of earthworms for soil fungi. Pedobiologia 44, 666-676.

Cesarz, S., Fender, A., Beyer, F., Valtanen, K., Pfeiffer, B., Gansert, D., Hertel, D., Polle, A., Daniel, R., Leuschner, C., Scheu, S., submitted. Beech promotes rhizosphere functioning by favoring fungi.

Crotty, F.V., Blackshaw, R.P., Murray, P.J., 2011. Tracking the flow of bacterially derived ^{13}C and ^{15}N through soil faunal feeding channels. Rapid Communications in Mass Spectrometry 25, 1503-1513.

Chapman, S.K., Langely, J.A., Hart, S.C., Koch, G.W., 2006. Plants actively control nitrogen cycling: uncorking the microbial bottleneck. New Phytologist 169, 27-34.

Chahartaghi, M., Langel, R., Scheu, S., Ruess, L., 2005. Feeding guilds in Collembola based on nitrogen stable isotope ratios. Soil Biology & Biochemistry 37, 1718–1725.

Curry, J.P., Schmidt, O., 2007. The feeding ecology of earthworms - A review. Pedobiologia 50, 463–477.

Dennis, P.G., Miller, A.J., Hirsch, P.R., 2010. Are root exudates more important than other sources of rhizodeposits in structuring rhizosphere bacterial communities? FEMS Microbiology Ecology 72, 313-327.

Ferlian, O., Scheu, S., Pollierer, M.M., 2012. Trophic interactions in centipeds (Chilopoda, Myriapoda) as indicated by fatty acid patterns: Variations with life stage, forest age and season. Soil Biology & Biochemistry 52, 33-42.

Fischer, B.M., Schatz, H., Maraun, M., 2010. Community structure, trophic position and reproductive mode of soil and bark-living oribatid mites in an alpine grassland ecosystem. Experimental and Applied Acarology 52, 221–237.

Geissler, D., Horwath, W.R., Joergensen, R.G., 2010. Pathways of nitrogen utilization by soil microorganisms - A review. Soil Biology & Biochemistry 42, 2058-2067.

Gunn, A., Cherrett, J.M., 1983. The exploitation of food resources by soil meso- and macro invertebrates. Pedobiologia 37, 303–320.

Hättenschwiler, S., Gasser, P., 2005. Soil animals alter plant litter diversity effects on decomposition. Proceedings of the National Academy of Science of the USA 102, 1519-1524.

Heidemann, K., Scheu, S., Ruess, L., Maraun, M., 2011. Molecular detection of nematodes predation and scavenging in oribatid mites: Laboratory and field experiments. Soil Biology & Biochemistry 43, 2229–2236.

Hobbie, J.E., Hobbie, E.A., 2006. ^{15}N in symbiotic fungi and plants estimates nitrogen and carbon flux rates in arctic tundra. Ecology 87, 816–822.

Högberg, P., Högberg, M.N., Göttlicher, S.G., Betson, N.R., Keel, S.G., Metcalfe, D.B., Campbell, C., Schindlbacher, A., Hurry, V., Lundmark, T., Linder, S.,

Näsholm, T., 2008. High temporal resolution tracing of photosynthate carbon from tree canopy to forest soil microorganisms. New Phytologist 177, 220-228.

Högberg, M.N., Briones, M.J.I., Keel, S.G., Metcalfe, D.B., Campbell, C., Midwood, A.J., Thornton, B., Hurry, V., Linder, S., Näsholm, T. and Högberg, P., 2010. Quantification of effects of season and nitrogen supply on tree below-ground carbon transfer to ectomycorrhizal fungi and other soil organisms in a boreal pine forest. New Phytologist 154, 791-795.

Illig, J., Langel, R., Norton, R.A., Scheu, S., Maraun, M., 2005. Where are the decomposers? Uncovering the soil food web of a tropical montane rain forest in southern Ecuador using stable isotopes (^{15}N). Journal of Tropical Ecology 21, 589–593.

Kautz, G., Zimmer, M., Topp, W., 2000. Responses of the parthenogenetic isopod *Trichoniscus pusillus* (Isopoda: Oniscidea) to changes in food quality. Pedobiologia 44, 75-85.

Kempson, D., Lloyd, M., Ghelardi, R., 1963. A new extractor for woodland litter. Pedobiologia 3, 1–21.

Lang, C., Polle, A., 2011. Ectomycorrhizal fungal diversity, tree diversity and nutrient relations in a mixed Central European forest. Tree Physiology 31, 531-538.

Lang, C., Seven, J., Polle, A., 2011. Host preferences and differential contributions of deciduous tree species shape mycorrhizal species richness in a mixed Central European forest. Mycorrhiza 21, 297-308.

Leake, J.R., Ostle, N.J., Rangel-Castro, J.I., Johnson, D., 2006. Carbon fluxes from plants through soil organisms determined by field $^{13}CO_2$ pulse labeling in an upland grassland. Applied Soil Ecology 22, 152-175.

Leuschner, C., Hertel, D., Schmidt, I., Koch, O., Muhs, A., Hölscher, D., 2004. Stand fine root biomass and fine root morphology in old-growth beech forests as a function of precipitation and soil fertility. Plant and Soil 258, 43–56.

Leuschner, C., Jungkunst, H.F., Fleck, S., 2009. Functional role of forest diversity: Pros and cons of synthetic stands and across-site comparisons in established forests. Basic and Applied Ecology 10, 1-9.

Lummer, D., Scheu, S., Butenschoen, O., 2012. Nitrogen transfer between decomposing litter species is an important but not the only factor responsible for synergistic mixture effects on litter decomposition. Oikos, 121, 1649-1655..

Marhan, S., Scheu, S., 2005. The influence of mineral and organic fertilisers on the growth of the endogeic earthworm *Octolasion tyrtaeum* (Savigny). Pedobiologia 49, 239-249.

Martens, J., 1978. Weberknechte, Opiliones. In: Senglaub, K., Hannemann, H.-J., Schumann, H. (eds) Die Tierwelt Deutschlands, Band 64, G. Fischer, Jena, Germany.

Muraoka, M., Ishibashi, N., 1976. Nematode-feeding mites and their feeding behaviour. Applied Entomology and Zoology 11, 1–7.

Moore, J.C., Hunt, H.W., 1988. Resource compartmentation and the stability of real ecosystems. Nature 333, 261-263.

Moore, J.C., McCann, K., de Ruiter P.C., 2005. Modeling trophic pathways, nutrient cycling, and dynamic stability in soils. Pedobiologia 49, 499-510.

Moore-Kucera, J., Dick, R.P., 2008. Application of ^{13}C-labeled litter and root materials for in situ decomposition studies using phospholipids fatty acids. Soil Biology & Biochemistry 40, 2485-2493.

Oelbermann, K. and Scheu, S., 2010. Trophic guilds of generalist feeders in soil animal communities as indicated by stable isotope analysis (^{15}N/^{14}N). Bulletin of Entomological Research 100, 511-520.

Pollierer, M.M., Langel, R., Korner, C,.Maraun, M., Scheu, S., 2007. The underestimated importance of belowground carbon input for forest soil animal food webs. Ecology Letters 10, 729-736.

Pollierer, M.M., Langel, R., Scheu, S., Maraun, M., 2009. Compartmentalization of the soil animal food web as indicated by dual analysis of stable isotope ratios (^{15}N/^{14}N and ^{13}C/^{12}C). Soil Biology & Biochemistry 41, 1221–1226.

Pollierer, M.M., Dykmans, J., Scheu, S., Haubert, D., 2012. Carbon fluxes through fungi and bacteria into the forest soil animal food web as indicated by compound-specific ^{13}C fatty acid analysis. Functional Ecology, doi: 10.1111/j.1365-2435.2012.02005.x.

Poser, G., 1988. Chilopoda as predators in a beech wood. Pedobiologia 31, 261-281.

Poser, G., 1990. Die Hundertfüßer (Myriapoda, Chilopoda) eines Kalkbuchenwaldes: Populationsökologie, Nahrungsboilogie und Gemeinschaftsstruktur. Dissertation, University of Göttingen, Göttingen, Germany.

Rockett, C.L., Woodring, J.P., 1966. Oribatid mites as predators of soil nematodes. Annals of the Entmological Society of America 59, 669–671.

Ruf, A., Kuzyakov, Y., Lopatovskaya, O., 2006. Carbon fluxes in soil food webs of increasing complexity revealed by ^{14}C labeling and ^{13}C natural abundance. Soil Biology & Biochemistry 38, 2390-2400.

Scheu, S., Falca, M., 2000. The soil food web of two beech forests (*Fagus sylvatica*) of contrasting humus type: stable isotope analysis of a macro- and a mesofauna-dominated community. Oecologia 123, 285–286.

Scheu, S., 2002. The soil food web: structure and perspectives. European Journal of Soil Biology 38, 11−20.

Scheu, S., 2005. Linkages between tree diversity, soil fauna and ecosystem processes. In: Scherer-Lorenzen, M., Köhler, C., Schulze, E.-D., (Eds.) Forest Diversity and Function: Temperate and Boreal Systems, Ecological Studies 176, Springer, Berlin, Germany, pp. 211-233.

Scheunemann, N., Scheu, S., Butenschoen, O., 2010. Incorporation of decade old soil carbon into the soil animal food web of an arable system. Applied Soil Ecology 46, 59-63.

Schmidt, I., Leuschner, C., Mölder, A., Schmidt, W., 2009. Structure and composition of the seed bank in monospecific and tree species-rich temperate broad-leaved forests. Forest Ecology and Management 257, 695–702.

Smith, S.E., Read, D.J., 1997. Mycorrhizal Symbiosis, 3rd ed. Elsevier, Oxford, UK.

Schneider, K., Migge, S., Norton, R.A., Scheu, S., Langel, R., Reineking, A., Maraun, M., 2004. Trophic niche differentiation in soil microarthropods (Oribatida, Acari): evidence from stable isotope ratios ($^{15}N/^{14}N$). Soil Biology & Biochemistry 36, 1769–1774.

Schneider, K., Renker, C., Maraun, M., 2005. Oribatid mite (Acari, Oribatida) feeding on ectomycorrhizal fungi. Mycorrhiza 16, 67-72.

Sticht, C., Schrader, S., Giesemann, A., Weigel, H.J., 2008. Effects of elevated atmospheric CO_2 and N fertilization on abundance, diversity and C-isotopic signature of collembolan communities in arable soil. Applied soil Ecology 34, 219-229.

Swift, M.J., Heal, 0.W., Anderson, J.M., 1979. Decomposition in terrestrial ecosystems. Blackwell, Oxford, UK.

Tiunov, A.V., 2007. Stable isotopes of carbon and nitrogen in soil ecological studies. Biology Bulletin 34, 395-407.

Van der Heijden, M.G.A., Bardgett, R.D., van Straalen N.M., 2008. The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. Ecology Letters 11, 296-310.

Vockenhuber, E., Scherber, C., Langenbruch, C., Meißner, M., Seidel, D., Tscharntke, T., 2011. Tree diversity and environmental context predict herb species richness cover in Germany´s largest connected deciduous forest. Perspectives in Plant Ecology, Evolution and Systematics 13, 111-119.

Wallander, H., Mörth, C.M., Giesler, R., 2009. Increasing abundance of soil fungi is a driver for ^{15}N enrichment in soil profiles along a chronosequence undergoing isostatic rebound in northern Sweden. Oecologia 160, 87-96.

Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setälä, H., van der Putten, W.H., Wall, D.H., 2004. Ecological linkages between aboveground and belowground biota. Science 304, 1629-1633.

Wolters, V., Ekschmitt, K., 1997. Gastropods, isopods, diplopods and chilopods: neglected groups of the decomposer food web. In: Benksier, G. (Ed.) Fauna in Soil Ecosystems: Recycling processes, Nutrient Fluxes and Agricultural Production. Marcel Dekker, New York, USA, pp. 265-306.

Supplementary material

Appendix: Soil animal species studied as assorted to trophic groups (primary decomposers, secondary decomposers, predators).

Trophic group	Taxonomic group	Species	Reference
Primary decomposer	**Oribatida**	*Achipteria coleoptrata* (Linnaeus, 1758)	Schneider et al. (2004, 2005), Pollierer et al. (2009, 2012)
		Eupelops plicatus (C.L. Koch, 1836)	Schneider et al. (2004)
		Eupleops hirtus (Berlese, 1916)	Maraun et al. (2011)
		Hermannia gibba (C.L. Koch, 1839)	Schuster (1956), A´Bear et al. (2010), Maraun et al. (2011)
		Hermanniella punctulata Berlese, 1908	Norton and Behan-Pelletier (2009)
		Platynothrus peltifer (C.L. Koch, 1839)	Schneider et al. (2004, 2005), Pollierer et al. (2009, 2012), Mauraun et al. (2011), Heidemann et al. (2011)
		Steganacarus magnus (Nicolet, 1855)	Maraun and Scheu (2000), Schneider et al. (2004, 2005), Pollierer et al. (2009, 2012), A´Bear et al. (2010), Heidemann et al. (2011)
		Steganacarus striculus (C.L. Koch, 1835)	Schneider et al. (2004)
		Xenillus tegeocranus (Hermann, 1804)	Norton and Behan-Pelletier (2009)
	Diplopoda	*Glomeris helvetica* (Voerhoff, 1894)	Scheu and Falca (2000)
		Glomeris undulata (C.L. Koch, 1844)	Pollierer et al. (2009), Oelbermann and Scheu (2010), Semenyuk and Tuinov (2011)
	Lumbricidae	*Octolasion tyrtaeum* (Örley, 1881)	Marhan and Scheu, (2005), Butenschoen et al. (2007), Curry and Schmidt (2007), Scheunemann et al. (2010)

Trophic group	Taxonomic group	Species	Reference
Secondary decomposer	**Oribatida**	*Chamobates voigtsi* (Oudemans, 1902)	Riha (1951), Schuster (1956), Luxton (1972), Kaneko (1988), Schneider et al. (2004), Maraun et al. (2011)
		Damaeidae undetermined Berlese, 1896	Maraun et al. (1998), Schneider et al. (2004)
		Metabelba pulverosa Strenzke, 1953	Schneider et al. (2004)
	Collembola	*Nothrus palustris* C.L. Koch, 1839	Schneider et al. (2004, 2005)
		Lepidocyrtus cyaneus Tullberg, 1871	Chaharthaghi et al. (2005), Scheunemann et al. (2010), Crotty et al. (2011), Pollierer et al. (2012)
		Sinella/Pseudo-sinella spp. undetermined	Scheunemann et al. (2010), Crotty et al. (2011)
	Diplopoda	*Craspeodsoma* sp. undetermined	Bellmann (2001)
	Isopoda	*Trichoniscus pusillus* Brandt, 1883	Kautz et al. (2000), Scheu and Falca (2000), Pollierer et al. (2012)
		Philoscia muscorum (Scopoli, 1763)	Scheu and Falca (2000)
		Porcellio scaber Latreille, 1804	Ihnen and Zimmer (2008), Crowther et al. (2011)
		Oniscus assellus Linnaeus, 1758	Oelbermann and Scheu, (2010), Crowther et al. (2011)
	Lumbricidae	*Aporrectodea longa* (Ude, 1885)	Curry and Schmidt (2007), Pollierer et al. (2009, 2012)
		Lumbricus terrestris Linnaeus, 1758	Gunn and Cherret (1983), Bonkowski et al. (2000), Curry and Schmidt (2007), Pollierer et al. (2009, 2012), Scheunemann et al. (2010)
		Aporrectodea caliginosa (Savigny)	Bonkowski et al. (2000), Scheu and Falca (2000)
		Aporrectodea rosea (Savigny, 1826)	Bonkowski et al. (2000), Pollierer et al. (2009)
		Lumbricus rubellus Hofmeister, 1843	Bonkowski et al. (2000)

Trophic group	Taxonomic group	Species	Reference
Predator	**Oribatida**	*Acrogalumna longipluma* (Berlese, 1904)	Rockett and Woodring (1966), Rockett (1980), Wunderle (1992), Schneider et al. (2004)
		Hypochthonius luteus Oudemans, 1917	Riha (1951),Schneider et al. (2004), Ruf et al. (2006), Pollierer et al. (2009, 2012), Maraun et al. (2011), Heidemann et al. (2011)
	Araneida	*Hahnia pusilla* C.L. Koch, 1841	Scheu and Falca (2000)
		Ozyptila trux (Blackwell, 1846)	Bellmann (2001)
	Collembola	*Clubiona compta* C.L. Koch, 1839	Bellmann (2001)
	Geophilo-morpha	*Necrophleophagus longicornis* (Leach, 1858)	Poser (1988), Poser (1990), Ferlian et al. (2012)
		Strigamia accuminata (Leach, 1814)	Poser (1990), Wolters and Eckschmitt (1997), Ferlian et al. (2012)
	Lithobio-morpha	*Lithobius muticus* C.L. Koch, 1847	Poser (1988), Scheu and Falca (2000), Pollierer et al. (2009, 2010)
		Lithobius piceus (C.L. Koch, 1862)	Poser (1988), Scheu and Falca (2000), Pollierer et al. (2009, 2010)
		Lithobius erythrocephalus C.L. Koch, 1847	Poser (1988), Scheu and Falca (2000), Pollierer et al. (2009, 2010)
		Lithobius curtipes C.L. Koch, 1847	Poser (1988), Scheu and Falca (2000), Pollierer et al. (2009, 2010)
		Trogulus tricarinatus (Linnaeus, 1767)	Martens et al. (1978)
		Lophopilio sp. undetermined	Oelbermann and Scheu (2010)
		Nemastoma sp. undetermined	Martens et al. (1978)
		Neobisium carcinoides (Hermann, 1804)	Scheu and Falca (2000), Oelbermann and Scheu (2010), Pollierer et al. (2012)

References

A´Bear, A.D., Boddy, L., Raspoting, G., 2010. Non-trophic effects of oribaitd mites on cord-forming basidomycetes in soil microcosms. Ecological Entomology 35, 477-484.

Bellmann, H., 2001. Kosmosatlas der Spinnentiere Europas. Frankh-Kosmos, Stuttgart, Germany.

Butenschoen, O., Poll, C., Langel, R., Kandeler, E., Marhan, S., Scheu, S., 2007. Endogeic earthworms alter carbon translocation by fungi at the soil–litter interface. Soil Biology & Biochemistry 39, 2854-2864.

Bonkowski, M., Griffiths, B.S., Ritz, K., 2000. Food preferences of earthworms for soil fungi. Pedobiologia 44, 666-676.

Curry, J.P., Schmidt, O., 2007. The feeding ecology of earthworms - a review. Pedobiologia 50, 463–477.

Crotty, F.V., Blackshaw, R.P., Murray, P.J., 2011. Tracking the flow of bacterially derived ^{13}C and ^{15}N through soil faunal feeding channels. Rapid Commununications in Mass Spectrometry 25, 1503-1513.

Crowther, T.W., A´Bear, A.D., 2011. Impacts of grazing soil fauna on decomposer fungi are species specific and density-dependent. Fungal Ecology 5, 277-281.

Eisenhauer, N., Scheu, S., 2008. Invasibility of experimental grassland communities: the role of earthworms, plant functional group identity and seed size. Oikos 117, 1026-1036.

Erdmann, G., Otte, V., Langel, R., Scheu, S., Maraun, M., 2007. The trophic structure of bark-living oribatid mite communities analysed with stable isotopes (^{15}N, ^{13}C) indicates strong niche differentiation, Experimental and Applied Acarology 41, 1-10.

Ferlian, O., Scheu, S., Pollierer, M.M., 2012.Trophic interactions in centipeds (Chilopoda, Myriapoda) as indicated by fatty acid patterns: Variations with life stage, forest age and season. Soil Biology & Biochemistry 52, 33-42.

Fischer, B.M., Schatz, H., Maraun, M., 2010. Community structure, trophic position and reproductive mode of soil and bark-living oribatid mites in an alpine grassland ecosystem. Experimental and Applied Acarology 52, 221–237.

Gunn, A., Cherrett, J.M., 1983. The exploitation of food resources by soil meso- and macro invertebrates. Pedobiologia 37, 303–320.

Heidemann, K., Scheu, S., Ruess, L., Maraun, M., 2011. Molecular detection of nematodes predation and scavenging in oribatid mites: Laboratory and field experiments. Soil Biology & Biochemistry 43, 2229–2236.

Ihnen, K., Zimmer, M., 2008. Selective consumption and digestion of litter microbes by *Porcellio scaber* (Isopoda: Oniscidea). Pedobiologia 51, 335-342.

Kaneko, N., 1988. Feeding habits and cheliceral size of oribatid mites in cool temperate forest soils in Japan. Revue d'Ecologie et de Biologie du Sol 25, 353–363.

Kautz, G., Zimmer, M., Topp, W., 2000. Responses of the parthenogenetic isopod *Trichoniscus pusillus* (Isopoda: Oniscidea) to changes in food quality. Pedobiologia 44, 75-85.

Luxton, M., 1972. Studies on the oribatid mites of a Danish beech wood soil. I. Nutritional biology. Pedobiologia 12, 434–463.

Maraun, M., Visser, S., Scheu, S., 1998. Oribatid mites enhance the recovery of the microbial community after a strong disturbance. Applied Soil Ecology 9, 175–181.

Maraun, M., Erdmann, G., Fischer, B.M., Pollierer, M.M., Norton, R.A., Schneider, K., Scheu, S., 2011. Stable isotopes revisited: Their use and limits for oribatid mite trophic ecology. Soil Biology & Biochemistry 43, 877–882.

Marhan, S., Scheu, S., 2005. The influence of mineral and organic fertilisers on the growth of the endogeic earthworm *Octolasion tyrtaeum* (Savigny). Pedobiologia 49, 239-249.

Martens, J., 1978. Weberknechte, Opiliones. In: Senglaub, K., Hannemann, H.-J., Schumann, H. (eds) Die Tierwelt Deutschland, Band 64., G. Fischer, Jena, Germany.

Norton, R.A., Behan-Pelletier, V.M., 2009. Suborder Oribatida. In: Krantz GW, Walter DW (eds.) A manual of Acarology, Texas Technical University Press, Lubbock, USA, pp. 430-565.

Oelbermann, K., Scheu, S., 2010. Trophic guilds of generalist feeders in soil animal communities as indicated by stable isotope analysis ($^{15}N/^{14}N$).Bulletin of Entomological Research100, 511-520.

Pollierer, M.M., Langel, R., Korner, C., Maraun, M., Scheu, S., 2007. The underestimated importance of belowground carbon input for forest soil animal food webs. Ecology Letters 10, 729-736.

Pollierer, M.M., Langel, R., Scheu, S., Maraun, M., 2009. Compartmentalization of the soil animal food web as indicated by dual analysis of stable isotope ratios ($^{15}N/^{14}N$ and $^{13}C/^{12}C$). Soil Biology & Biochemistry 41, 1221–1226.

Pollierer, M.M., Scheu, S., Haubert, D., 2010. Taking it to the next level: Trophic transfer of marker fatty acids from basal resource to predators. Soil Biology & Biochemistry 42, 919–925.

Pollierer, M.M., Dykmans, J., Scheu, S., Haubert, D., 2012. Carbon fluxes through fungi and bacteria into the forest soil animal food web as indicated by compound- specific ^{13}C fatty acid analyses. Functional Ecology, doi: 10.1111/j.1365-2435.2012.02005.x.

Poser, G., 1988. Chilopoda as predators in a beech wood. Pedobiologia 31, 261-281.

Poser, G., 1990. Die Hundertfüßer (Myriapoda, Chilopoda) eines Kalkbuchenwaldes: Populationsökologie, Nahrungsbiologie und Gemeinschaftsstruktur. Dissertation, University of Göttingen, Göttingen, Germany.

Riha, G., 1951. Zur Ökologie der Oribatiden in Kalksteinböden. Zoologische Jahrbücher Abteilung für Systematik, Ökologie und Geographie der Tiere 80, 407–450.

Rockett, C.L., Woodring, J.P., 1966. Oribatid mites as predators of soil nematodes. Annals of the Entomological Society of America 59, 669–671.

Ruf, A., Kuzyakov, Y., Lopatovskaya, O., 2006. Carbon fluxes in soil food webs of increasing complexity revealed by ^{14}C labeling and ^{13}C natural abundance. Soil Biology & Biochemistry 38, 2390–2400.

Scheu, S., Falca, M., 2000. The soil food web of two beech forests (*Fagus sylvatica*) of contrasting humus type: stable isotope analysis of a macro- and a mesofauna-dominated community. Oecologia 123, 285–286.

Scheunemann, N., Scheu, S., Butenschoen, O., 2010. Incorporation of decade old soil carbon into the soil animal food web of an arable system. Applied Soil Ecology 46, 59–63.

Schneider, K., Migge, S., Norton, R.A., Scheu, S., Langel, R., Reineking, A., Maraun, M., 2004. Trophic niche differentiation in soil microarthropods (Oribatida, Acari): evidence from stable isotope ratios ($^{15}N/^{14}N$). Soil Biology & Biochemistry 36, 1769–1774.

Schneider, K., Renker, C., Maraun, M., 2005. Oribatid mite (Acari, Oribatida) feeding on ectomycorrhizal fungi. Mycorrhiza 16, 67-72.

Schuster, R., 1956. Der Anteil der Oribatiden an den Zersetzungsvorgängen im Boden. Zeitschrift für Morphologie und Ökologie der Tiere 45, 1–33.

Semenyuk, I.I., Tiunov, A.V., 2011. Isotopic Signature (15N/14N and 13C/12C) Confirms Similarity of Trophic Niches of Millipedes (Myriapoda, Diplopoda) in a Temperate Deciduous Forest. Biology Bulletin 38, 283-291.

Wolters, V., Ekschmitt, K., 1997. Gastropods, isopods, diplopods and chilopods: neglected groups of the decomposer food web. In: Benksier G (ed.) Fauna in Soil Ecosystems: Recycling processes, Nutrient Fluxes and Agricultural Production. Marcel Dekker, New York, USA, pp. 265-306.

Wunderle, I., 1992. Die Oribatiden-Gemeinschaften (Acari) der verschiedenen Habitate eines Buchenwaldes. Carolinea 50, 79–144.

4 Incorporation of carbon and nitrogen from leaf litter of different structural complexity into forest soil food webs

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Abstract

It has been suggested that forest soil food webs predominantly rely on root rather than leaf litter derived carbon, but it is also well documented that saprophagous soil invertebrates process leaf litter material. The aim of the present study was to investigate which soil animal species incorporate resources from leaf litter material rich (European beech, *Fagus sylvatica*) and poor in structural compounds (European ash, *Fraxinus excelsior*) obtained from fertilized tree seedlings with little differences in litter nitrogen concentrations. Further, we aimed at testing if soil animal species preferably incorporate C and N from ash leaf litter when both ash and beech leaf litter are available. We placed ^{13}C and ^{15}N labeled beech and ash leaf litter separately and in combination in mesocosms and measured the incorporation of litter derived C and N into soil animal taxa after five month. We hypothesized that more C and N is incorporated into the soil animal food web from ash with low as compared to beech litter with high structural compounds. Further, we hypothesized that the signal of litter ^{13}C and ^{15}N is preferentially incorporated into primary decomposers less into secondary decomposers and least into predators. Conform to the first hypothesis soil animals incorporated more C from ash than from beech litter. However, soil animals incorporated similar amounts of N from both ash and beech indicating that the availability of N did not vary with litter structure. In contrast to our second hypothesis incorporation of litter C and N was in the order secondary decomposers > primary decomposers > predators indicating that litter resources enter the soil animal food web most quickly via microbial feeding soil animals. Overall, the results underline the importance of leaf litter poor in structural compounds such as ash for fuelling soil animal food webs.

Keywords

Soil fauna, litter decomposition, litter quality, primary decomposers, secondary decomposers, predators, fungal energy channel

1. Introduction

The soil animal food web of forest ecosystems relies on products of aboveground primary producers. Two different flows of energy and nutrients connect plants with the belowground system, i.e. litter input and root exudates (Scheu, 2005; Högberg and Read, 2006). It has been emphasized that the soil food web is fuelled mainly via resources entering the soil via the root pathway (Albers et al., 2006; Ruf et al., 2006; Pollierer et al., 2007; Högberg et al., 2008). On the other hand, up to 90% of the primary production in temperate forests ends up as litter entering the decomposer system (Hättenschwiler et al., 2005; Gessner et al., 2010). This dead organic material does not accumulate but is decomposed resulting in cycling of carbon and nutrients contributing fundamentally to ecosystem functioning (Polis and Strong, 1996; Moore et al., 2004; Meier and Bowman, 2008). Litter decomposition is controlled by a number of drivers such as climate, litter quality and decomposers including soil microorganisms and soil fauna (Swift et al., 1979; Hieber and Gessner, 2002; Szanzer et al., 2011; Swan and Kominoski, 2012). In fact, dead organic material has been assumed to form the main resource nourishing soil microorganisms (Swift et al., 1979; Thoms et al., 2010) and decomposer animals (Hättenschwiler and Gasser, 2005; Scheu, 2005).

Decomposition of litter by soil animals depends on litter quality and therefore varies with litter species (Hättenschwiler and Gasser, 2005). In early stages of decay, litter quality is mainly defined by leaf chemistry (Perez-Harguindeguy et al., 2000; Cornwell, 2008). Contents of nutrients, and structural and secondary compounds drive the quality of litter materials (Couteaux et al., 2005; Wardle et al., 2006), with concentrations of C and N, and the C-to-N and lignin-to-N ratio being among the most important factors (Mellilo et al., 1982; Berg and McClaugherty, 2008). Accessibility of litter C and N are determined by the complexity of structural litter compounds (Joergensen, 2010; Gessner et al., 2010; Dungait et al., 2012). Decomposition of litter rich in structural compounds, such as European beech, is dominated by saprotrophic fungi (Osono, 2007; Snaijdr et al., 2011).

Nitrogen is of crucial importance for plants, soil microorganisms and soil animals. During decomposition of litter microorganisms immobilize N in soil and thereby compete with plants for N resources (Chapman et al., 2006; Lindahl et al., 2006). Soil animal nutrition and growth often are also constrained by the N content of their food, and protein deficiency is widespread (Scheu, 2005). In leaf litter N is bound in complex insoluble polymers, such as proteins or nucleic acids, and often enmeshed

in recalcitrant compounds, such as cellulose and lignin (Swift et al., 1979; Vitousek et al., 2002). Therefore, the release of N from decomposing organic matter is closely coupled to the decomposition of structural litter compounds by microorganisms (Schimel and Hättenschwiler, 2007).

Not only litter type but also mixtures of different litter species affect decomposition rates (Gartner and Cardon, 2004; Hättenschwiler and Gasser, 2005; Ball et al., 2009). Mixing of functionally distinct litter species likely alleviate nutrient limitation thereby causing non-additive decomposition patterns (Lecerf et al., 2011). Although the underlying mechanisms are still debated, the transport of N through fungal networks between litter types of different quality is likely to play an important role (Frey et al. 2000; Lummer et al., 2012). Further, detritivores that feed on litter mixtures accelerate the decomposition of recalcitrant leaf species in mixtures (Hättenschwiler and Gasser, 2005; Gessner et al., 2010).

The soil animal food web has been described to rely on different resources processed along different energy channels (Moore and Hunt, 1988). Two channels, i.e. the bacterial and the fungal energy channel, are most important with each having distinct functions being associated with fast and slow cycling of C and N (Coleman et al., 1983; Moore and Hunt, 1988; Wardle et al., 2002). Saprotrophic fungi dominate in ecosystems with acidic soil, high organic matter content and low litter quality (Coleman et al., 1983), such as boreal and in part temperate forests (Wardle et al., 2004). There is increasing evidence that only few animal species live on resources from decomposing litter material, i.e. function as primary decomposers (Pollierer et al., 2009). Further, there is evidence that many primary decomposers form unsuitable prey for soil and litter predators due to strong sclerotization or large body size. In contrast, fungal feeders such as collembolans form a major fraction of the diet of predators (Oelbermann and Scheu, 2008; Schneider et al., 2012).

Natural variations in stable isotope ratios of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) have been shown to be a powerful tool for investigating the trophic structure of soil food webs (Minagwa and Wada, 1984; Post, 2002; Tiunov, 2007). $\delta^{15}N$ signatures are used to assign soil animals to trophic levels or food web compartments (Pollierer et al., 2009; Oelbermann and Scheu, 2010). In contrast, $\delta^{13}C$ signatures are only slightly enriched per trophic level and allow identifying basal resources of animal food webs (Oelbermann et al., 2008; Pollierer et al., 2009). However, labeling experiments with enriched ^{13}C and ^{15}N litter material are

indispensible for tracing the flux of C and N from decomposing litter through the soil food web (Zeller et al., 2000; Elfstrand et al., 2008; Lummer et al., 2012).

In this study, ^{13}C and ^{15}N labeled leaf litter were exposed in monocultures and mixtures in mesocosms in the field. Litter of European beech [*Fagus sylvatica* (L.)] and European ash [*Fraxinus excelsior* (L.)] were chosen for the experiment since litter of these species differs strongly in structural litter compounds (Jacob et al., 2010). Litter of ash is rich in easily accessible carbon, whereas litter of beech contains high amounts of recalcitrant compounds including cellulose and lignin (Jacob et al., 2009 and 2010; Gessner et al., 2010). To focus on the role of such structural compounds for the flux of C and N into soil food webs we used beech and ash litter with similar N concentration obtained by beech and ash seedlings at similar soil nutrient concentrations. Using these litter materials we followed the incorporation of C and N from litter into the soil animal food web of a deciduous forest.

We hypothesized that (1) the signal of the ^{13}C and ^{15}N of labeled litter can be traced through the soil animal food web, i.e. from primary decomposers to secondary decomposers to predators, and that (2) more C and N from ash with low than from beech with high amounts of structural compounds is incorporated into the soil animal food web. Further, we hypothesized that (3) the transfer of litter C and N from beech into primary decomposers is particularly low whereas the transfer of litter C and N into microbial feeders, i.e. secondary decomposers, is higher and differs little between beech and ash.

2. Material and Methods

2.1. Study site

The experiment was set up in a beech forest in the Hainich National Park near the village of Mülverstedt (51°06'N, 10°27'E) at 370 m a.s.l. The Hainich National Park is located in Central Germany (Thuringia) and covers 13,000 ha. Mean annual temperature is 7.5^{o}C and mean annual precipitation is 670 mm (Meteomedia station Weberstedt). The beech forest stocks on Luvisol underlain by Triassic Limestone (Guckland et al., 2009). The forest floor is classified as mull-like moder and the mean thickness of the litter layer is 2.8 ± 0.1 cm (Jacob et al., 2010; Langenbruch et al., 2012). The topsoil (0-10 cm) is rather acid with a pH_{KCl} of 3.3 (Guckland et al., 2009).

2.2. Litter material

For ^{13}C labeling young beech and ash trees were exposed to $^{13}CO_2$ enriched atmosphere (1,200 ppm) in a greenhouse for five month; average temperature and humidity were 22.8°C and 70%, respectively. For ^{15}N labeling and to establish similar nutrient conditions tree saplings were irrigated daily with a Hoagland-based nutrient solution containing 0.1 mM $^{15}NO_3{}^{15}NH_4$, 5 mM NO_3NH_4, 0.6 mM $CaCl_2$, 0.4 mM $MgSO_4$, 0.4 mM K_3PO_4, 0.01 mM $FeCl_3$, 1.80 µM $MnSO_4$, 0.15 µM $ZnCl_2$, 0.10 µM MoO_3 0.06 µM CuCl and 0.01 mM H_3BO_3, (Euriso-top, Saint-Aubin, Essonne, France).

Before experimental setup $\delta^{13}C$ and $\delta^{15}N$ values (measurement and calculation see below) and chemical composition of labeled leaf litter material were determined. $\delta^{13}C$ and $\delta^{15}N$ values of beech were 118.1 ± 1.7‰ and 3,143 ± 229.2‰, respectively. $\delta^{13}C$ and $\delta^{15}N$ values of ash were 155.0 ± 5.2‰ and 26,923 ± 1,813‰, respectively. Labeled beech and ash litter had similar N contents (21.3 ± 0.4 and 19.9 ± 0.9 mg g^{-1} litter dry weight, respectively) and C-to-N ratios (23.1 and 22.9), but differed in concentrations of cellulose (135.2 ± 5.5 and 95.3 ± 4.2 mg g^{-1}) and lignin (241.0 ± 4.1 and 178.1 ± 2.1 mg g^{-1} litter dry weight).

2.3. Experimental setup

A total of 42 mesocosms were installed within a 50 x 50 m fenced area of the study site in December 2008. Undisturbed cores of the upper 5 cm of the mineral soil of a diameter of 24 cm were placed into plastic cylinders. The litter layer was removed and replaced by 14.4 g of labeled litter with mixed litter treatments receiving 7.2 g of each beech and ash litter; the amount of litter added resembled the amount present in the litter layer of the study site. Cylinders were covered by 50 µm gauze at the bottom and by 1 mm gauze at the top allowing water to pass but preventing animals entering or leaving.

Mesocosms were placed at a distance of 1 m from each other and 2 m apart from tree stems into the soil matching in depth with the surrounding soil. Four treatments differing in litter composition were established: (1) labeled beech litter only, (2) labeled ash litter only, (3) mixture of labeled beech and unlabeled ash litter, (4) mixture of labeled ash and unlabeled beech litter. To investigate natural variations in stable isotope signatures in soil animals and to allow calculations of shifts in stable isotope values due to the addition of labeled litter three control

treatments with unlabeled litter were established: (1) pure beech litter, (2) pure ash litter and (3) mixture of beech and ash litter. Unlabeled beech and ash litter was sampled in the Hainich National Park; signatures of $\delta^{13}C$ and $\delta^{15}N$ did not differ significantly and averaged -28.8 ± 0.5‰ and -0.9 ± 1.0‰, respectively (Langenbruch et al., 2012). Each treatment was replicated six times.

2.4. Stable isotope analyses of soil animals

After five months, in May 2009, the experiment was destructively sampled. For collection of soil animals, the litter layer was separated from the mineral soil and animals in both layers were extracted by heat using a high-gradient canister method (Kempson et al., 1963). Thereafter, soil animals were transferred into 70% ethanol and determined to species level. For stable isotope analyses, animals were transferred into tin capsules at weights corresponding to a minimum of 5 µg N per sample. For most mesofauna species several individuals had to be pooled. Macrofauna species were dried, crushed and appropriate amounts were used for the analyses. Analyses of $^{15}N/^{14}N$ and $^{13}C/^{12}C$ ratios were carried out using a coupled system consisting of an elemental analyzer (NA 1500, Carlo Erba, Mailand) and a mass spectrometer (MAT 251, Finnigan, Bremen, Germany). The abundances (δX) of ^{13}C and ^{15}N are expressed using the δ notation with δ sample [‰] = $[(R_{sample} - R_{standard}) / R_{standard}] \times 1000$. R_{sample} and $R_{Standard}$ represent the $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios of samples and standard, respectively. For ^{13}C PD Belemnite (PBD) and for ^{15}N atmospheric nitrogen served as the primary standard. Acetanilide (C_8H_9NO, Merck, Darmstadt) was used for internal calibration.

2.5. Assigning soil animal species to trophic groups

Based on natural variations in $\delta^{15}N$ signatures soil animals from treatments with unlabeled litter were ascribed to trophic groups, i.e. primary decomposers, secondary decomposers and predators. The mean $\delta^{15}N$ signature of unlabeled beech and ash litter which did not differ significantly was taken as a baseline (-0.9 ± 1.0‰; Fig. 1). Assuming a maximum enrichment in $\delta^{15}N$ in primary decomposers of 1.7‰, i.e. half that of the commonly used trophic level enrichment of 3.4‰ (Gannes et al., 1997; Vanderklift and Ponsard, 2003; Tiunov, 2007), soil animals with $\delta^{15}N$ signatures lower than 1.7 δ units above the litter signature, i.e. below 0.8‰ were

assigned primary decomposers. Soil animals with $\delta^{15}N$ signatures of up to 3.4 δ units above the maximum $\delta^{15}N$ signature of primary decomposers, i.e. $\delta^{15}N$ signatures between 0.8 and 4.2‰, were assigned secondary decomposers. Animals with $\delta^{15}N$ signatures higher than 4.2‰ were assigned predators (Fig. 1).

2.6. Calculation of incorporated litter derived C and N into soil animals

Percentages of C and N in soil animal tissue originating from labeled litter were calculated using a modified two source mixing model (Fry, 2006). Assuming that soil animal species only fed on these two sources the fractions of source 1 (labeled litter; f1) and source 2 (unlabeled litter; f2) add up to unity (f1 + f2 = 1). The fraction incorporated from labeled litter was calculated as:

$f1 = |\delta A^* - \delta A| / |\delta L^* - \delta L|$

with $\delta A^* - \delta A$ representing the difference in delta values of C or N in soil animal tissue between treatments with labeled litter (A*) and control treatments (A); respectively, $\delta L^* - \delta L$ represents differences in delta values of C or N of labeled (L*) and control litter (L).

Incorporation of C and N into soil animal species was calculated for each of the four treatments with labeled litter (see above). For δA mean stable isotope signatures of soil animal species in the three treatments with unlabeled litter were used (see above). Percentages of C or N incorporated by the animals from labeled litter were calculated as f1 × 100.

2.7. Statistical analyses

Percentages of incorporated litter C and N into soil animals were analyzed using three factorial ANOVA differences in the incorporation of C and N from beech and ash litter from pure treatments as compared to the two respective mixture treatments. Fixed factors were litter species (beech, ash), mixture (single litter species, two litter species) and trophic group (primary decomposer, secondary decomposer and predator). Percentages of incorporated litter C and N into single soil animal taxa were analyzed using two factorial ANOVA; fixed factors were litter species (beech, ash) and mixture (single litter species, two litter species).

Prior to statistical analysis homogeneity of variances was inspected using Lévene test and data were log transformed if necessary. Percentage data were arcsine-square root transformed. For post-hoc comparisons of means Scheffé test was used. Data given in text and figures represent means and standard errors. Statistical analyses were conducted using SAS 9.2 (SAS Institute; Cary, NC, USA).

3. Results

3.1. Trophic structure of the soil animal food web

Primary decomposers included nine taxa of Oribatida, *Folsomia quadrioculata* (Collembola) and *Glomeris undulata* (Diplopoda; Fig. 1). $\delta^{15}N$ signatures of primary decomposers ranged between -3.0 ± 0.5‰ for *Achipteria coleoptrata* and 0.6 ± 0.2‰ for Damaeidae. $\delta^{13}C$ signatures ranged between -25.3 ± 0.2‰ for *Eupelops hirtus* and -19.9 ± 0.2‰ for *Steganacarus magnus*. Secondary decomposers included two taxa of Oribatida, two taxa of Collembola, *Lumbricus* spp. juv. (Lumbricida) and *Trichoniscus pusillus* (Isopoda; Fig. 1). $\delta^{15}N$ signatures of secondary decomposers ranged between 1.3 ± 1‰ for *Liacarus xylariae* and 4.0 ± 2.5‰ for *Ceratophysella* spp.; $\delta^{13}C$ signatures ranged between -24.8 ± 0.2‰ for *Ceratophysella* spp. and -21.8 ± 0.5‰ for *L. xylariae*. Predators included *Lepidocyrtus cyaneus* (Collembola), three taxa of Gamasida, Campodeidae, two taxa of Lithobiidae and three taxa of Coleoptera (Fig. 1). $\delta^{15}N$ signatures of predators ranged between 4.5 ± 1.3‰ for *Haplocerus capillicornis* and 8.3 ± 0.5‰ for *Uroseius cylindricus*; $\delta^{13}C$ signatures ranged between -25.1 ± 0.2‰ for *H. capillicornis* and -22.5 ± 0.2‰ for *U. cylindricus*.

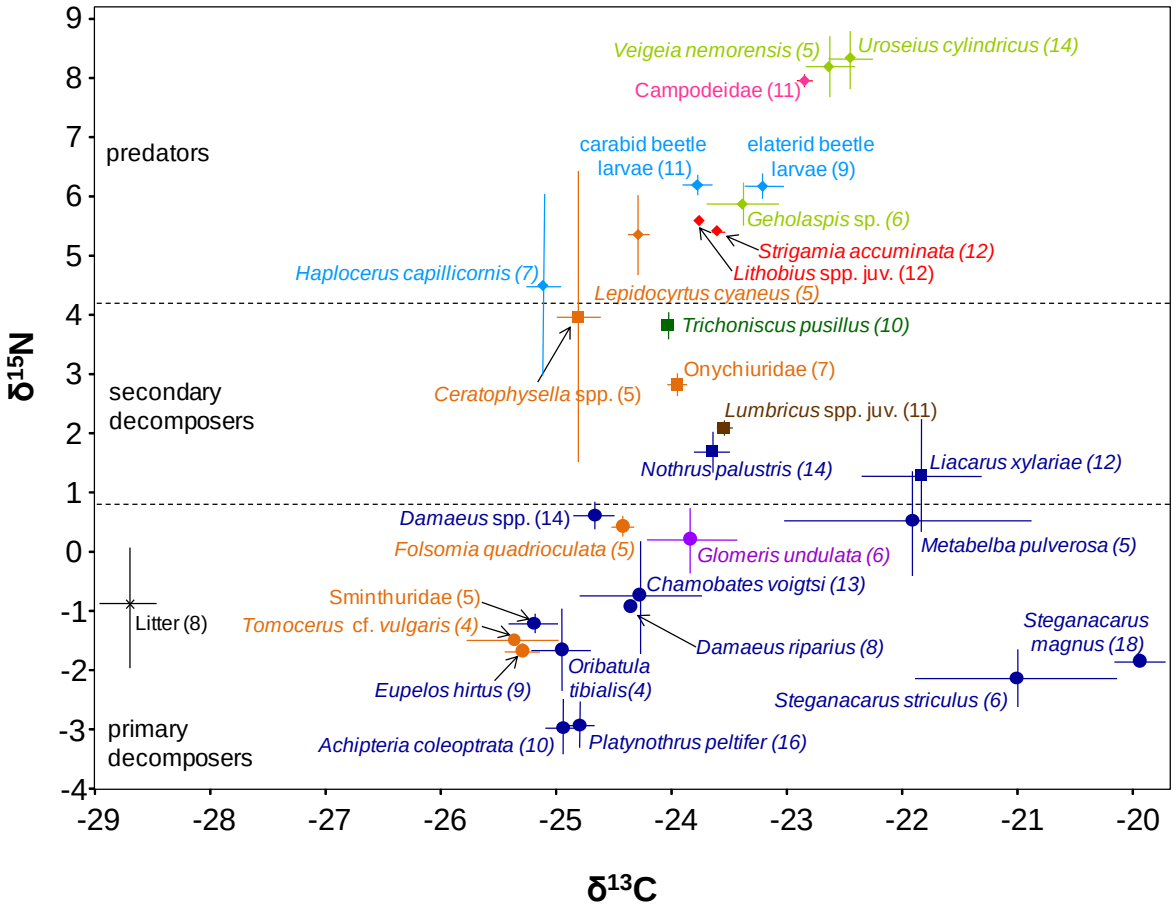

Fig. 1: $\delta^{13}C$ and $\delta^{15}N$ signature (means ± standard error) of unlabeled beech and ash litter (black cross). Mean (± standard error) $\delta^{13}C$ and $\delta^{15}N$ signatures of Oribatida (dark blue), Collembola (orange), *Glomeris undulata* (purple), *Lumbricus* spp. juv. (brown), *Trichoniscus pusillus* (dark green), Lithobiidae (red), Gamasida (light green), Coleoptera (light blue) and Campodeidae (pink) of treatments with unlabeled beech and ash litter. Primary decomposers are marked with circles, secondary decomposers with squares and predators with diamonds. Numbers of replicates are given in brackets.

3.2. Incorporation of C and N into soil animal taxa

Soil animals were significantly enriched in $\delta^{15}N$ and $\delta^{13}C$ in treatments with labeled beech or ash litter. On average, soil animals incorporated 10.4 ± 1.3% and 10.5 ± 1.0% of litter derived C and N, respectively. Similar amounts of N were incorporated into soil animal taxa in treatments with labeled beech and ash litter but incorporation of litter C differed between beech and ash litter ($F_{11,103}$ = 15.51, p = 0.0002; Table 1). In labeled ash litter treatments soil animals incorporated on average 15.7 ± 1.2% litter C whereas in labeled beech litter treatments they only incorporated 9.7 ± 1.0% of litter C.

Table 1: F- and p-values of three factorial ANOVAs on the effect of tree species ("tree": beech and ash), litter mixture ("mix": pure and mixed) and trophic group ("tropic group": primary decomposer, secondary decomposer and predator) on the incorporation of C and N into soil animals.

Element	**C**		**N**	
Fixed factor	**F-value**	**p-value**	**F-value**	**p-value**
Tree	**15.51**	**0.0002**	0.11	0.7447
Mix	0.06	0.8090	1.20	0.2752
Trophic group	**6.34**	**0.0026**	**5.46**	**0.0057**
Tree × Mix	1.14	0.2886	0.47	0.4931
Tree × Trophic group	2.07	0.1314	0.77	0.4651
Mix × Trophic group	0.38	0.6881	0.38	0.6857
Tree × Mix × Trophic group	0.95	0.3890	1.08	0.3449

Incorporation of litter C and N into soil animals differed between trophic groups ($F_{2,92}$ = 6.34, p = 0.0026 and $F_{2,92}$ = 5.46, p = 0.0057 for C and N, respectively; Fig. 2, Table 1). Generally, incorporation was in the order secondary decomposers (overall mean for C and N of 17.5 ± 0.3%) > primary decomposers (12.8 ± 0.2%) > predators (10.3 ± 0.4%). Incorporation of N from beech and ash did not differ in any of the trophic groups and this also applied to incorporation of C for secondary decomposers and predators. However, primary decomposers incorporated significantly more C from ash than from beech litter ($F_{1,40}$ = 15.96, p = 0.0003; Table 2).

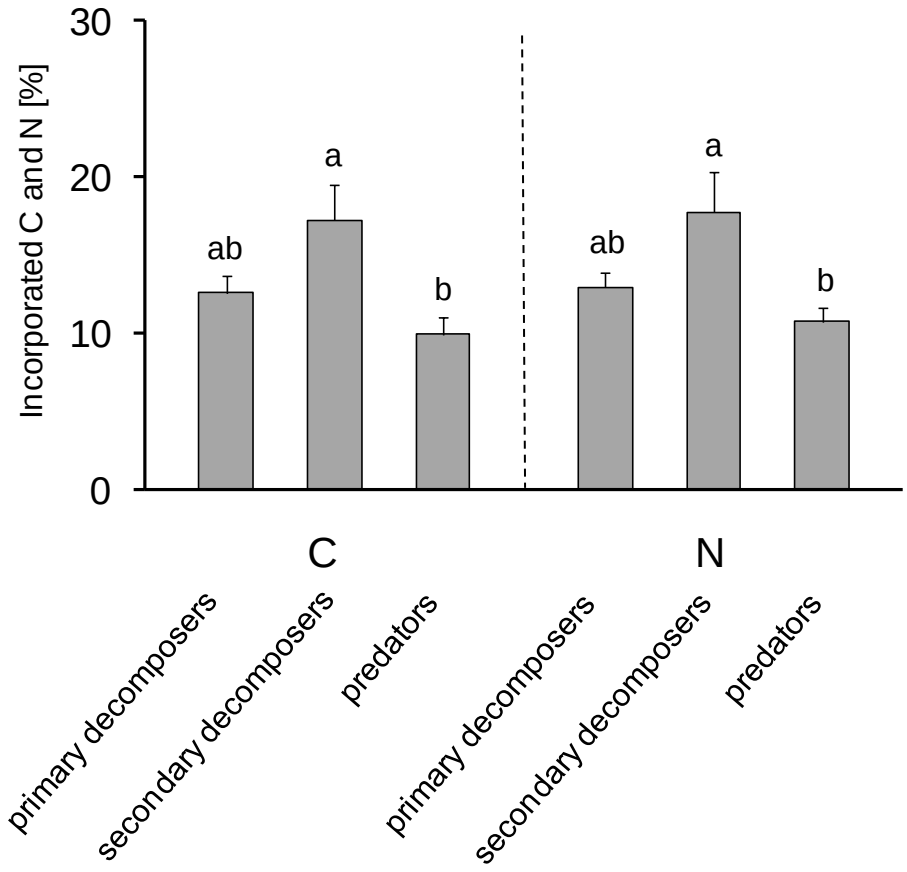

Fig. 2: Incorporation of carbon and nitrogen (means ± standard error) into primary decomposers, secondary decomposers and predators derived from beech and ash litter.

Tab. 2: F-values of two factorial ANOVAs on the effect of tree species ("tree": beech and ash) and litter mixture ("mix": pure and mixed) on the incorporation of leaf litter C into primary decomposers, secondary decomposers and predators. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

	Primary decomposers	**Secondary decomposers**	**Predators**
Fixed factor	**F-value**	**F-value**	**F-value**
Tree	**15.96*** **	4.20(*)	0.59
Mix	0.02	0.40	0.03
Tree x Mix	0.80	1.26	0.10

In primary decomposers incorporation of litter C and N was at a maximum in *Folsomia quadrioculata* with 21.3 ± 2.4% and 19.3 ± 1.0%, respectively, and at a minimum in *Eupelops hirtus* with respective values of 3.9 ± 1.4% and 3.3 ± 0.6%. Eight of the eleven taxa of primary decomposers incorporated significantly more C from ash than from beech litter whereas for N it was only three taxa (Fig. 3, Table 4).

In secondary decomposers incorporation of litter C and N was at a maximum in *Ceratophysella* spp. with 20.9 ± 1.8% and 19.1 ± 3.6%, respectively, and at a minimum in *Nothrus palustris* with respective values of 4.3 ± 1.9% and 5.2 ± 0.7%. Three of the six taxa of secondary decomposers incorporated significantly more C from ash than from beech litter; for N it was only two taxa (Fig. 4, Table 4).

In predators incorporation of litter C and N was at a maximum in *Lepidocyrtus cyaneus* with 20.9 ± 1.3% and 19.6 ± 1.5%, respectively, and at a minimum in elaterid larvae with respective values of 2.7 ± 1.7% and 3.9 ± 0.7%. Three of the nine taxa of predators incorporated more C from ash than from beech litter; no predator species incorporated more N from ash than from beech litter (Fig. 5, Table 4).

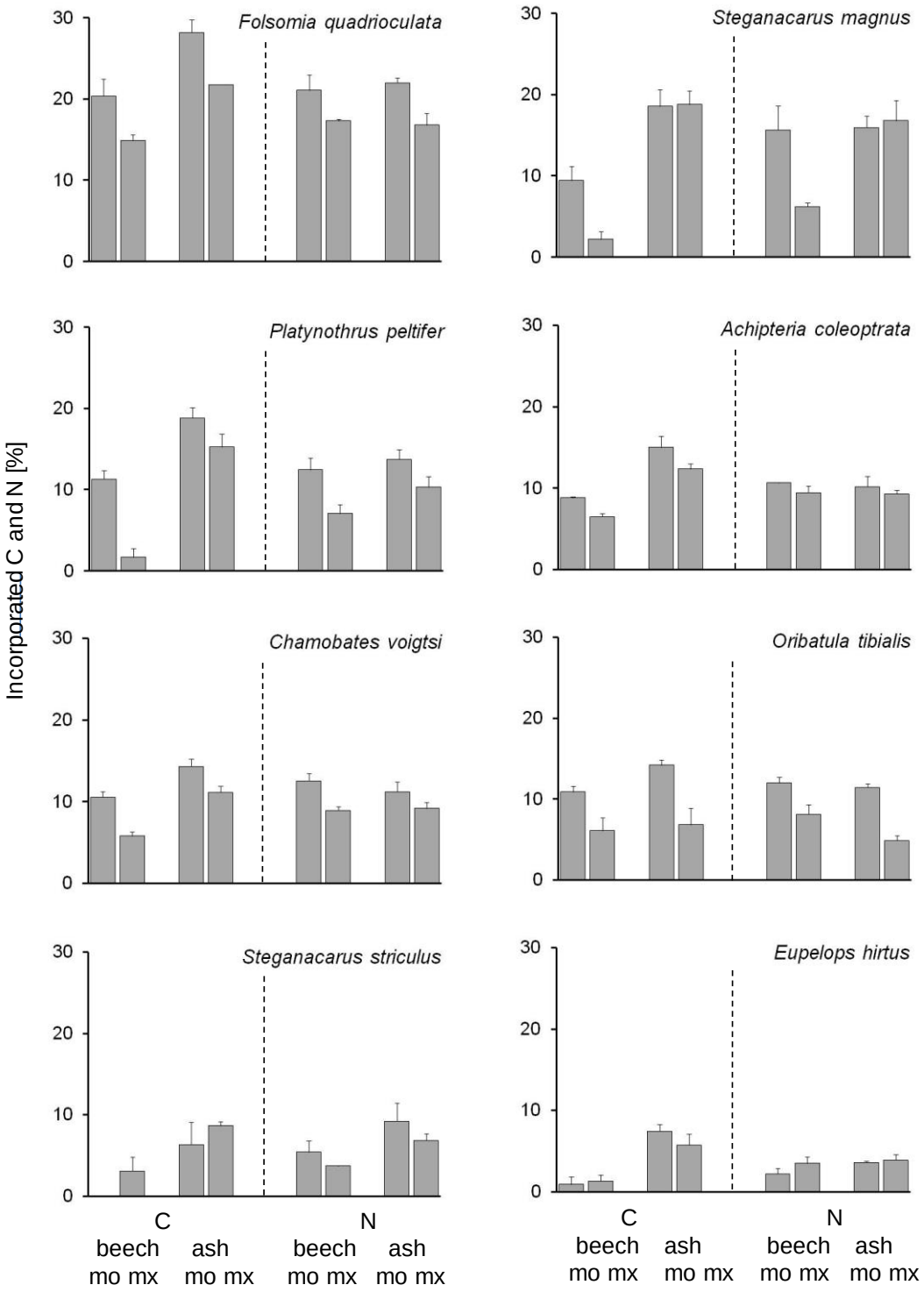

Fig. 3: Incorporation of carbon and nitrogen (means ± standard error) into primary decomposer species derived from beech and ash litter in monocultures (mo) of labeled beech and ash litter, and mixtures (mx) of labeled beech and unlabeled ash litter, and labeled ash and unlabeled beech litter.

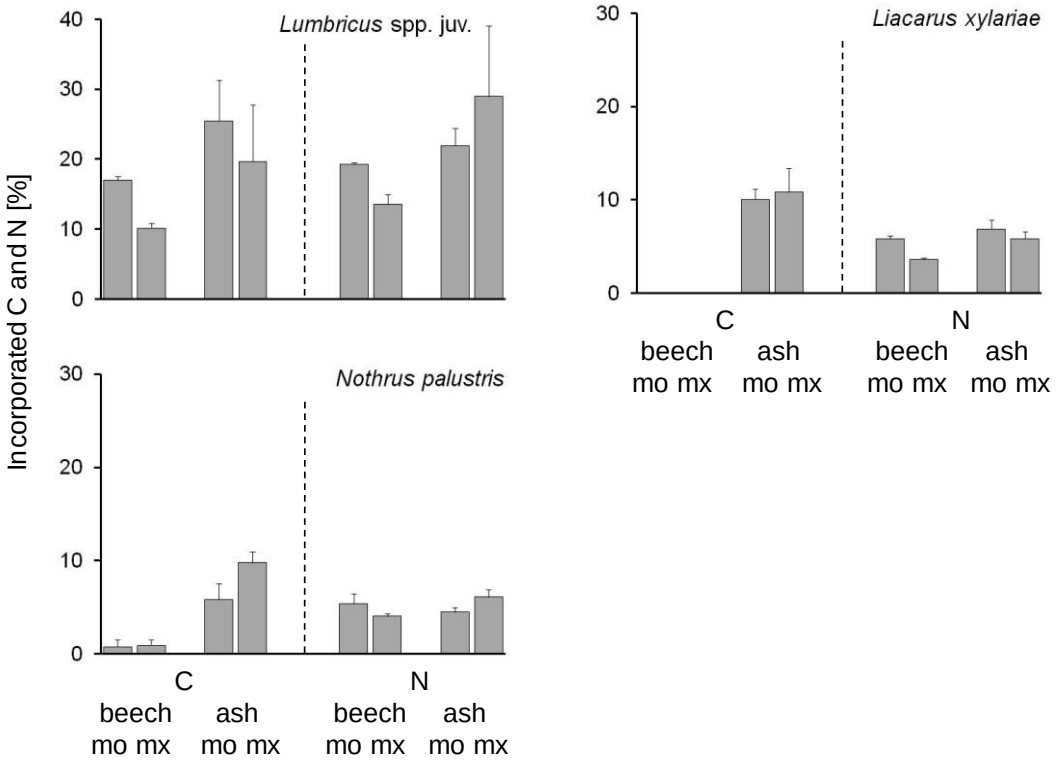

Fig. 4: Incorporation of carbon and nitrogen means ± standard error) into secondary decomposer species derived from beech and ash litter in monocultures (mo) of labeled beech and ash litter, and mixtures (mx) of labeled beech and unlabeled ash litter, and labeled ash and unlabeled beech litter.

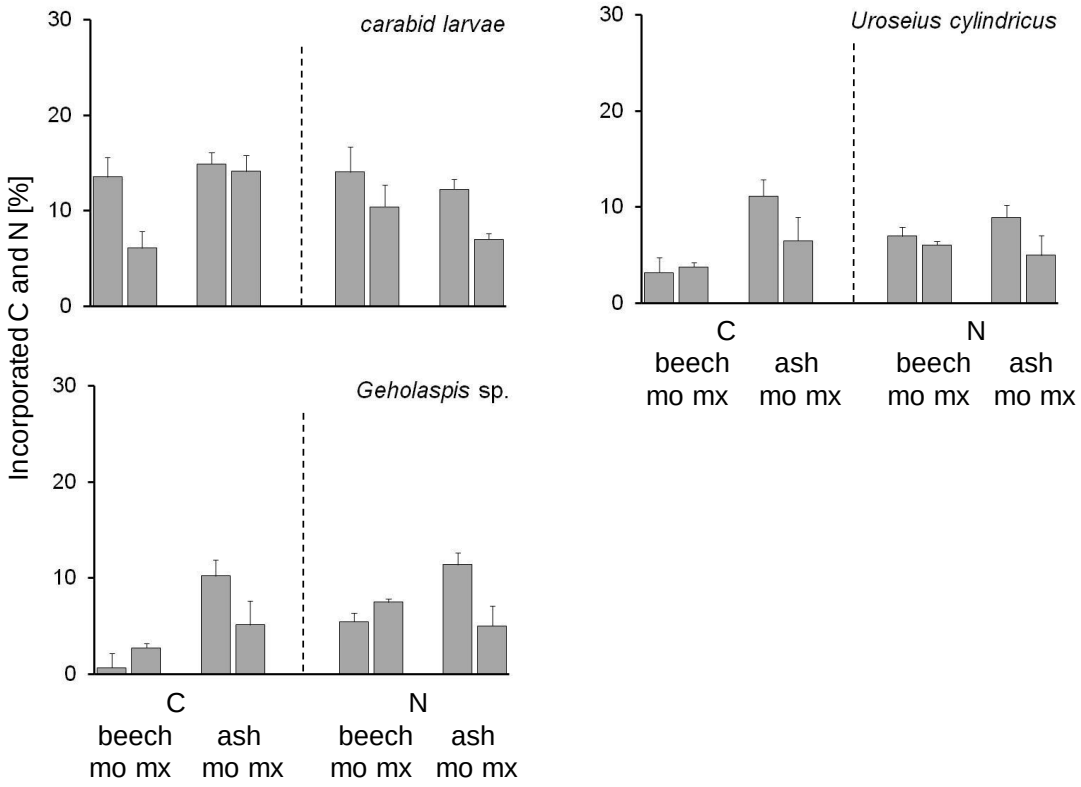

Fig. 5: Incorporation of carbon and nitrogen (in % ± standard error) into predator species derived from beech and ash litter in monocultures (mo) of labeled beech and ash litter, and mixtures (mx) of labeled beech and unlabeled ash litter, and labeled ash and unlabeled beech litter.

Table 3: Means (±standard errors) and F-values of two factorial ANOVA on the effect of tree species ("tree": beech and ash) and litter mixture ("mix": pure and mixed) on the incorporation of leaf litter C into primary decomposers, secondary decomposers and predators. *, P < 0.05; **, P < 0.01; ***, P < 0.001.

Trophic group	Taxonomic group	Species	mean	SE	Tree	Mix	Tree × Mix
Primary decomposer	Collembola	*Folsomia quadrioculata*	21.3	2.4	**44.90****	2.38	0.86
	Diplopoda	*Glomeris undulata*	13.1	2.1	1.31	0.55	3.86
	Oribatida	*Steganacarus magnus*	12.3	1.6	**74.23*****	0.06	**14.97****
		Damaeus riparius	12.1	2.5	4.11	0.0	0.65
		Platynothrus peltifer	11.8	3.2	**60.29*****	2.90	**12.23****
		Achipteria coleoptrata	10.7	1.6	**45.04*****	2.62	1.06
		Chamobates voigtsi	10.5	1.5	**35.85*****	0.02	4.17
		Oribatula tibialis	9.5	1.6	1.33	3.44	0.42
		Damaeidae	7.5	1.0	1.69	0.03	2.19
		Steganacarus striculus	4.5	1.2	**14.47***	**7.75***	0.17
		Eupelops hirtus	3.9	1.4	**25.57*****	0.41	0.01

Table 3: continued

Trophic group	Taxonomic group	Species	mean	SE	Tree	Mix	Tree × Mix
Secondary decomposer	Collembola	*Ceratophysella* sp.	20.9	1.8	0.74	0.11	2.41
	Collembola	Onychiuridae	19.5	1.9	2.46	0.0	3.22
	Lumbricida	*Lumbricus* spp. juv.	18.1	3.8	7.70*	0.19	3.02
	Isopoda	*Trichoniscus pusillus*	13.7	1.6	0.76	0.57	0.19
	Oribaitda	*Liacarus xylariae*	5.2	2.6	**87.57*** **	3.51	4.21
		Nothrus palustris	4.3	1.9	**53.17*** **	**10.35** **	**8.22** **
Predator	Collembola	*Lepidocyrtus cyaneus*	20.9	1.3	3.89	0.16	3.77
	Coleoptera	carabid larvae	12.2	1.7	**13.02** **	4.61	2.45
	Diplura	Campodeidae	8.7	1.7	0.37	1.17	0.95
	Coleoptera	*Haplocerus cappilicornis*	6.1	2.2	0.20	1.64	1.60
	Lithobiidae	*Lithobius* spp. juv.	6.7	2.5	0.31	2.68	0.03
	Gamasida	*Uroseius cylindricus*	6.1	1.5	**23.19** **	0.77	0.30
	Lithobiidae	*Strigamia accuminata*	5.5	1.6	1.37	1.99	0.05
	Gamasida	*Geholaspis* sp.	4.7	1.1	3.13	0.04	**17.41***
	Coleoptera	elaterid larvae	2.7	1.7	2.84	1.04	0.02

Table 4: Means (±standard errors) and F-values of two factorial ANOVA on the effect of tree species ("tree": beech and ash) and litter mixture ("mix": pure and mixed) on the incorporation of leaf litter N into primary decomposers, secondary decomposers and predators. *, P < 0.05; **, P < 0.01; ***, P < 0.001.

Trophic group	Taxonomic group	Species	mean	SE	Tree	Mix	Tree × Mix
Primary decomposer	Collembola	*Folsomia quadrioculata*	19.3	1.0	0.05	4.66	0.34
	Diplopoda	*Glomeris undulata*	15.7	2.7	1.84	0.49	4.12
	Oribatida	*Steganacarus magnus*	13.7	1.9	**9.88****	0.0	**9.16****
		Damaeus riparius	12.2	2.6	0.75	0.63	1.28
		Platynothrus peltifer	10.9	1.3	3.50	0.22	1.14
		Achipteria coleoptrata	9.9	0.3	0.11	**8.35***	0.02
		Chamobates voigtsi	10.5	0.8	0.10	1.09	0.66
		Oribatula tibialis	9.1	0.8	**17.17****	2.31	**13.12***
		Damaeidae	7.4	0.7	2.56	0.37	0.65
		Steganacarus striculus	6.3	1.1	**8.42***	0.02	0.06
		Eupelops hirtus	3.3	0.6	1.46	**8.03***	0.28

Table 4: continued

Trophic group	Taxonomic group	Species	mean	SE	Tree	Mix	Tree × Mix
Secondary decomposer	Collembola	*Ceratophysella* sp.	19.1	3.6	2.03	0.0	0.68
	Collembola	Onychiuridae	17.4	2.1	1.27	0.30	0.22
	Lumbricida	*Lumbricus* spp. juv.	21.0	2.2	3.22	1.06	1.76
	Isopoda	*Trichoniscus pusillus*	14.5	1.5	0.20	0.05	0.01
	Oribaitda	*Liacarus xylariae*	5.6	0.6	**5.19***	0.09	1.56
		Nothrus palustris	5.2	0.7	1.98	**5.72***	**4.74***
Predator	Collembola	*Lepidocyrtus cyaneus*	19.6	1.5	4.82	0.09	0.57
	Coleoptera	carabid larvae	10.9	1.7	1.29	0.03	0.34
	Diplura	Campodeidae	8.9	1.3	3.65	2.32	0.13
	Coleoptera	*Haplocerus cappilicornis*	6.8	1.8	2.76	0.75	0.73
	Lithobiidae	*Lithobius* spp. juv.	7.5	1.6	3.47	0.18	0.68
	Gamasida	*Uroseius cylindricus*	6.7	1.2	0.88	0.46	0.41
	Lithobiidae	*Strigamia accuminata*	6.1	1.3	0.58	2.65	0.0
	Gamasida	*Geholaspis* sp.	7.3	1.1	1.31	0.55	3.86
	Coleoptera	elaterid larvae	3.9	0.7	0.41	1.18	0.88

4. Discussion

4.1. The soil animal food web

The aim of the present study was to follow the flux of C and N derived from leaf litter into the soil animal food web of temperate deciduous forests. To trace the flux of C and N into the soil animal food web we used litter enriched in ^{13}C and ^{15}N. For studying the role of structural litter compounds for incorporation of litter elements into the soil animal food web we used labeled beech and ash litter with very similar C-to-N ratio, but different concentrations of recalcitrant structural components such as cellulose and lignin (see Materials and Methods).

Based on natural variations in $\delta^{15}N$ signatures we assigned soil animal species to trophic levels. $\delta^{15}N$ signatures of soil animal species spanned over 11.3 δ units which resembles previous studies of forest floor food webs (Ponsard and Arditi, 2000; Scheu and Falca, 2000; Pollierer et al., 2009). Assuming maximum enrichment of 1.7 δ units for primary decomposers and a trophic level enrichment of 3.4 δ units for higher trophic levels (Post, 2002; Vanderklift and Ponsard, 2003; Tiunov, 2007), the soil animal food web comprised three trophic groups, i.e. primary decomposers, secondary decomposers and predators.

4.2. Incorporation of litter derived C and N into the soil animal food web

$\delta^{13}C$ and $\delta^{15}N$ signatures of soil animals were highly enriched in treatments with labeled beech and ash litter indicating that ^{13}C and ^{15}N from decomposing litter was incorporated into soil animal species. This is in line with other studies reporting high incorporation of litter derived C and N into soil animal food webs (Elfstrand et al., 2008; Lummer et al., 2012). Notably, soil animals incorporated similar amounts of leaf litter derived C and N documenting that litter resources to a very similar extend covered energy (C) and nutrient (N) demands of soil animals.

Consistent with our first hypothesis, the signal of ^{13}C and ^{15}N of labeled litter propagated through the soil animal food web, i.e. from primary decomposers to secondary decomposers to predators. This suggests that both litter C and N are used by primary and secondary decomposers and are processed to higher trophic levels, i.e. predators. Pollierer et al. (2012) also found ^{13}C from litter of deciduous forests to be incorporated into soil animals of all trophic levels.

4.2.1. Primary decomposers

Consistent with our second hypothesis, most animal species ascribed to primary decomposers, i.e *F. quadrioculata* (Collembola), *S. magnus*, *Platynothrus peltifer*, *A. coleoptrata*, *Chamobates voigtsi*, *Oribatula tibialis*, *S. striculus* and *E. hirtus* (all Oribatida) incorporated more C derived from ash litter low in structural compounds than from beech litter high in structural compounds. Commonly, food quality of litter materials for decomposer animals is assumed to vary mainly with litter N concentrations. Results of the present study suggest that structural litter compounds are also of significant importance (Meier and Bowman, 2008). This indicates that soil animals preferentially use leaf litter with high amounts of easily accessible energy-rich C compounds. Soluble compounds such as sugars, hemicelluloses and starch are preferentially digested by detritivores (Gleixner et al., 1993; Pollierer et al., 2009), whereas lignin and cellulose remain undigested and are voided with casts (Scheu and Wolters, 1991; Gillon and David, 2001; Rawlins et al., 2006). This is in line with results of Hättenschwiler and Bracht-Joergensen (2010) who focused on the role of litter compounds for the decomposer system in tropical forests. They found increased mass loss of litter species rich in easily accessible C compounds, such as non-structural carbohydrates, and poor in recalcitrant C compounds, such as condensed tannins and lignin, and concluded that tropical decomposer food webs are limited primarily by energy derived from easily accessible C compounds of leaf litter and only secondarily by litter stoichiometry. This likely is also the case for decomposers of temperate forests, e.g. those dominated by beech, since leaf litter in these systems often also contains high amounts of recalcitrant C bound in complex structure-forming molecules such as cellolose, lignin, polyphenols and tannins (Webster and Benfield, 1986; Wardle et al., 2004). Therefore, detritivorous soil animals are likely to rely on food resources rich in labile compounds to satisfy their needs in energy and nutrients (Scheu and Setälä, 2002; Bardgett et al., 2005; Swan and Kominoski, 2012).

G. undulata incorporated high amounts of C and N from both beech and ash litter indicating that this species is able to acquire litter resources irrespective of the amount of litter structural C components. Large diplopods such as Glomerida are able to comminute leaf litter thereby getting access to inner litter compartments (Scheu and Wolters, 1991; Hättenschwiler and Gasser, 2005; Hedde et al., 2007). Thereby, Glomerida and other large detritivores with sclerotized mandibles are well

adapted to live on litter material of poor nutritional quality such as beech litter (Gillon and David, 2001; Pollierer et al., 2007).

Two taxa of oribatid mites that were ascribed to primary decomposers according to natural variations in $\delta^{15}N$ values, i.e. Damaeidae spp. and *Damaeus riparius,* incorporated similar amounts of C and N from ash and beech litter. As Damaeidae have small piercing mouthparts and are unable to fragment intact litter materials their diet is likely based on microorganisms rather than leaf litter. Leaf litter is quickly colonized by microorganisms including both fungal hyphae growing inside of the leaves, and bacteria and fungi forming mats on the leave surface (Berg and McClaughtery, 2008). Colonization of leaf litter by microorganisms is known to improve the nutritional value of leaf litter for detritivores and stimulate litter consumption (Hättenschwiler and Gasser, 2005). Therefore, detritivorous soil animals commonly feed on two trophic levels, i.e. leaf tissue and microbes, forming a gradient from primary to secondary decomposers (Lussenhop, 1992; Scheu and Setälä, 2002). Relying predominantly on a fungal diet Damaeidae might better be ascribed to secondary decomposers as also indicated in previous studies using natural variations in stable isotopes (Schneider et al., 2004). We assumed a maximum enrichment for primary decomposers of 1.7 δ units, i.e. half of the commonly used trophic level enrichment of 3.4‰, which is higher than the suggested value of 0.8‰ by Vanderclift and Ponsard (2003). The higher trophic level enrichment used for ascribing species to primary decomposers might have resulted in overestimating the number of primary decomposer species in the present study.

In contrast to our expectations, soil animals incorporated similar amounts of N from beech and ash litter indicating that litter N availability varied little between litter species differing in structural litter compounds. In fact, most litter N is bound in easily digestible compounds such as amino acids and proteins which in primary decomposers might be used directly or in secondary decomposers via feeding on microorganisms which sequestered the nutrients in these compounds. Overall, the results suggest that the concentration of litter nutrients rather than that of structural litter compounds drives nutrient acquisition of primary and secondary decomposers.

Conform to our third hypothesis, compared to secondary decomposers and predators, primary decomposers incorporated low amounts of leaf litter derived C and N. This indicates that soil animals feeding directly on leaf litter, i.e. nutritionally poor food, are facing particular problems in getting access to the nutrients therein.

In fact, there is increasing evidence that only few soil animals are able to satisfy their nutritional needs by feeding directly on leaf litter (Illig et al., 2005; Pollierer et al., 2009), and the animal species able to do that typically are large, equipped with strong mandibles, and grow slowly, i.e. live for many years (Scheu, 2002; Pollierer et al., 2007; Gessner et al., 2010). Various adaptations to nutritionally poor food resources, such as leaf litter, have been postulated, such as “protein sparing” and catabolism with slow metabolic rates (Swift et al., 1979; Castellini and Rea, 1992; Pollierer et al., 2009). Overall, the results underline the importance of litter resources rich in labile compounds and nutrients for primary decomposers to satisfy their energy needs and overcome stoichiometric imbalances of their body tissue (Scheu and Setälä, 2002; Bardgett et al., 2005; Martinson et al., 2008).

4.2.2. Secondary decomposers

Microbial feeders, i.e. secondary decomposers, incorporated higher amounts of C and N from beech and ash litter than primary decomposers suggesting that more litter derived C and N is available for detritivore soil animals feeding on a microbial diet than for primary decomposers feeding on litter. Saprotrophic fungi are the primary agents of leaf litter decomposition at early stages of decay and built fine filamental hyphal mats overgrowing leaf litter (Swift et al., 1979; Osono, 2003). Fungal feeding soil invertebrates presumably graze on these hyphal structures that are easier to digest than recalcitrant leaf litter rich in structural C compounds. Notably, secondary decomposers incorporated similar amounts of C and N from beech and ash litter indicating that the fungi they grazed on mobilized litter N thereby making it available for fungal grazers.

Decomposition of leaf litter involves a succession of saprotrophic fungal species with the initial phase of litter decomposition being dominated by fungal species degrading labile C and N compounds (Hudson, 1968; Berg, 2000; Osono, 2007). This implies that fungal feeding soil animals get access to labile C and N litter compounds inside of the leaves without the necessity to fragment the litter. Fungi are particularly effective in capturing litter C and N as they grow into leaves e.g., via stomata and transport nutrients from patches with high supply to sites where nutrients (in particular N) limit resource exploitation by microorganisms (Berg and Staaf, 1981, Berg, 2000; Schimel and Hättenschwiler, 2007).

There is increasing evidence that carbon and nutrients in decomposer systems are predominantly channeled to higher trophic levels via the fungal energy channel (Oelbermann et al., 2008; Crowther et al. 2012). This likely applies in particular to forests of late succession stages as late succession trees such as beech produce low-quality litter favouring fungi and fungal consumers (Wardle et al., 2002; Maraun et al., 2003; Hättenschwiler et al., 2005; Pollierer et al., 2009). Results of the present study provide evidence that the dominance of the fungal energy channel in decomposer systems receiving litter of high structural litter compounds i.e., litter of low quality, is due to fungi able to capture both litter C and N and thereby making it available to fungal grazers.

Three secondary decomposers, *Ceratophysella* spp., Onychiuridae and *T. pusillus*, incorporated high amounts of C and N from beech and ash litter indicating a fungal based diet. *Ceratophysella* spp. feeds on a wide range of diets, including fungi and animals, whereas Onychiuridae predominantly feed on fungi (Chahartaghi et al., 2005). *T. pusillus* is likely to feed on a mixture of litter, microorganisms and root associated fungi (Kautz et al., 2000; Pollierer et al., 2012). High incorporation of beech litter N into these species suggests that processing of litter N by fungi improves N availability for detritivores. *L. xylariae*, *N. palustris* (both Oribatida), and *Lumbricus* spp. juv. (Lumbricida) incorporated higher amounts of N and C from ash than from beech litter indicating that these species feed on a fungal based diet in presence of recalcitrant (beech) litter, but also directly on litter if high quality (ash) litter is available. Mixing diets to optimize nutrient uptake and switching to more favorable food resources if becoming available presumably is common among secondary decomposers (Scheu and Simmerling, 2004; Endlweber et al., 2009).

4.2.3. Predators

Predators comprised a similar fraction of litter derived C and N than primary decomposers but a considerably lower fraction than secondary decomposers indicating that (1) predatory species might have fed predominantly on primary decomposers, (2) predatory species fed on prey not investigated in this study relying on other than litter resources and/or (3) propagation of litter C and N to higher trophic levels has been delayed. In contrast to primary decomposers, secondary decomposers typically are smaller and less sclerotized thereby forming more suitable prey for soil predators (Scheu and Falca, 2000; Peschel et al., 2006;

Pollierer et al., 2009); predominant feeding on primary decomposers therefore is unlikely. Prey relying on other than litter C and N likely contributed to low incorporation of litter derived C and N into predators. E.g., *Strigamia accuminata* hunts in soil pores for enchytraeids and endogeic earthworms (Wolters and Eckschmitt, 1997) which likely incorporate predominantly soil rather than litter resources; both likely were present in the microcosms but not extracted by the heat extraction technique used.

On average, the body mass of predator species (overall mean 0.90 ± 0.60 mg) considerably exceeded that of secondary decomposer species (overall mean 0.19 ± 0.31 mg; V. Eissfeller, unpubl. data). Therefore, incomplete replacement of predator body tissue during the exposure in the field for five months likely contributed to low incorporation of litter derived C and N into predators. Compared to small secondary decomposers such as Collembola (Haubert et al., 2005; Chamberlain et al., 2006), replacement of body tissue in large predators such as spiders is markedly slower (Rickers et al., 2006; Oelbermann et al., 2008).

Juveniles of *Lithobius* spp. incorporated similar amounts of C from beech and ash litter and are likely to feed on a mixed diet of primary and secondary decomposers since this species hunts preferentially on small mobile prey such as mites and collembolans in the humus layer (Poser, 1990; Ferlian et al., 2011). Carabid lavae, *U. cylindricus* and *Geholaspis* sp. (both Mesostigmata) incorporated more C and N from ash than from beech litter. These species are highly mobile and probably hunt collembolans or nematodes relying on litter derived C and N within the upper litter layer. Klarner et al. (2013) stated recently that the majority of mesostigmata species hunt predominantly on fungivorous nematodes relying mostly on root derived C rather than on litter derived C sources. However, they suggested for some mesostigmata preying on nematodes nourished saprotrophic fungi. Campodeidae and *L. cyaneus* (Collembola) incorporated litter derived C and N excluding any difference of beech and ash litter. Despite being described as a fungal feeder (Chahartaghi et al., 2005), *L. cyaneus* likely lives on litter associated nematodes within the upper litter layer. Campodeidae have been described to hunt for nematodes (Scheu and Falca, 2000) and might prey on nematodes nourished by saprotrophic or mycorrhizal fungi.

4.3. Mixing of beech and ash litter

Treatments with mixed beech and ash litter allowed testing if soil animals switch to litter low in structural compounds (ash) if added to litter high in structural compounds (beech). Unexpectedly, mixing of litter affected the incorporation of litter derived C and N of only few soil animal species indicating that the processing of C and N of individual litter species varies little between pure and mixed stands. This supports our conclusion that incorporation of litter resources into the soil animal food web is mainly based on the fungal energy channel and fungal capture of litter resources is driven mainly by the concentration of litter nutrient rather than the concentration of litter structural compounds (see above). This view is further supported by the fact that mixing of leaf litter mainly affected primary decomposers, i.e. *S. magnus*, *P. peltifer* and *S. striculus* (all Oribatida) suggesting that predominantly species feeding directly on leaf litter benefit from high quality litter.

4.4. Conclusions

Results of the present study highlight the importance of leaf litter poor in structural compounds such as ash for fuelling soil animal food webs. Litter derived C and N was utilized by primary and secondary decomposers and was processed to higher trophic levels, i.e. predators. Primary decomposers incorporated low amounts of litter derived C and N pointing to low nutritional quality of leaf litter rich in structural compounds. Secondary decomposers incorporated most C and N derived from leaf litter suggesting that litter derived resources mainly propagate into the soil animal food web via the fungal energy channel. Higher incorporation of litter resources into predators as compared to primary decomposers indicate that predators predominantly feed on secondary decomposers but due to larger body size replacement of predator body tissue by prey resources was incomplete during the experimental duration of five months. Mixing of litter low and high in structural compounds affected the incorporation of litter resources into the food web only little suggesting that resource capture by fungi and incorporation into higher trophic levels via the fungal energy channel is rather independent of litter structural compounds.

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References

Albers, D., Schaefer, M., Scheu, S., 2006. Incorporation of plant carbon into the soil animal food web of an arable system. Ecology 87, 235–245.

Ball, B.A., Bradford, M.A., Hunter. M.D., 2009. Nitrogen and phosphorous release from mixed litter layers is lower than predicted from single species decay. Ecosystems 12, 87-100.

Bardgett, R.D., Bowman, W.D., Kaufmann, R., Schmidt, S.K., 2005. A temporal approach to linking aboveground and belowground ecology. Trends in Ecology and Evolution 20, 634–641.

Berg, B., 2000. Litter decomposition and organic matter turnover in northern forest soils. Forest Ecology and Management 133, 13-22.

Berg, B., McClaugherty, C., 2008. Plant Litter - Decomposition, Humus Formation, Carbon Sequestration. Springer, Berlin, Germany.

Berg, B. and Staaf H., 1981. Leaching, accumulation and release of nitrogen in decomposing forest litter. Terrestrial nitrogen cycles, Ecological Bulletins (Stockholm). Ecological Bulletin 33, 163–178.

Castellini, M.A. and Rea, L.D., 1992. The biochemistry of natural fasting at its limits. Experientia 48, 575-582.

Chahartaghi, M., Langel, R., Scheu, S., Ruess, L., 2005. Feeding guilds in Collembola based on nitrogen stable isotope ratios. Soil Biology and Biochemistry 37, 1718–1725.

Chapman, S.K., Langely, J.A., Hart, S.C., Koch, G.W., 2006. Plants actively control nitrogen cycling: uncorking the microbial bottleneck. New Phytologist 169, 27-34.

Chamberlain, P.M., Bull, I.D., Black, H.I.J., Ineson, P., Evershed, R.P., 2006. The effect of diet on isotopic turnover in Collembola examined using the stable carbon isotopic compositions of lipids. Soil Biology and Biochemistry 38, 1146-1157.

Coleman, D.C., Reid, C.P.P., Cole, C.V., 1983. Biological strategies of nutrient cycling in soil systems. Advances in Ecological Research 13, 1-55.

Cornwell, W.K., Cornelissen, J.H.C., Amatangelo, K., et al., 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. Ecology Letters 11, 1065-1071.

Crowther, T.W., A´Bear, A.D., 2011. Impacts of grazing soil fauna on decomposer fungi are species-specific and density-dependent. Fungal Ecology 5, 277-281.

Crowther, T.W., 2012. Impacts on grazing soil fauna on decomposer fungi are species-specific and density dependent. Fungal Ecology 5, 277-281.

Couteaux, M.M., Bottner, P., Berg, B., 1995. Litter decomposition, climate and litter quality. Tree 10, 63-66.

DeNiro, M.J., Epstein S., 1978. Influence of diet on distribution of carbon isotopes in animals. Geochimica Cosmochimica Acta 42, 495-506.

Dungait, J.A.J., Hopkins, D.W., Gregory, A.S., Whitmore A.P., 2012. Soil organic matter turnover is governed by accessibility not recalcitrance. Global Change Biology 18, 1781-1796.

Elfstrand, S., Lagerlöf, J., Hedlund, K., Martensson, A., 2008. Carbon routes from decomposing plant residues and living roots into soil food webs assessed with ^{13}C labeling. Soil Biology and Biochemistry 40, 2530-2539.

Eissfeller V., Maraun M., Scheu S., submitted. Incorporation of plant carbon and microbial nitrogen into the rhizosphere food web of beech and ash.

Endlweber, K., Rueß, L., Scheu, S., 2009. Collembola switch diet in presence of plant roots thereby functioning as herbivores. Soil Biology and Biochemistry 41, 1151-1154.

Ferlian, O., Scheu, S., Pollierer, M.M., 2012. Trophic interactions in centipeds (Chilopoda, Myriapoda) as indicated by fatty acid patterns: Variations with life stage, forest age and season. Soil Biology and Biochemistry 52, 33-42.

Frey, S.D., Elliott, E.T., Paustian, K., Peterson, G.A., 2000. Fungal translocation as a mechanism for soil nitrogen inputs to surface residue decomposition in a no-tillage agroecosystem. Soil Biology and Biochemistry 32, 1001-1004.

Fry, B., 2006. Mixing. In: Stable Isotope Ecology. Springer, New York, USA, 308 pp.

Gartner, T.B., Cardon Z.G., 2004. Decomposition dynamics in mixed species leaf litter. Oikos 104, 230-246.

Gannes, L.Z., D.M. O´Brien, et al., 1997. Stable isotopes in animal ecology: assumptions, caveats, and a call for more laboratory experiments. Ecology 78, 1271-1276.

Geissler, D., Horwath, W.R., Joergensen, R.G., 2010. Pathways of nitrogen utilization by soil microorganisms - A review. Soil Biology and Biochemistry 42, 2058-2067.

Gessner, M.O., Swan, M.S., Dang, C.K., McKie, B.G., Bardgett, R.D., Wall, D.H., Hättenschwiler S., 2010. Diversity meets decomposition. Trends in Ecology and Evolution 25, 372-380.

Gillon, D. and David, J.F., 2001. The use of near infrared reflectance spectroscopy to study chemical changes in the leaf litter consumed by saprophagous invertebrates. Soil Biology and Biochemistry 33, 2159-2161.

Gleixner, G., Danier, H.J., Werner, R.A., Schmidt, H.L., 1993. Correlations between the ^{13}C content of primary and secondary plant-products in different cell compartments and that in decomposing Basidiomycetes. Plant Physiology 102, 1287-1290.

Guckland, A., Flessa, H., Prenzel, J., 2009. Controls of temporal and spatial variability of methane uptake in soils of a temperate deciduous forest with different abundance of European beech (*Fagus sylvatica* L.). Soil Biology and Biochemistry 41, 1659-1667.

Haubert, D., Langel, R., Scheu, S., Ruess, L., 2005. Effects of food quality, starvation and life stage on stable isotope fractionation in Collembola. Pedobiologia 49, 229-237.

Hättenschwiler, S., Bracht-Joergensen, H., 2010. Carbon quality rather than stoichiometry controls litter decomposition in a tropical rain forest. Journal of Ecology 98, 754-763.

Hättenschwiler, S., Gasser, P., 2005. Soil animals alter plant litter diversity effects on decomposition. Proceedings of the National Academy of Science of the USA 102, 1519-1524.

Hättenschwiler, S., Tiunov, A.V., Scheu S., 2005. Biodiversity and litter decomposition in terrestrial ecosystems. Annual Reviews of Ecology, Evolution and Systematics 36, 191-218.

Hedde, M., Bureau, F., Akpa-Vinceslas, M., Aubert, M., Decaens, T., 2007. Beech leaf degradation in laboratory experiments: effects of eight detritivorous invertebrate species. Applied Soil Ecology 35, 291-301.

Hieber, M., Gessner, M.O., 2002. Contribution of stream detritivores, fungi and bacteria to leaf breakdown based on biomass estimates. Ecology 83, 1026-1038.

Högberg, P., Read, D.J., 2006. Towards a more plant physiological perspective on soil ecology. Trends in Ecology and Evolution 21, 548-554.

Högberg, P., Högberg, M.N., Göttlicher, S.G., 2008. High temporal resolution tracing of photosynthate carbon from the tree canopy to forest soil microorganisms. New Phytologists 177, 220-228.

Hudson, H. J., 1968. The ecology of fungi on plant remains above the soil. New Phytologist 67, 837-874.

Illig, J., Langel, R., Norton, R.A., Scheu, S., Maraun, M., 2005. Where are the decomposers? Uncovering the soil food web of a tropical montane rain forest in southern Ecuador using stable isotopes (^{15}N). Journal of Tropical Ecology 21, 589–593.

Jacob, M., Weland, N., Platner, C., Schaefer, M., Leuschner, C., Thomas, F.M., 2009. Nutrient release from decomposing leaf litter of temperate deciduous forest trees along a gradient of increasing tree species diversity. Soil Biology and Biochemistry 41, 2122-2130.

Jacob, M., Leuschner C., Thomas F.M., 2010. Productivity of temperate broad-leaved forest stands differing in tree species diversity. Annals of Forest Science 67, 503.

Kautz, G., Zimmer, M., Topp, W., 2000. Responses of the parthenogenetic isopod *Trichoniscus pusillus* (Isopoda: Oniscidea) to changes in food quality. Pedobiologia 44, 75-85.

Klarner B., Maraun M., Scheu S., 2013. Trophic diversity and niche partitioning in a species rich predator guild - Natural variations in stable isotope ratios ($^{13}C/^{12}C$, $^{15}N/^{14}N$) of mesostigmatid mites (Acari, Mesostigmata) from Central European beech forests. Soil Biology and Biochemistry 57, 327-333.

Langenbruch, C., Helfrich M., Joergensen R.G., Gordon J., Flessa, H., 2012. Effects of nutrient cycling through litter of different broadleaved deciduous tree

species on soil biochemical properties and the dynamics of carbon and nitrogen in soil. University of Göttingen. Dissertation. Göttingen.

Lecerf, A., Marie, G., Kominoski, J.S., 2011. Incubation time, functional litter diversity, and habitat characteristics predict litter mixing effects on decomposition. Ecology 92, 219-227.

Lindahl, B.D., Ihrmark, K., Boberg J., Trumbore, S.E., Högberg, P., Stenlid, J., Finlay, R.D., 2006. Spatial separation of litter decomposition and mycorrhizal nitrogen uptake in a boreal forest. New Phytologist 173, 611-620.

Lummer, D., Scheu, S., Butenschoen, O., 2012. Nitrogen transfer between decomposing litter species is an important but not the only factor responsible for synergistic mixture effects on litter decomposition. Oikos, 121, 1649-1655.

Lussenhop, J., 1992. Mechanisms of microarthropod - microbial interactions in soil. Advances in Ecological Research 23, 1-33.

Maraun, M., Martens, H., Migge, S., Theenhaus A., Scheu, S., 2003. Adding to „the enigma of soil animal diversity“: fungal feeders and saprophagous soil invertebrates prefer similar food substrates. European Journal of Soil Biology 39, 85-95.

Maraun, M., Erdmann, G., Fischer, B.M., Pollierer, M.M., Norton, R.A., Schneider, K., Scheu, S., 2011. Stable isotopes revisited: Their use and limits for oribatid mite trophic ecology. Soil Biology and Biochemistry 43, 877-882.

Martinson, H. M., Schneider, K., Gilbert K., Hines J., Hamback J.E., Fagan P.A., 2008. Detritivory: stoichiometry of a neglected trophic level. Ecological Research 23: 487-491.

Mellilo, J.M., Aber, J.D., Muratore, J.F., 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology 63, 621-626.

Meier, C.L., Bowman, W.D., 2008. Linke between plant litter chemistry, species diversity, and belowground ecosystem function. Proceedings of the National Academy of Sciences 105, 19780-19785.

Minagwa, M., Wada, E., 1984. Stepwise enrichment of ^{15}N along food chains: Further evidence and the relationship between ^{15}N and animal age. Geochimica et Cosmochimica Acta 48, 1135-1140.

Moore, J.C., Hunt, H.W., 1988. Resource compartmentation and the stability of real ecosystems. Nature 333, 261-263.

Moore, J.C., Berlow, E.L., Coleman, D.C., de Ruiter, P.C., Dong, Q., Hastings, A., Johnson, N.C., McCann, K.S., Melville, K., Morin, P.J., Nadelhoffer, K.,

Rosemond, A.D., Post, D.M., Sabo, J.L., Scow, K.M., Vanni, M.J., Wall, D.H., 2004. Detritus, trophic dynamics and biodiversity. Ecology Letters 7, 584-600.

Nielsen, U.N., Ayres, E., Wall, D.H., Bardgett, R.D., 2011. Soil biodiversity and carbon cycling: a review and synthesis of studies examining diversity-function relationships. European Journal of Soil Science 62, 105-116.

Oelbermann, K., Langel, R., Scheu, S., 2008. The role of prey out of the decomposer system for generalist predators of grassland. Oecologia 155, 605-617.

Oelbermann, K. and Scheu, S., 2010. Trophic guilds of generalist feeders in soil animal communities as indicated by stable isotope analysis ($^{15}N/^{14}N$). Bulletin of Entomological Research 100, 511-520.

Osono, T., Fukasawa Y., et al., 2003. Roles of diverse fungi in larch needle-litter decomposition. Mycologia 95, 820-826.

Osono, T., 2007. Ecology of lignolytic fungi associated with leaf litter decomposition. Ecology Research 22, 955-974.

Pérez-Harguindeguy, N., Díaz, S., Cornelissen, J.H.C., Vendramini, F., Cabido M., and Castellanos, A., 2000. Chemistry and toughness predict litter decomposition rates over a wide spectrum of functional types and taxa in central Argentinia. Plant and Soil 218, 21-30.

Peschel, K., R. A. Norton, et al., 2006. Do oribatid mites live in enemy-free space? Evidence from feeding experiments with the predatory mite *Pergamasus septentrionalis*. Soil Biology and Biochemistry 38, 2985-2989.

Pollierer, M.M., Langel, R., Korner, C,.Maraun, M., Scheu, S., 2007. The underestimated importance of belowground carbon input for forest soil animal food webs. Ecology Letters 10, 729-736.

Pollierer, M.M., Langel, R., Scheu, S., Maraun, M., 2009. Compartmentalization of the soil animal food web as indicated bydual analysis of stable isotope ratios ($^{15}N/^{14}N$ and $^{13}C/^{12}C$). Soil Biology & Biochemistry 41, 1221–1226.

Pollierer, M. M., S. Scheu, et al., 2010. Taking it to the next level: trophic transfer of marker fatty acids from basal resource to predators. Soil Biology and Biochemistry 42, 919-925.

Pollierer, M.M., Dykmans, J., Scheu, S., Haubert, D., 2012. Carbon fluxes through fungi and bacteria into the forest soil animal food web as indicated by compound-specific ^{13}C fatty acid analysis. Functional Ecology, doi: 10.1111/j.1365-2435.2012.02005.x.

Polis, G.A., Strong D.R., 1996. Food web complexity and community dynamics. American Naturalist 147, 813-846.

Ponsard, S., Arditi R., 2000. What can stable isotopes (delta N-15 and delta C-13) tell about the food web of soil macro-invertebrates? Ecology 81, 852-864.

Post, D.M., 2002. Using stable isotopes to estimate trophic position: models, methods and assumptions. Ecology 83, 703-718.

Rawlins, A. J., Bull I.D., Poirier, N., Ineson, P., Evershed, R.P, 2006. The biochemical transformation of oak (*Quercus robur*) leaf litter consumed by the pill millipede (*Glomeris marginata*). Soil Biology and Biochemistry 38, 1063-1076.

Rickers, S., R. Langel, Scheu S., 2006. Dietary routing of nutrients from prey to offspring in a generalist predator: effects of prey quality. Functional Ecology 20, 124-131.

Ruf, A., Kuzyakov, Y., Lopatovskaya, O., 2006. Carbon fluxes in soil food webs of increasing complexity revealed by ^{14}C labeling and ^{13}C natural abundance. Soil Biology and Biochemistry 38, 2390-2400.

Scheu, S., Falca, M., 2000. The soil food web of two beech forests (*Fagus sylvatica*) of contrasting humus type: stable isotope analysis of a macro- and a mesofauna-dominated community. Oecologia 123, 285–286.

Scheu, S., 2002. The soil food web: structure and perspectives. European Journal of Soil Biology 38, 11−20.

Scheu, S., Setälä H., 2002. Multitrophic interactions in decomposer communities. Multitrophic level interactions, Cambridge University Press, New York.

Scheu, S., 2005. Linkages between tree diversity, soil fauna and ecosystem processes. In: Scherer-Lorenzen, M., Köhler, C., Schulze, E.-D., (Eds.) Forest Diversity and Function: Temperate and Boreal Systems, Ecological Studies 176, Springer, Berlin, Germany, pp. 211-233.

Scheu, S., Simmerling, F., 2004. Growth and reproduction of fungal feeding Collembola as affected by fungal species, melanin and mixed diets. Oecologia 139, 347-353.

Scheu, S., Wolters, V., 1991. The influence of fragmentation and bioturbation on the decomposition of carbon-14-labelled beech leaf litter. Soil Biology & Biochemistry 23, 1029-1034.

Scheunemann, N., Scheu, S., Butenschoen, O., 2010. Incorporation of decade old soil carbon into the soil animal food web of an arable system. Applied Soil Ecology 46, 59-63.

Schmidt, O., Curry J.P., et al., 2004. Dual stable isotope analysis (delta C-13 and delta N-15) of soil invertebrates and their food sources. Pedobiologia 48, 171-180.

Schneider, K., Migge, S., Norton, R.A., Scheu, S., Langel, R., Reineking, A., Maraun, M., 2004. Trophic niche differentiation in soil microarthropods (Oribatida, Acari): evidence from stable isotope ratios ($^{15}N/^{14}N$). Soil Biology and Biochemistry 36, 1769–1774.

Schneider, F.D., Scheu, S., Brose, U., 2012. Body mass constraints on feeding rates determine the consequences of predator loss. Ecology Letters 15, 436-443.

Schimel J.P., Hättenschwiler, S., 2007. Nitrogen transfer between decomposing leaves of different N status. Soil Biology and Biochemistry 39, 1428-1436.

Swan, C.M., Kominoski, J.S., 2012. Biodiversity and Ecosystem Function of Decomposition. In: eLS. John Wiley & Sons, Ltd: Chichester. doi: 10.1002/9780470015902.a0023601.

Swift, M.J., Heal, O.W., Anderson, J.M., 1979. Decomposition in terrestrial ecosystems. Blackwell, Oxford, UK.

Szanzer, M., Ileva-Makulec, K., Kajak, A., et al., 2011. Impact of litter diversity on decomposition processes and communities of soil organisms. Soil Biology and Boichemistry 43, 9-19.

Thoms, C., Gattinger, A., Jacob, M., Thomas, F.M., Gleixner G., 2010. Direct and indirect effects of tree diversity drive soil microbial diversity in a temperate deciduous forest. Soil Biology and Biochemistry 42, 1558-1565.

Tiunov, A.V., Scheu, S., 2005. Arbuscular mycorrhiza and Collembola interact in affecting community composition of saprotrophic microfungi. Oecologia 142, 636-642.

Tiunov, A.V., 2007. Stable isotopes of carbon and nitrogen in soil ecological studies. Biology Bulletin 34, 395-407.

Tiunov, A. V., 2009. Particle size alters litter diversity effects on decomposition. Soil Biology and Biochemistry 41, 176-178.

VanderClift, M.A., Ponsard, S., 2003. Sources of variation in consumer-diet delta N-15 enrichment: a meta-analysis. Oecologia 136, 169–182.

Vitousek, P.M., Hättenschwiler, S., Olander, L., Allison S., 2002. Nitrogen and Nature. Ambio 31, 97-101.

Wardle, D.A., 2002. Communities and Ecosystems: Linking the Aboveground and Belowground Components. Monographs in Population Biology. Princeton University Press, Princeton, USA.

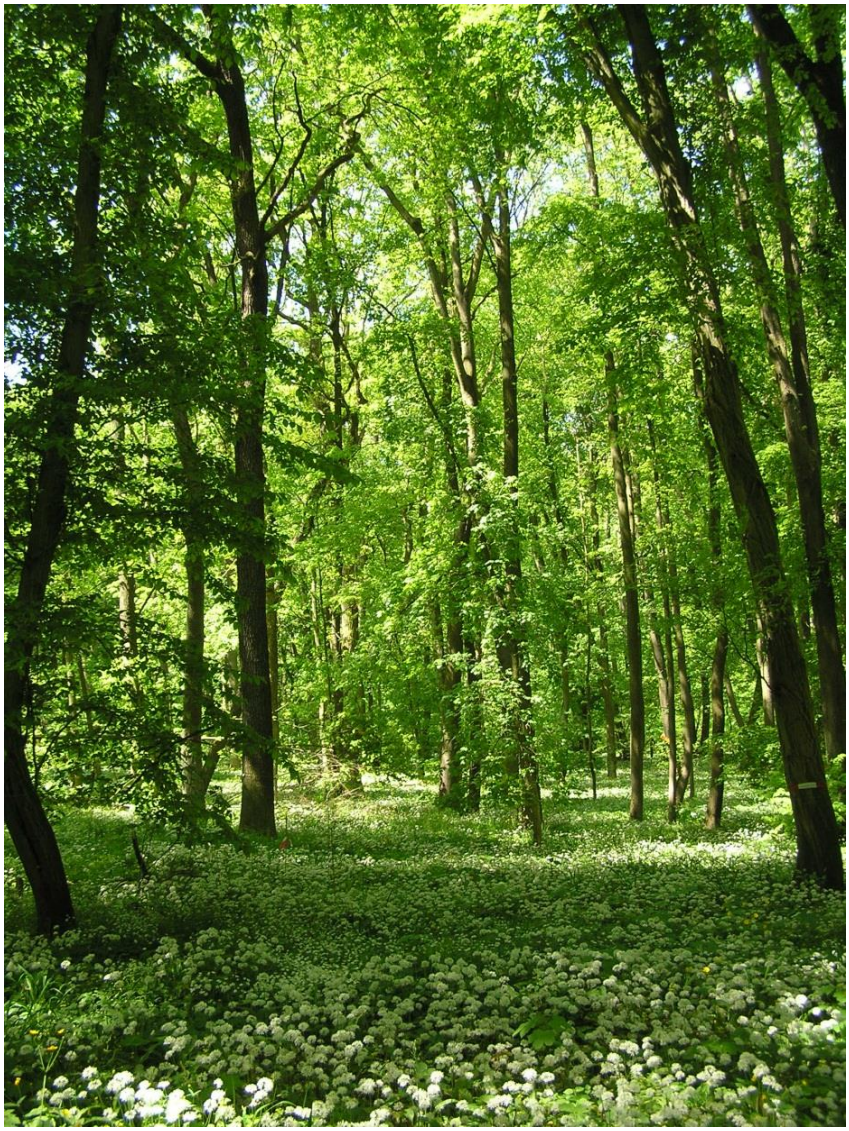
Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setälä, H., van der Putten, W.H., Wall, D.H., 2004. Ecological linkages between aboveground and belowground biota. Science 304, 1629-1633.

Wardle, D.A., 2006. The influence of biotic interactions on soil biodiversity. Ecology Letters 9, 870-886.

Webster J.R., and Benfield, E.F, 1986. Vascular plant breakdown in freshwater ecosystems. Annual Review of Ecology and Systematics 17,567–594.

Zeller, B., Coiln-Belgrand, M., Dambrine, E., Martin, F., Bottner, P., 2000. Decomposition of ^{15}N-labeled beech litter and fate of nitrogen derived from litter in a beech forest. Oecologia, 550-559.

5 General Discussion



General Discussion

The main focus of this dissertation was to investigate the role of trees for the structure and functioning of soil animal food webs in temperate forest ecosystems. Major outcomes of the field study presented in Chapter 2 allowed separating effects of tree diversity from tree identity. The results suggest that tree species identity is of major importance as structuring force for the soil mesofauna community as exemplified by investigating oribatid mites. Further, I gained insight into the impact of tree species traits on the flux of C and N through the soil animal food web. Results from stable isotope labeling experiments presented in Chapters 3 and 4 highlighted the importance of tree species traits for the above- and belowground input of C and N and the flux of these elements through the soil animal food web.

1. Tree species as drivers of soil animal community composition

The experimental design of the field study presented in Chapter 2 allowed separating impacts of tree diversity from tree identity on oribatid mite communities. In contrast to our hypothesis, tree species diversity neither beneficially affected the abundance of oribatid mites nor altered their community structure. These findings were rather surprising since they indicate that higher diversity of leaf litter and higher diversity of fine roots are of minor importance for soil animal communities of deciduous forest ecosystems. This contrasts results of the study of Hansen et al. (2000) who found oribatid mites to benefit from litter mixtures and associated microhabitat diversity. Different litter types were assumed to serve complementary functions, i.e. recalcitrant leaf litter providing habitable space and high quality litter serving additional spatial niches and resources.

In contrast to tree diversity we found evidence for strong effects of tree identity on oribatid mite communities which surpassed effects of tree diversity and this supported our second hypotheses. However, in contrast to our assumption tree identity effects were not driven by nutritional quality of the litter material. Oribatid mites reached highest densities in beech clusters indicating that they benefitted from the presence of beech providing recalcitrant litter material rather than being detrimentally affected by low nutritional quality of beech litter. Presumably, oribatid mites benefitted from low quality beech litter since it decomposes slowly and thereby provides habitable space by assembling in organic layers. Pronounced humus layers favour high oribatid mite abundances (Migge et al., 1998; Maraun et

al., 2000) due to providing habitably space but also a range of food resources (Schneider et al., 2004). Saprotrophic fungi as well as beech fine roots and associated ectomycorrhizal fungi are likely to serve as food source for fungivorous microarthropods (Maraun et al., 2003; Schneider et al., 2005). Similar to oribatid mites, nematode densities were highest in beech clusters (S. Cesarz; unpubl. data) and it is increasingly recognized that many species of oribatid mites act as predators or scavengers (Heidemann et al., 2011; Maraun et al., 2011), with nematodes likely forming the most important animal prey.

In contrast to our hypotheses, tree species providing litter of high nutritional quality, i.e. ash and lime, detrimentally affected oribatid mite density. Notably, density was particularly low in clusters with only ash and lime trees indicating that in general oribatid mites were unable to take advantage from the input of high quality leaf litter. Obviously, detrimental effects of the lack of pronounced humus layers were not compensated by high quality litter resources. Detrimental effects of shallow humus layers suggest that oribatid mites suffer from strong seasonal fluctuations, in particular desiccation in summer (Taylor and Wolters, 2005). Besides harsh microclimatic conditions, oribatid mites are sensitive to disturbances (Salamon et al., 2006; Eisenhauer, 2010) which are more pronounced in ash and lime than in beech clusters due to high activity of macrofauna benefitting from high quality leaf litter of ash and lime (Cesarz et al., 2007; Weland, 2009). Further, oribatid mites may suffer from low belowground input in ash clusters. Fine roots of ash are rather thick and associated with arbuscular mycorrhizal fungi providing little food for soil animals (S. Cesarz, submitted). In summary, the results highlight the importance of organic layers for oribatid mite communities and support the view that oribatid mite communities are fuelled predominantly by belowground rather than aboveground resources. This is in the line with recent findings that soil animal food webs of temperate forests are fuelled to a substantial extent by belowground resources (Pollierer et al., 2007, 2012).

The results showed that oribatid mite communities of the Hainich National Park comprised mainly species of higher trophic levels with 65% functioning as fungivores, predators and/or scavengers. About half of the individuals found were Oppioidea and ~15% were Suctobelbidae, Hypochthoniidae or Damaeidae, i.e. taxa known to occupy higher trophic levels (Maraun et al., 2011; Perdomo et al., 2012). This underlines recent conclusions that only a small fraction of oribatid mite species

act as primary decomposers (Schneider et al., 2004; Pollierer et al., 2009; Maraun et al., 2011).

In the studied clusters, tree diversity did not significantly affect oribatid mite community structure, whereas the composition of oribatid mite communities varied markedly with tree identity. Thick organic layers in beech clusters favoured Oppioidea and Suctobelbidae, i.e. species that act as fungivores or predators (Maraun et al., 2011; Perdomo et al., 2012), suggesting that saprotrophic fungi and nematodes contribute substantially to oribatid mite nutrition.

By contrast, in ash and lime clusters, dominant oribatid mite groups were Phthiracaridae and Enarthronota, i.e. species that are able to withstand harsh environmental conditions associated with shallow humus layers. Further, Phthiracaridae and Enarthronota are likely to be less sensitive to disturbances caused by macrofauna such as earthworms than small species such as Oppioidea and Suctobelbidae (Maraun et al., 2003). Enarthronota are known to predominantly live in the upper soil layers (Schulz, 1991) where they may benefit from litter of ash and lime incorporated by earthworms (Thoms et al., 2010).

Similar to oribatid mite density, the diversity of oribatid mites also remained unaffected by tree diversity, but was strongly influenced by tree identity. As in density oribatid mite diversity was highest in beech clusters. This again highlights the major importance of organic layers providing habitable space and food resources for most oribatid mite species.

2. Tracing belowground resources of carbon and nitrogen into the soil animal food web

It is increasingly recognized that soil animal food webs are fuelled substantially by belowground inputs (Albers et al., 2006; Pollierer et al., 2007; Eisenhauer and Reich, 2012; see also Chapter 2), but few experiments investigated if belowground tree species traits, such as root architecture or associated mycorrhiza, impact C and N inputs into soil animal food webs. Labelling tree saplings allowed novel insight into how tree species affect the flux of plant C and mineral N into the soil animal food web. Beech and ash saplings differing in rhizosphere architecture and type of mycorrhiza (EM vs. AM fungi) were used to explore variations in food web structure with tree species and root traits.

2.1. The role of tree species for channeling belowground resources into the soil animal food web

By using a $^{13}CO_2$ enriched atmosphere, we traced the flux of freshly assimilated photosythates into fine roots of beech and ash, and further into ectomycorrhizal fungi and soil animals. In parallel, nutrient solution containing $^{15}NO_3{}^{15}NH_4$ was added to the soil allowing to trace the flux of mineral nitrogen into ectomycorrhizal fungi and subsequently into beech roots. In beech treatments the ^{15}N signal of ectomycorrhizal fungi exceeded that of beech fine roots. Notably, the amount of ^{13}C and ^{15}N in soil and litter was low. Therefore, incorporation of ^{13}C or ^{15}N into soil animals of higher trophic level likely was due to feeding on roots and/or mycorrhizal fungi. However, algae which assimilated $^{13}CO_2$ and took up ^{15}N from the added nutrient solution may have contributed to the incorporation of ^{13}C and ^{15}N into the soil animal food web.

In accordance to our expectations the experimental setup allowed tracing the flux of plant ^{13}C and mineral ^{15}N into the soil animal food web. We expected higher incorporation of ^{13}C into soil animals in beech as compared to ash treatments. Unexpectedly and in contrast to our hypotheses, we found no differences in $\delta^{13}C$ signatures of soil animals from beech and ash treatments. This indicates that belowground tree species traits and associated mycorrhizal fungi little affect the incorporation of the ^{13}C into higher order consumers. In beech treatments soil animals presumably incorporated plant ^{13}C via ectomycorrhizal fungi, whereas in ash treatments the plant ^{13}C was channeled into soil animals via rhizosphere bacteria (Cesarz et al., submitted). This indicates that tree species impact the way how plant C sources are channeled to higher trophic levels. Recently, Pollierer et al. (2012) followed the propagation of plant carbon to higher trophic levels via different energy channels. Results of the present study indicate that differences in belowground tree species traits drive the relative importance of individual energy channels.

Similar incorporation of C and N from beech and ash into the soil animal food web contrasts results of Chapter 2 documenting that beech rather than ash favours oribatid mite communities. This supports our conclusion that beneficial effects of beech were due to providing habitable space rather than food resources via root derived resources such as ectomycorrhizal fungi

We expected soil animals to preferentially feed on saprotrophic fungi and therefore assumed that the incorporation of ^{15}N from added ammonium nitrate into

soil animals varies little with tree species. Indeed, soil animals' $\delta^{15}N$ signatures were similar to those of litter and associated saprotrophic fungi, but markedly lower than those of ectomycorrhizal fungi indicating preferential feeding on saprotrophic fungi. Conform to our hypothesis, $\delta^{15}N$ signatures of soil animals in beech and ash treatments were similar. These results indicate that the diet of fungivorous soil animals was based mainly on saprotrophic fungi which incorporate litter derived resources (Lindahl et al., 2006).

2.2. Incorporation of belowground C and N differs between trophic levels

As expected, incorporation of label into trophic groups of the soil animal food web, i.e. primary decomposers, secondary decomposers and predators, differed significantly. However, in contrast to our expectations primary decomposers received least plant ^{13}C and microbial ^{15}N. This suggests that primary decomposers fed little on root derived resources but mainly on litter and soil organic matter as also indicated by analysis of body lipids (Pollierer et al., 2012). However, primary decomposers were trophically diverse and comprised species incorporating virtually no plant C and microbial N as well as those incorporating root derived resources. This indicates that primary decomposers as defined in the present study include taxa which in addition to dead organic matter to some extend digest microorganisms colonizing these resources.

In contrast to our expectations, secondary decomposers incorporated significantly more ^{13}C and ^{15}N than primary decomposers suggesting that they essentially rely on plant C and microbial N. However, as in primary decomposers, secondary decomposers also formed a gradient from species exclusively incorporating litter C to those exclusively feeding on microorganisms as assumed earlier (Scheu and Falca, 2000). In fact, species rich taxa, such as Collembola and Oribatida, have been assumed to rely predominantly on fungal based diets, but also to utilize other resources ranging from plant litter to microorganisms to animal prey (Schneider et al., 2004; Chahartaghi et al., 2005). This is in line with results presented in Chapter 2 documenting that abundant oribatid mite species predominantly rely on fungal based diets and little on plant litter materials.

Interestingly, and in contrast to our expectations, $\delta^{13}C$ and $\delta^{15}N$ signatures of soil animals were highest in predators. This indicates that predators, despite not being

linked to root resources themselves, incorporated highest amounts of plant C and microbial N. Some predatory taxa had overlapping $\delta^{13}C$ and $\delta^{15}N$ signatures with secondary decomposer species, indicating that these species, i.e. the two measured spider taxa and *Neobisium carcinoides*, relied on diets based on secondary decomposer prey as has been suggested earlier (Scheu, 2002). However, most of the predators studied, i.e. two oribatid mite species, Opilionida and Lithobiidae, had $\delta^{13}C$ and $\delta^{15}N$ signatures that exceeded those of secondary decomposers. This suggests that there is a "missing link" not measured in this study which is of major importance for nourishing predators, i.e. prey species being heavily associated with rhizosphere derived C and N resources. Potentially, predators hunted species that cannot be trapped by the heat extraction method, such as tiny collembolans, nematodes and enchytraeids. Supporting this conclusion two oribatid mite species known to feed on nematodes, i.e. *Acorgalumna longipluma* and *Hypochthonius luteus*, were highly labeled (Rockett and Woodring, 1966; Muraoka and Ishibashi, 1976). Again, this is in line with results presented in Chapter 2 suggesting that the many oribatid mite species function as predators. Centipedes presumably hunted litter dwelling collembolans (Poser, 1988; Ferlian et al., 2012) which included the highly labeled species *Lepidocyrtus cyaneus* which presumably fed on algae. $\delta^{13}C$ and $\delta^{15}N$ signatures of Geophilomorpha also were high and resembled those of earthworms confirming them to feed on earthworms (Wolters and Eckschmitt, 1997).

In summary, high stable isotope signatures in predators indicated that they rely on different primary sources of carbon, including resources derived from roots and rhizosphere associated microorganisms but also algae. These carbon resources are channeled to higher trophic levels via collembolans, nematodes, enchytraeids and lumbricids or via algal feeders such as *Lepidocyrtus cyaneus*.

3. Structural leaf litter compounds as drivers for the incorporation of litter resources into soil animal food webs

In contrast to the rhizotron experiment which focused on carbon flux from living plants into the decomposer system (Chapter 3) the field microcosm experiment presented in Chapter 4 focused on the flux of leaf litter resources into the soil animal food web. Again, variations with tree species were investigated. For the first time we investigated the role of structural litter compounds as determinants of the

incorporation of litter resources into the soil animal food web. In the experiment beech and ash leaves differing in structural compounds but containing similar concentrations of N were used. Similar N concentrations were obtained by fertilizing beech and ash seedlings with the same nutrient solution (for details on the litter material see Material and Methods in Chapter 4).

3.1. Trophic groups of the soil animal food web

In a first step, we used natural variations in $\delta^{15}N$ signatures of soil animals to assign species to trophic levels. $\delta^{15}N$ signatures of soil animals spanned 11.3 δ units which resembled earlier studies (Scheu and Falca, 2000; Pollierer et al., 2009). Assuming lower $\delta^{15}N$ enrichment in decomposers as compared to higher trophic level consumers (Post, 2002; VanderKlift and Ponsard, 2003; Tiunov, 2007) the animal species were ascribed to three trophic levels, i.e. primary decomposers, secondary decomposers and predators.

3.2. Incorporation of C and N from litter differing in structural compounds

Soil animals incorporated ^{13}C and ^{15}N from decomposing litter which is in the line with earlier studies of Elfstrand et al. (2008) and Lummer et al. (2012). Interestingly, soil animals incorporated similar amounts of C and N from leaf litter suggesting that by utilizing litter resources soil animals covered both the demand for energy (C) and nutrients (N). The results indicate that both litter derived C and N propagate through all trophic levels which is in the line with results of Pollierer et al. (2012) who also found ^{13}C from litter in deciduous forests to be incorporated into soil animals of all trophic levels.

Soil animals incorporated lower amounts of C and N from beech litter rich in structural compounds than from ash litter low in structural compounds. This supports our first hypothesis that the amount of litter structural compounds is of major importance for incorporation of litter C and N resources into the soil animal food web. The results further suggest that tree species identity significantly impact the flux of litter C and N through the soil fauna food web with leaf litter poor in structural compounds such as ash being of major importance for fuelling soil animal food webs.

3.2.1. Primary decomposers

In accordance to our second hypothesis, differences in incorporation of litter resources between litter types were most pronounced in soil animal species acting as primary decomposers, e.g. *Steganacarus magnus* and *Folsomia quadrioculata*. Primary decomposers incorporated low amounts of litter derived C and N from beech and high amounts from ash litter pointing to low nutritional quality of leaf litter rich in structural compounds. Litter quality for decomposers is commonly assumed to be related to litter N concentration, but results of this study highlight that structural compounds of litter are also of significant importance (Meier and Bowman, 2008). This indicates that soil animals preferentially utilize leaf litter containing high amounts of easily accessible energy-rich C compounds. Thereby, detritivores preferably digest soluble C compounds of the litter material such as sugars, hemicelluloses and starch as suggested earlier (Pollierer et al., 2009), whereas lignin and cellulose remain undigested and are voided with casts (Scheu and Wolters, 1991; Rawlins et al., 2006). Similar conclusions were drawn by Hättenschwiler and Bracht-Joergensen (2010) investigating tropical soil systems. They concluded that tropical decomposer food webs are limited primarily by energy derived from easily accessible C compounds of leaf litter and only secondarily by litter nutrients. The same likely applies to beech forests since beech leaf litter contains high amounts of recalcitrant C compounds such as cellulose, lignin, polyphenols and tannins (Webster and Benfield, 1986, Wardle et al., 2004). Overall, these findings suggest that to satisfy their needs in energy and nutrients detritivorous soil animals heavily rely on food resources rich in labile compounds (Scheu and Setälä, 2002; Bardgett et al., 2005; Swan and Kominoski, 2012). The results provide additional support for the view that belowground input of root derived C is fuelling soil fauna food webs as root derived C comprises mainly substances that are easily available for soil organisms, i.e. amino acids, sugars and peptides (Dennis et al., 2010; see also Chapters 2 and 3).

Among primary decomposers only one macrofauna species, *Glomeris undulata*, incorporated high amounts of C and N from both beech and ash litter. This indicates that only large decomposers such as Glomeridae are able to live on beech litter low in nutritional quality and high in structural C components (Scheu and Wolters, 1991; Hättenschwiler and Gasser, 2005). With their sclerotized mandibles they are able to comminute recalcitrant leaf litter thereby getting access to inner litter compartments (Pollierer et al., 2007).

In contrast, Damaeidae (Oribatida), which were ascribed to primary decomposers, incorporated similar amounts of C and N from both beech and ash litter. As these species are unable to fragment litter material, this points to a diet based on microorganisms associated with litter material rather than feeding on litter tissue, presumably mainly fungi (Schneider et al., 2004). Leaf litter is colonized quickly by microorganisms including fungal hyphae growing inside of the leaves, and bacteria and fungi forming mats on the leave surface (Berg and McClaughtery, 2008). Detritivores preferentially feed on litter material in later stages of decay since it is of higher nutritional quality due to the colonization of microorganisms (Hättenschwiler and Gasser, 2005). This suggests that most detritivorous soil animals feed on two trophic levels, i.e. leaf tissue and microbes, and therefore form a gradient from primary to secondary decomposers (Lussenhop, 1992; Scheu and Setälä, 2002). This is in line with results presented in Chapters 2 and 3 documenting that oribatid mite species are trophically diverse with only few species functioning as primary decomposers.

Interestingly, and in contrast to litter derived C resources, soil animals incorporated similar amounts of N from beech and ash litter. This indicates that litter N availability varied little between the two litter species although they differed markedly in structural compounds. Irrespective of litter type, most litter N is bound in easily digestible compounds such as amino acids and proteins. Probably, primary decomposers are able to digest these compounds and secondary decomposers get access to litter N via feeding on microorganisms. The high importance of saprotrophic fungi for fuelling the N demands of many soil animals has also been stressed in Chapter 3.

3.2.2. Secondary decomposers

Secondary decomposers incorporated higher amounts of C and N from beech and ash litter than primary decomposers suggesting that more litter derived C and N is available for detritivore soil animals feeding on microbial based diets than for primary decomposers feeding directly on litter material. Saprotrophic fungi quickly form filamental hyphal mats covering the surface of decomposing leaves (Swift et al., 1979; Osono, 2003) which likely serve as food for fungal feeding soil animals. As in primary decomposers secondary decomposers also incorporated similar amounts of litter N from beech and ash. Thereby, fungal feeders took advantage of

fungi which captured N from litter thereby making it available to fungal grazers (Lummer et al., 2011). Fungi are highly efficient in degradation of labile C and N compounds (Hudson, 1968; Berg, 2000; Osono, 2007) implying that fungal feeders get access to these compounds even though they may not be able to fragment the litter themselves.

Unexpectedly, secondary decomposers incorporated most litter C and N. The results highlight the importance of the fungal energy channel for temperate forest soil food webs as stressed before (Oelbermann et al., 2008; Crowther, 2012). Particularly mature forests dominated by late successional tree species such as beech producing low-quality litter favor the dominance of fungi and thereby fungal consumers (Wardle, 2002; Maraun et al., 2003; Hättenschwiler et al., 2005; Pollierer et al., 2009; see also Chapter 2). Overall, results of the present study suggest the fungal energy channel to be of particular importance for soil animal food webs of temperate forest ecosystems and indicate that this is due to the high efficiency of fungi in capturing C and N from low quality litter thereby making it available to fungal grazers. Fungal grazers form an important compartment of soil animal food webs of temperate forests (Pollierer et al., 2009) and they contribute substantially to their diversity (Schneider et al., 2004; Chahartaghi et al., 2005).

Incorporation of litter C and N into species of Collembola, Oribatida and Isopoda did not differ between beech and ash (Kautz et al., 2000; Pollierer et al., 2012). Additionally, three species, i.e. *L. xylariae*, *N. palustris* (both Oribatida), and *Lumbricus* spp. juv. (Lumbricida) incorporated higher amounts of N and C from ash than from beech litter indicating that they directly fed on the high quality ash litter.

3.2.3. Predators

In contrast to our expectations, predators incorporated more litter C and N than primary decomposers indicating that predators preferentially relied on secondary decomposers as prey as hypothesized earlier (Scheu, 2002). Higher body mass of predators as compared to secondary decomposers likely contributed to lower stable isotope signatures in predators as compared to secondary decomposers due to incomplete replacement of predator body tissue during the exposure in the field for five months (Rickers et al., 2006; Oelbermann et al., 2008).

3.3. Impact of mixing of litter material

By establishing treatments with mixed beech and ash litter we aimed at testing if soil animals switch to litter low in structural compounds (ash) if added to litter high in structural compounds (beech). Surprisingly, mixing of the two litter types little affected the incorporation of litter derived C and N into the soil animal food web. This supports our conclusion that incorporation of litter resources into the soil animal food web is mainly based on the fungal energy channel supporting conclusions of Chapters 2 and 3.

4. Conclusions

In conclusion, we found tree species to strongly impact the structure and functioning of the soil animal food web in deciduous temperate forest ecosystems (Chapter 2). Overall, the results underlined the importance of belowground resources in fuelling soil animal food webs (Chapter 3), but we also found litter derived C and N to be of significant importance (Chapter 4). Focusing on tree species with contrasting litter and root traits (including mycorrhiza), i.e. beech and ash, the results suggested root C to be channeled into soil animal food web mainly via the fungal energy channel in beech but via the bacterial energy channel in ash. The use of labelled litter indicated that both litter derived C and N was channeled into the soil animal food web via fungal feeding soil animal species. Overall, results highlighted the outstanding importance of the fungal energy channel for incorporating plant resources into the soil animal food web of temperate forest ecosystems. Only a minor fraction of the investigated soil animal species functioned as primary decomposers, whereas secondary decomposers form a major control point for channeling plant resources to higher trophic levels.

Primary decomposers most strongly were related to aboveground tree species traits, i.e. the amount of structural compounds of leaf litter (Chapter 4). In contrast to primary decomposers, secondary decomposers were little affected by both aboveground (Chapter 4) and belowground tree species traits (Chapter 3). They heavily relied on belowground resources but also incorporated litter resources via saprotrophic fungi. Predators also incorporated high amounts of belowground C and N suggesting fungal feeding species to form a major part of their prey, but the results also point to incorporation of label via prey groups not investigated in this study, presumably mainly nematodes and enchytraeids.

References

Albers, D., Schaefer, M., Scheu, S., 2006. Incorporation of plant carbon into the soil animal food web of an arable system. Ecology 87, 235–245.

Bardgett, R.D., Bowman, W.D., Kaufmann, R., Schmidt, S.K., 2005. A temporal approach to linking aboveground and belowground ecology. Trends in Ecology and Evolution 20, 634–641.

Berg, B., 2000. Litter decomposition and organic matter turnover in northern forest soils. Forest Ecology and Management 133, 13-22.

Berg, B., McClaugherty, C., 2008. Plant Litter - Decomposition, Humus Formation, Carbon Sequestration. Springer, Berlin, Germany.

Cesarz S., Fahrenholz, N., Migge-Kleian, S., Platner, C., Schaefer M., 2007. Earthworm communities in relation to tree diversity in a deciduous forest. European Journal of Soil Biology 43, 61-67.

Cesarz, S., Ruess, L., Jacob, M., Jacob, A., Schaefer, M., Scheu, S. Soil energy channels of forests differing in tree species identity and diversity as indicated by nematode communities. Submitted.

Chahartaghi, M., Langel, R., Scheu, S., Ruess, L., 2005. Feeding guilds in Collembola based on nitrogen stable isotope ratios. Soil Biology & Biochemistry 37, 1718–1725.

Crowther, T.W., 2012. Impacts on grazing soil fauna on decomposer fungi are species-specific and density dependent. Fungal Ecology 5, 277-281.

Dennis, P.G., Miller, A.J., Hirsch, P.R., 2010. Are root exudates more important than other sources of rhizodeposits in structuring rhizosphere bacterial communities? FEMS Microbiology Ecology 72, 313-327.

Elfstrand, S., Lagerlöf, J., Hedlund, K., Martensson, A., 2008. Carbon routes from decomposing plant residues and living roots into soil food webs assessed with ^{13}C labeling. Soil Biology and Biochemistry 40, 2530-2539.

Eisenhauer, N., 2010. The action of an animal ecosystem engineer: Identification of the main mechanisms of earthworm impacts on soil microarthropods. Pedobiologica 53, 343-352.

Eisenhauer, N., Reich, P.B., 2012. Above- and below-ground plant inputs both fuel soil food webs. Soil Biology & Biochemistry 45, 156-160.

Ferlian, O., Scheu, S., Pollierer, M.M., 2012. Trophic interactions in centipeds (Chilopoda, Myriapoda) as indicated by fatty acid patterns: Variations with life stage, forest age and season. Soil Biology & Biochemistry 52, 33-42.

Hansen, R.A., 2000. Effects of habitat complexity and composition on a diverse litter microarthropod assemblage. Ecology 81, 1120-1132.

Hättenschwiler, S., Gasser, P., 2005. Soil animals alter plant litter diversity effects on decomposition. Proceedings of the National Academy of Science of the USA 102, 1519-1524.

Hättenschwiler, S., Tiunov, A.V., Scheu S., 2005. Biodiversity and litter decomposition in terrestrial ecosystems. Annual Reviews of Ecology, Evolution and Systematics 36, 191-218.

Hättenschwiler, S., Bracht-Joergensen, H., 2010. Carbon quality rather than stoichiometry controls litter decomposition in a tropical rain forest. Journal of Ecology 98, 754-763.

Heidemann, K., Scheu, S., Ruess, L., Maraun, M., 2011. Molecular detection of nematodes predation and scavenging in oribatid mites: Laboratory and field experiments. Soil Biology & Biochemistry 43, 2229–2236.

Hudson, H. J., 1968. The ecology of fungi on plant remains above the soil. New Phytologist 67, 837-874.

Kautz, G., Zimmer, M., Topp, W., 2000. Responses of the parthenogenetic isopod *Trichoniscus pusillus* (Isopoda: Oniscidea) to changes in food quality. Pedobiologia 44, 75-85.

Lindahl, B.D., Ihrmark, K., Boberg, J., Trumbore, S.E., Högberg, P., Stenlid, J., Finlay, R.D., 2006. Spatial separation o flitter decomposition and mycorrhizal nitrogen uptake in a boreal forest. New Phytologist 173, 611-620.

Lummer, D., Scheu, S., Butenschoen, O., 2012. Nitrogen transfer between decomposing litter species is an important but not the only factor responsible for synergistic mixture effects on litter decomposition. Oikos, 121, 1649-1655.

Lussenhop, J., 1992. Mechanisms of microarthropod - microbial interactions in soil. Advances in Ecological Research 23, 1-33.

Muraoka, M., Ishibashi, N., 1976. Nematode-feeding mites and their feeding behaviour. Applied Entomology and Zoology 11, 1–7.

Maraun, M., Scheu, S., 2000. The structure of oribatid mite communities (Acari Oribatida): patterns mechanisms and implications for future research. Ecography 23, 374–383.

Maraun, M., Martens, H., Migge, S., Theenhaus A., Scheu, S., 2003. Adding to „the enigma of soil animal diversity“: fungal feeders and saprophagous soil

invertebrates prefer similar food substrates. European Journal of Soil Biology 39, 85-95.

Maraun, M., Erdmann, G., Fischer, B.M., Pollierer, M.M., Norton, R.A., Schneider, K., Scheu, S., 2011. Stable isotopes revisited: Their use and limits for oribatid mite trophic ecology. Soil Biology and Biochemistry 43, 877-882.

Meier, C.L., Bowman, W.D., 2008. Linke between plant litter chemistry, species diversity, and belowground ecosystem function. Proceedings of the National Academy of Sciences 105, 19780-19785.

Migge, S., Maraun, M., Scheu, S., Schaefer, M., 1998. The oribatid mite community (Acarina: Oribatida) of pure and mixed stands of beech (*Fagus sylvatica*) and spruce (*Picea abies*) of different age. Applied Soil Ecology 9, 115-121.

Oelbermann, K., Langel, R., Scheu, S., 2008. The role of prey out of the decomposer system for generalist predators of grassland. Oecologia 155, 605-617.

Osono, T., 2007. Ecology of lignolytic fungi associated with leaf litter decomposition. Ecology Research 22, 955-974.

Perdomo, G., Evans, A., Maraun, M., Sunnucks, P., Thompson R., 2012. Mouthpart morphology and trophic postion of microarthropods from soils and mosses are strongly correlated. Soil Biology and Biochemistry, in press.

Pollierer, M.M., Langel, R., Korner, C,.Maraun, M., Scheu, S., 2007. The underestimated importance of belowground carbon input for forest soil animal food webs. Ecology Letters 10, 729-736.

Pollierer, M.M., Langel, R., Scheu, S., Maraun, M., 2009. Compartmentalization of the soil animal food web as indicated by dual analysis of stable isotope ratios ($^{15}N/^{14}N$ and $^{13}C/^{12}C$). Soil Biology & Biochemistry 41, 1221–1226.

Pollierer, M.M., Dykmans, J., Scheu, S., Haubert, D., 2012. Carbon fluxes through fungi and bacteria into the forest soil animal food web as indicated by compound-specific ^{13}C fatty acid analysis. Functional Ecology, doi: 10.1111/j.1365-2435.2012.02005.x.

Poser, G., 1988. Chilopoda as predators in a beech wood. Pedobiologia 31, 261-281.

Post, D.M., 2002. Using stable isotopes to estimate trophic position: models, methods and assumptions. Ecology 83, 703-718.

Rawlins, A. J., Bull I.D., Poirier, N., Ineson, P., Evershed, R.P, 2006. The biochemical transformation of oak (*Quercus robur*) leaf litter consumed by the pill millipede (*Glomeris marginata*). Soil Biology and Biochemistry 38, 1063-1076.

Rickers, S., R. Langel, Scheu S., 2006. Dietary routing of nutrients from prey to offspring in a generalist predator: effects of prey quality. Functional Ecology 20, 124-131.

Rockett, C.L., Woodring, J.P., 1966. Oribatid mites as predators of soil nematodes. Annals of the Entmological Society of America 59, 669–671.

Salamon, J., Alphei, J., Ruf, A., Schaefer, M., Scheu, S., Schneider, K., Sührig, A., Maraun, M., 2006. Transitory dynamic effects in the soil invertebrate community in a temperate deciduous forest: effects of resource quality. Soil Biology and Biochemistry 38, 209-221.

Scheu, S., Wolters, V., 1991. The influence of fragmentation and bioturbation on the decomposition of carbon-14-labelled beech leaf litter. Soil Biology & Biochemistry 23, 1029-1034.

Scheu, S., Falca, M., 2000. The soil food web of two beech forests (*Fagus sylvatica*) of contrasting humus type: stable isotope analysis of a macro- and a mesofauna-dominated community. Oecologia 123, 285–286.

Scheu, S., 2002. The soil food web: structure and perspectives. European Journal of Soil Biology 38, 11−20.

Scheu, S., Setälä H., 2002. Multitrophic interactions in decomposer communities. Multitrophic level interactions, Cambridge University Press, New York.

Scheunemann, N., Scheu, S., Butenschoen, O., 2010. Incorporation of decade old soil carbon into the soil animal food web of an arable system. Applied Soil Ecology 46, 59-63.

Schneider, K., Migge, S., Norton, R.A., Scheu, S., Langel, R., Reineking, A., Maraun, M., 2004. Trophic niche differentiation in soil microarthropods (Oribatida, Acari): evidence from stable isotope ratios ($^{15}N/^{14}N$). Soil Biology and Biochemistry 36, 1769–1774.

Schneider, K., Renker, C., Maraun, M., 2005. Oribatid mite (Acari, Oribatida) feeding on ectomycorrhizal fungi. Mycorrhiza 16, 67-72.

Schulz E., 1991. Die Milbenfauna (Acari: Mesostigmata und Cryptostigmata) in Lebensräumen auf Kalkstein: Populationsökologie, Sukzession and Beziehungen von Lebensraum. University of Göttingen, Dissertation, Göttingen. Forschungszentrum Waldökosysteme 91, 245 pp.

Swan, C.M., Kominoski, J.S., 2012. Biodiversity and Ecosystem Function of Decomposition. In: eLS. John Wiley & Sons, Ltd: Chichester. doi: 10.1002/9780470015902.a0023601.

Swift, M.J., Heal, O.W., Anderson, J.M., 1979. Decomposition in terrestrial ecosystems. Blackwell, Oxford, UK.

Taylor A.R., Wolters V., 2005. Responses of oribatid mite communities to summer drought: The influence of litter type and quality. Soil Biology and Biochemistry 37, 2117-2130.

Thoms, C., Gattinger, A., Jacob, M., Thomas, F.M., Gleixner G., 2010. Direct and indirect effects of tree diversity drive soil microbial diversity in a temperate deciduous forest. Soil Biology and Biochemistry 42, 1558-1565.

Tiunov, A.V., 2007. Stable isotopes of carbon and nitrogen in soil ecological studies. Biology Bulletin 34, 395-407.

VanderClift, M.A., Ponsard, S., 2003. Sources of variation in consumer-diet delta N-15 enrichment: a meta-analysis. Oecologia 136, 169–182.

Wardle, D.A., 2002. Communities and Ecosystems: Linking the Aboveground and Belowground Components. Monographs in Population Biology. Princeton University Press, Princeton, USA.

Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setälä, H., van der Putten, W.H., Wall, D.H., 2004. Ecological linkages between aboveground and belowground biota. Science 304, 1629-1633.

Webster J.R., and Benfield, E.F, 1986. Vascular plant breakdown in freshwater ecosystems. Annual Review of Ecology and Systematics 17,567–594.

Weland, N., 2009. Diversity and trophic structure of the soil fauna and its influence on litter decomposition in deciduous forests with increasing tree diversity. Dissertation, University of Göttingen, Göttingen, 110 pp.

Wolters, V., Ekschmitt, K., 1997. Gastropods, isopods, diplopods and chilopods: neglected groups of the decomposer food web. In: Benksier, G. (Ed.) Fauna in Soil Ecosystems: Recycling processes, Nutrient Fluxes and Agricultural Production. Marcel Dekker, New York, USA, pp. 265-306.

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Declaration of originality and certificate of authorship

I, Verena Eißfeller, declare that I am the sole author of the present dissertation entitled “Tree species as determinants of the structure of oribatid mite communities (Oribatida) and the incorporation of plant carbon and nitrogen into the soil animal food web”.
All sentences and passages quoted and all data sources from other people’s work that have been used in the dissertation are specifically acknowledged by clear cross-referencing. All co-authors contributed to finalizing the manuscripts and are mentioned by name in the single chapters.

The study in Chapter 2 was conducted in an interdisciplinary approach of the RGT 1086. I was involved in establishing the clusters in the field and the sampling of the soil fauna in May 2008. I did the determination work for oribatid mites. For the manuscript, I did the statistical analyses, made the figures and the table and wrote the text. Christina Langenbruch contributed data on litter input and Andreas Jacob data on fine roots. Both provided comments on the manuscript. PLFA data were provided by Andrea Scheibe and data on nematode densities by Simone Cesarz.

Chapter 3 is submitted to a pear reviewed journal. I was involved in the study design, the experimental setup, the implementing and the harvest of the experiment. I collected the data on soil animals. The data on plants where provided by Friderike Beyer who also was involved in the setup and the harvest of the experiment. Data on mycorrhizal fungi were provided by Kerttu Valtanen. I analyzed the data, prepared the figures, wrote the text and the Appendix. All authors provided constructive comments on the manuscript.

The experiment presented Chapter 4 was conducted in an interdisciplinary work by projects A1, B5 and B6 of the RGT 1086. I was involved in the preparation of the litter material and the mesocosms as well as the setup and the sampling of the experiment. I collected the data for soil animals in May 2009. For the manuscript, I did the statistical analyses, prepared the tables and graphs and wrote the text. Data

on lignin and cellulose contents of beech and ash leaves were measured by Guido Humpert and Christina Langenbruch provided data on litter chemical composition.

The cover-photographs of Chapters 1, 2, 5 and the front page are shared ownership of the RGT 1086.

I have not submitted the dissertation in any form for another degree at any other University or Institute.

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Verena Eißfeller
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Publications

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Eißfeller, V., Scheu, S., 2010. Muster und Mechanismen der Wirkung unterschiedlicher Baumartendiversität auf die Bodenfauna an der Schnittstelle Boden-Streu und in der Rhizosphäre. BfN-Skripten 265 (2010) 9-15.

Coloured cover images by Göttingen Centre for Biodiversity and Ecology
(legend top to bottom)

1 Mixed deciduous forest in the Hainich region (Central Germany)
2 Different insect taxa on the flowers of a thistle (*Cirsium* sp.)
3 *Glomeris* sp., a member of the decomposing soil fauna in forest ecosystems
4 *Pleodorina californica* (Chlorophyceae), colony-forming freshwater phytoplankton species
5 Grasshopper *Tettigonia cantans*, distributed from the Pyrenees to Northeastern China
6 *Microcebus berthae* (Cheirogaleidae), the smallest extant Primate species (Madagascar)
7 Tropical rain forest (Greater Daintree, Australia)
8 *Lethocolea glossophylla* (Acrobolbaceae), a liverwort of alpine mountain ranges in South America
9 Part of a coral reef in the Red Sea

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