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Community Structure and Guild Patterns of Soil Decomposers in Pure and Mixed Forests of European Beech, Norway Spruce and Douglas Fir

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To achieve a high level of simplicity requires a high level of sophistication.

— **Tim Hunt**

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Summary

Anthropogenic global warming is creating new challenges for forest management in many parts of the world. One vital aspect is the choice of tree species and whether to cultivate monospecific or mixed timber plantations. Because Central Germany applies close-to-nature forest management, each piece of land needs to fulfil multiple services, including timber production and biodiversity conservation. However, scientific understanding of the effect of forest type on ecosystem functioning, especially decomposer communities, is still limited. To better understand the linkages between forest types and decomposer communities, I investigated decomposer communities in pure and mixed forests of native European beech, range-expanding Norway spruce, and non-native Douglas fir across a range of environmental conditions. Based on a review of previous work (**Chapter 1**). I developed the overarching hypothesis that, compared to native European beech, Douglas fir detrimentally affects the community structure of decomposers. Further, available data suggest that mixed forests may mitigate the adverse effects of pure coniferous forests.

To test these hypotheses, I first investigated the structure and functioning of microbial communities using microbial respiration and phospholipid-derived fatty acid analyses (**Chapter 2**). The response of microbial community structure and functional indicators depends strongly on soil nutrient concentrations in the study site. Douglas fir and Norway spruce adversely affected soil microbial communities and compromised their functioning, particularly in unfavorable environments. These findings, published in Lu and Scheu (2021), call for caution when deciding whether to plant pure Douglas fir under less-favorable site conditions and overall contribute to a context-wise understanding of tree–soil interactions.

Building on the concept of microbial communities as basal resources connecting trees and soil animals, I next investigated collembolans and oribatid mites in association with biotic and abiotic environmental variables (**Chapter 3**). Species composition of Oribatida, but not of Collembola, sensitively responded to forest type, differing most between Douglas-fir and European-beech forests. Although microarthropod richness and diversity did not differ among forest types, the abundance of both euedaphic Collembola and predatory Oribatida were lower in Douglas fir than in European beech, presumably due to lower provisioning of root-associated resources in Douglas-fir forests. The results suggest that non-native Douglas fir generally does not affect the diversity of soil microarthropods, but the limitation of root-derived resources may restrict the population development of some microarthropods in Douglas-fir forests.

To further understand the intraspecific variation in food resources of oribatid mites, stable isotope ratios of $^{15}N/^{14}N$ and $^{13}C/^{12}C$ were quantified for 40 Oribatida species that occur in both litter and soil (**Chapter 4**). Across five forest types,

Oribatida species were found to occupy virtually identical trophic niches irrespective of the soil depth at which they were recovered. Such low intraspecific variability may facilitate Oribatida niche differentiation and species coexistence. These findings are an important contribution to the understanding of the trophic ecology of oribatid mites in temperate forest ecosystems. Although basal resources of Oribatida vary between coniferous and deciduous forests, basal resources and trophic positions of Oribatida species in mixed forests are similar to those in European beech, supporting the use of mixed forests in mitigating adverse impacts of coniferous trees.

Taken together, my results suggest that tree identity is an important driver for microbial and microarthropod communities. In mixed forests, microbial and microarthropod responses are intermediate compared to respective pure stands, suggesting that tree species are singular, that is, loss or addition of tree species causes detectable changes. Furthermore, the microbial response also depends on site conditions and mixture types, reflecting different responses of the tree species to environmental conditions. This also supports the idea that mixed forests provide better insurance against the changing climate (**Chapter 5**). Overall, mixed forests help to maintain soil microbial and microarthropod communities close to the state of native European-beech forests and mitigate the adverse impacts of coniferous forests. As a whole, this dissertation contributes to a better understanding of the structure and resource utilization of soil decomposer communities and serves as a stepping stone for the next phase of the research training group.

Contributions to the research chapters

Chapter 2. Microbial community structure and functioning (published)

Jing-Zhong Lu[1], Stefan Scheu[2]

Authorship: SS and JZL designed the study. JZL collected the data, analyzed the data, and wrote the first draft of the manuscript. SS contributed to all stages of the manuscript.

Chapter 3. Microarthropod guilds and communities (in preparation)

Jing-Zhong Lu, Christian Bluhm[3], Estela Foltran[4], Alicia Rivera[5], Jonas Glatthorn[6], Norbert Lamersdorf[7], Andrea Polle[8], Christian Ammer[9], Mark Maraun[10], Stefan Scheu

Authorship: SS, CA, JZL designed the study. JZL collected the data, with contribution from CB, MM, EF, AR, JG, CA, NL and AP. JZL analyzed the data and wrote the first draft of the manuscript. All authors contributed substantially to result interpretations and revisions.

Chapter 4. Trophic niches and stable isotopes (submitted)

Jing-Zhong Lu, Peter Cordes[11], Mark Maraun, Stefan Scheu

Authorship: JZL, SS, MM designed the study. JZL, PC collected the data. JZL analyzed the data and wrote the first draft of the manuscript. All authors contributed significantly to interpretations and revisions.

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Chapter 1

General introduction

1.1 Forest management and biodiversity

Temperate forests occupy about 16% of the world's forested area and serve as major source of the world's timber production (FAO and UNEP, 2020). Given that temperate forests are widely distributed in the mid-latitudinal regions, the effects of anthropogenic climate change on temperate forests are of global importance (Saxe et al., 2001; Allen et al., 2015; Schuldt et al., 2020). Temperate forests receive between 750–1500 mm precipitation annually (Adams et al., 2019). However, rising temperatures are projected to cause drier summers and tree mortality, which has indeed increased over the past decades (Allen et al., 2010, 2015). To better cope with future climate, the choice of tree species and the decision on monospecific or mixed cultures for timber plantations are of vital importance (Knoke et al., 2008; Ammer, 2019).

Central Europe applies close-to-nature forest management (Messier et al., 2013). This means that the same piece of land needs to fulfill multiple services, including timber production and biodiversity conservation. Although monocultures have been traditionally applied, mixtures hold many advantages in fluctuating environments especially in a changing climate (Knoke et al., 2008; Morin et al., 2011; Ammer, 2019). In addition to better conserving biodiversity, mixed forests may lead to overyielding due to complementarity or lower competition between tree species (Cavard et al., 2011; Morin et al., 2011). The risk of failure due to an extreme climatic event is also distributed across tree species in mixed forests, providing insurance for future forestry (Yachi and Loreau, 1999).

In addition to mixed forest management, the choice of tree species for plantation help to better cope with future climate change. Norway spruce has become one of the most frequent timber species in Central Europe due to forest plantation (Schütz et al., 2006). However, although being economically important, Norway spruce is vulnerable to extreme weather conditions and bark beetle outbreaks, events predicted to occur more often under global warming (Pettit et al., 2020). Alternative tree species, such as non-native Douglas fir, are under discussion (Schmid et al., 2014). Douglas fir provides valuable timber and other ecosystem services, but there are still many assumptions that need to be tested, such as to what extent will Douglas fir cope with warmer climate and increased drought conditions and how does Douglas fir affect ecosystem functioning at a large scale (Schmid et al., 2014; Ammer et al., 2018; Pötzelsberger et al., 2020). To better understand the effects of tree identity and diversity on ecosystem functioning, pure and mixed stands of European beech, Douglas fir, Norway spruce will be studied in this dissertation.

1.2 Decomposer communities and resources

Substantial quantities of the biomass acquired by trees during photosynthesis are not consumed by herbivores but enter the decomposer system (Cebrian, 1999; Polis, 1999; Wardle, 2013). Plants fuel decomposers through several pathways, including root exudation, root microbial symbionts, and deposits of leaf and woody materials (Nielsen, 2019; Angst et al., 2021). Communities of soil microorganisms and animals function in a broad sense as decomposers because they influence decomposition either by direct consumption or by indirectly altering decomposition processes (Bardgett et al., 2005; Bardgett and Van der Putten, 2014). Decomposer communities are amongst the most species-rich components in temperate forests (Giller, 1996). Their high species and genetic diversity exceed that of plants by orders of magnitude (Scheu et al., 2005; Binkley and Fisher, 2013). High soil biodiversity ensures the physical and chemical properties of soils, and at large ecosystem functioning (Loreau et al., 2001; Bardgett and Van der Putten, 2014; Tilman et al., 2014). By studying the soil decomposers in pure and mixed forest stands, this dissertation will contribute a better understanding of ecosystem functioning in temperate forests.

Microorganisms comprise the great majority of species in soil and are the engine for litter decomposition and nutrient cycling (Bardgett, 2010). They form the base of soil food webs and account for a large part of the belowground biomass (Fierer et al., 2009; Nielsen et al., 2015; Bar-On et al., 2018). Soil microbial communities are mainly composed of bacteria and fungi, and they can be broadly grouped into a few guilds (Bardgett and Van der Putten, 2014; Nielsen et al., 2015). Guilds are defined as groups of species that utilize similar classes of resources (Root, 1967; Simberloff and Dayan, 1991; Blondel, 2003). Gram^{-} bacteria benefit in particular from labile carbon compounds, whereas Gram^{+} bacteria are adapted to use more recalcitrant carbon resources (Fierer et al., 2003; Fanin et al., 2019; Waller et al., 2020). Similarly in fungi, while saprotrophic fungi are major decomposers of plant litter including recalcitrant compounds, mycorrhizal fungi are more abundant in deeper soil and receive labile carbon compounds from plant roots (Lindahl et al., 2007; Nacke et al., 2016). The study of microbial communities often is limited by the method used. Compared to molecular approaches such as meta-barcoding and metagenomics that focus on taxonomic community composition, phospholipid fatty acid (PLFA) analysis quantifies bacteria and fungi based on biomolecules in their cell membrane in a cost-effective way (Frostegård et al., 2011). PLFA analysis has been demonstrated as a sensitive method indicating microbial responses to environmental change and will be used to quantify microbial community composition in this dissertation (Frostegård and Bååth et al., 1993; Ramsey et al., 2006; Waller et al., 2020).

Soil mesofauna range in the body width from 0.1 to 2 mm (Swift et al., 1979; Nielsen, 2019). They include several groups, but the most abundant ones are oribatid mites (Oribatida, Acari) and collembolans (Collembola, Hexapoda). Oribatida and Collembola typically live in air-fill pore space in the soil and do not alter the soil structure (Nielsen, 2019). So far, more than 10,000 Oribatida and 9,000 Collembola species have been described (Weigmann, 2006; Potapov et al., 2020). Although many new species in soil are waiting to be discovered worldwide, species description in Germany is relatively complete so species identification is mostly possible (Maraun et al., 2007). In contrast to the adults of Oribatida that are normally heavily sclerotized, Collembola jump for self-defense against predators using the furcula at their ventral side. Oribatida and Collembola are broadly classified as saprophages, but trophic niche differentiation has been widely reported in soil microarthropods (Scheu and Falca, 2000; Schneider et al., 2004; Chamberlain et al., 2006; Klarner et al., 2013). Typically, three to four trophic guilds can be found in Oribatida and Collembola communities (Schneider et al., 2004; Chahartaghi et al., 2005; Maraun et al., 2011), and trophic niche differentiation suggests that microarthropods differentiate in resource use and thereby better coexist (Anderson, 1975; Schneider et al., 2004; Nielsen et al., 2010).

Litter- and root-derived resources

Resources are limited in soil (Hairston et al., 1960; Scheu and Schaefer, 1998). Although the majority of root- and litter-derived resources is consumed by decomposers over geological scales, physiochemical and biological processes keep organic carbon stored in soil as an ecosystem property, less available to decomposer communities (Schmidt et al., 2011; Berg and McClaugherty, 2020). Litter is an important resource for decomposer communities, but the importance of root-derived resources is increasingly recognized (Pollierer et al., 2007; Bluhm et al., 2021). Both litter- and root-derived resources need to be considered as resources fueling soil microbial and microarthropod communities (Ruf et al., 2006; Kramer et al., 2010).

Litter is mainly composed of chemical compounds such as lignin, cellulose, hemicellulose, and water-soluble materials (Berg and McClaugherty, 2020). In temperate broadleaved forests, around 30% of the annual carbon fixed is used for leaf production (Leuschner and Ellenberg, 2017). This is about 300–350 g leaf mass m^{-2} $year^{-1}$ in European-beech forests (Leuschner et al., 2006). According to a recent meta-analysis, litter mass does not differ much between coniferous and deciduous tree species (Augusto et al., 2015). Reflecting the importance of litter as a resource for decomposers, soil communities are concentrated in the uppermost organic horizon where the majority of litter gets fragmented and decomposed (Petersen and Luxton, 1982). Old organic matters that are physically protected and become an ecosystem property may be not accessible to decomposers (Schmidt et al., 2011). Because few animals can digest litter components like lignin and cellulose, soil microorganisms that break down these litter components form an important food resource for many soil animals (Pollierer et al., 2009; Potapov et al., 2019).

Root-derived resources contribute to the nutrition of decomposer communities (Albers et al., 2006; Pollierer et al., 2007). Root exudates mainly comprise carbohydrates, amino acids, and organic acids (Smith, 1976; Vives-Peris et al., 2020). The contribution of roots and root exudates to soil respiration and long-term carbon sequestration in soil have been stressed (Högberg et al., 2001; Clemmensen et al., 2013; Jiang et al., 2020). Up to half of the photosynthetically fixed carbon may be lost from the soil by respiration, pointing to the importance of root exudation as a driver of the dynamics of soil biological communities (Badri and Vivanco, 2009; Bardgett and Van der Putten, 2014). However, despite the importance of root-derived resources, the soil system is also highly resistant in a root trenching experiment likely due to the buffering of other organic resources (Bluhm et al., 2021). The questions of how root-derived resources fuel decomposer communities and the role of root-derived resources for forest production are still unanswered (Meier et al., 2017).

1.3 Tree–soil interactions and variations with environmental conditions

Soils provide trees with water and nutrients, and as feedback trees shape soil decomposer communities through multiple pathways. However, studies on the linkages between plants and decomposer communities have focused on grasslands (Zak et al., 2003; Milcu et al., 2006; Schuldt et al., 2010; Scherber et al., 2010). Our understanding of forest–decomposer interactions is still limited (Scheu et al., 2005). Forest types, including pure and mixed forests, may affect soil communities by changing productivity, tree species traits, and biotic interactions (Callaway and Ridenour, 2004; Endara and Coley, 2011; Waller et al., 2020). Here I break down forest type effects into identity effects and diversity effects for further discussions.

Tree species identity affects decomposer communities through three pathways. First, tree species differ in productivity and resource availability to decomposers; this may be affected by the quantity and quality of primary productivity and also the way how tree species allocate their biomass into litter and root (Korboulewsky et al., 2016). Second, tree species differ in traits, such as secondary metabolism (e.g., allelochemicals), litter physical structure (e.g., habitats), or canopy structure (e.g., moisture and light) (Endara and Coley, 2011; Leuschner and Ellenberg, 2017; Fujii et al., 2020). Third, biotic interactions vary between tree species; Interspecific interactions, such as competition and predation, may vary for a focal decomposer community depending on tree species (Terborgh et al., 2001; Scheu et al., 2003). These pathways are not mutually exclusive and may all contribute to tree identity effects.

Diversity effects influence decomposer communities by modifying tree identity effects. In mixed forests, interspecific interaction of tree species may drive synergistic or antagonistic effects on ecosystem processes depending on facilitation or competition between tree species (over-yielding or under-yielding in the context of tree growth) (Korboulewsky et al., 2016; Ammer, 2019). Synergistic effects can result from complementarity between tree species in space and in time (Loreau et al., 2001; Tilman et al., 2001; Fargione et al., 2007). Likewise, antagonistic effects may happen when there is strong competition of limited resources between tree species. The competition or facilitation of tree species in mixed stands may further drive the changes in forest productivity, species traits, and biotic interactions, thereby influencing decomposer communities.

Environmental conditions

Both tree identity and diversity effects can be modified by environmental conditions. Tree species cope differently with environmental stress, and change in morphology and physiology with environments (Leuschner et al., 2004; Meier et al., 2005; Meier and Leuschner, 2008; Palacio-López and Gianoli, 2011). Resource availability, tree species traits, and biotic interactions in forests can all be modified by environmental conditions, but the differences among tree species may be larger under stress conditions. For example, under nutrient-poor or acidic conditions, plants generally allocate more resources to roots than to shoots, and this likely applies to many tree species but a different extent (Keyes and Grier, 1981; Karst et al., 2017; Ostonen et al., 2017; Meier et al., 2020). Although in European-beech forests fine root biomass, root exudates and root traits have been reported to vary with site condition, their litter quantity and quality appear to be rather constant irrespective of site conditions (Meier et al., 2005, 2020; Meier and Leuschner, 2008). It is also emerging that plants produce more carbon than needed (surplus carbon) under the stress, e.g., stress of nutrients, water, and temperature (Prescott et al., 2020). More surplus carbon is released via roots under less favorable environments, potentially linking tree species and soil decomposer communities to a greater extent (Prescott et al., 2020).

Diversity effects also depend on environmental context. Under less favorable conditions, facilitation among species is greater according to the stress gradient hypothesis (Ratcliffe et al., 2017; Wright et al., 2021). Indeed, overyielding in mixed forests typically occurs at low-quality sites (Pretzsch et al., 2014; Toïgo et al., 2015). Diversity effects, therefore, interact with environmental conditions, and environmental contexts are important in understanding the relationship of biodiversity and ecosystem functioning (Ratcliffe et al., 2017). It is also important to point out that multiple environmental factors also interact and likely amplify each other's effects on ecosystem functioning (Rillig et al., 2019). For instance, soil type may interact with precipitation in determining tree productivity, and nutrient limitation may be magnified under drought conditions (Binkley and Fisher, 2013). Warming is likely to increase drought, leading to greater vulnerability of trees to mortality (Allen et al., 2015). Complex environmental drivers will be considered in this dissertation because field conditions are multifactorial by nature (Karban et al., 2014).

1.4 The Research Training Group 2300

The RTG 2300 investigates ecosystem functioning in temperate forests, with a special focus on Douglas fir and mixed forests. Eleven closely linked subprojects focus on functional traits of tree species and associated biota and the mechanisms that link them to ecosystem functioning (Glatthorn et al., 2021). Eight study sites were established in 2017, covering a range of nutrient and water conditions (Figure **1.1**).

The four sites located in the south of Lower Saxony are richer in soil nutrients and precipitation than the four northern sites (Site no. 1–4 and 5–8, respectively). Five forest types were established in each site, mostly in 50 m x 50 m square. The five forest types comprised pure stands of European beech, Douglas fir, Norway spruce, and two mixtures of European beech with the respective coniferous species. These forest types are not only of major interest to forest management in Central Europe but also provide contrasting ecosystems to study the ecology of decomposer communities. Under the framework of the Research Training Group 2300 (RTG 2300), I investigated microbial and microarthropod communities in *Subproject 5* ("Decomposer communities and decomposition processes").

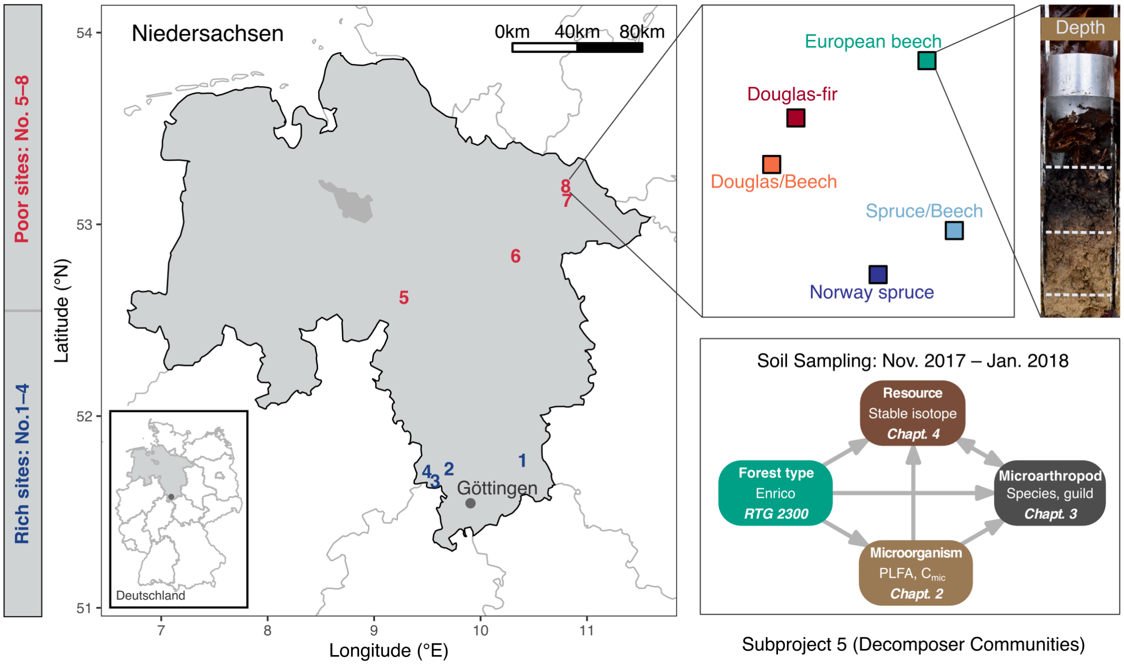

Figure 1.1: Study design and the structure of the dissertation. Subproject 5 is conducted under the framework of the Research Training Group 2300 (40 plots = 8 sites x 5 forest types). The five forest types are located at nutrient-rich (no. 1–4 in blue) and nutrient-poor (no. 5–8 in red) sites, covering pure stands of European beech, Douglas fir, Norway spruce, and two mixtures (Douglas/Beech, Spruce/Beech). Soil cores were separated into litter, 0–5, and 5–10 cm depth.

Deciduous and evergreen tree species

European beech (*Fagus sylvatica*) is a deciduous species that forms the climax forest in the lowland and lower mountain ranges of Central Europe (Leuschner and Ellenberg, 2017; Cai et al., 2021). In Central Europe, tree diversity is low, and managed forests are typically dominated by a few tree species (Bauhus et al., 2010). Many coniferous tree species are well adapted to the habitat of European beech, but European beech is relatively competitive due to shade tolerance, especially at a young stage (Leuschner and Ellenberg, 2017). European beech recolonized large parts of Europe from refugia since the last ice age (Hewitt, 2000; Magri et al., 2006). Further, the organic layer in European-beech forests is relatively shallow compared to coniferous forests, likely an ecosystem property developed from litter quality, decomposer communities, and specific local abiotic environment (Albers et al., 2004; Schmidt et al., 2011; Berger and Berger, 2012).

Norway spruce (*Picea abies*) naturally grows at high latitudes and altitudes, but has been widely planted in lowland and lower latitudes as well (Knoke et al., 2008). Conifer monocultures have been the major type of forests planted in Central Europe until today (Pretzsch et al., 2017). Norway spruce promotes podzolization and leads to increased rock weathering under base-rich soils (Binkley and Valentine, 1991; Lundström et al., 2000; Binkley and Fisher, 2013). Plantations of Norway spruce are generally richer in bryophytes likely due to their low pH (Leuschner and Ellenberg, 2017). Norway spruce promotes the formation of humus with an increase in C/N and C/P ratios (Leuschner and Ellenberg, 2017). The biomass of soil fauna has been reported to be negatively correlated with soil organic matter and is lower in Norway spruce than European-beech forests (Schaefer, 1990). Bioturbation typically is lower in spruce than in beech forests as earthworms and other large invertebrates are replaced by small mesofauna taxa such as enchytraeids, collembolans, and mites (Scheu et al., 2003). Further, although spruce forest soil is relatively cool in temperature, its topsoil is typically drier due to greater precipitation interception by the stand (Leuschner and Ellenberg, 2017). The shallow roots of Norway spruce also make the stands prone to storm and drought (Knoke et al., 2008). Further, Norway spruce is prone to bark beetle outbreaks (Pettit et al., 2020). All these risks are magnified in the face of climate change with increasing average temperature and extreme weather conditions (Allen et al., 2015).

Douglas fir (*Pseudotsuga menziesii*) originated from North and Central America (Schmid et al., 2014). Since its introduction (>150 years ago), Douglas fir has become the most abundant non-native tree species in Central Europe (Schmid et al., 2014). Although it is listed as invasive in South America and New Zealand, Douglas fir is not likely to be invasive in Central Europe (Spiecker et al., 2019). Douglas fir has become the most abundant non-native cultivated tree species in Central Europe (Schmid et al., 2014). So far, Douglas fir has not been subjected to large-scale outbreaks of pests in Europe, and it has been suggested to be more drought tolerant than Norway spruce (Vitali et al., 2017). However, there are concerns about non-native tree species for conservational reasons (Pötzelsberger et al., 2020). The average yearly interception of precipitation in the crown of Douglas fir (~42%) is stronger than of European beech (~20%), leading to drier soil under Douglas fir (Leuschner and Ellenberg, 2017). It has also been suggested that further introduction of exotic organisms associated with Douglas fir in its native range could be more problematic than the introduction of Douglas fir itself (Schmid et al., 2014).

1.5 Scope of the dissertation

The overarching hypothesis of this dissertation is that, compared to native European beech, Douglas fir detrimentally affects the community structure of decomposers; mixed forests mitigate the adverse effects of pure coniferous forests. Across all 40 plots (8 sites x 5 forest types), soil samples were taken between November 2017 to January 2018 and soil cores were separated into the litter, 0–5, and 5–10 cm soil depths (Figure **1.1**). The sampling campaign covered soil microorganisms (three cores each plot, pooled at each depth, diameter 5 cm), mesofauna (two soil cores each plot, diameter 5 cm), and macrofauna (two soil cores each plot, diameter 20 cm).

Soil microorganisms form the base of soil food webs and in this dissertation, I first investigated the structure and functioning of microbial communities in litter and soil using microbial respiration and phospholipid-derived fatty acid analyses (**Chapter 2**). Building on microbial communities, I associated microarthropod communities with biotic and abiotic environmental variables to disentangle the environmental drivers of Collembola and Oribatida communities (**Chapter 3**). Soil microarthropods are ubiquitous soil-pore dwellers, to further understand their variation in food resources with environmental conditions, I studied the stable isotope ratios of $^{15}N/^{14}N$ and $^{13}C/^{12}C$ in Oribatida species across soil depth and forest type (**Chapter 4**). Stable isotope values of Oribatida species from Chapter 4 also served to differentiate Oribatida species into trophic guilds in Chapter 3. Overall, these interconnected studies contributed to a better understanding of the linkages between forest types and soil decomposer communities. The effects of pure and mixed forests of non-native Douglas fir on decomposer communities further provide timely knowledge for future forest management.

Chapter 2

Response of soil microbial communities to mixed beech–conifer forests varies with site conditions[1]

Jing-Zhong Lu, **Stefan Scheu**

Abstract

Tree–soil interactions depend on environmental conditions. Planting trees may affect soil microbial communities and compromise their functioning, particularly in unfavorable environments. To understand the effects of tree species composition on soil microbial communities, we quantified structural and functional responses of soil microorganisms to tree species planted in various environments using substrate-induced respiration and phospholipid fatty acid analyses. Five forest types were studied including pure stands of native European beech (*Fagus sylvatica*), range expanding Norway spruce (*Picea abies*), and non-native Douglas fir (*Pseudotsuga menziesii*), as well as the two conifer–beech mixtures. We found that microbial functioning depends strongly on soil nutrient concentrations in the studied forest sites. At nutrient-poor sites, soil microorganisms were more stressed in pure and mixed coniferous forests, especially in Douglas fir, compared to beech forests. By contrast, microbial structure and functional indicators in beech forests varied little with site conditions, likely because beech provided ample amounts of root-derived resources for microbial growth. Since soil microbial communities are sensitive to Douglas fir, planting Douglas fir may compromise ecosystem functioning, especially at nutrient-poor sites. Overall, root-derived resources are important for determining the structure and functioning of soil microbial communities, so soil microbial responses to tree species will depend upon the provisioning of these resources as well as site-specific environmental conditions.

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2.1 Introduction

Trees affect soil microorganisms through several pathways, most importantly by litter and root exudates (Wardle et al., 2004; Högberg and Read, 2006). These resources are likely to shape microbial community composition because dissimilar carbon resources favor different guilds of microorganisms (Lindahl et al., 2007; Fanin et al., 2019). Despite that microbial community composition may change in response to variations in tree species composition, the relative role of litter and root exudates in structuring soil microbial communities remains controversial (Bluhm et al., 2019). The typically thicker organic layers in coniferous compared to deciduous forests have been attributed to the recalcitrance of needles (Augusto et al., 2015), but root and mycorrhizal fungi also affect soil carbon storage (Clemmensen et al., 2013; Averill et al., 2014). Studying the linkage between trees and soil microorganisms may allow uncovering the pathways by which trees drive microbial community composition.

Planting coniferous trees beyond their native range has become common worldwide (Castro-Díez et al., 2019). Although providing timber and other benefits to humans, conifers may detrimentally affect soil microorganisms, compromising carbon and nutrient cycling (Berger and Berger, 2012; Castro-Díez et al., 2019). To improve microbial functioning, admixing conifers to deciduous forests has been suggested as it may increase resource availability to soil microorganisms in mixed litter (Hättenschwiler et al., 2005; Cremer et al., 2016). Further, broadleaf mixed forests are likely to increase both aboveground and belowground biomass due to interspecific facilitation and improved resource partitioning, resulting in higher resource availability to microorganisms (Cardinale et al., 2007; Emmett Duffy et al., 2017). The importance of mixed stands for ecosystem functioning is increasingly recognized, particularly under unfavorable environmental conditions (Ratcliffe et al., 2017; Wright et al., 2021). However, it is little understood how effects of tree species composition on soil microorganisms vary with site conditions, such as soil nutrient status (Malchair and Carnol, 2009).

Facilitation among plants is more pronounced in nutrient-poor soil according to the stress-gradient hypothesis, and such positive interspecific interactions are likely to be mediated by soil microorganisms (Defossez et al., 2011; David et al., 2020). Plants do not passively tolerate environmental stress, but respond in various ways to unfavorable growth conditions, such as by shifting the allocation of resources towards roots in nutrient-poor soil (Callaway et al., 2003; Yan et al., 2016). Recently, De Vries et al. (2019) has shown that under stress conditions herbaceous species change the quality of root exudates and induce higher microbial respiration, presumably facilitating nutrient capture by stimulating microorganisms. Phenotypic plasticity or morphological changes induced by the environment may differ between species, exacerbating differences in resource availability to soil microorganisms under nutrient-poor conditions (Meier and Leuschner, 2008; Schall et al., 2012). Thus, the impact of tree species composition on microbial community composition and functioning may be more pronounced at nutrient-poor than nutrient-rich sites.

A better understanding of the effects of tree species composition on soil microorganisms has implications for forest management, especially in temperate and boreal regions where tree species richness is low and managed forests are dominated by one or a few species (Knoke et al., 2008; Bauhus et al., 2010). European beech is the climax species in lowland and lower montane regions in Central Europe (Leuschner and Ellenberg, 2017). The most popular timber species, Norway spruce originally occurred in higher mountain ranges and boreal regions, but has been planted widely in lowlands (Knoke et al., 2008). In recent years, Norway spruce has been damaged severely by extreme weather and bark beetle outbreaks, events predicted to become more frequent in the future (Pettit et al., 2020). Although the admixture of Norway spruce to native European beech forests may reduce the risk of damage while maintaining economic gains, Douglas fir is increasingly planted (Schmid et al., 2014). Since its introduction from North America over 150 years ago, Douglas fir has become the most abundant non-native cultivated tree species in Central Europe (Schmid et al., 2014). To date, the impact of planting Douglas fir on biodiversity and functioning of forests is little studied, and this applies in particular to the belowground system, although e.g., Douglas fir has been suggested to affect soil chemistry in a similar way than spruce (Prietzel and Bachmann, 2012; Schmid et al., 2014). Overall, we lack a comprehensive evaluation of forest types on soil microorganisms across soil nutrient conditions.

Here, we studied microbial community composition and functioning in litter and soil of five forest types of different soil-nutrient status. Forest types included pure stands of European beech, Norway spruce, Douglas fir, and the two conifer–beech mixtures. We analyzed the structure of microbial communities using phospholipid fatty acid patterns, and their functioning using microbial basal respiration, biomass and stress indicators. In general, we assumed the structure of microbial communities to be closely linked to their functioning. In particular, we hypothesized that (1) coniferous trees will more detrimentally affect microbial structure and functioning compared to European beech, with the effects being similar in Norway spruce and Douglas fir forests, and intermediate in mixed forests. Further, we hypothesized that (2) microbial community structure and functioning will be strongly impacted by forest type at nutrient-poor sites, but less at nutrient-rich sites. Since the litter layer is less buffered against environmental harshness than the organic and mineral soil, we also hypothesized that (3) forest types will affect soil microorganisms more strongly in litter than in soil.

2.2 Methods

2.2.1 Field sites

The study included five forest types arranged as quintets at eight sites in northern Germany, covering a range of environmental conditions (5 forest types x 8 sites; Figure **1.1**. The four sites in the south stock on fertile soil and receive higher precipitation. Mean annual precipitation is 821–1029 mm. Parental rock is either loess influenced Triassic sandstone or Paleozoic shares of greywacke, sandstone, quartzite and phyllite, resulting in soil types of partly podsolic Cambisol and Luvisol. The four sites in the north are located on out-washed sand with the soil type of Podzol. The mean annual precipitation is 672–746 mm. The southern sites are richer in nutrients than

Table 2.1: General information as well as soil physical and chemical properties of the study sites. Soil texture is based on 5–30 cm mineral soil, and soil chemical properties are based on 0–5 cm mineral soil. Soil moisture is expressed as percentage of dry mass, and was measured in litter, 0–5, and 5–10 cm soil. Ca^{2+} concentration was analyzed in exchangeable form by NH_4Cl extraction, and total P was determined by pressure digestion (for detailed see Methods and Foltran et al. 2020).

	Rich site				Poor site			
	1	2	3	4	5	6	7	8
(a) General Information								
Site name	Harz	Dassel	Winnefeld	Nienover	Nienburg	Unterlüß	Göhrde II	Göhrde I
Latitude (°*N*)	51.77	51.726	51.662	51.696	52.621	52.837	53.127	53.201
Longitude (°*E*)	10.397	9.704	9.574	9.526	9.281	10.331	10.814	10.801
MAT (°*C*)	7.712	8.663	8.961	9.074	9.769	9.099	9.262	9.271
MAP (*mm*)	1015.226	816.793	818	872.037	729.206	741.14	678.505	669.354
Slope (°)	15.518	2.963	4.969	6.56	1.855	1.19	1.429	2.049
Elevation (*m*)	510.8	426.169	349.065	323.368	92	161.2	129.8	120
(b) Texture & Moisture								
Sand%	16	26	20	20	80	79	79	73
Silt%	16	53	57	57	13	15	15	24
Clay%	68	21	23	23	7	6	6	3
Water% (*litter*)	237.2	221.2	235.5	232.4	245.9	303.1	328.5	265.7
Water% ($0-5$)	135.5	106.6	84.7	62.7	71.4	120.2	88.1	76.2
Water% ($5-10$)	59.1	39.6	37.8	29.6	22.4	26.9	23.9	22.9
(c) Chemical Properties								
C%	7.086	5.898	7.505	5.303	7.975	4.031	9.315	5.362
N%	0.368	0.33	0.372	0.294	0.282	0.169	0.34	0.245
C/N ratio	19.354	17.46	20.651	18.371	28.946	23.969	27.32	22.231
CEC ($mmol\ dm^{-3}$)	237.31	117.537	114.907	95.958	74.813	47.785	71.096	67.716
pH (*KCl*)	3.424	3.213	3.336	3.474	3.002	3	2.711	3.006
P ($mg\ kg^{-1}$)	0.607	0.505	0.44	0.457	0.16	0.113	0.166	0.243
Ca^{2+} ($mmol\ dm^{-3}$)	28.353	15.902	32.563	27.881	20.384	12.907	7.896	11.279

Note:

MAT: mean annual temperature. MAP: mean annual precipitation. CEC: cation exchange capacity.

the northern sites as reflected by higher total soil P, cation exchange capacity and pH; more details on site characteristics and soil chemical properties are given in Table **2.1** (Ammer et al., 2020; Foltran et al., 2020). Hereafter, we refer to the southern sites as nutrient-rich sites and to the northern sites as nutrient-poor sites.

Each site comprised pure stands of European beech (*Fagus sylvatica* L.; Be), Douglas fir (*Pseudotsuga menziesii* [Mirbel] Franco.; Do) and Norway spruce (*Picea abies* [L.] Karst.; Sp), as well as two conifer-beech mixtures (Douglas fir/European beech and Norway spruce/European beech; Do/Be and Sp/Be). On average, trees were more than 50 years old. Within sites, the distance between stands ranged from 76 m to 4600 m, and the distance between sites ranged from 5 to 190 km. Within each stand, plots of 2500 m^2 were established, mostly in rectangular shape (50 × 50 m). Tree species in pure stands comprised more than 90% of the total basal area, and that in mixed stands 33–53% for beech and 53–60% for conifers.

2.2.2 Soil sampling and physio-chemical analyses

Samples were taken between November 2017 and January 2018. Soil cores of 5 cm diameter were taken by a metal cylinder, and were separated into litter, 0–5, and 5–10 cm soil depth. In each plot, three cores spaced by 5 m were taken. Samples from the same depth were pooled, resulting in 120 samples (40 plots × 3 depths). The soil was sieved through 2 mm mesh, and the litter was cut into pieces (<25 mm^2) (Maraun and Scheu, 1995). Roots >2 mm in diameter and stones were removed. Samples were stored at -20°C. The pH was determined using a ratio of sample to solution (g/ml; KCl, 1 M) of 1:10 for litter, 1:5 and 1:2.5 for 0–5, and 5–10 cm soil, respectively. Moisture content was measured by drying samples at 105°C for 48 h. Water content did not differ consistently between nutrient-rich and nutrient-poor sites across layers; it was higher in litter but lower in soil at nutrient-poor than at nutrient-rich sites (Site condition × Depth interaction; $F_{2,68} = 26.21$, $P < 0.001$). Dried samples were grinded in a ball mill, and total carbon and nitrogen concentrations were determined by an elemental analyzer (NA 1110, CE-instruments, Rodano, Milano, Italy). Litter mass was estimated by drying at 50°C for >48 h (Macfadyen, 1961).

2.2.3 Microbial basal respiration and biomass

Microbial biomass was measured by substrate-induced respiration with respiration measured as O_2 consumption (Anderson and Domsch, 1978; Scheu, 1992). Samples stored at -20°C were thawed and incubated overnight at room temperature (20°C) before placing in an automated micro-respirometer. The system absorbs CO_2 using KOH solution and the O_2 consumed by microorganisms is replaced through electrolytic release of O_2 from $CuSO_4$ solution. Microbial basal respiration was measured as mean consumption of O_2 during 10–23 h after attachment of the vessels to the respirometer (μg O_2 g^{-1} h^{-1}). Microbial biomass was determined after the addition of glucose to saturate microbial glycolytic enzymes based on the maximum initial respiratory response 4–7 h after the addition of D-glucose (MIRR; μl O_2 g^{-1} h^{-1}) and converted to microbial biomass (C_{mic}; μg C_{mic} g^{-1}) as 38 × MIRR (Beck et al., 1997). Basal respiration and substrate-induced respiration were measured at 22°C in a water bath. Fresh litter and soil from 0–5 and 5–10 cm depth equivalent to approximately 0.3, 1.0 and 3.5 g dry mass was supplemented with 80, 20 and 8 mg glucose solved in 400 μl H_2O, respectively. The ratio between microbial basal respiration and microbial biomass was taken as microbial specific respiration (qO_2; μg O_2 μg^{-1} C_{mic} h^{-1}).

2.2.4 Phospholipid fatty acid analysis

To quantify the composition of phospholipid fatty acids (PLFAs), lipids were extracted using a modified Bligh and Dyer method (Frostegård and Bååth et al., 1993; Pollierer et al., 2015). In short, lipids were fractionated into neutral lipids, glycolipids and phospholipids by elution through silica acid columns using chloroform, acetone and methanol, respectively (0.5 g silicic acid, 3 ml; HF BOND ELUT-SI, Varian Inc., Darmstadt, Germany). Phospholipids were subjected to mild alkaline methanolysis and fatty acid methyl esters were identified by chromatographic retention time compared to standards (FAME CRM47885, C11 to C24; BAME 47080-U, C11 to C20; Sigma-Aldrich, Darmstadt, Germany) using a GC-FID Clarus 500 (PerkinElmer Corporation, Norwalk, USA) equipped with an Elite 5 column (30 m × 0.32 mm inner diameter, film thickness 0.25 μm). The temperature program started with 60°C (hold time 1 min) and increased by 30°C per min to 160°C, and then by 3°C per min to 280°C. The injection temperature was 250°C and helium was used as carrier gas. Approximately 2 g of fresh litter and 4 g of fresh soil were used for the extraction.

2.2.5 Stress indicators and fatty acid markers

The ratio of cyclopropyl PLFAs to their monoenoic precursors [cy/pre; (cy17:0 + cy19:0)/(16:1ω7 + 18:1ω7)] and the ratio of saturated to monounsaturated PLFAs [sat/mono; (14:0 + 15:0 + 16:0 + 17:0 + 18:0)/(16:1ω7 + 17:1 + 18:1ω9 + 18:1ω7)] were used as indicators of physiological or nutritional stress (Pollierer et al., 2015). The ratio of Gram$^+$ to Gram$^-$ bacteria was used as indicator of carbon availability (Fanin et al., 2019). The saturated fatty acids i15:0, a15:0, i16:0, i17:0 were used as markers for Gram$^+$ bacteria, and the fatty acids cy17:0, cy19:0, 16:1ω7 and 18:1ω7 were assigned as markers for Gram$^-$ bacteria (Zelles, 1999; Fanin et al., 2019). Bacteria were represented by the sum of Gram$^+$ and Gram$^-$ bacteria. Linoleic acid 18:2ω6, 9 was used as fungal marker (Frostegård and Bååth, 1996). Total amount of PLFAs included all identified PLFAs (n = 40; nmol g^{-1} dry weight) and was used to calculate PLFA proportions. All stress indicators and PLFA markers were analyzed from proportions (mole percentage).

2.2.6 Statistical analyses

To estimate the effect size of Forest type and Site condition, we first fitted linear mixed models (*LMM*s) to log-transformed response variables and then applied planned contrasts (Piovia-Scott et al., 2019). All *LMM*s included Forest type (European beech, Douglas fir, Douglas fir/European beech, Norway spruce, Norway spruce/European beech), Site condition (nutrient-rich and nutrient-poor sites), and Depth (litter, 0–5, and 5–10 cm) as fixed effects. Models were stepwise selected by likelihood ratio test, and minimal models included all main effects and the interaction of Forest type and Site condition. The 40 forest plots were included as random effects to account for non-independence of samples from the same plot. Based on Akaike Information Criterion (AIC), the eight sites were included as random effect, and the mean-variance relationship was accounted for by a dispersion parameter to meet the assumption of homogeneity of variance (Zuur et al., 2009). Univariate response variables included microbial basal respiration, microbial biomass, microbial specific respiration, stress indicators and PLFA markers.

Contrasts for the effect size of Forest type were designed to compare coniferous and mixed forests to beech forests. European beech, the climax tree species in lowland and lower montane regions of Central Europe, was used as reference (Leuschner and Ellenberg, 2017). Due to the property of log-transformed response variables, the planned contrasts are analog to log response ratios (Piovia-Scott et al., 2019). To improve interpretation, we back transformed the log response ratio into response ratio and defined it as effect size. Effect sizes of Forest type were estimated for nutrient-poor and nutrient-rich sites. In addition, we applied contrasts between nutrient-poor vs. nutrient-rich sites in a similar manner to estimate the effect sizes of Site condition.

To inspect for effects of Forest type, Site condition and their interactions on microbial community structure, we first arcsine root transformed PLFA composition, and then reduced the dimensions of fatty acids by principal component analysis at each sample depth. Multivariate analyses of variance (*MANOVA*s) at each sample depth were applied to principal components (PCs) to test for statistical significance. Further, selected environmental variables were included into *MANOVA*s as covariates to test whether they explain main effects in the models (Bennett et al., 2020). Significant PCs were determined by broken stick criterion. Covariates were selected according to permutation tests based on adjusted R^2 in redundancy analyses (RDA). Only fatty acids $\geq 0.2\%$ mean mole proportion were included in the analyses.

All analyses were done in R 4.0.3 (`https://www.r-project.org/`). We used the 'nlme' package to fit *LMM*s and the 'emmeans' package to conduct planned contrasts. All mixed models met the assumptions of normality of residuals and homogeneity of variance.

2.3 Results

2.3.1 Functional indicators of microorganisms

Forest type consistently affected microbial basal respiration, microbial biomass and stress indicators at nutrient-poor but not at nutrient-rich sites (Forest type x Site condition interactions; all $P < 0.08$; Figures **2.1**, **2.2**, Table **2.2**), and this was generally true across soil layers (Figure **A.1**). At nutrient-poor sites, microbial basal respiration and microbial biomass in Douglas fir were 65% and 59% lower compared to pure beech forests. Forest type effects were similar in the two conifer-beech mixtures (-46 to -56%) and least pronounced in pure spruce forests (-33 to -36%; Figure **2.1**). In addition, at nutrient-poor sites microbial specific respiration was 19% lower in Douglas fir than in beech forests.

At nutrient-poor sites, stress indicators, the cy/pre ratio, the sat/mono ratio as well as the $\text{Gram}^{+}/\text{Gram}^{-}$ bacteria ratio, all were lower in beech forests than in the other forest types (Figure **2.2**). Forest type effects on the cy/pre and sat/mono ratio were more pronounced in Douglas fir (+87% and +74%) and less pronounced in spruce and conifer-beech mixtures (+37 to +46%). Effects of Forest type on the $\text{Gram}^{+}/\text{Gram}^{-}$ bacteria ratio also were strongest in Douglas fir forests (+46%) and less strong in the other forest types (+21 to +29%). Stress indicators generally did not differ significantly at nutrient-rich sites ($P > 0.31$; Figures **2.2**, **A.1**, Table **A.1**).

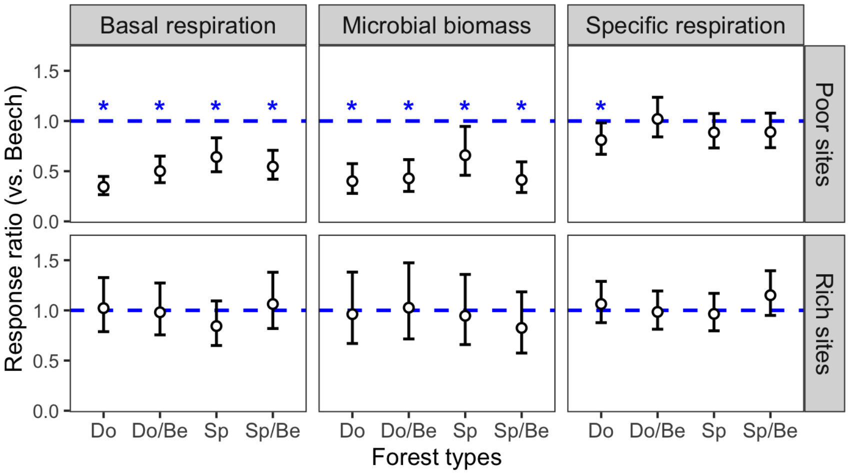

Figure 2.1: Effects of conifers and conifer-beech mixtures on microbial basal respiration (μg O_2 g^{-1} C h^{-1}), microbial biomass (μg C_{mic} g^{-1} C) and microbial specific respiration (μg O_2 μg^{-1} C_{mic} h^{-1}) at nutrient-poor and nutrient-rich sites (Douglas fir [Do], Douglas fir with beech [Do/Be], Norway spruce [Sp], and Norway spruce with beech [Sp/Be]). Effect sizes are given as back transformed log response ratios compared to beech forests [ln (value in coniferous or mixed forest types / values in beech)]. Values smaller than 1 indicate higher values in beech. Asterisks indicate significant effects ($P < 0.05$). Bars represent 95% confidence intervals ($n = 12$).

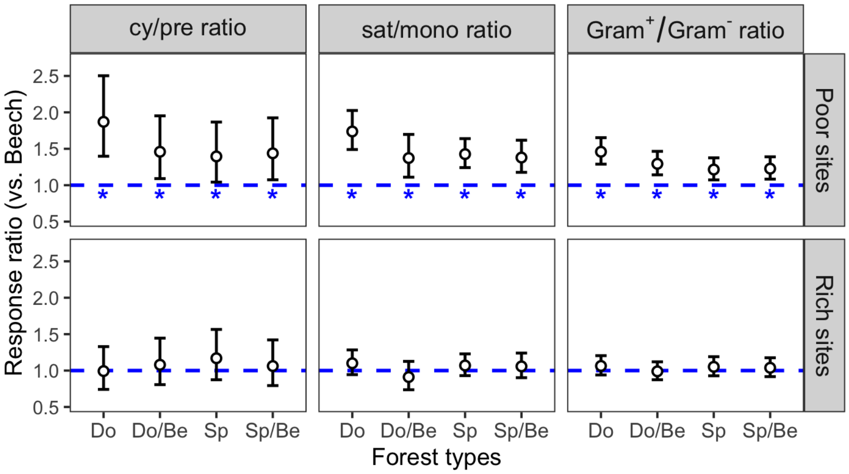

Figure 2.2: Effects of conifers and conifer-beech mixtures on stress indicators: ratio of cyclopropyl PLFAs to its monoenoic precursors (cy/pre), ratio of saturated to monounsaturated PLFAs (sat/mono), and ratio of $Gram^+$ to $Gram^-$ bacteria ($Gram^+/Gram^-$) at nutrient-poor and nutrient-rich sites (Douglas fir [Do], Douglas fir with beech [Do/Be], Norway spruce [Sp], and Norway spruce with beech [Sp/Be]). Asterisks indicate significant effects ($P < 0.05$). Bars represent 95% confidence intervals ($n = 12$).

Table 2.2: F- and P-values of linear mixed-effects models on the effect of Forest type (European beech, Douglas-fir, Norway spruce, mixture of European beech with Douglas-fir, and mixture of European beech with Norway spruce), Site condition (nutrient-poor and nutrient-rich sites) and Depth (litter, 0–5, and 5–10 cm) on (a) basal respiration, microbial biomass and microbial specific respiration, (b) stress indicators (ratio of cyclopropyl PLFAs to its monoenoic precursors [cy/pre], ratio of saturated to monounsaturated PLFAs [sat/mono], Gram$^+$/Gram$^-$ ratio), and (c) percentages of fungal and bacterial PLFAs (of total PLFAs), and fungi/bacteria ratio. Significant effects are given in bold ($P < 0.05$).

Factor	df	F	P	df	F	P	df	F	P
(a)									
		Basal respiration			Microbial biomass			Specific respiration	
Forest type (F)	4,24	7.51	**<0.001**	4,30	5.95	**0.001**	4,24	0.92	0.47
Site condition (S)	1,6	3.26	0.121	1,30	16.93	**<0.001**	1,6	0.52	0.498
Depth (D)	2,78	181.58	**<0.001**	2,70	271.27	**<0.001**	2,78	17.37	**<0.001**
F x S	4,24	8.83	**<0.001**	4,30	4.61	**0.005**	4,24	2.36	0.082
S x D									
F x D				8,70	2.15	**0.042**			
(b)									
		cy/pre ratio			sat/mono ratio			*$Gram^+/Gram^-$ ratio*	
Forest type (F)	4,24	2.75	0.052	4,24	11.12	**<0.001**	4,24	6.86	**0.001**
Site condition (S)	1,6	3.48	0.111	1,6	1.27	0.304	1,6	8.24	**0.028**
Depth (D)	2,68	337.3	**<0.001**	2,76	21.68	**<0.001**	2,76	291.1	**<0.001**
F x S	4,24	2.69	0.055	4,24	5.89	**0.002**	4,24	4.08	**0.012**
S x D	2,68	6.2	**0.003**	2,76	10.71	**<0.001**	2,76	7.51	**0.001**
F x D	8,68	3.72	**0.001**						
(c)									
		Fungi percent			Bacteria percent			Fungi/bacteria ratio	
Forest type (F)	4,30	1.77	0.161	4,30	2.19	0.094	4,24	0.83	0.52
Site condition (S)	1,30	6.46	**0.016**	1,30	4.34	**0.046**	1,6	4.98	0.067
Depth (D)	2,68	982.11	**<0.001**	2,78	149.46	**<0.001**	2,68	995.4	**<0.001**
F x S	4,30	1.99	0.121	4,30	0.73	0.577	4,24	1.6	0.207
S x D	2,68	18.54	**<0.001**				2,68	16.92	**<0.001**
F x D	8,68	3.61	**0.001**				8,68	2.84	**0.009**

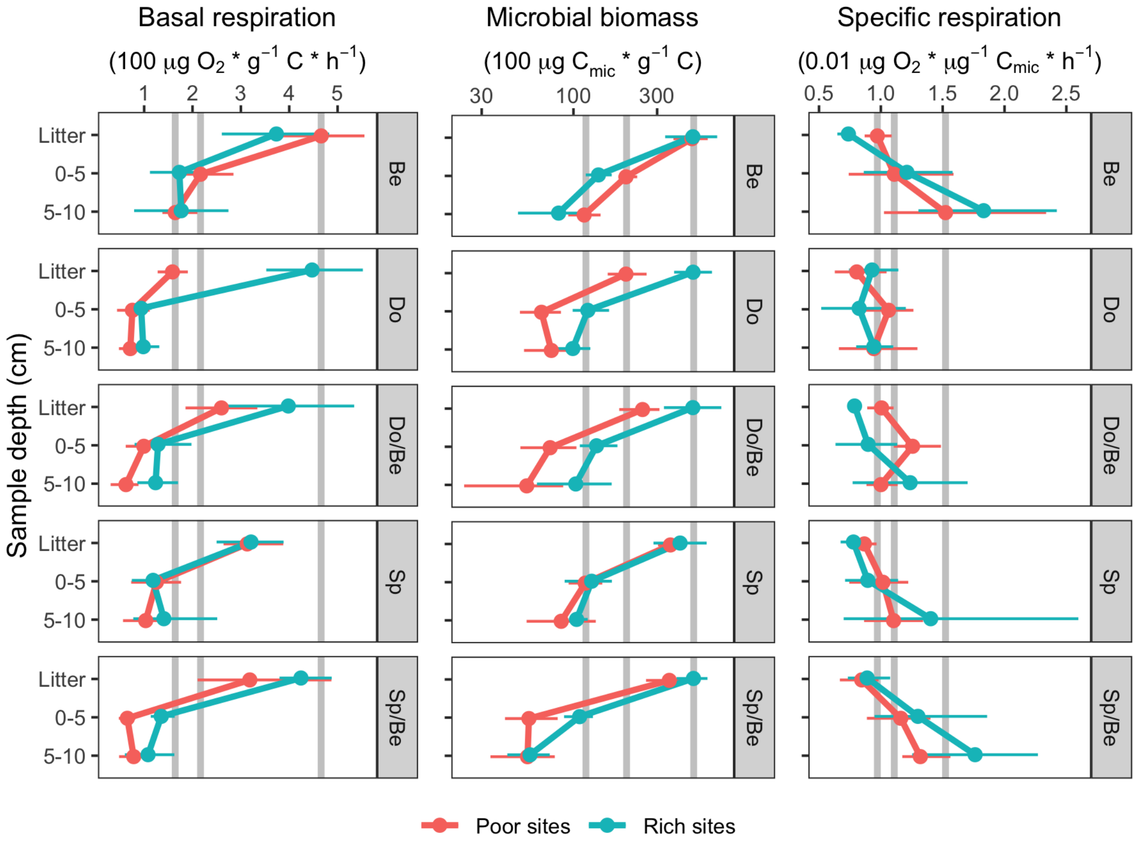

Figure 2.3: Changes in microbial basal respiration (μg O_2 g^{-1} C h^{-1}), microbial biomass (μg C_{mic} g^{-1} C) and microbial specific respiration (μg O_2 μg^{-1} C_{mic} h^{-1}) with soil depth (litter and 0–5, and 5–10 cm soil) in five forest types (European beech [Be], Douglas fir [Do], Douglas fir with beech [Do/Be], Norway spruce [Sp], and Norway spruce with beech [Sp/Be]) at nutrient-poor and nutrient-rich sites. Points and horizontal bars represent means and standard errors (n = 4). The grey vertical bars represent respective values in beech forests at nutrient-poor sites in litter, 0–5, and 5–10 cm soil. Note log scale for microbial biomass.

The response of microorganisms to changes in site conditions also varied with forest types. Differences between nutrient-rich and nutrient-poor sites were largest in Douglas fir and smallest in beech forests (Figures **2.3**, **2.4**, Table **A.2**). At nutrient-poor sites, microbial basal respiration in Douglas fir forests was 57% lower and microbial biomass in pure and mixed forests of Douglas fir both were 47% lower compared to nutrient-rich sites. In parallel, but less strong, microbial biomass in spruce mixed forests was 36% lower at nutrient-poor than that at nutrient-rich sites.

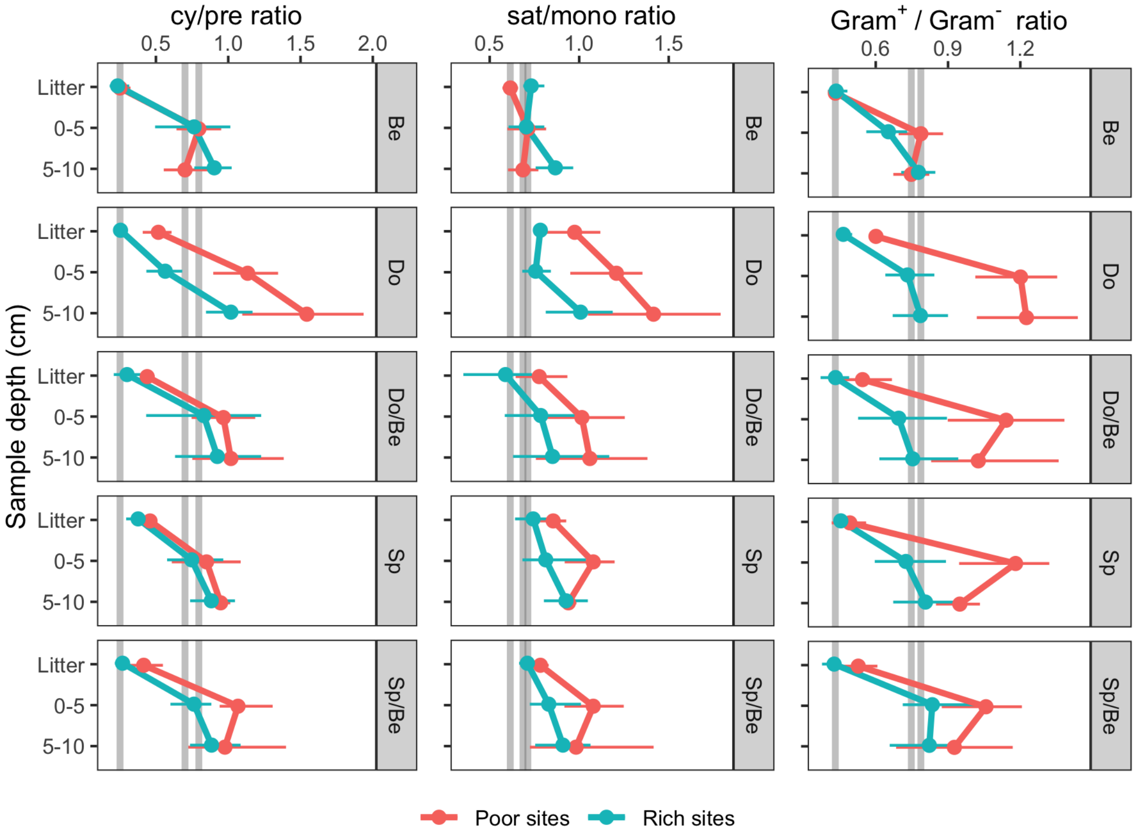

Figure 2.4: Changes in stress indicators (ratio of cyclopropyl fatty acids to its precursors [cy/pre], ratio of saturated to monounsaturated fatty acids [sat/mono] and ratio of Gram$^+$ to Gram$^-$ bacteria [Gram$^+$/Gram$^-$]) with soil depth (litter and, 0–5, and 5–10 cm soil) in five forest types (European beech [Be], Douglas fir [Do], Douglas fir with beech [Do/Be], Norway spruce [Sp], and Norway spruce with beech [Sp/Be]) at nutrient-poor and nutrient-rich sites. Points and horizontal bars represent means and standard errors (n = 4). The grey vertical bars represent respective values in beech forests at nutrient-poor sites in litter, 0–5, and 5–10 cm soil.

Likewise, in Douglas fir forests the stress indicator cy/pre ratio at nutrient-poor sites exceeded that at nutrient-rich sites by 82%, and similarly, the sat/mono and Gram$^+$/Gram$^-$ bacteria ratio at nutrient-poor sites exceeded that at nutrient-rich sites by 38–40% (Figure **2.4**, Table **A.2**). In Douglas fir mixed forests the Gram$^+$/Gram$^-$ bacteria ratio at nutrient-poor sites exceeded that at nutrient-rich sites by 34%. Further, the response of microbial stress to changes in site conditions varied with soil depth. In particular, the responses of the sat/mono ratio and the Gram$^+$/Gram$^-$ ratio to site conditions were most pronounced at 0–5 cm soil depth.

2.3.2 Microbial community structure

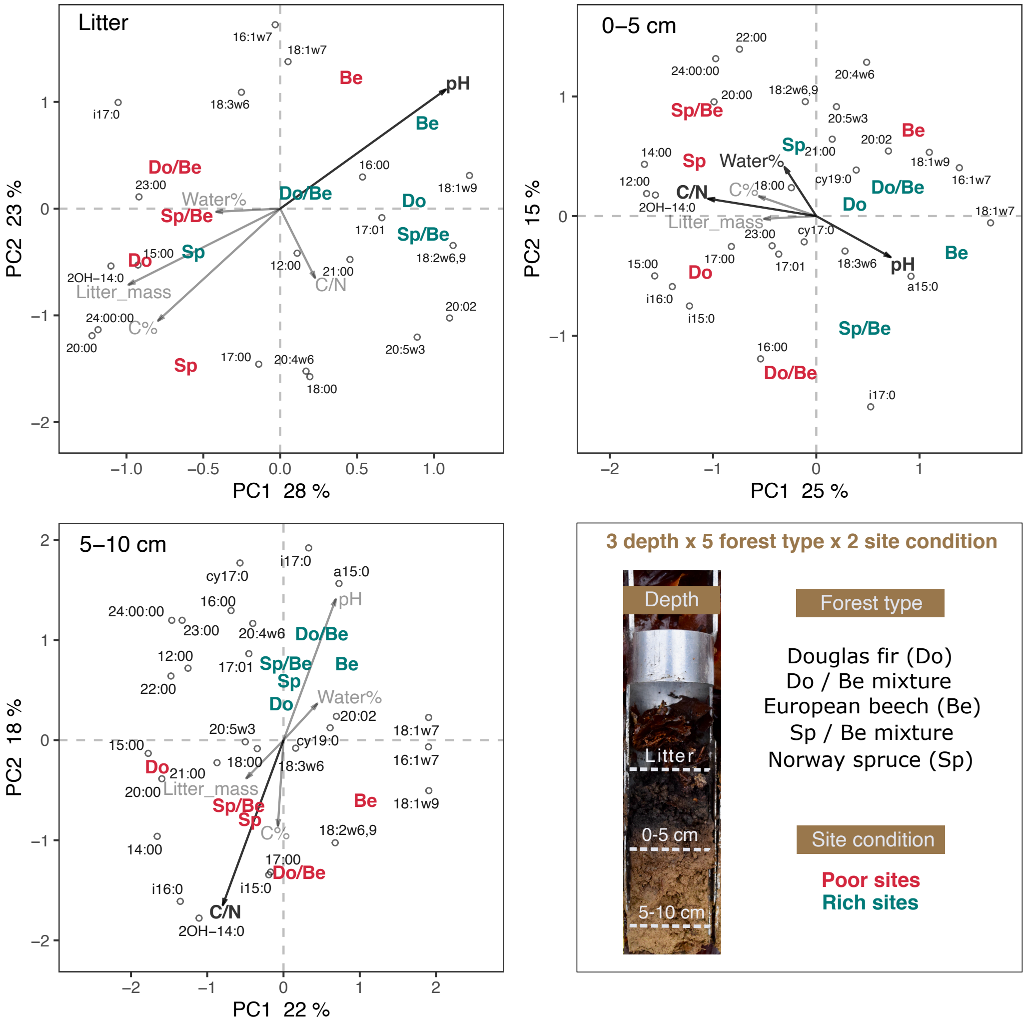

Figure 2.5: Principal component analysis of the microbial community structure (as indicated by phospholipid-derived fatty acids) in five forest types (European beech [Be], Douglas fir [Do], Douglas fir with beech [Do/Be], Norway spruce [Sp], and Norway spruce with beech [Sp/Be]) at nutrient-poor and nutrient-rich sites in litter, 0–5, and 5–10 cm soil. Positions of forest types represent centroids (n = 4). Nutrient-poor sites are given in red and nutrient-rich sites in green. C/N, pH, water content (water%), carbon content (C%) as well as litter mass were post-fitted into the plot. Significant variables selected by RDA permutation test were in bold (based adjusted R^2).

As indicated by the PLFA patterns, microbial community composition in beech forests differed from that in Norway spruce and Douglas fir forests, with mixed forests being intermediate between pure beech and coniferous forests (Figure **2.5**). Across layers, Forest type effects on microbial community composition were significant in litter and 0–5 cm soil, and marginally significant in 5–10 cm soil (Table **2.3**). Despite strong

Table 2.3: Results of two-way *MANOVA*s on PLFA composition (a) without covariates and (b) with covariates (pH, C/N ratio, water content) in litter, 0–5, and 5–10 cm soil. Factors include Forest type (European beech, Douglas-fir, Norway spruce and mixture of European beech with Douglas-fir, and mixture of European beech with Norway spruce), Site condition (nutrient-rich and nutrient-poor sites) and their interactions. *MANOVA*s were based on principal components from each sample depth (significant PCs were determined by broken stick criterion; see Methods). Type I sequential sum of square was used for models with and without covariates. Significant effects are given in bold (P < 0.05).

	(a) Without covariates					(b) With covariates			
Factor	df	Wilk's lambda	F	P	-	df	Wilk's lambda	F	P
Litter									
Forest type(F)	4,30	0.32	3.29	**0.001**		4,29	0.39	2.53	**0.008**
Site condition (S)	1,30	0.42	12.77	**0.000**		1,29	0.61	5.72	**0.004**
F x S	4,30	0.73	0.77	0.677		4,29	0.75	0.68	0.767
0–5 cm									
Forest type(F)	4,30	0.19	2.80	**0.001**		4,27	0.30	1.67	0.057
Site condition (S)	1,30	0.39	8.13	**0.000**		1,27	0.75	1.54	0.218
F x S	4,30	0.36	1.57	0.078		4,27	0.33	1.53	0.096
5–10 cm									
Forest type(F)	4,30	0.41	1.76	0.051		4,29	0.41	1.68	0.067
Site condition (S)	1,30	0.45	8.15	**0.000**		1,29	0.82	1.39	0.265
F x S	4,30	0.69	0.68	0.805		4,29	0.73	0.54	0.915

Covariates:

$in\ litter:\ pH;\quad in\ 0-5\ cm:\ C/N\ ratio+pH+water\ content;\quad in\ 5-10\ cm:\ C/N\ ratio.$

turnover of microbial community composition between nutrient-rich and nutrient-poor sites (Site condition effects; all P < 0.001), in beech forests microbial community structure in nutrient-poor and nutrient-rich sites was similar, and this was most apparent in 0–5 cm soil (Forest type × Site condition interaction; Figure **2.5**, Table **2.3**).

A number of fatty acids varied among forest types and with site conditions. Beech forests were characterized by unsaturated fatty acids at all depths, in particular by 16:1ω7, 18:1ω7, 18:1ω9 (Figure **2.5**). Norway spruce forests were associated with long-chain saturated fatty acids (22:0, 24:0), and Douglas fir forests with bacterial marker fatty acids (2OH-14:0, cy17:0). Further, nutrient-rich sites were associated with unsaturated fatty acids in litter, such as 18:1ω9 and 18:2$\omega 6, 9$. Litter at nutrient-rich sites was generally richer in fungi than at nutrient-poor sites, but the opposite was true for the soil (Site condition × Depth interaction; Figure **A.2**, Table **2.2**). The relative abundance of fungi and bacteria generally did not differ among forest types, but the relative abundance of fungi consistently decreased, whereas the relative abundance of bacteria increased with soil depth (Figures **A.2**, **A.3**). In addition, based on the contrast of Site condition, at nutrient-poor sites the relative abundance of fungi in pure beech and spruce forests was higher than at nutrient-rich sites. By contrast, in pure and mixed Douglas fir forests at nutrient-poor sites the relative abundance of fungi in soil was similar to that at nutrient-rich sites (Figure **A.2**, Table **A.2**).

Litter mass did not differ significantly among forest types, but was 58% higher at nutrient-poor than at nutrient-rich sites (Forest type: $F_{4,30} = 0.55$, $P = 0.70$; Site condition: $F_{1,30} = 13.21$, $P = 0.001$; Figure **A.4)**. Nutrient-poor sites also were more nitrogen-limited and acidic than nutrient-rich sites (Figure **2.5**). Soil C/N ratio, pH and soil moisture were among the most important environmental variables in explaining variations in PLFA composition (Table **A.3**). In litter, pH accounted for most (8%) of the variation explained by all environmental variables (13%). By contrast, in 0–5 cm as well as 5–10 cm soil depth, C/N ratio accounted for most of the variation explained by all environmental variables (22% out of the total of 37% and 13% out of the total of 15%, respectively; Table **A.3**). Underlining the importance of environmental factors in structuring microbial communities at the study sites, the main effect of Site condition became non-significant in soil after including C/N ratio, pH, water content (0–5 cm soil depth) and C/N ratio (5–10 cm soil depth) as covariates in *MANOVA*s. By contrast, in litter, including pH as covariate did not significantly affect the effects of Site condition. The effects of Forest type remained marginally significant in both depths of soil and significant in litter when including covariates (Figure **2.5**, Table **2.3**).

2.4 Discussion

2.4.1 Functional indicators

The present study evaluated effects of two coniferous trees in pure and mixed stands on the composition and functioning of soil microbial communities across a range of nutrient conditions, with native European beech as reference. Overall, the results partially support our first and second hypotheses. Forest type only affected the functioning of microbial communities at nutrient-poor sites, but not at nutrient-rich sites. At nutrient-poor sites, basal respiration, microbial biomass and stress indicators all were detrimentally affected in pure and mixed coniferous forests, with the effects being particularly strong in Douglas fir, but less pronounced in Norway spruce and mixed stands. Enrichment of beech with either Douglas fir or spruce compromised microbial functioning, suggesting that caution is needed when admixing conifers to European beech forests at nutrient-poor sites. By contrast, similar basal respiration, microbial biomass and stress indicators at nutrient-rich sites across the studied forest types contradict our second hypothesis and suggest that, at nutrient-rich sites, soil microbial communities are rather irresponsive to changes in tree species. This implies that, at nutrient-rich sites, planting Douglas fir in pure or mixed forests may provide an alternative to planting Norway spruce.

The site- and tree species-specific responses of microorganisms are likely caused by differences in the provisioning of carbon resources. Gram^{+} bacteria better cope with recalcitrant carbon resources, whereas Gram^{-} bacteria favor labile carbon compounds (Kramer and Gleixner, 2008; Fanin et al., 2019). High $\text{Gram}^{+}/\text{Gram}^{-}$ ratio in Douglas fir and low $\text{Gram}^{+}/\text{Gram}^{-}$ ratio in European beech at nutrient-poor sites therefore indicate more pronounced shortage of labile carbon resources in Douglas fir compared to beech forests. This is further supported by the lower microbial specific respiration in Douglas fir compared to beech forests, which was largely due to lower microbial basal respiration (Anderson and Domsch, 2010). Low availability of labile carbon favors oligotrophic microbial communities characterized by low respiration rates and biomass (Potthast et al., 2010; Fanin et al., 2019), consistent with our findings of low basal respiration and microbial biomass in pure and mixed coniferous forests at nutrient-poor sites.

Moreover, higher ratios of cyclopropyl PLFAs to their monoenoic precursors and higher ratios of saturated to monounsaturated PLFAs in pure and mixed coniferous compared to pure beech forests at nutrient-poor sites indicate that microorganisms in pure and mixed coniferous forests were more nutrient (and/or water) stressed (Moore-Kucera and Dick, 2008; Pollierer et al., 2015). Greater microbial stress in coniferous and mixed compared to pure beech forests at nutrient-poor sites also is indicated by lower proportions of the Gram^{-} bacteria marker fatty acids 16:1ω7 and 18:1ω7 in the former. Under stress, Gram^{-} bacteria change the composition of their cell membranes from 16:1ω7 and 18:1ω7 to cyclopropane fatty acids associated with slower growth rates (Kieft et al., 1994; Lundquist et al., 1999). The similarity of microbial indicators in beech forests at nutrient-rich and nutrient-poor sites indicates that, compared to coniferous stands, beech maintained microbial community functioning and prevented stress conditions by providing more labile carbon resources at nutrient-poor conditions, presumably by releasing high amounts of root-derived resources (Meier et al., 2020).

The suggestion that beech is able to alleviate microbial stress by maintaining or even increasing the release of root-derived resources at nutrient-poor sites is supported by higher fine root biomass in beech than in pure and mixed coniferous forests at nutrient-poor sites, whereas at nutrient-rich sites fine root biomass varies little among forest types (*A. Lwila, in prep.*). If soil nutrient availability declines, plants allocate surplus carbon into roots, associated with increased root exudation (Laliberté et al., 2017; Prescott et al., 2020). Recently, higher root exudation has been confirmed for beech forests at more acidic and nitrogen deficient stands (Meier et al., 2020), conditions similar to our nutrient-poor sites. Large amounts of root-derived resources were presumably also responsible for alleviating microbial resource deficiency and stress in beech forests at nutrient-poor sites. Trenching and girdling experiments confirm that reducing or omitting the flux of root-derived resources into the soil strongly reduces fungal and bacterial biomass, demonstrating the importance of root-derived resources for maintaining soil microbial biomass (Kaiser et al., 2010; Bluhm et al., 2019). Thus, beech may facilitate soil microorganisms at environmental stress conditions by increasing root exudation, unlike both of the studied coniferous species. This may also mitigate detrimental effects of Douglas fir on microorganisms at nutrient-poor sites in mixed forests. Generally, high amounts of root-derived resources in beech may be responsible for the facilitation of neighboring coniferous trees by beech, resulting in overyielding in mixed stands at nutrient-poor sites (Toïgo et al., 2015; Ammer, 2019; David et al., 2020).

Notably, we sampled litter and soil during autumn/winter after beech had shed its leaves, which might have affected microbial communities. However, any litter effect on microbial communities should have been similar in nutrient-rich and nutrient-poor sites, as litter input in beech forests varies little with site conditions (Meier et al., 2005). By contrast, we found microbial community characteristics to differ among forest types only at nutrient-poor sites, and litter mass on the forest floor did not differ among forest types (Figure **A.4**). Supporting the importance of root-derived resources, fine root biomass in beech forests at nutrient-poor sites exceeded that in coniferous forests by more than 1.6 times, whereas fine root biomass did not differ significantly among forest types at nutrient-rich sites (*A. Lwila, in prep.*). The hypothesis of high root-derived resources in beech forests implies that the impact of roots on microorganisms still was strong in autumn/winter indicating that not only recent photosynthates but also stored carbohydrates contribute to providing root-derived resources to soil microorganisms (Druebert et al., 2009). However, it remains open whether the effects of Forest type on microbial communities get stronger or weaker with time, hampering generalization of our finding across seasons. Although microbial communities fluctuate considerably with season (Koranda et al., 2013; Abramoff and Finzi, 2016; Nacke et al., 2016), comprehensive sampling in Douglas fir forests across seasons suggests that, except during summer drought, microbial stress indicators fluctuate little (Moore-Kucera and Dick, 2008). Further, although fine roots are generally concentrated in upper soil layers, we may not have captured the full effects of roots, as our sampling was limited to the upper 10 cm of the soil; beech roots, for example, may extend considerably deeper into the soil (Leuschner et al., 2004). Experimental manipulations of root-derived resources in the field are needed to fully resolve the role of root-derived resources in driving microbial community structure and functioning (Koranda et al., 2011; Bluhm et al., 2019).

Contrary to our third hypothesis, the effects of forest type were not stronger in litter than in soil. Forest type impacted microbial respiration, biomass and stress indicators similarly across layers at nutrient-poor sites. This uniformity further supports our conclusion that effects of forest type were not the result of different litter quantity and quality, but were due to root-derived resources. This contrasts earlier suggestions that, because litter is not buffered against environmental conditions, microbial responses in litter are more sensitive to environmental change than those in soil (Pollierer et al., 2015). Reflecting environmental changes, microbial biomass decreased while microbial stress indicators increased with soil depth. Actually, this sensitivity may be related to lower carbon availability deeper in soil, resulting in stronger resource limitation (Fierer et al., 2003). As indicated by Gram$^+$/Gram$^-$ ratios, the difference in resource limitation between litter and soil was greatest in pure coniferous and mixed forests at nutrient-poor sites.

2.4.2 Community structure

We assumed that microbial functioning ultimately relies on microbial community structure, and this is supported by the consistent turnover in microbial community composition, as well as the differences in microbial functioning between nutrient-rich and nutrient-poor sites. Despite increased resource limitation with soil depth, microbial community structure in 5–10 cm soil differed little between forest types at nutrient-rich sites. This suggests that the influence of forest types fades deeper in soil. By contrast, at nutrient-poor sites, microbial community structure differed between beech and coniferous forests in soil, particularly in 5–10 cm depth, supporting our conclusion that effects of tree species on microorganisms in nutrient-poor soil are predominantly due to differences in root-derived resources. Unlike Douglas fir and spruce, European beech maintained and stabilized microbial community structure and functioning in litter and soil irrespective of site conditions. Interestingly, in 5–10 cm depth at nutrient-poor sites, microbial community structure and carbon limitation under Douglas fir differed most strongly from beech. This implies that, among the tree species studied, root-derived resources are most limited under Douglas fir at nutrient-poor sites, resulting in pronounced resource shortage and marked changes in microbial community composition. Such changes in microbial community structure may significantly impact the functioning of soil microbial communities as the availability of carbon resources and carbon limitation affect the vertical distribution of saprotrophic fungi and decomposition processes, e.g., by shifting competition between saprotrophic and mycorrhizal fungi (Gadgil and Gadgil, 1971; Lindahl et al., 2007).

Our results support previous findings that regional factors more strongly shape microbial community structure than tree species (Richter et al., 2018). The relative abundance of fungi and bacteria as well as the fungi/bacteria ratio did not vary with forest types but rather with site conditions. Fungi were relatively more abundant at nutrient-poor sites, supporting earlier suggestions that the fungal energy channel dominates in low nutrient systems (Wardle et al., 2004). However, at nutrient-poor sites, the fungal energy channel did not dominate in Douglas fir forests, despite high C/N ratio and low pH. In fact, the relative abundance of fungi in Douglas fir forest soil was similar at nutrient-rich and nutrient-poor sites, resulting in lower fungal abundance in Douglas fir than beech forests, particularly in 5–10 cm depth. In addition to low amounts of root-derived resources, low fungal abundance in Douglas fir forest soil may be due to a mismatch between local and home (native range of Douglas fir) fungal communities, as only a subset of native-range fungal species has been recorded in the soils to which Douglas fir has been introduced (Schmid et al., 2014). Although molecular techniques are needed to identify the microbial taxa responsible for differences among forest types, particularly between Douglas fir and beech at nutrient-poor sites, our study supports the sensitivity of PLFA analysis in detecting changes in microbial community composition (Ramsey et al., 2006).

Forest type effects on microbial community composition were marginally significant after including covariates, indicating that forest types affected microbial community composition independently of the studied environmental variables. By contrast, the measured environmental variables clearly captured differences in soils between nutrient-poor and nutrient-rich sites, and explained much of the variance in site conditions. Among the environmental variables studied, C/N ratio and pH best explained variations in microbial community structure. Soil pH typically correlates with soil nutrient availability (Meier et al., 2020), further supporting the importance of nutrients in driving microbial responses to variations in site conditions. However, factors other than soil nutrient status and soil pH may have contributed to the observed differences between nutrient-rich and nutrient-poor sites. Despite inconsistent effects of site conditions on water content across layers, and little effects of water content on litter and soil microbial community structure, nutrient-poor sites are also characterized by lower precipitation. This is supported by higher δ^{13}C values of litter at nutrient-poor than at nutrient-rich sites (Figure **C.1**), reflecting high water stress at nutrient-poor sites (Peuke et al., 2006). Presumably, in addition to nutrients and pH, water stress contributed to the observed differences in microbial community composition between nutrient-poor and nutrient-rich sites. This is supported by the fact that soil water conditions are intricately linked to soil nutrient dynamics and the uptake of nutrients by plants (De Vries et al., 2019). To disentangle pathways linking forest stands and soil microbial communities, it is most promising to focus on water-deficient, low-pH and nutrient-poor stands.

2.4.3 Management implications

Due to increasing drought and associated outbreaks of bark beetles, Norway spruce forests are increasingly threatened in lowland regions of Europe. In the face of such challenges, mixed forests and alternative tree species such as Douglas fir provide promising options for provisioning long-term ecosystem services. By studying microbial communities in pure and mixed forests covering a range of nutrient and water conditions, we found that effects of forest type on soil microorganisms vary among tree species and mixed stands, but this strongly depends on the nutrient status of the sites. At nutrient-poor sites, Douglas fir strongly impacted microbial community structure and functioning compared to beech. Therefore, in long-term plantings, non-native tree species such as Douglas fir may compromise ecosystem functioning at nutrient-poor sites. This brings into question not only the advisability of establishing of pure Douglas fir forests, but also the enrichment of beech forests by Douglas fir at nutrient-poor sites. However, as Douglas fir in single-species and mixed stands with beech barely impacted the structure and functioning of soil microbial communities at nutrient-rich sites, Douglas fir may provide an alternative to Norway spruce at least at such sites. Although more information on ecosystem properties and processes is needed to gain a holistic understanding of the consequences of forest plantation on ecosystem functioning, we conclude that microbial stress is intensified in nutrient-poor soils by planting Douglas fir.

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Chapter 3

Guild patterns and variation in Collembola and Oribatida communities across soils of European beech, Norway spruce, non-native Douglas fir, and mixed conifer–beech forests: Biotic and abiotic drivers

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Abstract

Planting non-native trees may detrimentally affect decomposer communities, compromising biodiversity conservation and nutrient cycling. To evaluate the effects of tree species composition on soil microarthropods, we studied guild and community structure of collembolans (Collembola, Hexapoda) and oribatid mites (Oribatida, Acari) in temperate forests across a range of site conditions. Five forest types were studied, including pure stands of native European beech (*Fagus sylvatica*), non-native Douglas fir (*Pseudotsuga menziesii*), range-expanding Norway spruce (*Picea abies*) as well as respective conifer–beech forests. We assigned Collembola to life forms (epedaphic, hemiedaphic, and euedaphic) and Oribatida to trophic guilds (primary decomposers, secondary decomposers, and predators). We found that, although species richness and diversity did not differ among forest types, the abundance of euedaphic Collembola and that of predatory Oribatida were lower in Douglas fir than in European beech, presumably due to lower provisioning of root-associated resources in Douglas-fir

forests. Furthermore, species composition of Oribatida, but not that of Collembola, sensitively responded to forest type, differing most between Douglas fir and European-beech forests. Tree species composition explained more variation in Oribatida than in Collembola communities. Overall, the results suggest that non-native Douglas fir generally does not affect the diversity of soil microarthropods, but the limitation of root-derived resources may restrict the population development of microarthropods in Douglas-fir forests.

3.1 Introduction

Forest soils harbor a high diversity and abundance of invertebrates. Although many soil microarthropods function as generalist detritivores, they occupy a range of trophic positions (Scheu and Falca, 2000; Schneider et al., 2004; Chahartaghi et al., 2005). This challenges the view that the food of detritivores is homogeneous (Ponsard and Arditi, 2000; Moore et al., 2004). To better understand the link between forest types and soil animal communities, microarthropods might be grouped into guilds, i.e. species that use similar resources (Simberloff and Dayan, 1991). However, guilds have rarely been used in studies of microarthropod–tree interactions across ecosystems (Anderson, 1975; Maraun et al., 2003; Magilton et al., 2019).

Collembolans (Collembola, Hexapoda) and oribatid mites (Oribatida, Acari) play crucial roles in nutrient cycling and soil fertility. As indicated by bulk stable isotope analyses, Collembola and Oribatida span three to four trophic levels in temperate forests, including decomposers, fungal feeders and predators/scavengers (Schneider et al., 2004; Chahartaghi et al., 2005). While primary decomposers predominantly rely on plant litter, secondary decomposers heavily feed on microorganisms, in particular saprotrophic fungi (Schneider et al., 2004; Pollierer et al., 2021). High ^{15}N values of certain Oribatida species have been taken as evidence that they live as predators or scavengers (Maraun et al., 2011), but in Collembola high ^{15}N values may also result from consumption of old organic matter (*Z. Li, in prep.*). Variations in the amount and quality of litter and root-derived resources across ecosystems are likely to drive guild-specific responses of soil microarthropods, with potentially contrasting responses in low and high trophic guilds.

Animal communities are structured by both biotic and abiotic factors, but the relative importance of these two pathways drive the community structure of Collembola and Oribatida has never been disentangled (Maraun and Scheu, 2000; Pollierer and Scheu, 2017). Despite only a few environmental variables were included, previous studies suggest that regional factors are crucial for structuring microarthropod communities, especially abiotic environmental variables (Erdmann et al., 2012; Pollierer and Scheu, 2017; Bluhm et al., 2019). By contrast, biotic factors typically little explained variation in community structure (Scheu and Schaefer, 1998; Erdmann et al., 2012; Bluhm et al., 2016). The importance of niche processes has been stressed for soil Oribatida (Caruso et al., 2012; Mori et al., 2013), but the knowledge on which niches are important for soil microarthropods is limited. Tree species composition is likely to affect the community structure of soil animals via changing abiotic factors (Maraun and Scheu, 2000; Scheu et al., 2003; Eissfeller et al., 2013). Further, Collembola are generally assumed to be more sensitive than Oribatida to abiotic microhabitat conditions and recolonize disturbed habitats more quickly (González-Macé and Scheu, 2018). Thus, the relative importance of biotic and abiotic environmental variables for the community structure of soil microarthropods may differ between Collembola and Oribatida, but until today this has not been investigated.

A better understanding of the effects of tree species composition on soil microarthropods has implications for forest management. In temperate and boreal regions, species richness is low, and managed forests typically are dominated by one or a few species. European beech is the climax species in lowland and lower montane regions in Central Europe (Leuschner and Ellenberg, 2017). Douglas fir has become the most abundant non-native tree species cultivated in Central Europe since its introduction from North America over 150 years ago (Schmid et al., 2014). The popular timber species, Norway spruce, originally growing at high elevation and in boreal regions, has been managed widely in lowlands of the temperate zone (Knoke et al., 2008). However, in recent years, large areas of Norway spruce stands, the most popular timber species, have been severely affected by extreme weather and bark beetle outbreaks. Those events are predicted to become more frequent in the pace of climate change (Pettit et al., 2020). Growing Douglas fir or admixture conifers to beech may reduce the risk of damage while maintaining economic gains (Schmid et al., 2014). However, in contrast to Norway spruce, little is known about the effects of Douglas fir on soil microarthropods. Overall, we lack a comprehensive evaluation of forest types on communities of soil Collembola and Oribatida using European beech as reference.

Here, we studied guilds and communities of Collembola and Oribatida across a range of site conditions. Forest types included pure stands of European beech, Douglas fir, Norway spruce, and the two beech–conifer mixtures. We related species to abiotic and biotic environmental variables to disentangle environmental drivers for the community structure of Collembola and Oribatida. We hypothesized that (1) compared to beech, the diversity and abundance of Collembola and Oribatida will be detrimentally affected in Douglas-fir forests, but being higher in Norway spruce and mixed forests. Further, as resource availability may differ among forest types, we hypothesized that (2) effects of forest types on Collembola and Oribatida will vary with guilds, with the effects differing between guilds of low and high trophic levels. Finally, we hypothesized that (3) the community structure of Collembola and Oribatida will vary with forest type, with Collembola more sensitively responding to environmental changes than Oribatida.

3.2 Methods

3.2.1 Forest sites

This study was conducted in forests of Northern Germany at eight sites, covering a range of environmental conditions (8 sites × 5 forest types; Figure **1.1**). Four sites in the south (51.662–51.770°N) stocked on parent rock of either loess-influenced

Triassic sandstone or mixtures of Paleozoic greywacke, sandstone, quartzite, and phyllite, resulting in soil types of partly podzolic Cambisol and Luvisol. Mean annual precipitation was 821–1029 mm. Four sites in the north (52.621–53.201°N) were located on Podzols over parent material of out-washed sand. Mean annual precipitation was 672–746 mm. The southern sites were richer in nutrients than the northern sites, as reflected by higher cation exchange capacity and pH; more details on site characteristics and soil chemical properties were given in Foltran et al. (2020) and Lu and Scheu (2021). The distance between sites ranged from 5 to 190 km (Ammer et al., 2020). Each site comprised three pure forests of European beech (*Fagus sylvatica* L.), Douglas fir (*Pseudotsuga menziesii* [Mirbel] Franco.), Norway spruce (*Picea abies* [L.] Karst.), and two conifer–beech mixtures (Douglas fir/European beech and Norway spruce/European beech). Within sites, the distance between stands ranged from 76 to 4600 m. Within each stand, plots of 2500 m^2 were established, mostly 50 m × 50 m. Focal tree species in pure stands on average comprised more than 90% of total basal area, while in Douglas fir mixed stands, focal tree species comprised on average 34% European beech and 58% Douglas fir, and in Norway spruce mixed stands, focal tree species comprised on average 56% European beech and 37% Norway spruce. Trees were on average more than 50 years old.

3.2.2 Animal sampling

Soil animals were sampled by taking soil cores using a metal corer (diameter 5 cm) between November 2017 and January 2018. Samples were taken between trees of the same (pure stands) or different species (mixed stands). One core was taken in each plot, and soil cores were separated into litter, 0–5, and 5–10 cm soil depth, and soil arthropods were extracted for each layer separately using high-gradient heat extraction (Macfadyen, 1961). Animals were collected in 50% diethylene glycol and then transferred into 70% ethanol for determination. Specimens were identified using the keys of Gisin (1960), Fjellberg (1998), Fjellberg (2007), and Hopkin (2007) for Collembola, and Weigmann (2006) for Oribatida. Collembola and adult Oribatida were identified to species level, except for Brachychthoniidae, Suctobelbidae, Phthiracidae, and nymphs of Oribatida. Due to the small size of Brachychthoniidae (~170 μm) and a lack of keys for immature Oribatida, they were not included in the analyses (see Supplementary **B**).

3.2.3 Trophic guilds

Guilds were defined as groups of species exploiting particular classes of resources within a community (Root, 1967; Simberloff and Dayan, 1991; Blondel, 2003). We used published and original data to assign Collembola to three life-forms, epedaphic, hemiedaphic, and euedaphic (Table **B.1**), and Oribatida to three trophic guilds, primary decomposers, secondary decomposers, and predators/scavengers (Table **B.2**) (Schneider et al., 2004; Maraun et al., 2011; Potapov and Tiunov, 2016; Potapov et al., 2019). Life-forms, as ecomorphological traits, reflect the vertical distribution of Collembola in the soil profile, but stable isotopes suggest life-forms of Collembola to also reflect trophic niches (Potapov and Tiunov, 2016). Endophagous Oribatida were grouped as secondary decomposers as both occupy similar trophic positions (Maraun et al., 2011). Some endophagous Oribatida species may also live as primary decomposers, but for simplicity, this was ignored (Supplementary **B**). If the guilds were not known for a certain species, we inferred it from closely related species. However, we did not translate Collembola life-forms into trophic guilds because there is limited support that the same trophic levels of Collembola and Oribatida reflect similar resource use. For example, euedaphic Collembola and predatory Oribatida both occupy high trophic positions as indicated by stable isotopes, but euedaphic Collembola may incorporate older plant materials rather than live as predators (*Z. Li, in prep.*).

3.2.4 Environmental variables

Environmental variables were collected from parallel studies at our study sites (Ammer et al., 2020; Foltran et al., 2020; Lu and Scheu, 2021). The proportion of focal tree species, namely European beech, Douglas fir, and Norway spruce, was calculated for each stand based on basal area at sampling (*J. Glatthorn, unpubl. data*). Fine roots (<2 mm) were sampled from 0–10 cm soil, and carbon (C) and nitrogen (N) were analyzed by an elemental analyzer (Vario MSA 2.7S, Sartorius Lab Instrument GmbH & Co. KG, Germany) (*A. Rivera Pérez, unpubl. data*). Microbial communities and chemical properties of litter and 0–5 cm soil were taken from Lu and Scheu (2021). Microbial communities were quantified using phospholipid fatty acids (PLFA), and microbial biomass was measured by substrate-induced respiration (Anderson and Domsch, 1978; Frostegård and Bååth et al., 1993). We derived Gram$^-$ and Gram$^+$ bacteria, fungi, and total PLFAs from marker fatty acids (Lu and Scheu, 2021). Basal respiration and microbial biomass were measured by O_2 consumption without and with glucose addition, respectively (Scheu, 1992). To characterize litter and soil, we measured pH, C, and N concentrations, as well as C/N ratio. Litter mass was estimated by drying litter at 50°C for 48 h (Macfadyen, 1961).

Climate data comprised annual temperature and annual rainfall averaged from January 1981 to December 2018 (Ammer et al., 2020). The chemistry of the mineral soil (0–5 cm depth) was taken from Foltran et al. (2020). Exchangeable cations (Al^{3+}, Ca^{2+}, Fe^{2+}, K^+, Mg^{2+}, Mn^{2+}, Na^+, and H^+) were extracted in NH_4Cl. Elemental concentrations (Al, Ca, Fe, K, Mg, Mn, Na, P, and S) were determined by pressure digestion with nitric acid. Exchangeable cations and element concentrations were determined by inductively coupled plasma-optical emission spectrometry (ICP-OES; Spectro Genesis, Spectro, Kleve, Germany). Total cation exchange capacity (CEC; mmol kg^{-1}) was summed from all extracted cations. Soil C and N were measured by an elemental analyzer, and pH was measured in H_2O and KCl solution.

3.2.5 Statistical analyses

We used generalized linear mixed models (GLMMs) to analyze the guild-specific abundance of Collembola and Oribatida. Due to overdispersion in Poisson distribution, we fitted GLMM with negative binomial error distribution and log link function.

Models included forest type (European beech, Douglas fir, Douglas fir/European beech, Norway spruce, Norway spruce/European beech), site condition (nutrient-rich and nutrient-poor sites), guild (three trophic guilds), and their interactions as fixed effects. Nested random effects include guild nested within forest type within each site. Specimens from the same soil core were pooled before the analyses.

Planned contrasts were designated to compare coniferous and mixed forests with beech forests. European beech was used as reference because it represents the climax tree species in lowland and lower montane regions in Central Europe (Leuschner and Ellenberg, 2017). The contrasts were used as a measure of effect size. Due to the log-linked function in negative binomial model, the contrast is analogous to the log response ratio (Piovia-Scott et al., 2019). For other univariate analyses of species richness, Shannon diversity and abundance see Supplementary **B**.

To model species communities as a function of forest type and site condition, we applied permutational multivariate analyses of variance (*PERMANOVA*) separately for Collembola and Oribatida. Multivariate homogeneity of dispersion (beta-diversity) was tested between forest types (Anderson et al., 2006). We used nonmetric multidimensional scaling (*NMDS*) to visualize community structure; both *PERMANOVA* and *NMDS* were based on Bray-Curtis dissimilarities. For all multivariate analyses, only species that occurred in more than one plot were included in the analyses.

Redundancy analyses (RDA; Euclidean distance) were used to inspect the role of tree species composition and other environmental variables in driving the community structure of Collembola and Oribatida. Before RDA, Hellinger-transformation was applied to species data to reduce the effects of double zeros (Legendre and Gallagher, 2001). We first eliminated intercorrelated environmental variables ($|\text{Pearson's r}| < 0.7$) selecting variables first within groups and then between groups (two groups: trees and organic layers, mineral soil and climate; Figure **B.1**, **B.2**). The remaining variables were standardized before RDA (zero mean and unit variance).

We applied variance partitioning to evaluate the relative contribution of abiotic and biotic environmental variables in driving community structure (Borcard et al., 1992). Environmental variables ($|\text{Pearson's r}| < 0.7$) were grouped into three categories: tree-related variables [proportion of European beech (Beech%), proportion of Douglas fir (Douglas%), proportion of Norway spruce (Spruce%), root carbon (C), ratio of root carbon and nitrogen (C/N)], abiotic environmental variables (nutrients in 0–5 cm mineral soil, litter mass, pH and water content in litter and 0–5 cm soil) and biotic environmental variables (microbial community parameters in litter and 0–5 cm soil).

To identify the most influential environmental variables, we applied forward selection in RDA with adjusted R^2 and alpha level ($P \leq 0.05$) as two stopping criteria (Blanchet et al., 2008). We then refitted the RDA with the selected environmental variables for easier interpretation. To further understand how environmental variables moderated the effects of tree species composition, we applied RDA with tree species composition only as compared to partial RDA with tree species composition conditioned by the remaining covariates.

All analyses were performed in R 4.0.3 (www.r-project.org). We used ‘lmer4’ to fit GLMMs (‘glmmer.nb’), and ‘nlme’ to fit LMMs (‘lme’). Contrasts for models were calculated using ‘emmeans’ package. For all univariate models, residuals were plotted to check the assumptions of normality and homoscedasticity. For multivariate analyses, we used ‘vegan’ to analyze *PERMANOVA* (‘adonis2’), *NMDS* (‘metaMDS’), and RDA (‘rda’).

3.3 Results

3.3.1 Animal communities

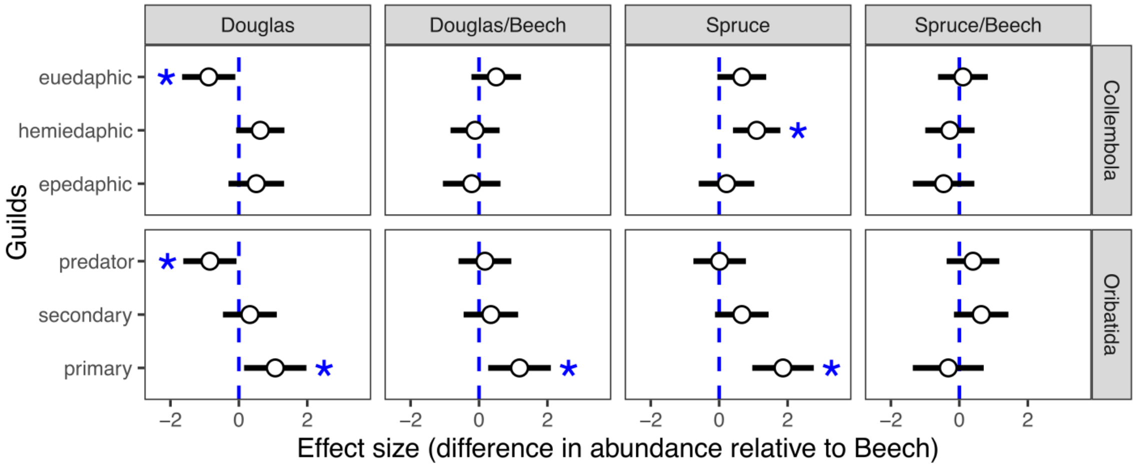

Figure 3.1: Variation in the abundance of Collembola and Oribatida guilds with forest type [Douglas-fir (Douglas), Norway spruce (Spruce), two conifer-beech mixtures (Douglas/Beech and Spruce/Beech)] given as effect size relative to European beech. Effect size is analog to the log response ratio [ln(abundance in conifer pure and mixed forests / abundance in European-beech forests)]. Guilds are represented by three life-forms in Collembola (euedaphic, hemiedaphic, and epedaphic) and three trophic groups in Oribatida (primary decomposers, secondary decomposers, predators/scavengers). Points represent means and bars represent 95% confidence intervals (n = 8). Asterisks indicate significant difference to European beech ($P \leq 0.05$).

Richness, Shannon diversity and total number of Collembola and Oribatida did not differ among forest types (all $P > 0.06$; Supplementary **B**; Figures **B.3**, **B.4**, **B.5**; Tables **B.3**, **B.4**). However, the guild-specific abundance varied with forest types (Figure **3.1**; Table **B.5**). Abundances of euedaphic Collembola and predatory Oribatida in Douglas fir were 50% and 47% lower than in European-beech forests, respectively. By contrast, the abundance of hemiedaphic Collembola in spruce forests was three times higher than in European beech (+199%). Primary decomposer oribatid mites in Douglas fir and Norway-spruce forests were more than two times higher than in European beech (+132%, +175%, respectively). Guild-specific abundances of Collembola and Oribatida in mixed forests were intermediate to the pure stands, and this was also true for the proportions of guilds (Figure **3.2**).

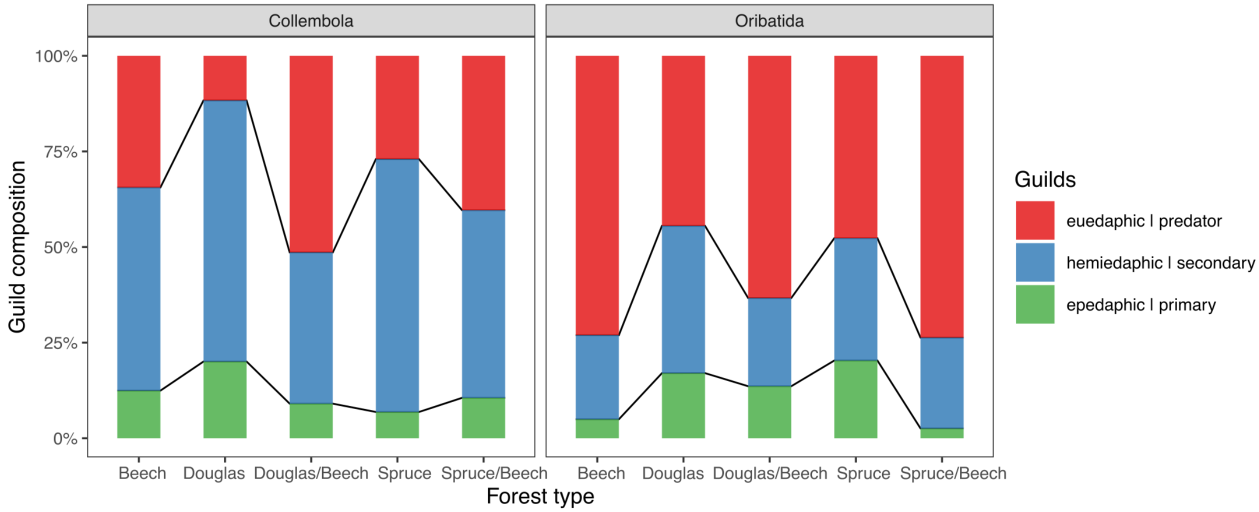

Figure 3.2: Abundance-based guild composition of Collembola and Oribatida in pure and mixed forest stands [European beech (Beech), Douglas-fir (Douglas), Norway spruce (Spruce), and two conifer–beech mixtures (Douglas/Beech and Spruce/Beech)]. Guilds were represented by three life-forms in Collembola (euedaphic, hemiedaphic, and epedaphic) and three trophic groups in Oribatida (primary decomposers, secondary decomposers, predators/scavengers).

Based on species abundance, Collembola communities did not differ among forest types, but Oribatida communities differed significantly and this was most pronounced between European beech and Douglas-fir forests, with Norway spruce and mixed forests being intermediate (Figure **3.3**; *PERMANOVA*, forest type effects for Collembola $F_{4,30} = 1.13$, $P = 0.298$ and for Oribatida $F_{4,30} = 1.52$, $P = 0.012$). The beta dispersion was not significant among forest types for Collembola ($F_{4,35} = 1.07$; $P = 0.385$) and for Oribatida ($F_{4,35} = 0.37$; $P = 0.825$). Despite strong effects of site conditions (*PERMANOVA*, site condition effect for Collembola $F_{1,30} = 3.81$, $P = 0.001$ and for Oribatida $F_{1,30} = 3.04$, $P = 0.002$), forest type effects on the community structure of Collembola and Oribatida did not vary with site conditions (*PERMANOVA*, Forest type x Site condition: all $P > 0.5$).

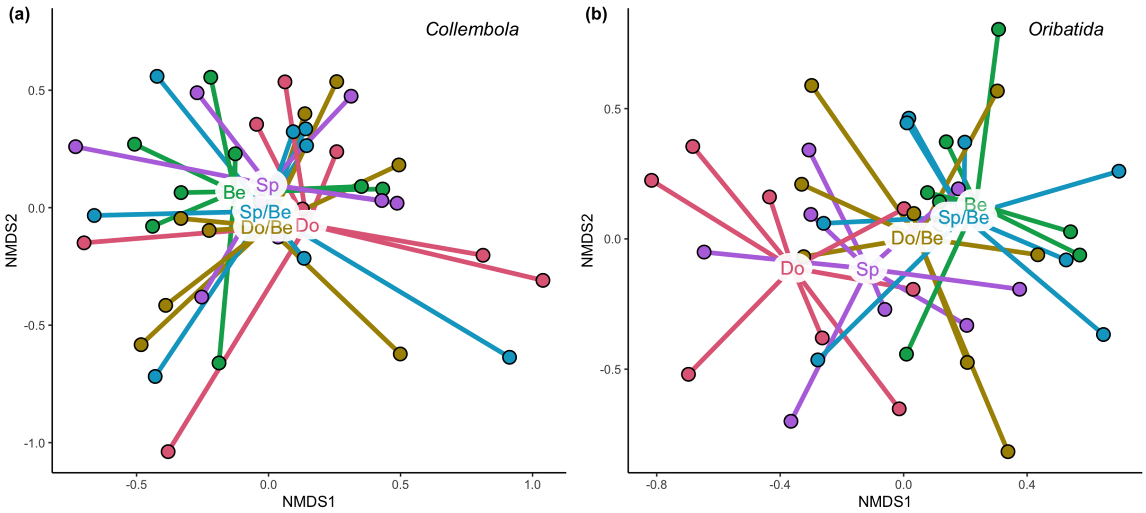

Figure 3.3: Nonmetric multidimensional scaling (*NMDS*) of (a) Collembola and (b) Oribatida communities in five forest types [European beech (Be), Douglas-fir (Do), Norway spruce (Sp), and two conifer–beech mixtures (Do/Be and Sp/Be)]. The positions of forest types are based on centroids. *NMDS* stress value of Collembola and Oribatida of 0.23 and 0.27, respectively (k = 2). *NMDS* based on Bray-Curtis dissimilarities of animal abundances.

3.3.2 Environmental drivers

Environmental variables explained 31.1% of the variation in Collembola data and 16.1% in Oribatida data (Table **B.6**). Based on forward selection, the structure of Collembola communities was explained by soil C/N ratio, soil CEC, litter mass, and proportion of beech. The most abundant euedaphic Collembola, such as *Isotomiella minor*, *Protaphorura armata*, and *Mesaphorura macrochaeta*, were associated with European beech (Figure **3.4**). In Oribatida, variation in community structure was explained by soil CEC, soil Fe concentration, soil pH, Gram$^-$ bacteria, and proportions of European beech and Douglas fir. The three most abundant Oribatida taxa, *Oppiella nova*, *Suctobelbella* spp., and *Oppiella subpectinata*, were negatively associated with Douglas fir (Figure **3.4**).

Variation partitioning supported the importance of tree species in driving the community structure of Oribatida and abiotic environmental variables in driving Collembola (Figure **3.5**). Tree-related variables explained 13% of the variation in Oribatida data and 9% of the variation in Collembola data. By contrast, abiotic variables in litter and soil explained 14% of the variation in Collembola data, but only 4% in Oribatida data. When partitioning out selected covariates in partial RDA (Table **3.1**), the effects of European beech on both Collembola and Oribatida communities were more pronounced, suggesting that tree identity effects on microarthropod community structure extended beyond those of measured environmental variables.

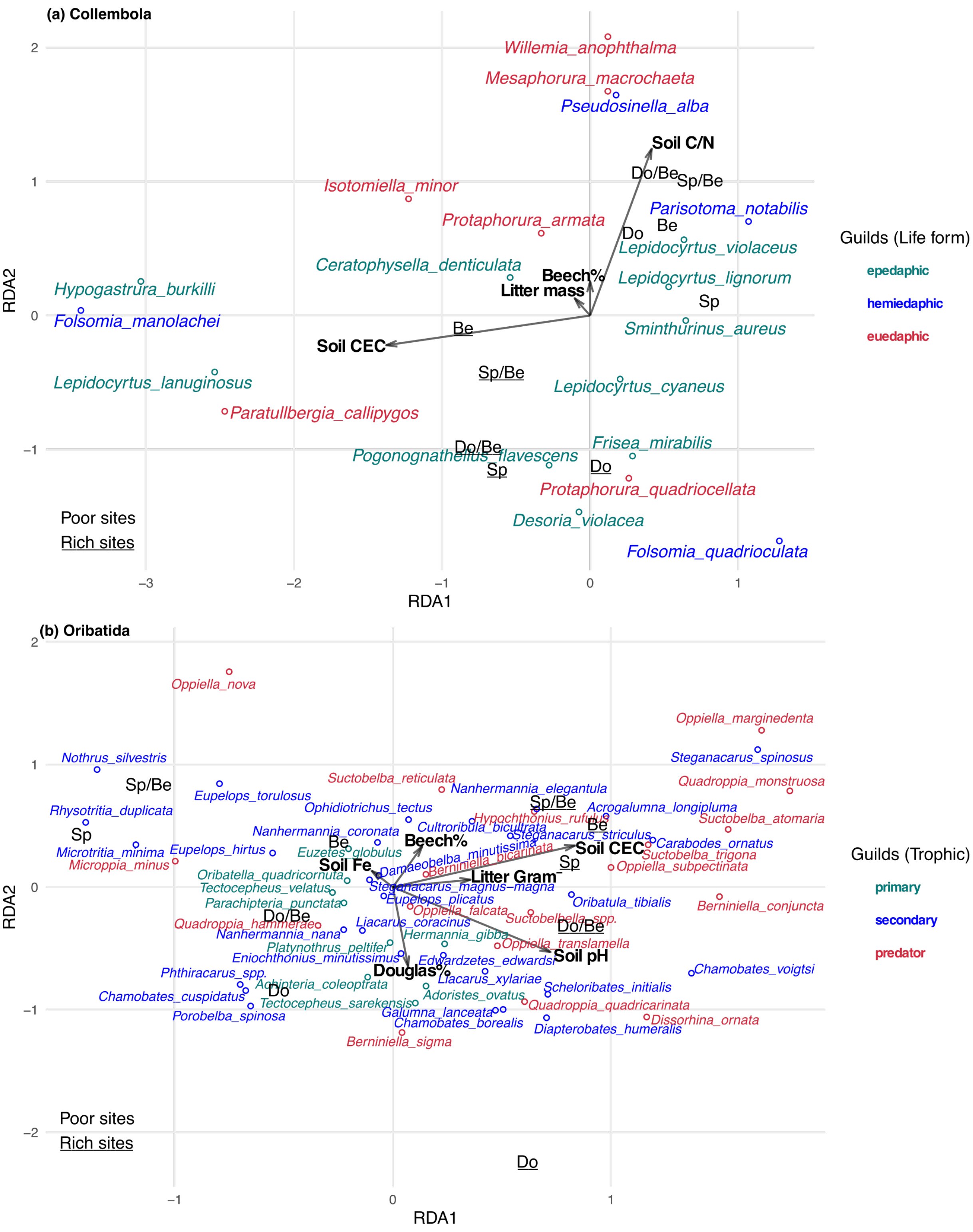

Figure 3.4: Redundancy analysis linking (a) Collembola and (b) Oribatida community composition in forests [European beech (Be), Douglas-fir (Do), Norway spruce (Sp), and two conifer–beech mixtures (Do/Be, Sp/Be)] to environmental drivers [for Collembola soil C/N ratio, soil cation exchange capacity (CEC), litter mass, proportion of European beech (Beech%); for Oribatida soil CEC, soil pH, soil Fe concentration, litter Gram$^+$ bacteria, proportion of Douglas-fir (Douglas%), proportion of European beech (Beech%)]. Centroids of forest types at nutrient-rich sites are underlined.

Table 3.1: Effects of tree species composition on Collembola and Oribatida communities, (a) not conditioned by covariates and (b) conditioned by covariates [for Collembola: soil C/N ratio, soil cation exchange capacity (CEC), litter mass; for Oribatida: soil CEC, soil pH, soil Fe concentration, litter Gram$^-$ bacteria] in redundancy analyses (RDA). Sequential 'anova' test based on 999 permutations. Significant effects are given in bold ($P \leq 0.05$).

	Not Conditioned by Covariate					Conditioned by Covariate			
Factor	Df	Variance	F	P	-	Df	Variance	F	P
Collembola									
Beech%	1	0.77	1.49	0.079		1	0.97	2.26	**0.002**
Douglas%	1	0.34	0.65	0.869		1	0.35	0.82	0.668
Spruce%	1	0.73	1.4	0.141		1	0.45	1.04	0.402
Residual	35	18.16				32	13.72		
Oribatida									
Beech%	1	2.44	1.69	**0.003**		1	2.41	1.84	**0.001**
Douglas%	1	2.13	1.48	**0.013**		1	1.80	1.37	**0.048**
Spruce%	1	1.98	1.38	0.054		1	1.34	1.02	0.41
Residual	35	50.44				31	40.72		

Covariate: for Collembola: Soil C/N, CEC, Litter mass; for Oribatida: Soil CEC, pH, Fe, Litter Gram$^-$

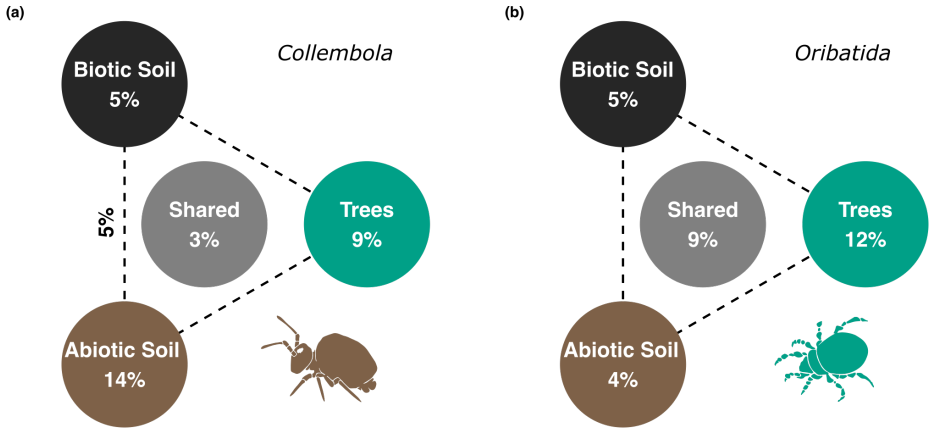

Figure 3.5: Variation partitioning of (a) Collembola and (b) Oribatida communities of five forest types (European beech, Douglas-fir, Norway spruce, and two conifer–beech mixtures) using soil biotic (Biotic Soil; total PLFAs, microbial biomass, percentages of fungi, Gram$^-$ bacteria in litter and 0–5 cm soil, Gram$^+$ bacteria in soil) and abiotic environmental variables (Abiotic Soil; percentages of C in litter, in organic soil and mineral soil, C/N ratio in litter, litter mass, soil pH, soil C/N ratio, soil CEC, soil Fe, K and Mn concentrations), and tree-related variables (Trees; proportion of European beech, Douglas-fir, and Norway spruce, concentration of root carbon, root C/N ratio). Unexplained variation in Collembola is 69% and in Oribatida 78%. Shared fractions between two groups are indicated along the dashed lines; fraction shared by all three groups of variables is given within the triangle. Animal drawings were kindly provided by Svenja Meyer (*Uni. Göttingen*).

3.4 Discussion

We evaluated the effects of forest types on soil Collembola and Oribatida across a range of environmental conditions. Contrasting our first hypothesis, we found that the diversity of Collembola and Oribatida did not significantly differ among the studied forest types and that the diversity of Collembola and Oribatida in Douglas fir was similar to that in European-beech forests. From a conservation perspective, planting Douglas fir therefore may not compromise the biodiversity of soil Collembola and Oribatida, and potentially also that of other soil invertebrates (Marian et al., 2020).

However, when considering guilds, the abundance of euedaphic Collembola and predatory Oribatida were both lower in Douglas fir than in European-beech forests. Potentially, lower root-derived resources in Douglas fir compared to European-beech forests were responsible for the lower abundance of high trophic guild Collembola and Oribatida (Meier et al., 2020; Lu and Scheu, 2021). Assuming that high trophic guilds of Collembola and Oribatida rely on similar resources, consistent lower abundance of these two guilds in Douglas-fir forests suggests that Douglas fir is particularly low in these resources. Euedaphic Collembola and predatory Oribatida, such as *Protaphorura armata* and *Oppiella nova*, both have been reported to be associated with roots and rely on root-derived resources (Salamon et al., 2004; Remén et al., 2008; Li et al., 2020). Supporting this assumption, at our study sites, fine root biomass of Douglas fir is lower than in European-beech forests (*A. Lwila, in prep.*). Therefore, lower root-derived resources may reduce the abundance of high trophic level microarthropods in Douglas-fir forests (Wang et al., 2019; Meier et al., 2020; Lu and Scheu, 2021). Our findings are consistent with those of a global meta-analysis suggesting that the abundance of soil predators was suppressed by living roots of non-native tree species through rhizosphere pathways (Zhang et al., 2019). Further, it is consistent with recent studies reporting soil mesofauna to be most strongly affected by the reduction of root-derived resources (Bluhm et al., 2021). To evaluate resource dependencies of soil mesofauna, different trophic guilds of Collembola and Oribatida should be considered in future root manipulation experiments.

High trophic level Oribatida, mainly Oppiidae, Suctobelbidae, and Quadroppiidae, are slender and small (~250 µm in length). They have been shown repeatedly to occupy high trophic positions (Schneider et al., 2004; Magilton et al., 2019), and therefore were suggested to live as predators or scavengers (Maraun et al., 2011). How these soil microarthropods are linked to roots and root-derived resources remains to be resolved. Potentially, limited availability of prey in soil, such as nematodes, contribute to the lower abundance of predatory Oribatida in Douglas fir than in European-beech forests (Heidemann et al., 2011, 2014). Trenching of roots has been shown to strongly reduce the abundance of root-feeding nematodes (Bluhm et al., 2021). However, incorporation of resources from old soil organic matter may also result in high ^{15}N values as shown for euedaphic Collembola (*Z. Li, in prep.*). Whether this applies to oribatid mites of high ^{15}N values needs further attention. Comparing the resource dependencies of euedaphic Collembola and predatory Oribatida may shed light on the pathways linking non-native Douglas fir and soil microarthropods.

We hypothesized that tree species vary in resource provisioning to soil animals.

Supporting our second hypothesis, responses of microarthropods to forest types differed among guilds. The contrasting responses mirror litter and root pathways between trees and microarthropods (Zhang et al., 2019). In addition to rhizosphere processes, the abundance of primary decomposer Oribatida species was higher in Douglas fir and Norway spruce than in European-beech forests, suggesting needles as favorable resources for primary decomposer Oribatida. Further, it suggests that contrary to root-based resources, litter resources are ample in Norway spruce and Douglas-fir forests. For Oribatida, litter of non-native Douglas-fir forests seems to be virtually as favorable as that of Norway spruce. The abundance of hemiedaphic Collembola, predominantly colonizing upper soil layers, was higher in coniferous forests, particularly in Norway spruce, than in beech forests, suggesting that their resources resemble those of primary decomposer Oribatida. Overall, such contrasting effects of tree species on different guilds of soil microarthropods reflect the reorganization of low and high trophic levels in soil food webs as response to different forest types (Laliberté et al., 2017; Nagelkerken et al., 2020).

By investigating both Collembola and Oribatida, we found that the community structure of Oribatida, but not that of Collembola, sensitively responded to forest types, contrasting our third hypothesis. European beech and Douglas fir significantly affected the community structure of Oribatida, but the effects of beech on Collembola were only significant when partitioning out environmental variation. Previous studies suggested high similarity in the community structure of both Collembola and Oribatida in European beech and Norway-spruce forests (Migge et al., 1998; Salamon et al., 2008). The results of our study suggest that this also applies to non-native Douglas fir and overall indicates that Collembola communities vary little with forest types. By contrast, Oribatida communities sensitively responded to forest types. Some Oribatida taxa including *Phthiracarus* spp., *Rhysotritia duplicata* and *Microtritia minima* evolved endophagous life cycles where immatures burrow in decaying needles. The association of endophagous mites with Norway spruce and Douglas fir, therefore, fits their life cycle. Generally, although Collembola have been studied frequently as indicators of environmental change, our results highlight the sensitivity of Oribatida to environmental changes suggesting that they may surpass Collembola as bioindicators (Weigmann and Kratz, 1987; Maraun and Scheu, 2000; Marian et al., 2020).

In our study, microbial parameters poorly predicted the community structure of soil microarthropods, agreeing with earlier studies (Scheu and Schaefer, 1998; Ferlian et al., 2015). Biotic environmental variables, such as microbial biomass and the relative abundance of fungi and bacteria in litter and soil, explained little of the variation in animal community structure. Previously, it has been found that Douglas fir only affects biomass and community structure of microorganisms at nutrient-poor sites (Lu and Scheu, 2021). As microbial indicators in our study proved to be poor predictors of animal community structure, it is not surprising that the response of soil microarthropods to forest types did not follow the response of microorganisms and did not vary with site conditions. However, this raises the question of mechanisms responsible for the reduced density of high trophic level Collembola and Oribatida in Douglas-fir forests besides reduced provisioning of root-derived resources. We focused on resource-based explanations in this study related to the guild structure of

Collembola and Oribatida neglecting other environmental variables, such as physical habitat conditions including the volume and size of soil pores, which may override the importance of resources in structuring microarthropod communities in soil (Elliott et al., 1980; Nielsen et al., 2008; Fujii et al., 2020).

Results of our study support earlier findings suggesting that regional factors are more influential than forest types in structuring communities of Collembola and Oribatida (Erdmann et al., 2012; Pollierer and Scheu, 2017). Our study covered a range of site conditions, which strongly affected the community structure of both Collembola and Oribatida. However, as site conditions such as soil nutrients intercorrelate with other environmental variables, such as precipitation, we cannot disentangle the drivers of the variation in microarthropod community structure with site conditions. However, we found that abiotic environmental variables, including soil C/N ratio, pH, and CEC explained more variation in Collembola than in Oribatida community structure, suggesting that environmental filtering is more important in Collembola than in Oribatida. In our study, by controlling for variations in environmental variables in partial constraint ordination, the effects of beech trees became more significant in both Collembola and Oribatida. This suggests that effects of tree species identity neither are reflected by the measured variables on microbial community structure nor by abiotic variables such as soil nutrients, supporting the importance of tree identity in structuring microarthropod communities (Eissfeller et al., 2013).

We highlight the usefulness of the guild approach in studying the response of microarthropod communities to forest types. In contrast to communities, the response of guilds varied with forest types in Collembola. This indicates that the guild approach reduces variability at the level of species thereby facilitating the understanding of structural attributes and organizing processes of animal communities (Simberloff and Dayan, 1991). However, using guilds has been underappreciated in studies on the response of soil microarthropods to environmental changes, particularly in Oribatida. In part this might be because trophic positions of Oribatida species have no phylogenetic signal (Schaefer and Caruso, 2019), complicating their association to guilds as it requires species-level information. However, as the trophic niche of Oribatida varies little among habitats (Chapter **4**), stable isotope data of oribatid mites may allow to reliably assign oribatid mite species to guilds. Overall, the results suggest that guilds, although representing a single trait, have the potential to shed light on resource-related processes, and to allow a better understanding of structuring forces of soil animal communities. Our study, therefore, calls for more intensive use of guilds in comparative studies of communities of soil microarthropods.

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Chapter 4

High consistency of trophic niches in soil microarthropod species (Oribatida, Acari) across soil depth and forest type[1]

Jing-Zhong Lu, **Peter Cordes**, **Mark Maraun**, **Stefan Scheu**

Abstract

Individuals of species may differ in resource use within and between populations. To better understand the intraspecific variation in trophic niches of oribatid mites (Oribatida, Acari), we quantified stable isotope ratios of carbon (δ^{13}C) and nitrogen (δ^{15}N) of 40 Oribatida species that co-occurred in litter and soil of five forest types (European beech, Douglas fir, Norway spruce, two beech–conifer mixed forests) in Germany covering a range of environmental conditions. We found that although stable isotopes in litter and soil varied among forest types, δ^{13}C and δ^{15}N values of Oribatida and their trophic niches were remarkably stable between litter and soil, and also among forest types. We considered four trophic guilds of Oribatida representing the guild composition of the regional species pool; notably, trophic niches of Oribatida guilds also did not vary with soil depth. Furthermore, δ^{13}C of Oribatida was more enriched (detrital shift) in European beech than in coniferous forests, but δ^{15}N of Oribatida did not vary among forest types, indicating that basal resources of Oribatida are variable, but trophic positions are highly consistent across forest ecosystems. We conclude that trophic positions of Oribatida species and guilds are consistent across different forest types, and Oribatida species occupy virtually identical trophic niches irrespective of the soil depth they are colonizing. Low intraspecific variability facilitates Oribatida niche differentiation and species coexistence.

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[1] Preprint in bioRxiv (`https://doi.org/10.1101/2021.07.24.453652`)

4.1 Introduction

In soil food webs, a large part of isotopic space is occupied by soil microarthropods (Scheu and Falca, 2000; Pollierer et al., 2009; Maraun et al., 2011; Potapov et al., 2019). Based on the analysis of natural variations in bulk stable isotope values of carbon (^{13}C) and nitrogen (^{15}N), trophic niche differentiation has been uncovered in major groups of soil microarthropods including Oribatida, Collembola, and Mesostigmata (Schneider et al., 2004; Chahartaghi et al., 2005; Klarner et al., 2013). While trophic niche differentiation contributes to the co-existence of species, high intraspecific variation in stable isotope values points toward large niche overlap potentially hampering species co-existence (Hart et al., 2016). For example, oribatid mites (Oribatida, Acari), typically occupy three to four trophic levels in temperate forests (Schneider et al., 2004; Maraun et al., 2011), but it remains poorly studied how trophic niches of Oribatida species vary with environmental conditions (Gan et al., 2014), such as soil depth and forest type.

Microarthropods dominate in the uppermost horizons of forest soils, especially the litter and the other organic horizons (Pande and Berthet, 1975; Mitchell, 1978; Arribas et al., 2021). Oribatida species were suggested to occupy similar trophic positions irrespective of soil depth (Scheu and Falca, 2000), but the variation in trophic niches of Oribatida species with soil depth has not been rigorously tested. Stable isotope ratios of carbon and nitrogen are typically enriched in soil compared to litter (Potapov et al., 2019; Högberg et al., 2020). If Oribatida species are feeding opportunistically (Maraun et al., 1998), their stable isotope values should increase with soil depth parallel to that in organic matter. If Oribatida species in soil incorporate older carbon than in litter, high stable isotope values should inflate their trophic position (Potapov et al., 2019). This may hamper understanding of their trophic ecology and incorporating them into soil food web models. Although the importance of microhabitats for the trophic ecology of Oribatida species has received considerable attention (Lehmitz and Maraun, 2016; Nae et al., 2021), variations in trophic positions among microhabitats have been little studied (Krause et al., 2019). Variations in trophic niches of Oribatida species with soil depth may also be related to shifts in microorganisms in their diet. In the litter of more advanced stages of decay deeper in the soil, the proportion of bacteria and mycorrhizal fungi increases relative to saprotrophic fungi dominating at earlier stages of decay in the litter layer (Lindahl et al., 2007; Lu and Scheu, 2021). Variations in stable isotope values with soil depth may allow deeper insight into opportunistic feeding and trophic niche differentiation of Oribatida species.

Similar to depth, early studies also suggested that trophic niches of Oribatida vary little with forest type (Schneider et al., 2004). However, forest types vary in litter quality, microbial communities, and internal nutrient cycling (Albers et al., 2004; Lu and Scheu, 2021). Contrasting resource availability across forest types may induce changes in the use of basal resources and trophic positions of Oribatida species (Krause et al., 2019; Maraun et al., 2020). To date, only a few Oribatida species have been shown to respond flexibly by adjusting their trophic positions across land-use systems, but no agreement has been reached why some Oribatida species change their trophic niches with forest type while others do not (Gan et al., 2014;

Krause et al., 2019; Maraun et al., 2020). The contrasting response calls for more detailed analyses including a wide range of Oribatida species with different traits across ecosystems. Including trophic guilds of Oribatida may allow deeper insight into whether the variation of trophic niches in Oribatida species between forest types differ among guilds, e.g., is more pronounced in species at bottom of the food web confronted with basal resources of different quality.

A better understanding of trophic niche variation in Oribatida species has important implications for forest management. In temperate and boreal regions, tree species richness is low, and managed forests are typically dominated by only one or few tree species (Knoke et al., 2008; Bauhus et al., 2010). Oribatida dominate in abundance and richness among soil mesofauna and macrofauna groups in temperate forest soils (Schaefer, 1990). The climax tree species in Central Europe is European beech (Leuschner and Ellenberg, 2017), and litter decomposition in European-beech forests is faster than e.g., in Norway-spruce forests (Albers et al., 2004). Norway spruce, the economically most important timber species in Central Europe, is at increasing risk due to climate change and associated bark beetle outbreaks (Pettit et al., 2020). Although the admixture of Norway spruce to native European-beech forests may reduce the risk of damage while maintaining economic gains, non-native Douglas fir is increasingly planted (Schmid et al., 2014). Recent studies indicated that the impact of Douglas fir on soil microbial communities is detrimental at nutrient-poor sites but not at nutrient-rich sites (Lu and Scheu, 2021), and Douglas fir changes the community composition of Oribatida communities (Chapter **3**). Overall, the effects of forest type including non-native tree species and mixed forests on the functioning of the belowground system are little studied (Schmid et al., 2014; Kriegel et al., 2021). The variation in trophic niches of Oribatida species across forest types may reflect changes in resource availability in soil food webs, allowing deeper insight into linkages between tree species composition and belowground biota (Wardle et al., 2004).

Here, we quantified trophic niches of 40 Oribatida species in litter and soil of different forest types using bulk stable isotope analysis of ^{13}C and ^{15}N. Five forest types were investigated, including pure stands of European beech, Norway spruce, Douglas fir, and two conifer - beech mixtures. Forest types were replicated covering a range of water and soil nutrient conditions. Assuming niche conservatism (Wiens and Graham, 2005), we hypothesized that (1) stable isotope ratios of Oribatida species generally vary little between litter and soil, but (2) variation with soil depth is more pronounced in Oribatida species of low than in those of high trophic level. Further, we hypothesized that (3) particularly Oribatida species of low trophic level occupy different trophic niches across different forest types, with the differences being most pronounced between forests with dissimilar basal resources, i.e., between beech and coniferous forests.

4.2 Methods

4.2.1 Study sites

The study was conducted in 40 forest stands located in Northern Germany (8 sites x 5 forest types). The forest sites covered a wide range of soil nutrient and water conditions. Four more southern sites stock on Cambisol and Luvisol, with mean annual precipitation of 821–1029 mm. Four more northern sites are located on nutrient-poor out-washed sand with Podzol soil, with mean annual precipitation of 672–746 mm. Each site comprises three pure stands of European beech (*Fagus sylvatica* L.), Norway spruce (*Picea abies* [L.] Karst.) and Douglas fir (*Pseudotsuga menziesii* (Mirbel) Franco.) as well as two beech-conifer mixtures (European beech/Douglas fir and European beech/Norway spruce). Focal tree species in pure stands on average comprised more than 90% of total basal area, while in mixed stands, focal tree species accounts on average 34% for European beech and 58% for conifer in Douglas fir mixed stands, and 56% for European beech and 37 % for conifer in Norway spruce mixed stands. Trees were on average more than 50 years old. More details on the sites are given in Ammer et al. (2020), Foltran et al. (2020), Lu and Scheu (2021).

4.2.2 Soil sampling

Animals were sampled by using a metal corer (diameter 20 cm) between November 2017 and January 2018. Samples were taken between trees of the same (pure stands) or different species (mixed stands). One core was taken in each plot, and samples were separated into the litter and 0–5 cm soil depth. Soil arthropods were extracted separately for litter and soil using high-gradient heat extraction (Kempson et al., 1963). Animals were collected in 50 % diethylene glycol and then transferred into 70 % ethanol. Species were identified using the key of Weigmann (2006). Separate soil samples (diameter 5 cm) were taken in close vicinity and were separated into the litter and 0–5 cm soil for bulk stable isotope analysis, see Chapter **2**.

4.2.3 Species selection

We sampled species that occurred both in litter and soil from the same soil core, as our primary focus was to understand the variation in stable isotope values of Oribatida species with soil depth. From each soil core, two to three pairs of species (adults) were selected for stable isotope analysis. We aimed at covering a wide range of species, which were selected a priori based on a previous study at the same sites to cover representative trophic guilds (Chapter **3**). Females were used in species with sexual dimorphism, i.e., *Acrogalumna longipluma* and *Adoristes ovatus.* In total, we analyzed 40 species including primary decomposers, secondary decomposers, as well as endophagous and predator/scavenger species (Table **C.1**). Each species on average occurred in two forest plots, on average four replicates per species. This allowed estimating trophic niche variation across forests by controlling for species identity in mixed-effects models (see below). Guilds were balanced in each of the forest types

(Table **C.2**), allowing to test for the interaction between forest type and trophic guild.

4.2.4 Bulk stable isotopes

We used bulk stable isotopes ($^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios) of Oribatida to quantify their trophic niches. Stable isotope values of bulk litter and soil were measured and used as the baseline for comparing Oribatida species across forest types (Klarner et al., 2013; Potapov et al., 2019). Different numbers of individuals were used for stable isotope analysis depending on the body size of the species (Table **C.1**), but for Oribatida species from the same soil core, the same number of individuals was used. Animals, litter, and soil were dried at 60°C for 48 h. Litter and soil were ground and homogenized using a ball mill. After weighing samples into tin capsules, the natural abundance of stable isotope ratios of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) of bulk litter and soil was determined by a coupled system of an elemental analyzer (NA 1110, CE-instruments, Rodano, Milano, Italy) and a mass spectrometer (Delta Plus, Finnigan MAT, Bremen, Germany). For animal samples, their isotopic signatures were analyzed similarly by a coupled system of an elemental analyzer (Flash 2000, Thermo Fisher Scientific, Cambridge, UK) and a mass spectrometer (Delta V Advantage, Thermo Electron, Bremen, Germany). Animal samples with a dry weight <100 µg were analyzed using a modified setup adopted for a small sample size (Langel and Dyckmans, 2014). Atmospheric nitrogen and Vienna PeeDee belemnite were used as primary standards. Acetanilide (C_8H_9NO, Merck, Darmstadt) was used as internal working standard. Natural variation in stable isotope ratios of carbon and nitrogen (δX) is expressed as δX (‰) = (R_{sample} - $R_{standard}$) / $R_{standard}$ x 1000, with R the ratio between the heavy and light isotopes ($^{13}C/^{12}C$ or $^{15}N/^{14}N$).

4.2.5 Data analyses

We used linear mixed-effects models (*LMM*s) to analyze the variation in $\delta^{13}C$ and $\delta^{15}N$ values of Oribatida species. Fixed effects included depth (litter and 0–5 cm soil), forest type (European beech, Douglas fir, Norway spruce, mixture of European beech with Douglas fir, mixture of European beech with Norway spruce), trophic guild (primary decomposer, secondary decomposer, endophagous, predatory/scavenging) and site condition (nutrient-rich and nutrient-poor sites). We included several two-factor interactions (depth x forest type, depth x site condition, depth x trophic guild, and forest type x trophic guild) as fixed effects because our primary focuses were (1) to evaluate depth effects and their dependencies on other factors, and (2) to evaluate forest type effects and their dependence on Oribatida guilds. The stable isotope values of litter and 0–5 cm soil were included as covariates to control for differences in the baseline across forests (Melguizo-Ruiz et al., 2017). The cross-random effects included 40 plots and 40 species, accounting for the non-independence of samples from the same soil core, and for the taxonomic identity analyzed across forests.

To confirm the trophic guilds that were assigned a priori, we calibrated stable isotopes of Oribatida species using the stable isotope values of litter from the same plot (Scheu and Falca, 2000; Schneider et al., 2004; Klarner et al., 2013). In addition, we also modeled the variation in stable isotope values of bulk material as a function of forest type (European beech, Douglas fir, Norway spruce, European beech/Douglas fir, European beech/Norway spruce), depth (litter and 0–5 cm soil), site condition (nutrient-rich and nutrient-poor) and their interactions.

For Oribatida, we applied contrasts to inspect differences in their δ^{13}C and δ^{15}N values between litter and 0–5 cm soil depth. The contrast was designated as the difference of estimated marginal means between litter and soil (Piovia-Scott et al., 2019). We estimated the contrast for each forest type and each trophic guild. For litter and soil, we similarly applied contrasts to compare depth differences in δ^{13}C and δ^{15}N values of bulk litter and soil for each forest type. Furthermore, to quantify differences in δ^{13}C and δ^{15}N values of Oribatida species between forest types, we compared δ^{13}C and δ^{15}N values of Oribatida between forest types using European beech, the climax tree species in Central Europe, as reference (Leuschner and Ellenberg, 2017; Lu and Scheu, 2021).

All analyses were done in R version 4.0.3 (`https://www.r-project.org/`). We used ‘lme4’ to fit *LMM*s (lmer) (Bates et al., 2015), and ‘emmeans’ to estimate marginal means. The package ‘lmerTest’ was used to derive p-values of *LMM*s with degrees of freedom estimated by Satterthwaite’s method (Kuznetsova et al., 2017). All *LMM*s met the assumptions of normality of residuals and homogeneity of variance.

4.3 Results

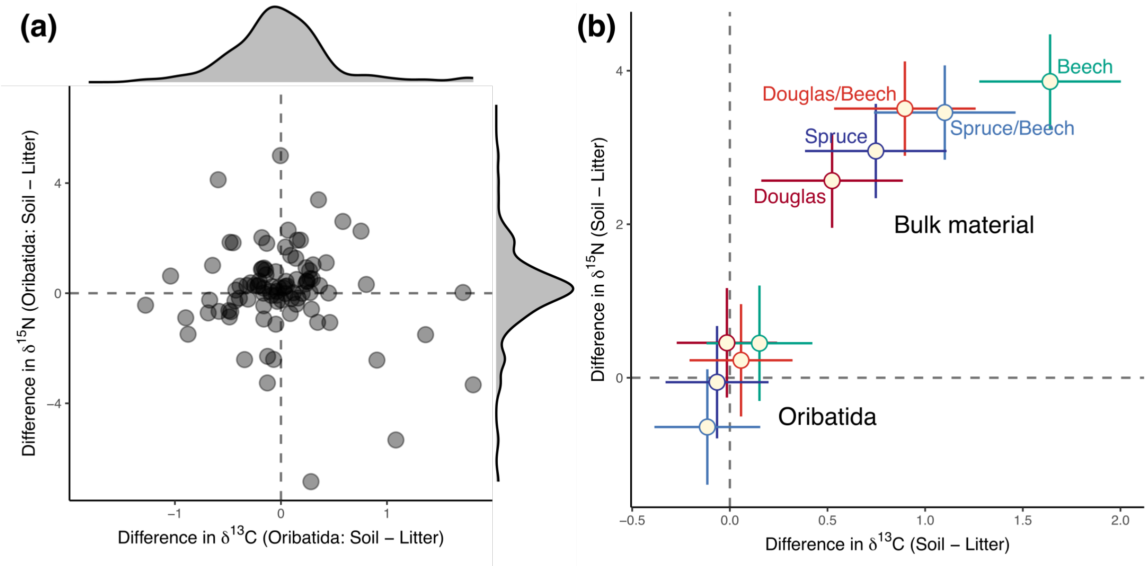

Figure 4.1: (a) Differences in δ^{13}C and δ^{15}N values of Oribatida species between soil and litter. (b) Differences in δ^{13}C and δ^{15}N values of Oribaitida and bulk soil between soil and litter in five forest types [European beech (Beech, green), Norway spruce (Spruce, blue), Douglas fir (Douglas, red), mixture of Norway spruce and European beech (Spruce/Beech, light-blue), mixture of Douglas fir and European beech (Douglas/Beech, light-red)]; means and 95% confidence intervals.

The difference in δ^{13}C and δ^{15}N values between bulk litter and soil was highest in European beech (1.64 ± 0.23 ‰ and 3.85 ± 0.34 ‰ for δ^{13}C and δ^{15}N, respectively) and lowest in Douglas-fir forests (0.52 ± 0.23 ‰ and 2.57 ± 0.34 ‰ for δ^{13}C and δ^{15}N, respectively). Despite differences in depth-gradients of bulk stable isotope values in the studied forests (Table **C.3**, Figure **C.1**), δ^{13}C and δ^{15}N of Oribatida species did not differ significantly between litter and soil (Table **4.1**, Figure **4.1**). The selected 40 species covered primary decomposers (n = 7), secondary decomposers (n = 17), endophagous (n = 9) and predatory/scavenging species (n = 7) (Table **C.1**, Figures **4.2**, **C.2**). Trophic guilds explained the majority of the variability in δ^{13}C and δ^{15}N values of Oribatida species (in both cases ca. 56 % out of 64 % of total variation explained). However, δ^{13}C and δ^{15}N values of trophic guilds of Oribatida did not significantly vary with soil depth and this was true for each of the Oribatida guilds (Figure **4.3**).

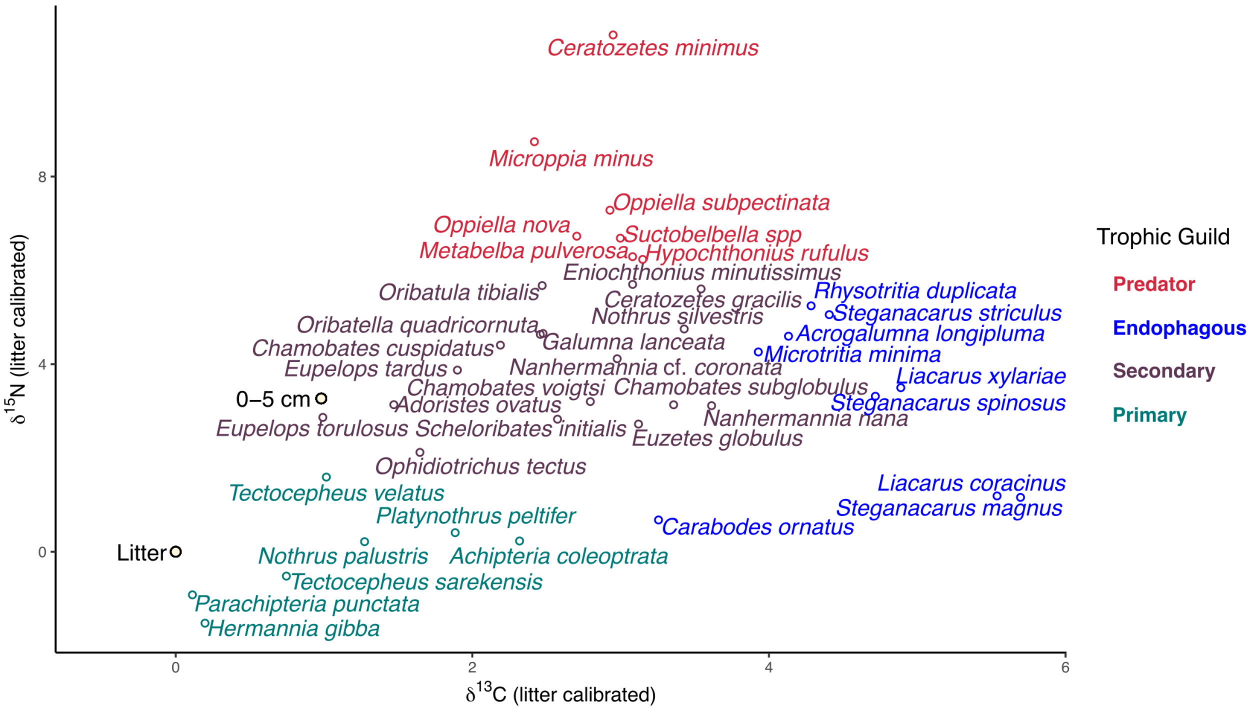

Figure 4.2: Trophic guilds of Oribatida species are assigned based on litter calibrated δ^{13}C and δ^{15}N values. Means of Oribatid species and bulk material of litter and soil are shown; trophic guilds are color-coded [primary decomposer (green), secondary decomposer (brown), endophagous (blue), and predatory (red)].

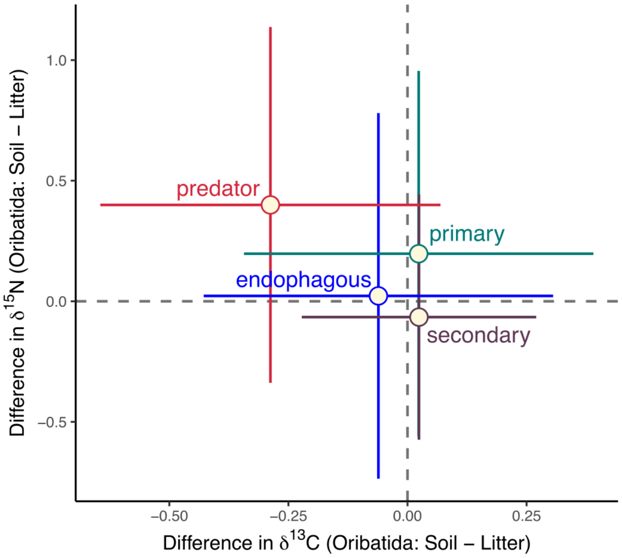

Figure 4.3: Differences in δ^{13}C and δ^{15}N values of trophic guilds of Oribatida [primary decomposer (green), secondary decomposer (brown), endophagous (blue), and predatory (red)]; means and 95% confidence intervals.

Table 4.1: Linear mixed-effects models on δ^{13}C and δ^{15}N values of Oribatida species (Type III ANOVA). Fixed effects include Depth (litter and soil), Forest type (European beech, Douglas fir, Norway spruce and mixed forests of European beech and Douglas fir and European beech and Norway spruce), Guild (primary decomposer, secondary decomposer, endophagous, predatory), Site condition (nutrient-rich and nutrient-poor sites), and interactions of depth with other categorical factors. δ values of bulk litter and soil were included as covariates to control for the variation in stable isotope values of basal resources across forest ecosystems. Random effects included 40 plots and 40 species. Satterthwaite's method was used to estimate denominator degrees of freedom (df). Significant P-values are in bold ($P \leq 0.05$).

δ ^{13}C Oribatida						δ ^{15}N Oribatida				
Factor	df	SumSq	F	P	-	Factor	df	SumSq	F	P
Depth (D)	1,103	0.24	0.88	0.350		Depth (D)	1,98	0.69	0.53	0.468
Forest type (F)	4,37	4.98	4.56	**0.004**		Forest type (F)	4,30	6.63	1.28	0.301
Guild (G)	3,28	24.20	29.54	**0.000**		Guild (G)	3,29	119.71	30.71	**0.000**
Site condition (S)	1,44	0.98	3.60	0.064		Site condition (S)	1,30	0.19	0.15	0.705
Soil δ^{13}C	1,27	0.06	0.24	0.631		Soil δ^{15}N	1,24	0.93	0.72	0.405
Litter δ^{13}C	1,31	0.34	1.25	0.273		Litter δ^{15}N	1,29	16.10	12.39	**0.001**
D x F	4,103	1.76	1.61	0.178		D x F	4,98	6.70	1.29	0.279
D x G	3,103	0.81	0.99	0.399		D x G	3,98	0.83	0.21	0.887
D x S	1,103	0.05	0.19	0.666		D x S	1,98	2.27	1.75	0.189
F x G	12,108	7.03	2.14	**0.020**		F x G	12,125	22.71	1.46	0.149

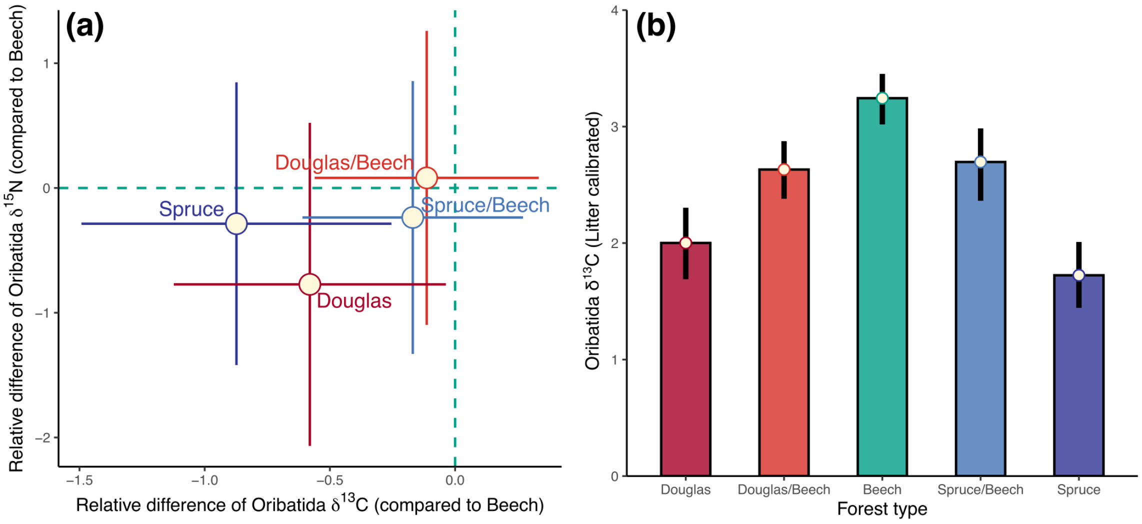

Figure 4.4: Trophic niche plasticity of Oribatida across forest types. (a) The difference in δ^{13}C and δ^{15}N values of Oribatida species in comparison to European-beech forests (Beech, green); means and 95% confidence intervals. (b) Comparison of δ^{13}C values of Oribatida species between forest types [European beech (Beech, green), Douglas fir (Douglas, red), Norway spruce (Spruce, blue), Douglas fir and European beech mixture (Spruce/Beech, light-red), and Norway spruce/European beech mixture (Spruce, light-blue)]; means and standard errors.

To account for variations in δ^{13}C and δ^{15}N values in basal resources across forest types, we included bulk stable isotope values of litter and 0–5 cm soil as covariates; stable isotope values of Oribatida species varied stronger with those of litter than with those of soil across forests (Table **4.1**). Further, δ^{13}C values of Oribatida species were higher in European beech than in Norway spruce (0.87) and Douglas-fir forests (0.58), and were intermediate in mixed forests (Figures **4.4**, **4.5**). The δ^{13}C enrichment of Oribatida guilds in European-beech forests was significant in secondary decomposer Oribatida, but not in primary decomposer and predatory/scavenging Oribaitda; in endophagous Oribaitda δ^{13}C enrichment was higher in mixed forests than in European-beech forests (Figure **C.3**). By contrast, as reflected by δ^{15}N, the trophic position of Oribatida species did not vary significantly between forest types (Figure **4.4**), and this was also true for each of the Oribatida guilds (Table **4.1**).

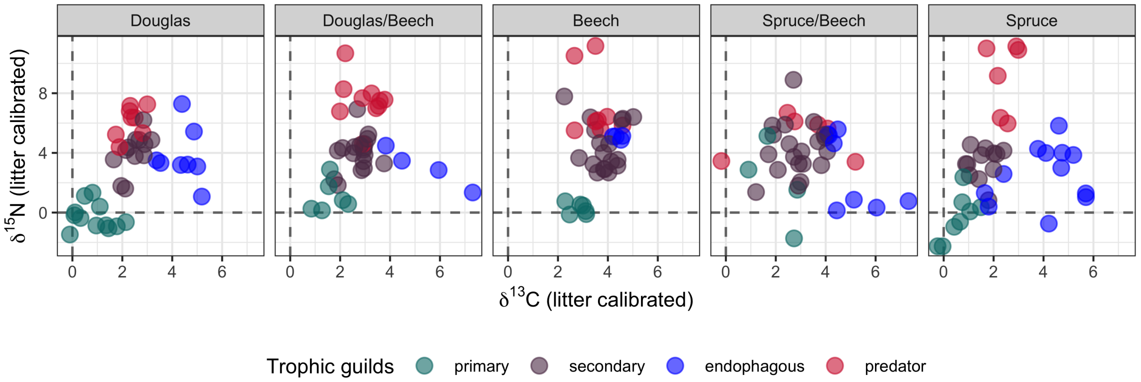

Figure 4.5: Litter calibrated δ^{13}C and δ^{15}N values of Oribatida guilds across forest types [Douglas fir (Douglas), mixture of Douglas fir/European beech (Douglas/Beech), European beech (Beech), mixture of Norway spruce/European beech (Spruce/Beech), Norway spruce (Spruce)]. Colors code for trophic guilds: primary decomposer (green), secondary decomposer (brown), endophagous (blue), and predatory species (red).

4.4 Discussion

Trophic niche differentiation of soil microarthropods has advanced our understanding of species co-existence (Schneider et al., 2004), and low intraspecific variation may further strengthen species niche differentiation. To better understand the intraspecific variation in trophic niches of Oribatida, we investigated if trophic niches of Oribatida species vary with soil depths and forest types. Based on 40 Oribatida species occurring in litter and soil of temperate forests, we found that trophic niches of Oribatida species in litter and soil are highly consistent, and their trophic positions are similar across deciduous and coniferous forests. This implies that intraspecific variability in trophic niches of Oribatida is low, further facilitating the co-existence of soil Oribatida species (Hart et al., 2016).

4.4.1 Variation with soil depth

Despite strong gradients in stable isotope values in bulk materials of the studied forest with soil depth, especially in European beech, trophic niches of Oribatida species were consistent irrespective of sampling depth. This supports our first hypothesis and suggests that "the actual environments of specimens do not inform us about where the majority of food resources have been acquired during the lifetime" of Oribatida species (Scheu and Falca, 2000). Although the decomposition rate and speed of internal nitrogen cycling differ between European beech and coniferous forests, as indicated by gradients in stable isotope values with depth, basal resources and trophic position of Oribatida species in litter and soil are highly consistent as indicated by stable isotope ratios of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ of Oribatida species. We sampled soil down to 5 cm depth, equivalent to ca. 50–200 times the body length of Oribatida. While Oribatida are less mobile compared to other soil microarthropods, such as Collembola and Mesostigmata mites (Åström and Bengtsson, 2011), our results suggest that Oribatida may be more mobile than commonly assumed. Oribatida may have access to their favorite resources irrespective of the soil depth they colonize. Further, stable isotope ratios in litter well explained the variation in stable isotope values of Oribatida species, suggesting that Oribatida species predominantly rely on fresh organic carbon in litter and/or root-derived resources irrespective of the actual depth they inhabit (Pollierer et al., 2007, 2021; Okuzaki et al., 2009; Melguizo-Ruiz et al., 2017; Potapov et al., 2019).

The lack of variation in trophic niches of Oribatida species with soil depth also applied to trophic guilds, contrasting our second hypothesis. In temperate forests, the relative availability of food resources, such as litter, bacteria, ectomycorrhizal and saprotrophic fungi, changes rapidly with soil depth, with increasing proportions of bacteria and ectomycorrhizal fungi deeper in soil (Lindahl et al., 2007; Lu and Scheu, 2021). We investigated four Oribatida guilds typically occurring in temperate forests, spanning from primary and secondary decomposers, endophagous species to predators/scavengers (Schneider et al., 2004; Maraun et al., 2011). As trophic guilds of Oribatida differ in food resources (Maraun et al., 2011), primary decomposer and predatory Oribatida, for example, differ most in trophic position, they may respond differently to soil depth. However, our results strongly suggest that Oribatida guilds occupy similar niches irrespective of soil depth, further supporting that despite resource quantity and quality change rapidly with soil depth (Lu and Scheu, 2021), the trophic niches of Oribatida remain unchanged (Scheu and Falca, 2000). Notably, this applies to a wide range of species ($n = 40$) including major trophic guilds of Oribatida ($n = 4$), colonizing pure and mixed forests of deciduous and coniferous trees ($n = 5$) arguing for the generality of these results.

The lack of variation in stable isotope values with soil depth in Oribatida species may point towards the high vertical mobility of these species; however, it also points to the presence of these niches irrespective of soil depth in the forest floor. In any case, the high consistency of trophic niches in Oribatida species underlines the importance of niche differentiation for the co-existence of Oribatida species in soil (Schneider et al., 2004). Trophic niche consistency in Oribatida species also indicates that intraspecific competition may be stronger than the interspecific competition, thereby facilitating niche differentiation of Oribatida species in soil (Hart et al., 2016). Although the contribution of bacteria and plants as basal resources to Oribatida species varies depending on species, compound-specific stable isotope analysis of amino acids suggests that saprotrophic fungi are the major food resource of primary and secondary decomposer Oribatida species (Pollierer et al., 2021). In contrast to Collembola (Potapov and Tiunov, 2016), the vertical distribution of Oribatida species has not yet been found to be related to morphological and life-history traits (Pande and Berthet, 1975; Potapov and Tiunov, 2016). The mechanisms responsible for maintaining species diversity, therefore, are likely to differ between Collembola and Oribatida. Our findings also challenge the view that Oribatida species are opportunistic feeders (Maraun and Scheu, 2000), but rather suggest that they occupy a distinct niche in the field irrespective of the depth and forest type they inhabit.

4.4.2 Variation with forest type

As indicated by our results, the detrital shift, i.e., the enrichment in δ^{13}C values relative to litter (Potapov et al., 2019), in oribatid mites is stronger in European beech than in coniferous forests. The detrital shift has been widely documented in terrestrial ecosystems (Pollierer et al., 2009; Potapov et al., 2019; Susanti et al., 2021), suggesting that it is a universal phenomenon in decomposer food webs. The contrasting detrital shift between European beech and coniferous forests suggests that the basal resources of Oribatida species differ between forest types, supporting our third hypothesis. Several non-mutually exclusive mechanisms may explain the contrasting detrital shift between deciduous and coniferous forests. The litter quality of European beech may be particularly poor and rich in lignin with saprotrophic microorganisms incorporating more palatable litter compounds less enriched in ^{13}C than lignin (Pollierer et al., 2009). δ^{13}C values of leaf litter of European beech (-29.58 ± 0.33 ‰) are about 1.34 ‰ lower than those in needle litter of coniferous trees (-28.17 ± 0.44 ‰ and -28.31 ± 0.37 ‰ for Norway spruce and Douglas fir, respectively; mean ± sd); further, the C/N ratio in the leaf litter of European beech (50.73 ± 6.26) is higher than that in needle litter of coniferous trees (39.26 ± 1.85 and 42.3 ± 5.21 for Norway spruce and Douglas fir, respectively; J.-Z. Lu, unpubl. data). Our results agree with earlier suggestions that spruce needles are not more recalcitrant than beech leaves and may even decompose faster (Albers et al., 2004; Berger and Berger, 2012). Notably, however, as indicated by microbial biomass and microbial basal respiration, microbial activity in European-beech forests may exceed that in coniferous forests, which may be due to more efficient decomposer communities and/or favorable abiotic conditions (Albers et al., 2004; Lu and Scheu, 2021). High microbial activity in European-beech forests drives faster carbon turnover, and increases the incorporation of microbial processed carbon into soil food webs (Potapov et al., 2019), presumably contributing to the pronounced detrital shift in European-beech forests. Supporting the importance of microbial activities, differences in the detrital shift between European beech and coniferous forests were strongest in secondary decomposers Oribatida, known as predominant fungal feeders (Schneider et al., 2004). Our findings on detrital shift likely also apply to other soil invertebrates feeding on microorganisms reflecting differential resource use in the respective soil food webs (Scheu and Falca, 2000; Pollierer et al., 2009; Klarner et al., 2013).

Although basal resources differ between European beech and coniferous forests, Oribatida species kept their trophic position and this was true across Oribatida guilds and forest types, contrasting our third hypothesis. Ratios of $^{15}N/^{14}N$ in Oribatida species depend on the isotopic signature of their food resources with respective enrichment in ^{15}N (Heethoff and Scheu, 2016). The high consistency of the trophic positions of Oribatida species supports the assumption that soil food webs are resistant to changes in forest types (Pollierer et al., 2021), agreeing with recent studies on variations in trophic niches in other mesofauna groups, such as Mesostigmata mites and Collembola between land-use systems (Klarner et al., 2017; Susanti et al., 2021). In tropical ecosystems ranging from rainforest to monoculture plantations, trophic plasticity of Oribatida has been suggested to depend on species (Krause et al., 2019), which we could not confirm for Oribatida species in temperate forest ecosystems. Adding to these findings, our results further suggest that, at least in temperate forests, the consistency of trophic positions of Oribatida species does not vary among trophic guilds. Overall, the results indicate that trophic positions of Oribatida species and guilds are very consistent across forest types.

High trophic level Oribatida living as predators or scavengers in our study on average were enriched in $\delta^{15}N$ by 6.7–11.0 ‰, consistent with the enrichment of other predators of temperate forests including Mesostigmata mites, Chilopoda and Araneida (Pollierer et al., 2009; Potapov et al., 2019). Incorporation of old organic carbon in detritivores may inflate their high trophic positions. However, the consistency in trophic positions of Oribatida species irrespective of soil depth indicates that tissue carbon in the diet of Oribatida is unlikely to be derived from old organic matter, rather it likely originates predominantly from litter and/or root-derived resources which are little decomposed (Klarner et al., 2013). If the detrital shift in Oribatida species would be due to the consumption of carbon derived from old organic matter, the shift should be stronger in soil than in litter, and Oribatida species should also be enriched in $\delta^{13}C$. Contrasting this assumption, $\delta^{13}C$ and $\delta^{15}N$ values of Oribatida species correlated more closely with those of litter than with those of soil. As stable isotope values of high trophic level Oribatida species also did not vary with soil depth, we suggest that they live as predators/scavengers rather than reflecting that they incorporate nitrogen originating from old organic matter, contrasting other mesofauna with high $\delta^{15}N$ values such as euedaphic Collembola (Potapov et al., 2019). However, some Oribatida species with high $\delta^{15}N$ values such as *Oppiella nova* may also feed on ectomycorrhizal fungi, known to be enriched in ^{15}N (Remén et al., 2008; Potapov and Tiunov, 2016). Notably, *O. nova* was the most abundant soil mesofauna species at our study sites, and resources used by this species, therefore, need further attention including experiments manipulating the input of root-derived resources (Bluhm et al., 2021).

The high consistency in trophic positions of Oribatida guilds across soil depth and forest types has implications for trophic guilds to be included in soil food webs. Early studies analyzing natural variations in stable isotope ratios indicated Oribatida species to live as primary and secondary decomposers (Scheu and Falca, 2000), but later Oribatida species have been shown to cover virtually the full range of the isotope space of soil food webs (Schneider et al., 2004; Maraun et al., 2011). Despite that high δ^{13}C in endophagous Oribatida may inflate their δ^{13}C niche due to incorporation of calcium carbonate (Maraun et al., 2011), the isotopic ranges of Oribatida covered 100 % of δ^{13}C and 67 % of δ^{15}N of the isotopic range of soil food webs (Potapov et al., 2019). Differentiating Oribatida into guilds better represents their roles and trophic structure in soil food webs, and reduces the complexity of soil food webs at the resolution of species (Nielsen, 2019). We also call to study the depth variation of trophic niches in other soil animal groups such as Collembola and Gamasina to move toward more spatially explicit trophic interactions in soil food webs.

4.4.3 Management implications

In face of climate change, Norway spruce is increasingly threatened in the lowland of Central Europe. Mixed forests and alternative tree species such as non-native Douglas fir may provide better options for provisioning long-term ecosystem services than monoculture plantations of Norway spruce. By studying the variation in trophic niches in an abundant group of soil microarthropods, we found that trophic positions of Oribatida are consistent across European beech and coniferous forests, suggesting that the trophic structure of Oribatida species is highly resistant against the plantation of different tree species including non-native species such as Douglas fir. Although basal resources of Oribatida vary between coniferous and deciduous forests, the effects of Douglas fir on basal resources of Oribatida species did not differ from that of Norway spruce. Further, the basal resources in mixed forests were similar to those in European-beech forests, supporting the potential of mixed forests to mitigate the detrimental effects of coniferous trees on ecosystem properties and functioning. Although to gain a holistic understanding of forest type effects on the functioning of decomposer system more information is needed on the energy flux through other taxa of soil food webs, we conclude that trophic niches of Oribatida species and guilds are highly consistent in European beech and Douglas fir mixed forests.

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Chapter 5

General discussion

Decomposers underpin essential ecosystem services in temperate forests. Planting trees may affect decomposer communities and compromise their functioning. I studied soil microbial and microarthropod communities in five forest types across a range of environmental conditions. I found that tree identities are important drivers for both microbial and microarthropod communities. Compared to native European-beech forests, Douglas fir significantly changed the community composition of decomposers, especially for Oribatida, and for microorganisms only at nutrient-poor sites (Chapters 2 and 3). Microbial stress is intensified and microbial biomass is diminished in nutrient-poor soils by planting Douglas fir, indicating functional compromises of soil microorganisms (**Chapter 2**). Further, microbial guilds do not explain the community structure of Collembola and Oribatida to a high degree, and euedaphic Collembola and predator/scavenger Oribatida are adversely affected by planting Douglas fir, pointing to the limitation of a particular class of resources in Douglas fir (**Chapter 3**). Based on environmental conditions from Chapter 2 and animal communities from Chapter 3, I further investigated the variation in trophic niches in Oribatida species across soil depth and forest type to better understand their resource utilization. Trophic niches in Oribatida species vary little with environmental conditions, suggesting strong trophic niche differentiation in Oribatida (**Chapter 4**). Overall, these studies focused on the base of soil food webs and contribute to a better understanding of tree–decomposer interactions.

5.1 Linkages between trees and soil biological communities

Studies on the linkages between plants and decomposer communities have focused on grasslands, and our understanding of the effects of tree species identity and diversity on decomposer communities are still limited (Zak et al., 2003; Milcu et al., 2006; Schuldt et al., 2010; Eisenhauer et al., 2013). I looked into soil decomposer communities under the framework of the RTG, in which forest types were well replicated across soil nutrient and water conditions (Chapter 1). In general, I identified that tree identity is an important driver for the community structure of soil microorganisms and microarthropods, but this also depends on site conditions and taxonomical groups.

Soil microbial communities are major players in litter decomposition, carbon storage, and nutrient cycling (Van Der Heijden et al., 2008). Deciduous forests generally have higher microbial biomass than coniferous forests (Priha and Smolander, 1997). In Chapter 2, I extend this claim and suggest that microbial response depends on site conditions, particularly on soil nutrients. Microbial biomass is higher in European-beech forests than coniferous forests, but only at nutrient-poor sites, not nutrient-rich sites. The higher microbial biomass in European-beech forests at nutrient-poor sites is also associated with higher microbial respiration and lower microbial stress. These are important ecosystem processes that may have other ecosystem-level consequences, such as litter decomposition, soil fertility, and soil carbon stock. Further, the higher microbial biomass in European-beech forests is also linked to higher fine root biomass (*A. Lwila, in prep.*), pointing to the importance of belowground root-derived resources in driving microbial community functioning (Bluhm et al., 2019). Overall, environmental conditions are crucial in understanding forest type effects on soil microbial communities and ecosystem functioning (Sapsford et al., 2020).

Soil microarthropods are abundant and diverse in temperate forests, functioning as webmasters in soil food webs (Schaefer, 1990; Coleman and Hendrix, 2000). However, the effects of non-native Douglas fir on the abundance and biodiversity of soil Collembola and Oribatida are understudied. Based on species-level identification, I assigned Collembola into life-forms and Oribatida into trophic guilds (Chapter 3). Although the overall abundance and diversity of Collembola and Oribatida do not significantly differ among forest types, the abundance of euedaphic Collembola and predator Oribatida in Douglas fir were much lower than European-beech forests, pointing to the limitation of root-derived resources in Douglas-fir forests. This finding supports the usefulness of guilds in comparative studies of Oribatida communities across forest ecosystems (Simberloff and Dayan, 1991). Further, linking trees and soil microarthropods, the community structure of Oribatida but less so of Collembola differ among tree species. The higher sensibility in Oribatida differs among tree species but less in Collembola, suggesting that Oribatida may surpass Collembola as bioindicators. For biotic environmental variables, the proportion of bacteria and fungi, contribute little to the variation of the community composition of Collembola and Oribatida. The effects of forest types on soil microarthropods are therefore not linked to variations in soil microbial communities, pointing to other directions linking tree–microarthropods. This also explains why forest type effects on microbial communities varied with site conditions, but forest type effects on microarthropod communities did not. These findings contribute to a better understanding of the effects of non-native tree species on soil microarthropods, and environmental drivers of microarthropod communities.

The lesson from the biodiversity and ecosystem functioning (BEF) relationship has stressed the importance of multitrophic biodiversity on ecosystem properties and processes above and below the ground (Hector and Bagchi, 2007; Scherber et al., 2010; Bardgett and Van der Putten, 2014; Schuldt et al., 2018; Trogisch et al., 2021; Glatthorn et al., 2021). BEF theories not only are of high theoretical interest but also call for practice, which is the strengths of the RTG 2300, that is, planting mixed forests vs. monocultures[1]. Although the tree diversity effects have not been explicitly tested in this dissertation, I discussed them here for conceptual integrity. Overall, microbial and microarthropod response are intermediate in mixtures compared to respective pure stands (Chapters 2, 3). This suggests that tree species are singular, in other words, loss or addition or tree species causes detectable changes (Naeem et al., 2002; Eisenhauer et al., 2010). However, the singular effects on microbial communities also depend on site conditions and mixture types. At nutrient-rich sites, there was no significant difference between mixtures and pure stands. By contrast, at nutrient-poor sites, effects on microbial responses were intermediate in Douglas fir mixed stands, but tended to be antagonistic in Norway spruce mixed stands. This context-dependent response of microbial communities reflects that tree species respond differently to environmental conditions (Yachi and Loreau, 1999). Despite this context-dependency, overall, mixed forests help to maintain soil microbial and microarthropod communities close to the state of native European-beech forests and mitigate the adverse impact of coniferous forests.

5.2 Niche variation and species coexistence in soil decomposers

It has been a long-standing question why so many animal species coexist in soil (Hutchinson, 1959; Anderson, 1975). Niche differentiation helps to explain high species diversity and co-existence as species occupy the same niche do not co-exist. Many niche dimensions can be important in soil habitats, such as differences in resource utilization and microhabitat differences (Anderson, 1975). The application of stable isotopes in soil food webs uncovered widespread trophic niche differentiation in soil microarthropods (Scheu and Falca, 2000; Schneider et al., 2004). However, an unanswered question is to what extent trophic niches of animal species vary with environmental conditions. High trophic niche overlap may diminish trophic niche differentiation and resource partitioning of Oribatida species. In Chapter 4, I studied trophic niche variation of 40 Oribatida species with soil depth and forest type. It turns out that the trophic niches of Oribatida species are highly consistent between litter and soil, and their trophic position is similar across forest types. The high consistency of trophic niches in Oribatida species suggests that the overlap in trophic niches between Oribatida species is small, further facilitating niche differentiation and species coexistence of Oribatida species. The high consistency of trophic niches across the studied depth and forest types also suggests that Oribatida are resistant to different forest plantations, and Oribatida species use similar basal resources and occupy similar trophic positions across forests (Nae et al., 2021; Susanti et al., 2021). This study also demonstrates that combing multispecies and mixed modeling is flexible and useful for testing ecological hypotheses across ecosystems by controlling for species identity.

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[1] Philosophers have hitherto only interpreted the world in various ways; the point is to change it. — **Karl Marx**, *Eleven Thesis on Feuerbach*

Unlike herbivores which have coevolved with plants and diversified, soil decomposers are typically generalists concerning their body size to food (Scheu et al., 2005). Oribatida are opportunistic feeders under lab conditions (Maraun et al., 1998), but, surprisingly, that Oribatida occupy consistent trophic niches irrespective of soil depths across forest type. For each Oribatida species, there must be a distinct niche irrespective of the soil depth they inhabit. Several theories may explain this paradox of theoretical generalist vs. actual specialization (Ehrlich and Raven, 1964; Bolnick et al., 2003): (1) Aphid theory — or animals ingest everything but assimilate selectively. This may be also related to gut microbiomes in Oribatida (Dixon, 1985; Gong et al., 2018); (2) Foraging theory — Animals consume all kinds of food resource but in different proportions (Stephens and Krebs, 2019); (3) Microhabitat hypothesis — Although stable isotope signatures in soil organic matter change with soil depth, microhabitats exist in different depths that are similar in food resources and isotopic signature (Christensen, 1992). Animal species may have access to these microhabitats. Here, I would also like to acknowledge that these ideas originated from fruitful discussions in a seminar, and the following people deserve the credits [aphid theory (*M. Maraun*), gut microbiota (*I. Schaefer*); foraging theory (*A. Potapov*); microhabitat hypothesis (*S. Scheu*)]. Although testing these ideas needs further contemplation, I summarized these ideas here for reflection. Overall, this work contributes to a better understanding of the resource utilization of soil microarthropods, and serves as the building block for the future phase of the research training group.

5.3 Forest management and contributions to the RTG 2300

Sustainable forest management keeps the balance between ecological interests and economic needs and provides integrated benefits to all (Bolte et al., 2009). In Central Europe, Norway spruce, the most economic important tree species, may face increasing risks of bark beetle outbreak and extreme weather in the face of climate change (Pettit et al., 2020). To reduce the risk of damage while maintaining economic gains, mixed forests and planting alternative tree species, such as non-native Douglas fir, may provide alternative options for the future (Schmid et al., 2014; Ammer, 2019; Pötzelsberger et al., 2020). I have focused on decomposer communities in the RTG to better understand the effects of tree species composition on ecosystem functioning. The results on the diversity, abundance, community structure, and functioning of decomposer communities contribute to better decision-making and interdisciplinary of the RTG (Glatthorn et al., 2021).

Non-native trees provide opportunities but also bring challenges to forestry (Pötzelsberger et al., 2020). Douglas fir has been introduced into Germany over 150 years ago, but its impact on belowground communities remains understudied (Schmid et al., 2014). Based on soil microorganisms and microarthropod communities, I found that the effects of Douglas fir on soil communities depend on the taxonomic groups and environmental conditions. For soil microarthropods, although Douglas fir did not change the overall diversity and density of Collembola and Oribatida, the abundance of high trophic levels of Collembola and Oribatida were adversely affected, suggesting a limitation of particular resources in Douglas fir soils (Chapter 3). For microorganisms, only at less favorable site conditions, microbial stress is intensified by planting Norway spruce and mixed forests, particularly by Douglas fir (Lu and Scheu, 2021). Although further studies are needed to disentangle the limited resources in Douglas fir, these findings call for caution in planting Douglas fir, particularly at less favorable site conditions. Further, although there are exceptions, such as Norway spruce mixed stands, planting mixed forests overall mitigates the detrimental effects of conifers on microbial and microarthropod communities. These results on decomposer communities, therefore, advocate the practice of mixed forest management.

The results of subproject 5 on decomposers (*Subproject 5*) have yielded plentiful links to other subprojects, particularly to soil carbon (*Subproject 3*), and fine root biomass (*Subproject 1*). Soil organic matter is the largest carbon reservoir in the world (Angst et al., 2021). *E. Foltran* (*Subproject 3*) quantified organic carbon stock in the organic and mineral soils down to a depth of 30 cm soil depth. As both plant- and microbial-derived carbon contribute to soil carbon stock, the role of microbial activity and carbon measured by me (*Subproject 5*) may better explain organic carbon stock. A starting point may be to look for correlations between carbon stock in the organic layer and microbial respiration and biomass. In the long run, a more promising approach may be to calculate ecosystem-level carbon budgets (Buchmann, 2000; Jiang et al., 2020). The carbon budget has the potential to serve to synthesize the results of the research training group in the future. Furthermore, the link between trees and soil microbial communities via fine-root biomass (*Subproject 1*) and root-derived resources has emerged (Meier et al., 2020; Prescott et al., 2020). The context-dependent phenotypic plasticity of trees may have consequences on the structure and functioning of soil microbial communities and other ecosystem processes and properties, such as soil fertility, plant–soil feedbacks, and plant–plant interactions. Ongoing litter bag experiments and future root-trenching experiments may approach some of these questions.

Effect-size thinking (‘new statistics’) rather than null hypothesis significance testing is increasingly welcomed in ecology (Cumming, 2014). Unlike post hoc pairwise comparisons, effect-size thinking applies contrast that has been set a priori and compares groups of major interests (Ruxton and Beauchamp, 2008). Effect size such as log response ratio has the potential to serve as a general statistical approach for the RTG to present and synthesize results within and across studies. With inspiration from the talk of *Dr. David Wise* invited by the RTG and the recent work by Piovia-Scott et al. (2019), I have used and demonstrated the value of effect sizes throughout this dissertation. Considering the complexity of the RTG design and multiple measurements done within plots across space and/or time, using European beech as a reference can serve as a simple but powerful way of synthesizing and communicating science.

5.4 Future directions

From a broader perspective, my work presented in this dissertation only covered a single sampling date and part of the soil food web, compromising the generalization of the findings through time and across taxa. Groups such as soil viruses, archaea, microfauna, other groups of mesofauna and macrofauna, were not covered. However, despite these limitations, microorganisms occupy the base of soil food webs and are key ecosystem-process drivers (Bardgett and Van der Putten, 2014). Microorganisms in numbers are the sheer majority of soil communities (Whitman et al., 1998). Likewise, Collembola and Oribatida are among the most abundant and diverse ones among soil mesofauna and macrofauna (Schaefer, 1990). They occupy the majority isotopic space of soil food webs, arguing for their importance in soil food webs (Potapov et al., 2019). Further adding to the value of my work, I had the fortune to contribute the empirical data included in this dissertation to several cutting-edge syntheses: (1) Global soil PLFA led by *G. Smith* (Smith et al., 2020); (2) Global Collembola initiated by *A. Potapov* (Potapov et al., 2020); (3) Perspective Oribatida review by *M. Maraun* (Maraun et al., 2011). These initiatives add to the increasing global synthesis of belowground carbon and biota, such as soil fungi, bacteria, carbon, nematodes, and earthworms (Tedersoo et al., 2014; Delgado-Baquerizo et al., 2018; Crowther et al., 2019; Van den Hoogen et al., 2019; Phillips et al., 2019). Community ecology is an exciting field, and life in the soil has a lot to offer general ecological theories (Wardle, 2013). The identification of soil animals needs patience, but this can be joyful. Here I further present ideas that I find appealing for future projects: seasonal dynamics of microbial communities and spatially explicit trophic interactions in soil food webs.

The patterns of seasonal growth are different between deciduous and coniferous forests. Litter- and root-derived resources are dynamic and vary with forest types (Högberg et al., 2010). However, temporal dynamics are poorly studied in microbial communities (Pollierer et al., 2015). Although soil sampling is labor-intensive, soil microbial communities vary with the season in temperate forests (Moore-Kucera and Dick, 2008; Kaiser et al., 2011; Koranda et al., 2013). Earlier studies reported high inter-annual variation in microbial community structure, but the processes leading to such variation remain unexplored. The effects of root-derived resources were suggested to be significant after a year but not after (Bluhm et al., 2019). This further calls for studies looking at a finer temporal resolution of microbial communities across seasons. Seasonal response of microbial communities may reflect the availability of litter- and root-derived resources and their seasonal dynamics, leading to a better understanding of the role of root-derived resources driving soil microbial communities (Lu and Scheu, 2021).

Resources and abiotic environments change rapidly with soil depth (Fierer et al., 2003; Lindahl et al., 2007; Lu and Scheu, 2021). Soil depths, therefore, provide an interesting environmental gradient to study the intraspecific variation in trophic niches of soil decomposers. The low intra-specific variation of trophic niches may contribute to niche differentiation and species co-existence of Oribatida (Chapter 4), but to what extent this applies to other mesofauna groups has not been investigated. The value of comparing vertical gradients of stable isotopes in microarthropods with soil organic matter has been proposed earlier (Potapov et al., 2019). This has the potential to identify soil-dwelling decomposers or litter-dwelling predators for species that have high ^{15}N values. Such information is also useful for establishing spatially explicit trophic interactions in soil, leading to a better understanding of niche differentiation in soil microarthropods and trophic interactions in soil food webs.

5.5 Concluding remarks

In face of climate change, forest management faces challenges on which tree species to plant and whether in mixtures. Based on this dissertation, although microbial and microarthropod communities are overall buffered against forest plantations, pure Douglas fir may compromise long-term ecosystem functioning by adverse effects on microbial communities at less favorable sites. As well as on high-trophic guild Collembola and Oribatida likely due to the limitation of root-derived resources. Caution is therefore needed when planting Douglas fir at less favorable site conditions. Generally, mixed-forest management is advocated because it mitigates the adverse impact of Norway spruce and Douglas fir.

Tree identity is an important driver of the community structure of soil microorganisms and microarthropods. Mixed forests generally have intermediate effects on microbial and microarthropod communities, supporting the singular hypothesis. The contribution of microbial communities to the variation of microarthropod community structure is small, agreeing with the stable isotope study that the actual environment informs little about their diets. The Oribatida paradox, that is, opportunistic feeding but occupation of distinct trophic niches irrespective of soil depth, calls for more detailed studies on the foraging behavior of Oribatida. Although other mechanisms need to be considered in linking forest types and soil biological communities, such as competition, top-down control, and habitat structure, this dissertation highlights the importance of resources linking forest types to soil microbial and microarthropod communities across environmental conditions.

We live in the Anthropocene with progressing loss of biodiversity. This applies not only to top predators but also to low-trophic level invertebrates (Estes et al., 2011; Dirzo et al., 2014). Soil as habitat is of great importance to biodiversity and human beings (Bardgett and Van der Putten, 2014). The high diversity and importance in functions of soil organisms call for a better understanding of the systems. Soil biological communities have a lot to offer to general theories in ecology. Many important problems may be answered using soil organisms as a study system.

Appendix A

Supplementary materials for Chapter 2

Response of soil microbial communities to mixed beech–conifer forests varies with site conditions[1]

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[1] Published in Soil Biology & Biochemistry, 2021, 155(108155)

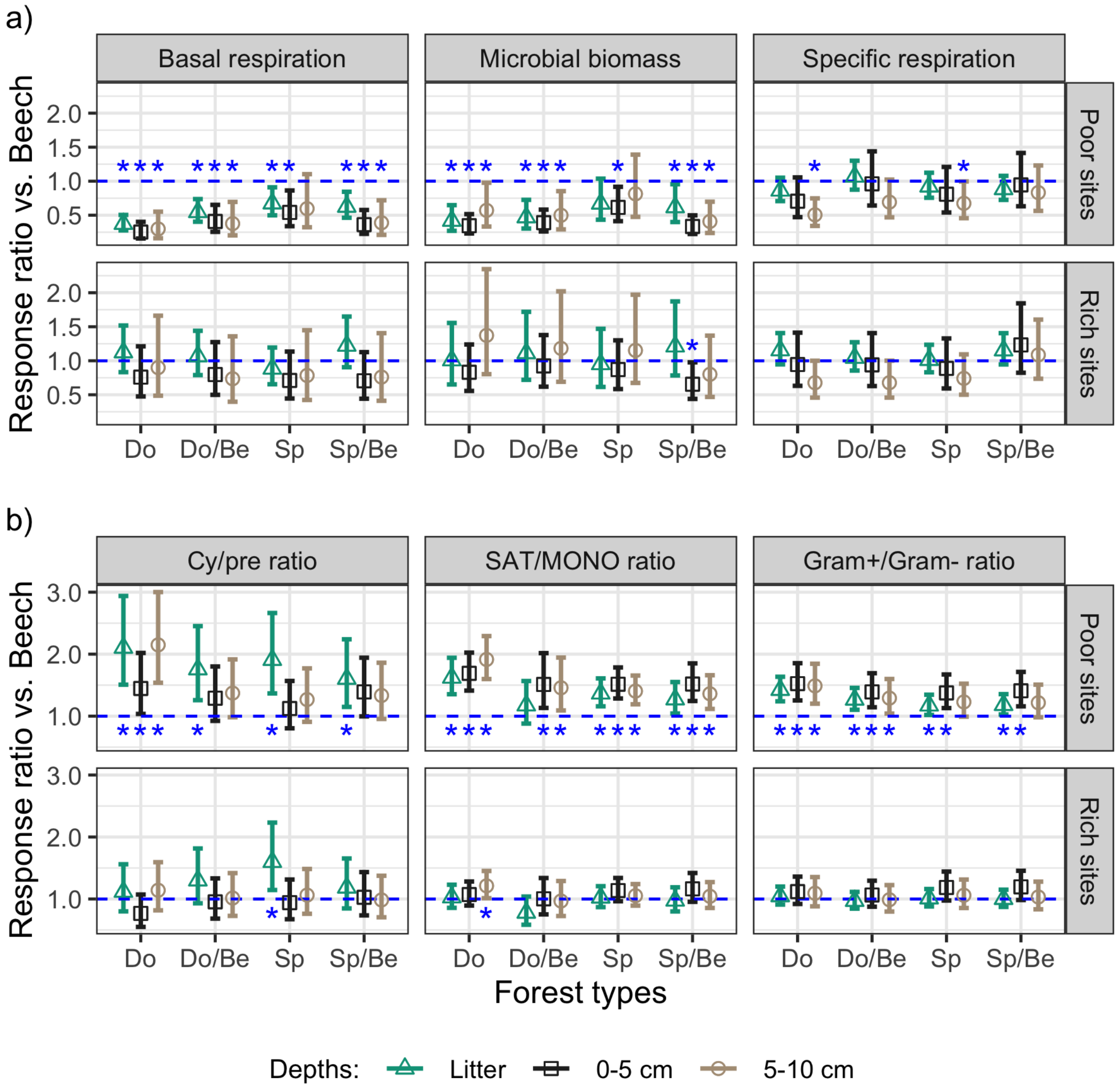

Figure A.1: (a) Depth-specific effects of conifers and conifer-beech mixtures (Douglas fir [Do], Douglas fir with European beech [Do/Be], Norway spruce [Sp] and Norway spruce with European beech [Sp/Be]) on microbial basal respiration (μg O_2 g^{-1} C h^{-1}), microbial biomass (μg C_{mic} g^{-1} C) and microbial specific respiration (μg O_2 μg^{-1} C_{mic} h^{-1}) at nutrient-poor and nutrient-rich sites; (b) depth-specific effects on the ratio of cyclopropyl PLFAs to its monoenoic precursors, saturated to monounsaturated PLFAs, and Gram positive to Gram negative bacteria ratio (cy/pre, sat/mono and Gram^{+}/Gram^{-}, respectively) at nutrient-poor and nutrient-rich sites. Effect sizes are given as back transformed log response ratios compared to beech forests [ln (value in coniferous or mixed forest types / values in beech)]. Effect sizes were estimated from litter, 0–5 and 5–10 cm soil depth based on mixed-effects models with all two-way interactions. Asterisks indicate significant effects ($P < 0.05$). Bars represent 95% confidence intervals ($n = 4$).

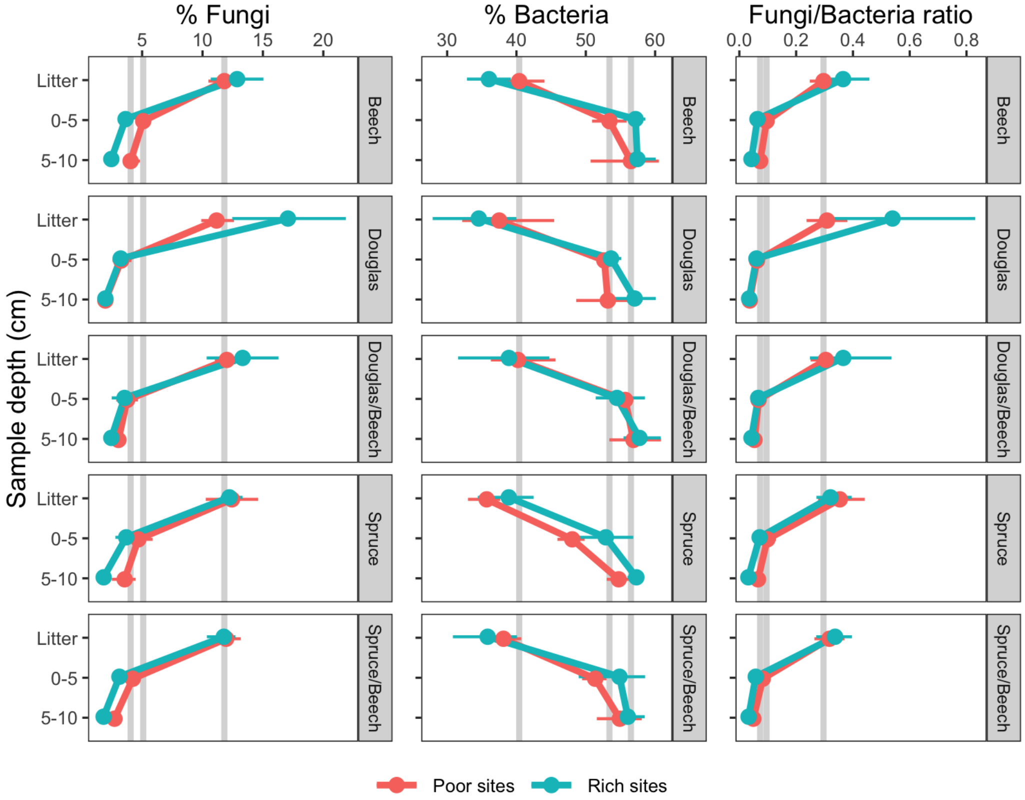

Figure A.2: Changes in the relative abundance of fungi, bacteria and fungi/bacteria ratio with soil depth (litter and 0–5 cm and 5–10 cm soil) in five forest types (European beech [Beech], Douglas fir [Douglas], Douglas fir with beech [Douglas/Beech], Norway spruce [Spruce], and Norway spruce with beech [Spruce/Beech]) at nutrient-poor and nutrient-rich sites. Points and horizontal bars represent means and standard errors (n = 4). The grey vertical bars indicate respective values in beech forests at nutrient-poor sites in litter, 0–5, and 5–10 cm depth.

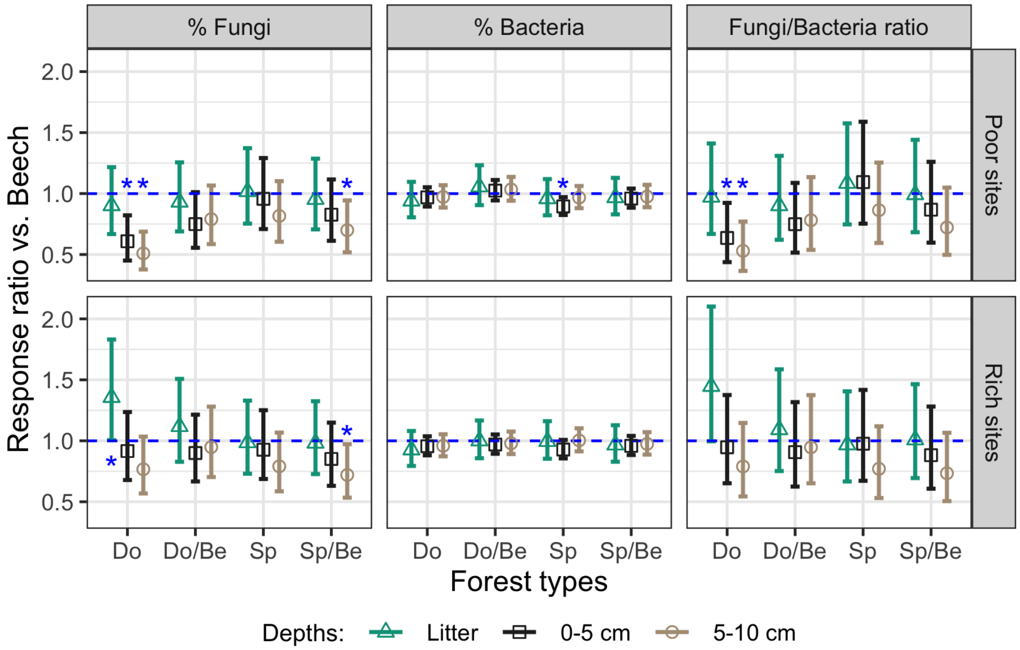

Figure A.3: Depth-specific effects of conifers and conifer-beech mixtures (Douglas fir [Do], Douglas fir with beech [Do/Be], Norway spruce [Sp] and Norway spruce with beech [Sp/Be]) on the relative abundance of fungi, bacteria and fungi/bacteria ratio at nutrient-poor and nutrient-rich sites. Effect sizes are given as back transformed log response ratios compared to beech forests [ln (value in coniferous or mixed forest types / values in beech)]. Effect sizes were estimated from litter, 0–5, and 5–10 cm soil depth based on mixed-effects models with all two-way interactions. Asterisks indicate significant effects ($P < 0.05$). Bars represent 95% confidence intervals ($n = 4$).

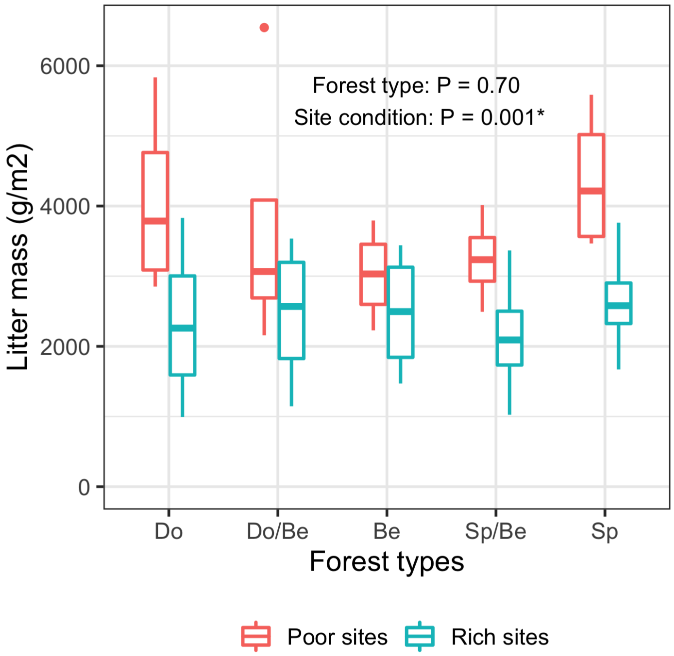

Figure A.4: Litter mass in the studied forest types (Douglas fir [Do], Douglas fir with beech [Do/Be], European beech [Be], Norway spruce with beech [Sp/Be] and Norway spruce [Sp]) at nutrient-poor and nutrient-rich sites. Litter mass includes leaves, needles and reproductive organs on the forest floor.

Table A.1: Contrasts comparing the studied forest types (Douglas fir [Do], Douglas fir and European beech mixture [Do/Be], Norway spruce and European beech mixture [Sp/Be], Norway spruce [Sp]) to European-beech forests (Be). Ratio was back-transformed from log response ratio. Significant p-values are given in bold ($P < 0.05$).

Variable	Contrast	Site condition	Ratio	p-value
Basal respiration	Do vs. Be	Nutrient-rich	1.011	0.938
Basal respiration	Do/Be vs. Be	Nutrient-rich	0.976	0.86
Basal respiration	Sp/Be vs. Be	Nutrient-rich	1.056	0.696
Basal respiration	Sp vs. Be	Nutrient-rich	0.841	0.224
Basal respiration	Do vs. Be	Nutrient-poor	0.345	**<0.001**
Basal respiration	Do/Be vs. Be	Nutrient-poor	0.499	**<0.001**
Basal respiration	Sp/Be vs. Be	Nutrient-poor	0.540	**<0.001**
Basal respiration	Sp vs. Be	Nutrient-poor	0.640	**0.004**
Microbial biomass	Do vs. Be	Nutrient-rich	0.962	0.829
Microbial biomass	Do/Be vs. Be	Nutrient-rich	1.027	0.883
Microbial biomass	Sp/Be vs. Be	Nutrient-rich	0.825	0.286
Microbial biomass	Sp vs. Be	Nutrient-rich	0.946	0.756
Microbial biomass	Do vs. Be	Nutrient-poor	0.400	**<0.001**
Microbial biomass	Do/Be vs. Be	Nutrient-poor	0.428	**<0.001**
Microbial biomass	Sp/Be vs. Be	Nutrient-poor	0.413	**<0.001**
Microbial biomass	Sp vs. Be	Nutrient-poor	0.659	**0.025**
Specific respiration	Do vs. Be	Nutrient-rich	1.064	0.514
Specific respiration	Do/Be vs. Be	Nutrient-rich	0.985	0.869
Specific respiration	Sp/Be vs. Be	Nutrient-rich	1.151	0.144
Specific respiration	Sp vs. Be	Nutrient-rich	0.965	0.706
Specific respiration	Do vs. Be	Nutrient-poor	0.810	**0.033**
Specific respiration	Do/Be vs. Be	Nutrient-poor	1.020	0.833
Specific respiration	Sp/Be vs. Be	Nutrient-poor	0.890	0.223
Specific respiration	Sp vs. Be	Nutrient-poor	0.887	0.208
cy/pre	Do vs. Be	Nutrient-rich	0.993	0.959
cy/pre	Do/Be vs. Be	Nutrient-rich	1.080	0.592
cy/pre	Sp/Be vs. Be	Nutrient-rich	1.062	0.674
cy/pre	Sp vs. Be	Nutrient-rich	1.169	0.279
cy/pre	Do vs. Be	Nutrient-poor	1.870	**<0.001**
cy/pre	Do/Be vs. Be	Nutrient-poor	1.459	**0.013**
cy/pre	Sp/Be vs. Be	Nutrient-poor	1.438	**0.017**
cy/pre	Sp vs. Be	Nutrient-poor	1.395	**0.027**
sat/mono	Do vs. Be	Nutrient-rich	1.100	0.211
sat/mono	Do/Be vs. Be	Nutrient-rich	0.911	0.373
sat/mono	Sp/Be vs. Be	Nutrient-rich	1.058	0.474
sat/mono	Sp vs. Be	Nutrient-rich	1.070	0.329
sat/mono	Do vs. Be	Nutrient-poor	1.738	**<0.001**
sat/mono	Do/Be vs. Be	Nutrient-poor	1.372	**0.005**
sat/mono	Sp/Be vs. Be	Nutrient-poor	1.379	**<0.001**
sat/mono	Sp vs. Be	Nutrient-poor	1.427	**<0.001**
$Gram^+/Gram^-$	Do vs. Be	Nutrient-rich	1.064	0.316
$Gram^+/Gram^-$	Do/Be vs. Be	Nutrient-rich	0.989	0.86
$Gram^+/Gram^-$	Sp/Be vs. Be	Nutrient-rich	1.038	0.542
$Gram^+/Gram^-$	Sp vs. Be	Nutrient-rich	1.051	0.415
$Gram^+/Gram^-$	Do vs. Be	Nutrient-poor	1.459	**<0.001**
$Gram^+/Gram^-$	Do/Be vs. Be	Nutrient-poor	1.293	**<0.001**
$Gram^+/Gram^-$	Sp/Be vs. Be	Nutrient-poor	1.227	**0.002**
$Gram^+/Gram^-$	Sp vs. Be	Nutrient-poor	1.215	**0.004**

Table A.2: Contrasts comparing the studied forest types (Douglas fir [Do], Douglas fir and European beech mixture [Do/Be], European beech [Be], Norway spruce and European beech mixture [Sp/Be] and Norway spruce [Sp]) at nutrient-poor sites (Poor) to nutrient-rich sites (Rich). Ratio was back-transformed from log response ratio. Significant p-values are given in bold ($P < 0.05$).

Variable	Contrast	Forest type	Ratio	p-value
Basal respiration	Poor vs. Rich	Do	0.436	**0.007**
Basal respiration	Poor vs. Rich	Do/Be	0.653	0.082
Basal respiration	Poor vs. Rich	Be	1.277	0.277
Basal respiration	Poor vs. Rich	Sp/Be	0.653	0.082
Basal respiration	Poor vs. Rich	Sp	0.972	0.893
Microbial biomass	Poor vs. Rich	Do	0.531	**0.001**
Microbial biomass	Poor vs. Rich	Do/Be	0.532	**0.001**
Microbial biomass	Poor vs. Rich	Be	1.276	0.179
Microbial biomass	Poor vs. Rich	Sp/Be	0.639	**0.017**
Microbial biomass	Poor vs. Rich	Sp	0.889	0.510
Specific respiration	Poor vs. Rich	Do	0.916	0.512
Specific respiration	Poor vs. Rich	Do/Be	1.246	0.133
Specific respiration	Poor vs. Rich	Be	1.203	0.195
Specific respiration	Poor vs. Rich	Sp/Be	0.930	0.585
Specific respiration	Poor vs. Rich	Sp	1.105	0.461
cy/pre	Poor vs. Rich	Do	1.817	**0.017**
cy/pre	Poor vs. Rich	Do/Be	1.303	0.198
cy/pre	Poor vs. Rich	Be	0.965	0.851
cy/pre	Poor vs. Rich	Sp/Be	1.306	0.194
cy/pre	Poor vs. Rich	Sp	1.151	0.471
sat/mono	Poor vs. Rich	Do	1.383	**0.030**
sat/mono	Poor vs. Rich	Do/Be	1.320	0.118
sat/mono	Poor vs. Rich	Be	0.876	0.235
sat/mono	Poor vs. Rich	Sp/Be	1.143	0.301
sat/mono	Poor vs. Rich	Sp	1.169	0.190
$Gram^+/Gram^-$	Poor vs. Rich	Do	1.402	**0.009**
$Gram^+/Gram^-$	Poor vs. Rich	Do/Be	1.336	**0.017**
$Gram^+/Gram^-$	Poor vs. Rich	Be	1.022	0.816
$Gram^+/Gram^-$	Poor vs. Rich	Sp/Be	1.208	0.078
$Gram^+/Gram^-$	Poor vs. Rich	Sp	1.181	0.111
Fungi	Poor vs. Rich	Do	0.866	0.274
Fungi	Poor vs. Rich	Do/Be	1.085	0.531
Fungi	Poor vs. Rich	Be	1.303	**0.049**
Fungi	Poor vs. Rich	Sp/Be	1.265	0.078
Fungi	Poor vs. Rich	Sp	1.345	**0.029**
Bacteria	Poor vs. Rich	Do	0.972	0.449
Bacteria	Poor vs. Rich	Do/Be	1.012	0.754
Bacteria	Poor vs. Rich	Be	0.961	0.293
Bacteria	Poor vs. Rich	Sp/Be	0.961	0.297
Bacteria	Poor vs. Rich	Sp	0.925	**0.046**
Fun/Bac	Poor vs. Rich	Do	0.868	0.404
Fun/Bac	Poor vs. Rich	Do/Be	1.067	0.697
Fun/Bac	Poor vs. Rich	Be	1.292	0.156
Fun/Bac	Poor vs. Rich	Sp/Be	1.271	0.180
Fun/Bac	Poor vs. Rich	Sp	1.449	0.058

Table A.3: Forward selection in redundancy analyses (RDA). Statistically significant covariates were determined using stepwise forward selection after Monte Carlo permutation test. P-values <0.05 and significant accumulated R^2 values are given in bold.

Based on odistep				*Based on ordiR2step*	
Tested term	F	P	-	Forward selected model	*Adjusted R^2*
Litter					
pH	4.45	**0.005**		pH	0.08
C/N	1.65	0.090		pH + C/N	0.10
water content	1.81	0.105		pH + water content	0.10
litter mass	1.35	0.215		pH + litter mass	0.09
carbon content	1.06	0.395		pH + carbon content	0.08
0-5 cm					
C/N	11.76	**0.005**		C/N	0.22
pH	5.61	**0.005**		C/N + pH	0.30
water content	4.79	**0.005**		C/N + pH + water content	0.37
litter mass	0.80	0.610		C/N + pH + water content + litter mass	0.36
carbon content	1.20	0.300		C/N + pH + water content + carbon content	0.37
5-10 cm					
C/N	7.01	**0.005**		C/N	0.13
carbon content	1.82	0.075		C/N + carbon content	0.15
water content	1.19	0.260		C/N + water content	0.14
pH	0.81	0.580		C/N + pH	0.13
litter mass	0.99	0.435		C/N + litter mass	0.13

Appendix B

Supplementary materials for Chapter 3

Guild patterns and variation in Collembola and Oribatida communities across soils of European beech, Norway spruce, non-native Douglas fir and mixed conifer–beech forests: Biotic and abiotic drivers

Supplementary methods

To model species richness, Shannon diversity and total abundance, we used linear mixed effects models (*LMM*s) with forest type (European beech, Douglas fir, Douglas fir/European beech, Norway spruce, Norway spruce/European beech), site condition (nutrient-rich and nutrient-poor sites) as fixed effects. Site (eight blocks) was included as random effects. Log transformation was applied to abundance data to meet normality assumptions. Specimens from the same soil cores were pooled prior to the analyses.

To model guild-specific richness, Shannon diversity and abundance, we used *LMM*s with forest type (European beech, Douglas fir, Douglas fir/European beech, Norway spruce, Norway spruce/European beech), site condition (nutrient-rich and nutrient-poor sites) and guilds (three trophic guilds) as fixed effects. Nested random effects include guild within forest type within site. Specimens from the same soil cores were pooled prior to the analyses. Log transformation was applied to abundance data to meet normality assumptions [log(x+1)]. We applied *LMM*s in addition to *GLMM*s because the p-values of the anova table from *LMM*s helps us to navigate major effects.

Supplementary results

In total, we recorded 26 species of Collembola and 69 species of Oribatida from 1941 individual of Collembola and 3797 adult individuals of Oribatida. The average species richness per sample for Collembola and Oribatida was 6 (range 2–9) and 13 (range 5–24), respectively.

Oribatida nymphs (juveniles) accounted for 54% of total Oribatida (7011). The abundance of nymph did not differ among forest types but tended to be lower in European beech than Norway-spruce forests (36.5 ± 27.9 ind./sample, in spruce: 127.0 ± 119.0 ind./sample, mean ± sd; $\text{Deviance}_{4,30} = 8.40$, $P = 0.078$; generalized linear model with negative binomial distribution).

Brachychthoniidae account for 2.7% of total Oribatida abundance. The abundance of Brachychthoniidae tended to be lower in Norway spruce than other forest types (5.7 ± 12.5 ind./sample; in spruce: 0.6 ± 1.4 ind./sample; mean ± sd; $\text{Deviance}_{4,30} = 8.88$, $P = 0.064$).

Carabodes labyrinthicus presumably feeds on lichens, but based on ^{15}N values the species was grouped as primary decomposer. *Edwardzetes edwardsi* feeds on mosses (Fischer et al., 2014), but based on ^{15}N values was grouped as secondary decomposer. In total, as there were two individuals of *C. labyrinthicus* and eight of *E. edwardsi*, the grouping therefore unlikely influenced the results.

Supplementary figures

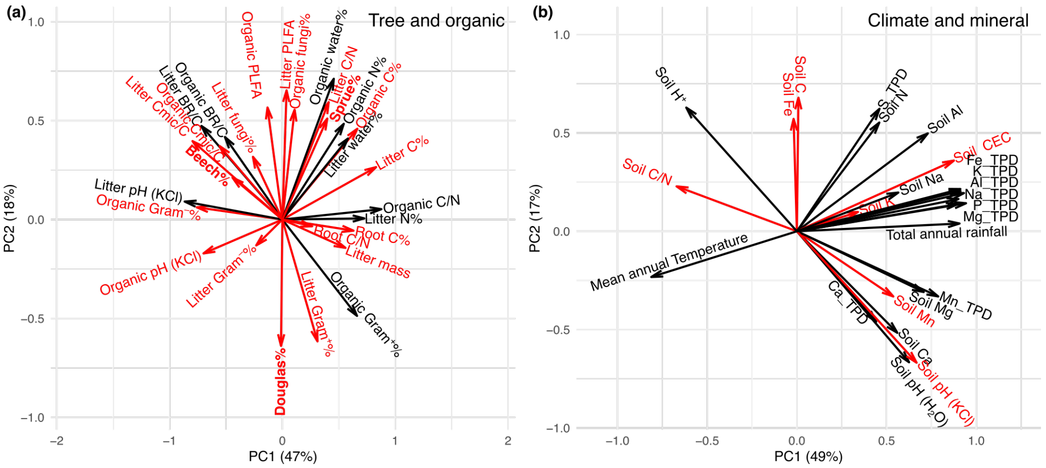

Figure B.1: Principal component analyses of environmental variables from (a) trees and organic soil layers (litter and 0–5 cm soil) and (b) climate and the mineral soil layer (0–5 cm mineral soil). Variables were pre-selected within group before RDA analyses (|Pearson's r| < 0.7; coded in red). Details of the abbreviations are: European beech proportion (Beech%), Norway spruce proportion (Spruce%), Douglas fir (Douglas%), 0–5 cm organic layer (Organic), carbon (C), nitrogen (N), Gram$^+$ bacteria (Gram$^+$), Gram$^-$ bacteria (Gram$^-$), cation exchange capacity (CEC), total concentration determined by pressure digestion (_TPD).

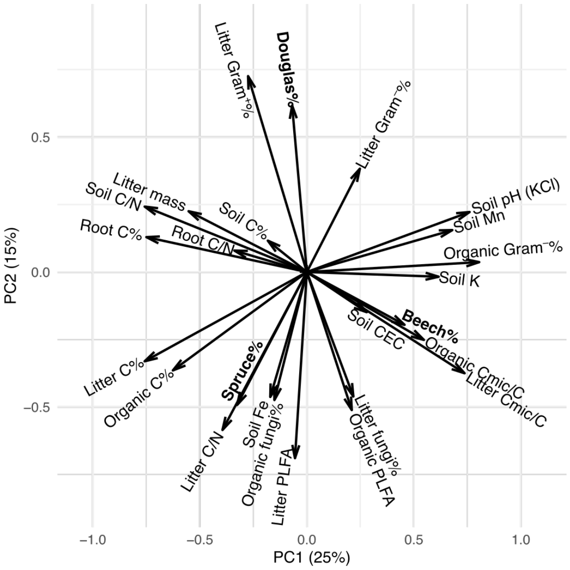

Figure B.2: Principal component analyses of all environmental variables (|Pearson's r| < 0.7). Forest tree compositions are given in bold. Note that organic pH was correlated with soil pH (r = 0.73) and only soil pH is included in the PCA. Details of the abbreviations are: European beech proportion (Beech%), Norway spruce proportion (Spruce%), Douglas fir (Douglas%), 0–5 cm organic layer (Organic), carbon (C), nitrogen (N), Gram$^+$ bacteria (Gram$^+$), cation exchange capacity (CEC).

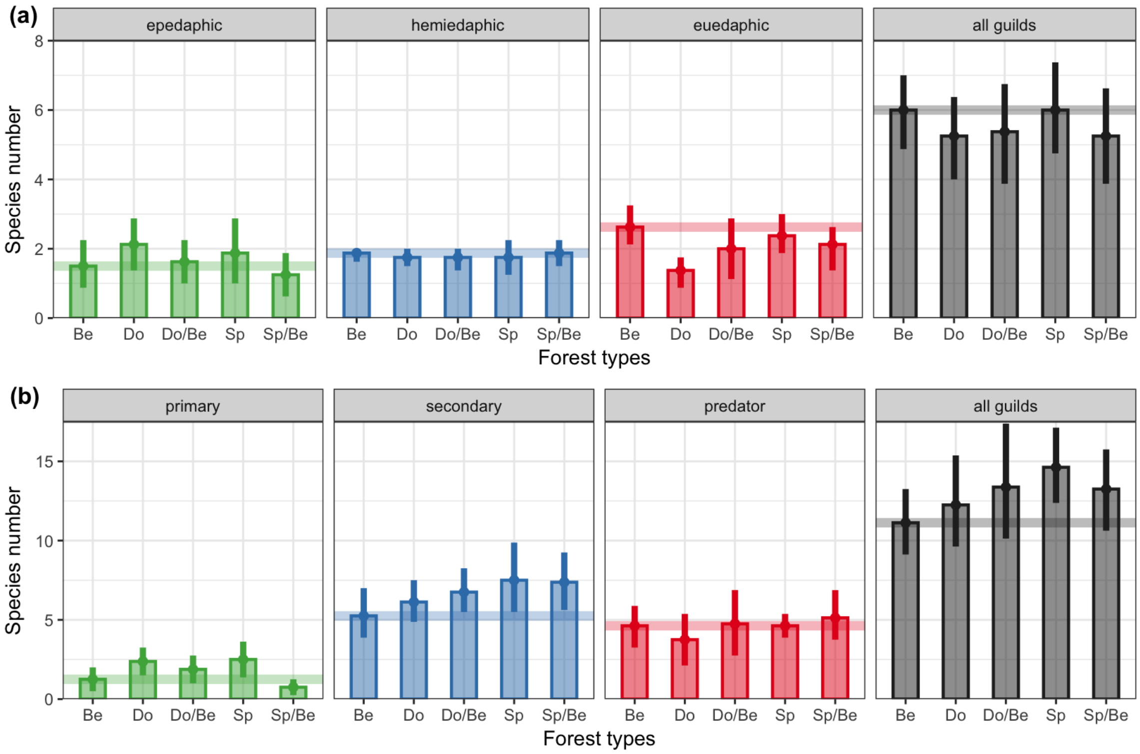

Figure B.3: Microarthropod species richness per sample. Guild-specific (epedaphic, hemiedaphic and euedaphic in Collembola; primary, secondary decomposer and predator in Oribatida) and total number of species of (a) Collembola and (b) Oribatida in European beech (Be), Douglas fir (Do), Norway spruce (Sp) and two conifer-beech mixtures (Do/Be and Sp/Be); means and standard errors (n = 8). Horizontal bars represent respective mean values in beech forests. Note that richness for Oribatida does not include Brachychthoniidae and nymphs.

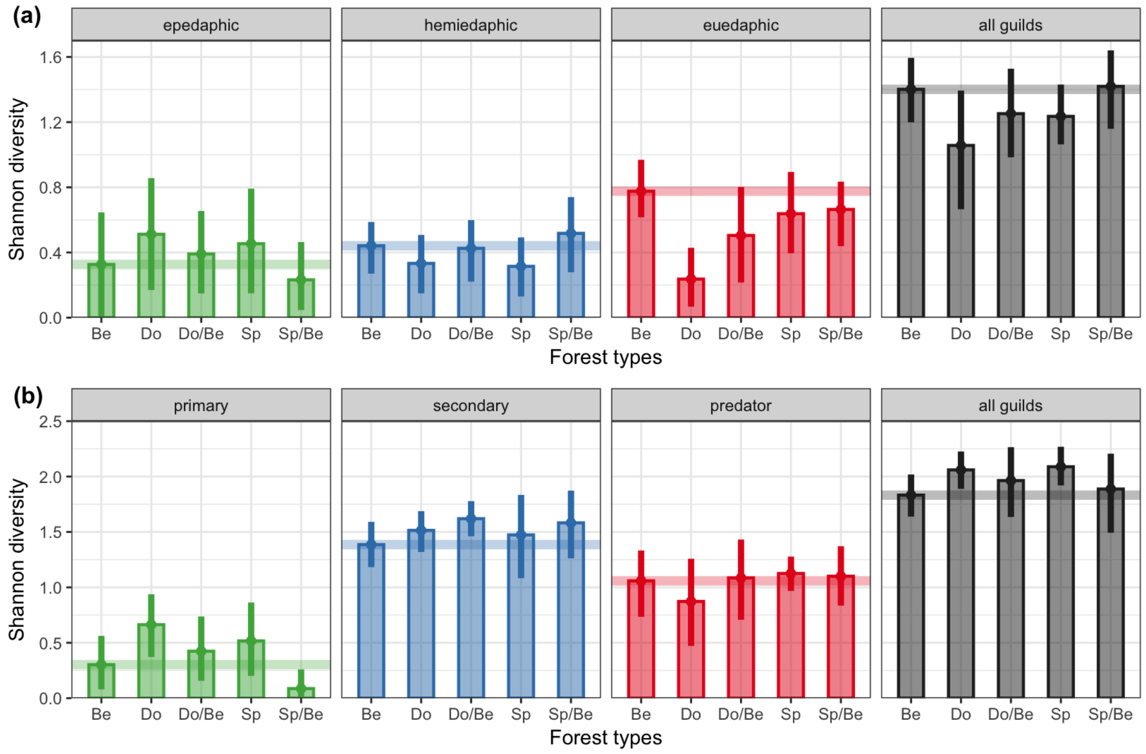

Figure B.4: Shannon diversity index of microarthropods. Diversity of each guild specific (epedaphic, hemiedaphic and euedaphic in Collembola; primary, secondary decomposer and predator in Oribatida) and all guilds of (a) Collembola and (b) Oribatida in European beech (Be), Douglas fir (Do), Norway spruce (Sp) and two conifer-beech mixtures (Do/Be and Sp/Be); mean and standard errors (n = 8). Horizontal bars represent respective mean values in beech forests. Note that diversity for Oribatida does not include Brachychthoniidae and nymphs.

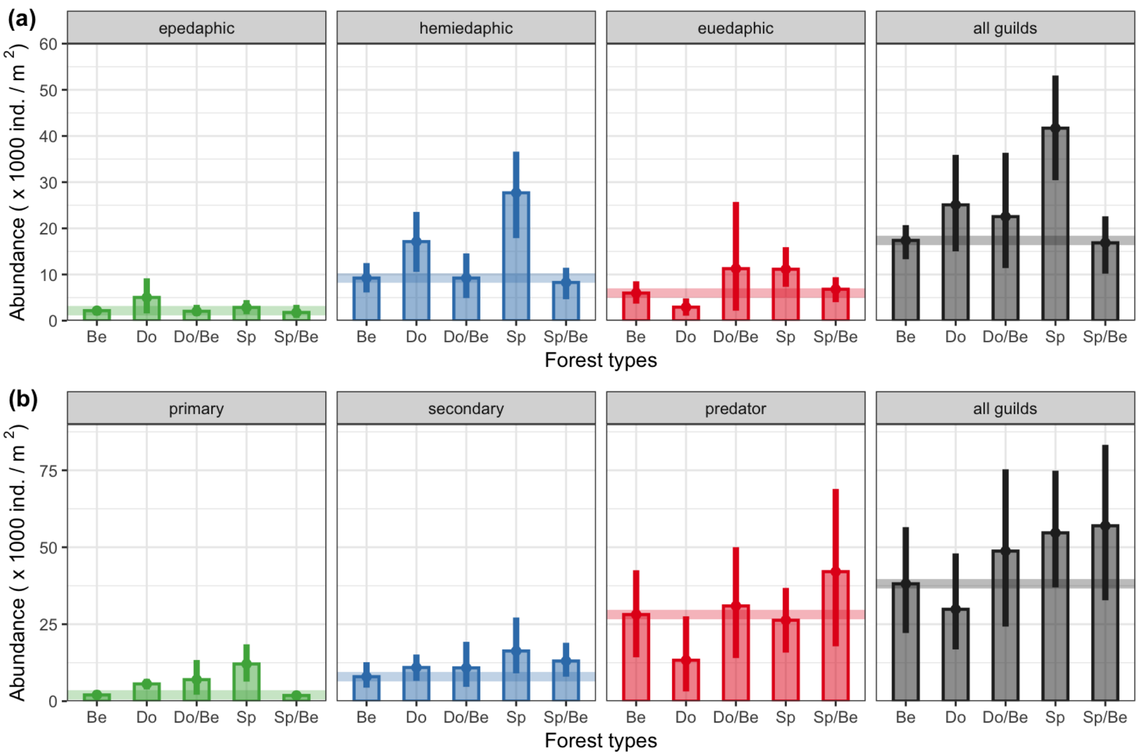

Figure B.5: Microarthropod abundance per square meter. Guild-specific (epedaphic, hemiedaphic and euedaphic in Collembola; primary, secondary decomposer and predator in Oribatida) as well as total number of (a) Collembola and (b) Oribatida in European beech (Be), Douglas fir (Do), Norway spruce (Sp) and two conifer-beech mixtures (Do/Be and Sp/Be) are presented. Bars and error bars are means and standard errors (n = 8). Horizontal bars represent respective mean values in beech forests. Note that diversity for Oribatida does not include Brachychthoniidae and nymphs.

Supplementary tables

Table B.1: List of Collembola species, families and guilds (life form). Life forms were assigned based on Potapov and Tiunov (2016).

Species name	Family	Life form
Frisea mirabilis (Tullberg, 1871)	Neanuridae	epedaphic
Pogonognathellus flavescens (Tullberg, 1871)	Tomoceridae	epedaphic
Sminthurinus aureus (Lubbock, 1862)	Katiannidae	epedaphic
Desoria violacea Tullberg, 1876	Isotomidae	epedaphic
Ceratophysella denticulata (Bagnall, 1941)	Hypogastruridae	epedaphic
Hypogastrura burkilli (Bagnall, 1940)	Hypogastruridae	epedaphic
Dicyrtomina ornata (Nicolet, 1842)	Dicyrtomidae	epedaphic
Orchesella bifasciata Nicolet, 1842	Entomobryidae	epedaphic
Entomobrya nivalis (Linnaeus, 1758)	Entomobryidae	epedaphic
Lepidocyrtus lanuginosus (Gmelin, 1788)	Entomobryidae	epedaphic
Lepidocyrtus cyaneus Tullberg, 1871	Entomobryidae	epedaphic
Lepidocyrtus violaceus Lubbock, 1873	Entomobryidae	epedaphic
Lepidocyrtus lignorum (Fabricius, 1775)	Entomobryidae	epedaphic
Pseudosinella alba (Packard, 1873)	Entomobryidae	hemiedaphic
Parisotoma notabilis Schäffer, 1896	Isotomidae	hemiedaphic
Folsomia quadrioculata (Tullberg, 1871)	Isotomidae	hemiedaphic
Folsomia manolachei Bagnall, 1939	Isotomidae	hemiedaphic
Xenyllodes armata Axelson, 1903	Odontellidae	hemiedaphic
Neanura muscorum (Templeton, 1835)	Neanuridae	hemiedaphic
Mesaphorura macrochaeta Rusek, 1976	Tullbergiidae	euedaphic
Isotomiella minor (Schäffer, 1896)	Isotomidae	euedaphic
Protaphorura quadriocellata (Gisin, 1947)	Onychiuridae	euedaphic
Protaphorura armata (Tullberg, 1869)	Onychiuridae	euedaphic
Paratullbergia callipygos (Börner, 1902)	Tullbergiidae	euedaphic
Willemia anophthalma Börner, 1901	Hypogastruidae	euedaphic
Willemia denisi Mills, 1932	Hypogastruidae	euedaphic

Table B.2: List of Oribatida species, families and guilds (trophic guilds). Endophagous Oribatida were assigned to secondary decomposers. References used for assigning guilds are given.

Species name	Family	Trophic guilds	Reference
Euzetes globulus (Nicolet, 1855)	Euzetidae	primary	Schneider2004
Hermannia gibba (C.L.Koch, 1839)	Hermanniidae	primary	Maraun2011, only genus, Pollierer2009
Platynothrus peltifer (C.L.Koch, 1839)	Camissidae	primary	Maraun2011
Nothrus palustris C.L.Koch, 1839	Nothridae	primary	Maraun2011
Achipteria coleoptrata (Linne, 1758)	Achipteriidae	primary	Maraun2011
Parachipteria punctata (Nicolet, 1855)	Achipteriidae	primary	Bluhm2015
Carabodes labyrinthicus (Michael, 1879)	Carabodidae	primary	Maraun2011
Tectocepheus minor Berlese, 1903	Tectocepheidae	primary	Maraun2011
Tectocepheus sarekensis Traegardh, 1910	Tectocepheidae	primary	Maraun2011
Tectocepheus velatus (Michael, 1880)	Tectocepheidae	primary	Maraun2011
Galumna lanceata (Oudemans, 1900)	Galumnidae	secondary	Maraun2011
Acrogalumna longipluma (Berlese, 1904)	Galumnidae	secondary	Migelton2019
Diapterobates humeralis (Hermann, 1804)	Ceratozetidae	secondary	Fischer2014, only to genus
Trichoribates novus (Sellnick, 1928)	Ceratozetidae	secondary	Fischer2014, only to genus
Edwardzetes edwardsi (Nicolet, 1855)	Ceratozetidae	secondary	Lu2021
Ceratozetes gracilis (Michael, 1884)	Ceratozetidae	secondary	Maraun2011
Nothrus silvestris Nicolet, 1855	Nothridae	secondary	Maraun2011
Scheloribates initialis (Berlese, 1908)	Scheloribatidae	secondary	Schneider2004
Scheloribates ascendens Weigmann,Wunderle, 1990	Scheloribatidae	secondary	Bluhm2015
Liebstadia longior (Berlese, 1908)	Scheloribatidae	secondary	Fischer2010
Nanhermannia elegantula Berlese, 1913	Nanhermanniidae	secondary	Schneider2004
Nanhermannia cf.coronata Berlese, 1913	Nanhermanniidae	secondary	Schneider2004
Nanhermannia nana (Nicolet, 1855)	Nanhermanniidae	secondary	Schneider2004
Adoristes ovatus (C.L.Koch, 1839)	Liacaridae	secondary	Lu2021
Chamobates borealis (Traegardh, 1902)	Chamobatidae	secondary	Bluhm2015
Chamobates voigtsi (Oudemans, 1902)	Chamobatidae	secondary	Maraun2011
Chamobates cuspidatus (Michael, 1884)	Chamobatidae	secondary	Maraun2011
Chamobates pusillus (Berlese, 1895)	Chamobatidae	secondary	Migelton2019
Eupelops torulosus (C.L.Koch, 1839)	Phenopelopidae	secondary	Maraun2011, only genus
Eupelops plicatus (C.L.Koch, 1835)	Phenopelopidae	secondary	Maraun2011, only genus
Eupelops hirtus (Berlese, 1916)	Phenopelopidae	secondary	Maraun2011, only genus
Carabodes rugosior Berlese, 1916	Carabodidae	secondary	expertguess
Oribatula tibialis (Nicolet, 1855)	Oribatulidae	secondary	Schneider2004
Ophidiotrichus tectus (Michael, 1884)	Oribatellidae	secondary	Magilton2019
Oribatella quadricornuta Michael, 1880	Oribatellidae	secondary	Lu2021
Eniochthonius minutissimus (Berlese, 1903)	Eniochthoniidae	secondary	Schneider2004
Porobelba spinosa (Sellnick, 1920)	Damaeidae	secondary	Maraun2011, Unkownsupp
Damaeobelba minutissima (Sellnick, 1920)	Damaeidae	secondary	Maraun2011, infer from family
Damaeus onustus C.L.Koch, 1844	Damaeidae	secondary	Bluhm2015
Damaeus riparius Nicolet, 1855	Damaeidae	secondary	Maraun2011
Spatiodamaeus verticillipes (Nicolet, 1855)	Damaeidae	secondary	Maraun2011, infer from family
Cultroribula bicultrata (Berlese, 1905)	Astegistidae	secondary	expertguess
Steganacarus striculus (C.L.Koch, 1835)	Phthiracaridae	endophagous	Schneider2004
Steganacarus spinosus (Sellnick, 1920)	Phthiracaridae	endophagous	Schneider2004
Phthiracarus spp Perty, 1841	Phthiracaridae	endophagous	Maraun2011, Magiltong2019
Rhysotritia duplicata (Grandjean, 1953)	Euphthiracaridae	endophagous	Schneider2004
Microtritia minima (Berlese, 1904)	Euphthiracaridae	endophagous	Lu2021
Steganacarus magnus (Nicolet, 1855)	Phthiracaridae	endophagous	Maraun2011, Pollierer2009
Liacarus xylariae (Schrandk, 1803)	Liacaridae	endophagous	Maraun2011, Schneider2004
Liacarus coracinus (C.L.Koch, 1841)	Liacaridae	endophagous	Bluhm2015, Schneider2004
Carabodes ornatus Storkan, 1925	Carabodidae	endophagous	Lu2021
Hypochthonius rufulus C.L.Koch, 1835	Hypochthoniidae	predator	Maraun2011
Metabelba pulverosa Strenzke, 1953	Damaeidae	predator	Lu2021
Oppiella subpectinata (Oudemans, 1900)	Oppiidae	predator	Maraun2011
Oppiella marginedenta (Strenzke, 1951)	Oppiidae	predator	Maraun2011
Oppiella nova (Oudemans, 1902)	Oppiidae	predator	Maraun2011
Oppiella translamella (Oudemans, 1900)	Oppiidae	predator	Maraun2011
Oppiella falcata (Paoli, 1908)	Oppiidae	predator	Maraun2011
Dissorhina ornata (Oudemans, 1900)	Oppiidae	predator	Maraun2011
Berniniella conjuncta (Strenzke, 1951)	Oppiidae	predator	Maraun2011
Berniniella bicarinata (Paoli, 1908)	Oppiidae	predator	Maraun2011
Microppia minus (Paoli, 1908)	Oppiidae	predator	Maraun2011
Berniniella sigma (Strenzke, 1951)	Oppiidae	predator	Maraun2011
Suctobelbella spp Jacot, 1937	Suctobelbidae	predator	Schneider2004
Suctobelba atomaria Moritz, 1970	Suctobelbidae	predator	Schneider2004
Suctobelba trigona (Michael, 1888)	Suctobelbidae	predator	Schneider2004
Suctobelba reticulata Moritz, 1970	Suctobelbidae	predator	Schneider2004
Suctobelba altvateri Moritz, 1970	Suctobelbidae	predator	Schneider2004
Quadroppia monstruosa Hammer, 1979	Quadroppiidae	predator	Magilton2019
Quadroppia hammerae Minguez,Ruiz,Subias, 1985	Quadroppiidae	predator	Magilton2019
Quadroppia quadricarinata (Michael, 1885)	Quadroppiidae	predator	Magilton2019

Table B.3: F- and P-values of linear mixed-effect models on the effects of forest type (European beech, Douglas fir, Norway spruce and two conifer- beech mixtures), site condition (nutrient-rich and nutrient-poor sites) on species richness, Shannon diversity and abundance of Collembola and Oribatida. Significant effects are given in bold ($p \leq 0.05$).

	Species richness			Shannon diversity			Abundance		
Factor	df	F	P	df	F	P	df	F	P
Collembola									
Forest type (F)	*4,24*	0.628	0.647	*4,24*	1.394	0.266	*4,24*	2.576	0.063
Site condition (S)	*1,6*	9.747	0.021	*1,6*	3.186	0.125	*1,6*	5.901	0.051
F x S	*4,24*	0.141	0.965	*4,24*	0.478	0.752	*4,24*	0.287	0.883
Oribatida									
Forest type (F)	*4,24*	1.147	0.358	*4,24*	0.687	0.608	*4,24*	1.225	0.327
Site condition (S)	*1,6*	3.370	0.116	*1,6*	5.183	0.063	*1,6*	0.283	0.614
F x S	*4,24*	0.936	0.460	*4,24*	0.472	0.756	*4,24*	0.485	0.746

Table B.4: F- and P-values of linear mixed-effect models on the effects of forest type (European beech, Douglas fir, Norway spruce and two conifer- beech mixtures), site condition (nutrient-rich and nutrient-poor sites) and guilds (epedaphic, hemiedaphic and euedaphic in Collembola; primary, secondary decomposer and predator in Oribatida) on guild-specific species richness, Shannon diversity and abundance of Collembola and Oribatida. Significant effects are given in bold ($p \leq 0.05$).

	Species richness			Shannon diversity			Abundance		
Factor	df	F	P	df	F	P	df	F	P
Collembola									
Forest type (F)	*4,24*	0.628	0.647	*4,24*	1.039	0.408	*4,24*	2.945	**0.041**
Site condition (S)	*1,6*	9.747	**0.021**	*1,6*	5.825	0.052	*1,6*	7.785	**0.032**
Guild (G)	*2,60*	3.067	0.054	*3,90*	83.869	**0.000**	*2,60*	39.625	**0.000**
F x S	*4,24*	0.141	0.965	*4,24*	0.210	0.930	*4,24*	0.616	0.655
F x G	*8,60*	1.862	0.083	*12,90*	1.886	**0.046**	*8,60*	2.023	0.059
S x G	*2,60*	1.701	0.191	*3,90*	2.151	0.099	*2,60*	0.019	0.981
F x S x G	*8,60*	0.429	0.899	*12,90*	0.609	0.829	*8,60*	0.163	0.995
Oribatida									
Forest type (F)	*4,24*	1.111	0.374	*4,24*	0.595	0.670	*4,24*	1.655	0.193
Site condition (S)	*1,6*	3.089	0.129	*1,6*	5.428	0.059	*1,6*	0.400	0.550
Guild (G)	*2,60*	43.326	**0.000**	*3,90*	105.480	**0.000**	*2,60*	28.061	**0.000**
F x S	*4,24*	0.850	0.508	*4,24*	0.824	0.523	*4,24*	0.924	0.466
F x G	*8,60*	0.907	0.517	*12,90*	0.829	0.621	*8,60*	2.556	**0.018**
S x G	*2,60*	4.034	**0.023**	*3,90*	2.455	0.068	*2,60*	1.067	0.351
F x S x G	*8,60*	0.828	0.581	*12,90*	0.917	0.534	*8,60*	0.812	0.595

Table B.5: Contrasts of animal abundance in Douglas fir (Do), mixture of Douglas fir and European beech (Do/Be), Norway spruce (Sp), and mixture of Norway spruce and European beech (Sp/Be) compared to European beech (Be) forests. Response variables are guild-specific abundance of Collembola and Oribatida. Significant p-values are given in bold ($p \leq 0.05$).

contrast	guild	estimate	SE	asymp.LCL	asymp.UCL	z.ratio	p.value
Collembola							
Do - Be	euedaphic	-0.939	0.404	-1.731	-0.147	-2.324	**0.02**
Do/Be - Be	euedaphic	0.327	0.390	-0.438	1.091	0.837	0.402
Sp/Be - Be	euedaphic	0.072	0.376	-0.664	0.808	0.192	0.848
Sp - Be	euedaphic	0.643	0.368	-0.077	1.364	1.750	0.08
Do - Be	hemiedaphic	0.628	0.363	-0.083	1.339	1.730	0.084
Do/Be - Be	hemiedaphic	-0.066	0.370	-0.790	0.659	-0.177	0.859
Sp/Be - Be	hemiedaphic	-0.272	0.370	-0.997	0.454	-0.734	0.463
Sp - Be	hemiedaphic	1.101	0.358	0.400	1.803	3.079	**0.002**
Do - Be	epedaphic	0.480	0.417	-0.338	1.298	1.150	0.25
Do/Be - Be	epedaphic	-0.238	0.433	-1.086	0.610	-0.550	0.582
Sp/Be - Be	epedaphic	-0.431	0.463	-1.338	0.476	-0.931	0.352
Sp - Be	epedaphic	0.263	0.419	-0.558	1.084	0.627	0.53
Oribatida							
Do - Be	predator	-0.863	0.395	-1.638	-0.088	-2.183	**0.029**
Do/Be - Be	predator	0.158	0.394	-0.614	0.929	0.400	0.689
Sp/Be - Be	predator	0.394	0.386	-0.362	1.151	1.021	0.307
Sp - Be	predator	0.015	0.384	-0.737	0.767	0.040	0.968
Do - Be	secondary	0.338	0.396	-0.437	1.113	0.854	0.393
Do/Be - Be	secondary	0.365	0.409	-0.437	1.166	0.891	0.373
Sp/Be - Be	secondary	0.680	0.401	-0.107	1.467	1.694	0.09
Sp - Be	secondary	0.684	0.395	-0.090	1.458	1.731	0.083
Do - Be	primary	1.183	0.456	0.290	2.077	2.595	**0.009**
Do/Be - Be	primary	1.206	0.461	0.301	2.110	2.613	**0.009**
Sp/Be - Be	primary	0.052	0.490	-0.909	1.013	0.106	0.915
Sp - Be	primary	1.875	0.451	0.991	2.759	4.158	**<0.001**

Table B.6: Forward selection of environmental variables in redundancy analyses (RDA). Significant variables were determined by adjusted R^2 and p values ($p \leq 0.05$; Monte Carlo permutations = 999). Summary table only shows top list of in total 25 variables. Details of the variables are: soil cation exchange capacity (CEC), carbon/nitrogen (C/N), litter mass, European beech proportion, soil Fe, total PLFA in litter (Litter total PLFA), Soil K, Gram^{-} bacteria in organic layer (Organic Gram^{-}), soil Mn, Gram^{+} bacteria in litter (Litter Gram^{+}), Norway spruce proportion, Douglas fir (Douglas) proportion, total PLFA in organic layer (Organic total PLFA).

Variable	R2.adj	df	AIC	F	P	Selection
Collembola						
+ Soil CEC	0.093	*1*	114.994	4.874	**0.001**	**Yes**
+ Soil C/N	0.131	*1*	114.227	2.647	**0.007**	**Yes**
+ Litter mass	0.159	*1*	113.859	2.191	**0.007**	**Yes**
+ Beech proportion	0.189	*1*	113.335	2.273	**0.002**	**Yes**
+ Soil Fe	0.204	*1*	113.437	1.646	0.052	
+ Litter total PLFA	0.217	*1*	113.6	1.543	0.083	
+ Soil K	0.227	*1*	113.844	1.428	0.129	
+ Organic Gram^{-}	0.233	*1*	114.272	1.234	0.244	
+ Soil Mn	0.245	*1*	114.313	1.494	0.102	
+ Litter Gram^{+}	0.255	*1*	114.436	1.381	0.153	
+ Litter carbon content	0.266	*1*	114.405	1.443	0.129	
+ Litter Cmic/C	0.273	*1*	114.595	1.236	0.237	
+ Spruce proportion	0.288	*1*	114.262	1.541	0.077	
+ Douglas proportion	0.300	*1*	114.009	1.427	0.138	
+ Organic total PLFA	0.307	*1*	113.962	1.239	0.252	
<All variables>	0.311	-	-	-	-	
Oribatida						
+ Soil CEC	0.037	*1*	158.15	2.466	**0.001**	**Yes**
+ Soil pH	0.062	*1*	158.057	1.985	**0.001**	**Yes**
+ Beech proportion	0.082	*1*	158.112	1.79	**0.001**	**Yes**
+ Soil Fe	0.102	*1*	158.141	1.762	**0.002**	**Yes**
+ Litter Gram^{-}	0.114	*1*	158.455	1.458	**0.024**	**Yes**
+ Douglas proportion	0.124	*1*	158.817	1.372	**0.05**	**Yes**
+ Litter mass	0.131	*1*	159.271	1.254	0.161	
+ Root C/N	0.137	*1*	159.681	1.249	0.145	
+ Litter total PLFA	0.142	*1*	160.163	1.151	0.249	
+ Organic Gram^{-}	0.147	*1*	160.572	1.166	0.248	
+ Soil carbon content	0.153	*1*	160.873	1.203	0.174	
+ Organic total PLFA	0.154	*1*	161.329	1.05	0.403	
+ Litter C/N	0.156	*1*	161.735	1.043	0.4	
+ Root carbon content	0.156	*1*	162.111	1.02	0.437	
<All variables>	0.161	-	-	-	-	

Appendix C

Supplementary materials for Chapter 4

High consistency of trophic niches in soil microarthropod species (Oribatida, Acari) across soil depth and forest type

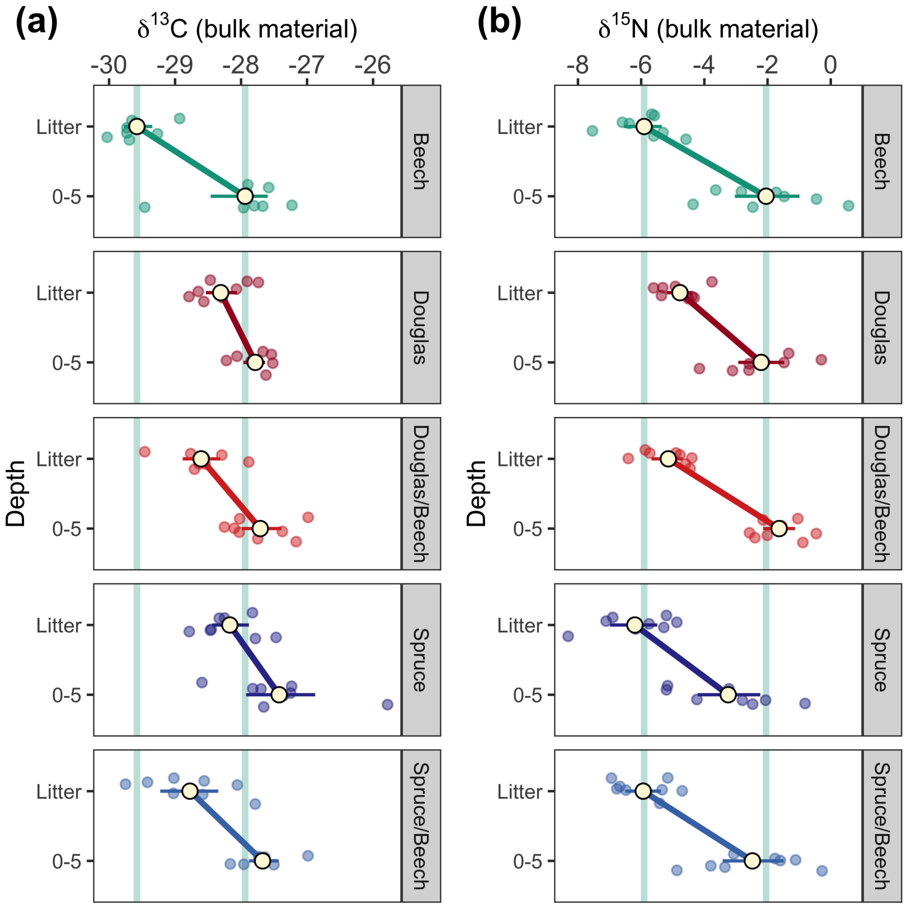

Figure C.1: Stable isotope values of δ^{13}C (a) and δ^{15}N (b) of bulk litter and 0–5 cm soil in European beech (Beech), Douglas fir (Douglas), Douglas fir/European beech (Douglas/Beech), Norway spruce (Spruce), Norway spruce/European beech (Spruce/Beech) forests. Horizontal bars are bootstrap estimated standard errors (n = 8). The green vertical bars represent respective values in beech forests in litter and 0–5 cm soil.

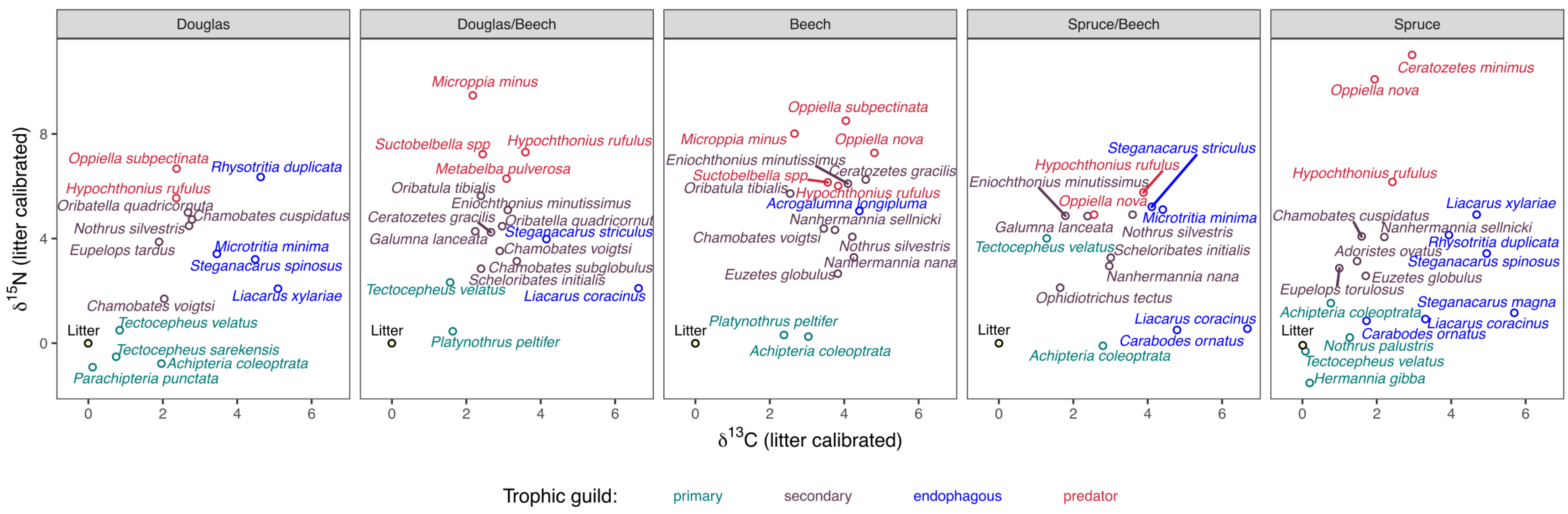

Figure C.2: Average of litter calibrated δ^{13}C and δ^{15}N values of Oribatida species in each of the forest type [Douglas fir (Douglas), mixture of Douglas fir/European beech (Douglas/Beech), European beech (Beech), mixture of Norway spruce/European beech (Spruce/Beech), Norway spruce (Spruce)]. Colors code for trophic guilds: primary decomposer (green), secondary decomposer (brown), endophagous (blue) and predatory species (red).

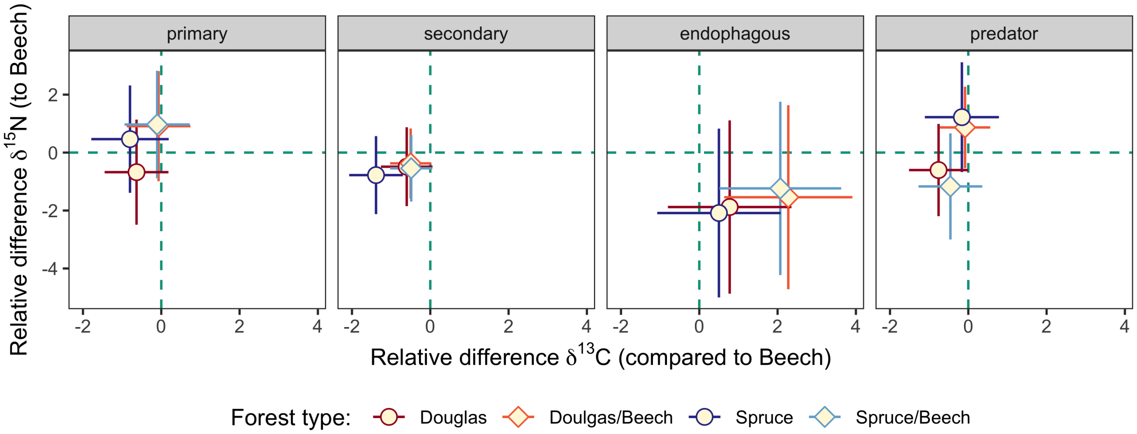

Figure C.3: Difference in δ^{13}C and δ^{15}N values of Oribatida guilds (primary decomposer, secondary decomposer, endophagous and predatory) in comparison to European-beech forests (Beech, dash line in green); Forest types include Douglas fir (Douglas, red), Norway spruce (Spruce, blue), Douglas fir and European beech mixture (Spruce/Beech, light-red) and Norway spruce/European beech mixture (Spruce, light-blue); means and 95% confidence intervals.

Table C.1: Species list Oribatida (n = 40). Trophic guilds were assigned according to litter calibrated δ^{13}C and δ^{15}N values: primary decomposer, secondary decomposer, endophagous Oribatida and scavenger/predator. Total number of animals for each species used for stable isotopes and their ranges (min - max) are given.

Oribatid taxa	Family	Trophic guilds	Total number (range)
Suctobelbella spp Jacot, 1937	Suctobelbidae	predator	22 (18-26)
Oppiella subpectinata (Oudemans, 1900)	Oppiidae	predator	9 (3-16)
Oppiella nova (Oudemans, 1902)	Oppiidae	predator	14 (8-17)
Microppia minus (Paoli, 1908)	Oppiidae	predator	19 (7-25)
Metabelba pulverosa Strenzke, 1953	Damaeidae	predator	3 (3-3)
Hypochthonius rufulus C.L.Koch, 1835	Hypochthoniidae	predator	4 (2-7)
Ceratozetes minimus Sellnick, 1928	Ceratozetidae	predator	10 (10-10)
Steganacarus striculus (C.L.Koch, 1835)	Phthiracaridae	endophagous	4 (3-5)
Steganacarus spinosus (Sellnick, 1920)	Phthiracaridae	endophagous	4 (1-8)
Steganacarus magnus (Nicolet, 1855)	Phthiracaridae	endophagous	1 (1-1)
Rhysotritia duplicata (Grandjean, 1953)	Euphthiracaridae	endophagous	8 (8-9)
Microtritia minima (Berlese, 1904)	Euphthiracaridae	endophagous	12 (10-15)
Liacarus xylariae (Schrandk, 1803)	Liacaridae	endophagous	2 (1-2)
Liacarus coracinus (C.L.Koch, 1841)	Liacaridae	endophagous	1 (1-2)
Carabodes ornatus Storkan, 1925	Carabodidae	endophagous	2 (1-3)
Acrogalumna longipluma (Berlese, 1904)	Galumnidae	endophagous	4 (3-5)
Scheloribates initialis (Berlese, 1908)	Scheloribatidae	secondary	4 (3-6)
Oribatula tibialis (Nicolet, 1855)	Oribatulidae	secondary	3 (1-5)
Oribatella quadricornuta Michael, 1880	Oribatellidae	secondary	2 (2-3)
Ophidiotrichus tectus (Michael, 1884)	Oribatellidae	secondary	6 (4-8)
Nothrus silvestris Nicolet, 1855	Nothridae	secondary	3 (1-5)
Nanhermannia cf.coronata Berlese, 1913	Nanhermanniidae	secondary	8 (2-14)
Nanhermannia nana (Nicolet, 1855)	Nanhermanniidae	secondary	3 (3-3)
Galumna lanceata (Oudemans, 1900)	Galumnidae	secondary	2 (1-2)
Euzetes globulus (Nicolet, 1855)	Euzetidae	secondary	1 (1-1)
Eupelops torulosus (C.L.Koch, 1839)	Phenopelopidae	secondary	1 (1-1)
Eupelops tardus (C.L.Koch, 1835)	Phenopelopidae	secondary	1 (1-1)
Eniochthonius minutissimus (Berlese, 1903)	Eniochthoniidae	secondary	8 (2-16)
Chamobates voigtsi (Oudemans, 1902)	Chamobatidae	secondary	6 (2-9)
Chamobates subglobulus (Oudemans, 1900)	Chamobatidae	secondary	1 (1-1)
Chamobates cuspidatus (Michael, 1884)	Chamobatidae	secondary	4 (2-7)
Ceratozetes gracilis (Michael, 1884)	Ceratozetidae	secondary	8 (6-10)
Adoristes ovatus (C.L.Koch, 1839)	Liacaridae	secondary	1 (1-1)
Tectocepheus velatus (Michael, 1880)	Tectocepheidae	primary	11 (5-19)
Tectocepheus sarekensis Traegardh, 1910	Tectocepheidae	primary	15 (15-15)
Platynothrus peltifer (C.L.Koch, 1839)	Camissidae	primary	2 (1-2)
Parachipteria punctata (Nicolet, 1855)	Achipteriidae	primary	2 (2-2)
Nothrus palustris C.L.Koch, 1839	Nothridae	primary	1 (1-1)
Hermannia gibba (C.L.Koch, 1839)	Hermanniidae	primary	2 (2-2)
Achipteria coleoptrata (Linne, 1758)	Achipteriidae	primary	6 (1-10)

Table C.2: Cross tabulation summarizing the study design. Frequency of trophic guilds (primary decomposer, secondary decomposer, endophagous and predator Oribatida) in each of the forest type [Douglas fir (Douglas), Douglas fir/European beech (Douglas/Beech), European beech (Beech), Norway spruce/European beech (Spruce/Beech), Norway spruce (Spruce)].

	Douglas	Douglas/Beech	Beech	Spruce/Beech	Spruce
primary	12	6	6	4	8
secondary	12	18	18	20	12
endophagous	8	4	4	8	12
predator	8	10	8	6	6

Table C.3: Linear mixed-effects models on δ^{13}C and δ^{15}N values of bulk soil and litter (Type III anova). Fixed effects include Depth (litter and soil), Forest type (European beech, Douglas fir, Norway spruce and mixed forests of European beech and Douglas fir and European beech and Norway spruce), Site condition (nutrient-rich and nutrient-poor sites), and their interactions. Random effects included 40 plots. Satterthwaite's method was used to estimate denominator degrees of freedom (df). Significant P-values are in bold ($P \leq 0.05$).

Factor	df	SumSq	F	P
δ ^{13}C Bulk material				
Depth (D)	*2,60*	33.705	142.996	**0.000**
Forest type (F)	*4,30*	1.834	3.891	**0.012**
Site condition (S)	*1,30*	0.379	3.218	0.083
D x F	*8,60*	4.604	4.883	**0.000**
D x S	*2,60*	5.701	24.189	**0.000**
F x S	*4,30*	0.152	0.323	0.861
D x F x S	*8,60*	1.254	1.330	0.246
δ ^{15}N Bulk material				
Depth (D)	*2,60*	735.873	762.106	**0.000**
Forest type (F)	*4,30*	4.902	2.538	0.060
Site condition (S)	*1,30*	25.685	53.201	**0.000**
D x F	*8,60*	13.700	3.547	**0.002**
D x S	*2,60*	3.589	3.717	**0.030**
F x S	*4,30*	1.280	0.663	0.623
D x F x S	*8,60*	2.079	0.538	0.823

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Thesis declarations

Declaration of the author's own contribution to manuscripts with multiple authors

Chapters 2 comprises a manuscript that has been published in a peer-reviewed journal; Chapter 3 and 4 comprise manuscripts that are currently in preparation to peer reviewed journals. In all manuscripts, I am the first author (Jing-Zhong Lu); I have collected and analyzed the data, written the manuscripts, developed the main ideas, created tables, figures and appendices and contributed significantly to the study design. All co-authors contributed to interpretation and finalizing the manuscripts.

Plagiarism declaration

I declare that I have written this doctoral dissertation independently. All persons contributing to the manuscripts have been named so. All sentences or passages quoted from other people's work have been specifically acknowledged by clear cross-referencing. I have not submitted this dissertation in any form for another degree at any university or institution. I bindingly confirm that the contents of the digital version are identical with the written version.

Jingzhong Lu
Göttingen, June 2021