Impacts of leaf litter diversity and root resources on microorganisms and microarthropods (Acari, Collembola) during early stages of decomposition in tropical montane rainforest ecosystems

Dissertation

zur Erlangung des mathematisch-naturwissenschaftlichen Doktorgrades

"Doctor rerum naturalium"

der Georg-August-Universität Göttingen

im Promotionsprogramm Biologie

der Georg-August University School of Science (GAUSS)

vorgelegt von

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Göttingen, 22 December 2020

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Tag der mündlichen Prüfung: 18 Februar 2021

“Look deep into nature and then you will understand everything better”

Albert Einstein

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Summary

Soil organisms influence organic matter turnover and nutrient cycling via processing of organic matter entering the soil as litter and root-derived resources. Plant species differ enormously in the quality and quantity of litter and roots that they produce, and this diversity strongly modifies decomposition of litter by decomposer organisms. Higher plant diversity is generally assumed to improve habitat conditions and availability of resources, thereby improving the abundance and activity of decomposer organisms. Tropical Andean montane rainforest ecosystems harbor an exceptional diversity of plant and animal species. However, little is known on how the huge diversity of plants and root resources affect the activity of soil communities and the overall decomposition rates, particularly during early stages of decomposition. This thesis aims to contribute to our understanding of the effects of leaf litter diversity and root resources on microorganisms and decomposer microarthropods during the early stages of litter decomposition in Andean tropical montane rainforest ecosystems. The studies were performed as field experiments at 2000 m (Chapter 2 and 4) and along an altitudinal gradient from 1000 to 2000 to 3000 m (Chapter 3) in a tropical montane rainforest in Southern Ecuador.

Chapter 2 investigates the effect of leaf litter diversity and identity on microbial functions and microarthropod abundance. The results suggest that decomposition and microbial parameters in litter vary with litter diversity as well as litter identity, while microarthropods respond only to litter identity. The results show that higher levels of diversity detrimentally affect soil microbial biomass and result in a decline in litter decomposition. Further, the results indicate that the differential response of soil biota was mostly due to differences in the initial chemical composition of litter species. However, the results also highlight the importance of leaf litter physical traits, particularly on the abundance of decomposer invertebrates. Overall, the results indicate that litter species identity functions as major driver of the abundance and activity of soil organisms and thereby exerts distinct effects on ecosystem processes such as decomposition and nutrient mobilization.

Chapter 3 investigates the contribution of soil microbes and decomposer microarthropods to the decomposition of leaf and root litter along an altitudinal gradient of the studied

tropical rainforests. The results suggest that the decomposition of both leaf and root litter in montane rainforests is mainly due to microorganisms, whereas the effect of microarthropods is minor along the altitudinal gradient. However, at higher altitudes soil microarthropods accelerate the decomposition of low-quality litter, such as root litter. Further, the study suggests that the abundance of microorganisms as food is of minor importance in structuring decomposer microarthropod communities, underscoring the role of litter quality. Overall, our findings highlight that resource quality or local interspecific variation in litter quality has stronger effects on decomposer organisms regardless climatic variations associated to altitude, at least during early stages of decomposition.

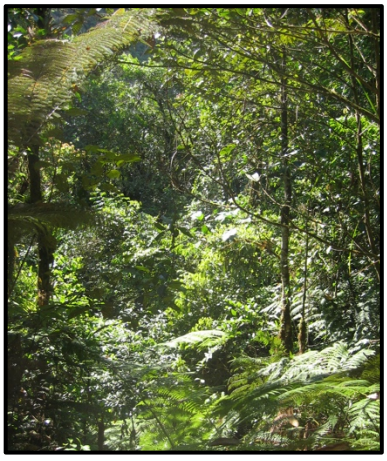
Chapter 4 investigates the response of arbuscular mycorrhizal (AM) fungi, microorganisms and microarthropods to the rotation of hyphal-ingrowth cores, defaunation and nitrogen addition. The results suggest that in the study site AM fungi are closely associated with living roots and do not form extensive extraradical hyphae that can be cut by rotation of the cores. Nonetheless, the results suggest that on top of the litter layer, AM fungi likely compete with saprotrophic microorganisms for litter-derived resources, with mycorrhizal fungi suppressing the activity of saprotrophic microorganisms. While in the soil layer interactions of mycorrhizal fungi with other soil biota are restricted to the close vicinity of roots. Nitrogen addition increased the quality of litter material produced by plants and beneficially affected microbial activity, highlighting that decomposition processes in the studied montane rainforests are strongly limited by nutrient availability and microorganisms in these forests even respond to moderate increase in nitrogen. The results also document a restricted recovery of microorganisms and microarthropods after defaunation of the rotated cores, highlighting the importance of root-derived resources for fueling soil food webs.

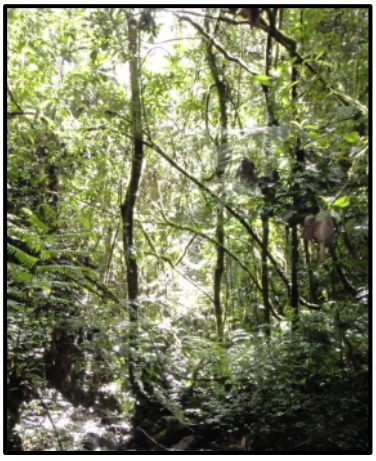
Chapter 5 presents a discussion and conclusions on the contribution of the research chapters to the overall state of knowledge. Generally, the results of this thesis suggest that during early stages of decomposition the abundance, diversity and activity of soil organisms are strongly associated with the quality and availability of the litter resources. Overall, the results suggest that decomposition processes in montane rainforests at early stages are mainly driven by microorganisms, whereas the contribution of microarthropods is of minor

importance. Further, the results also highlight the importance of root-derived resources for fueling soil microarthropod abundance during early stages of decomposition. In addition, the results point to AM fungi as an important player for determining the abundance and activity of microbial communities during early stages of decomposition in tropical montane rainforests.

Chapter 1

General introduction





Plant litter decomposition

Plant litter decomposition is an essential carbon-transforming process that drives nutrient cycling in terrestrial ecosystems (Swift et al. 1979; Bardgett 2005). The breakdown of plant litter material by soil organisms releases nutrients to the soil that are important for plant growth. Simultaneously, this process emits greenhouse gases such as carbon dioxide (CO_2) to the atmosphere fueling net primary production (Swift et al. 1979; Aerts 1997; Berg and McClaugherty 2008; Krishna and Mohan 2017). Decomposition of plant-litter substrates can be divided into two main stages: (1) the early stage characterized by the loss of ca. 40% of the litter mass, mostly by the decomposition of labile C compounds and leaching of water-soluble nutrients, and (2) the late stage in which the remaining mass, mostly recalcitrant material, like lignin, is degraded (Coûteaux et al. 1995; Berg and McClaugherty 2008; Djukic et al. 2018). Changes in the litter substrates during both stages supply different sets of intermediate degradation products that serve as energy and nutrient sources for different populations of soil organisms (Berg and McClaugherty 2008).

Climate, plant-litter quality and decomposer organisms are generally recognized as the main drivers of decomposition rates (Swift et al. 1979; Coûteaux et al. 1995; Aerts 1997). Climate is commonly considered the primary driver of decomposition rates at global scales because factors such as temperature or precipitation can directly alter the sensitivity of soil biological processes and consequently plant-litter quality and soil biota (Wardle et al. 2004; Kutsch et al. 2010; García-Palacios et al. 2013). Plant-litter quality is considered the main controlling factor of litter decomposition rates at the ecosystem level, even though recent studies suggest that litter quality can have stronger effects on decomposition than climate parameters at local to regional scales (Cornwell et al. 2008; Zhang et al. 2008; Fujii et al. 2017). However, the role of decomposer fauna in relation to climate and litter traits is still poorly understood. Therefore, elucidating the role of soil fauna in litter decomposition is necessary for a better understanding of decomposition process in terrestrial ecosystems and is of great importance for predicting carbon dynamics under the future climate-change scenarios.

Litter diversity and decomposition

Most of the above-ground plant material produced returns to the soil in form of leaves and woody tissue, representing the major resource of energy and matter for soil organisms (Berg et al. 1993; Berg & McClaugherty 2008). On the forest floor, a variety of leaf litter species accumulate and decompose as mixture of leaf species. The diversity of leaf litter in mixtures affects decomposer organisms and thereby litter decomposition rates by modifying the physical and chemical characteristics of the litter layer (Gartner and Cardon 2004; Hättenschwiler et al. 2005; Gessner et al. 2010; Handa et al. 2014). Differences in the chemical composition of litter species offer a variety of food resources to detritivores and microorganisms fulfilling their nutritional demands, but also impacting litter decomposition, e.g. by affecting the transfer of nutrients via fungal hyphae (Hättenschwiler et al. 2005; Gessner et al. 2010). Additionally, physical leaf litter characteristics (e.g., toughness, surface structures and shape) that do not necessarily correlate with higher nutrient concentrations, can modify microenvironmental conditions and increase microhabitat diversity for soil animals and, therefore, indirectly affect litter decomposition (Hättenschwiler et al. 2005; Makkonen et al. 2012; Bani et al. 2018).

Considering that more diverse leaf litter mixtures increase habitat variability and thereby may enhance nutrient acquisition by soil organisms, higher diversity of litter is likely to result in faster decomposition rates by maintaining a more abundant and diverse fauna community (Handa et al. 2014; Trogisch et al. 2016). Nonetheless, the current literature shows inconsistent effects of higher leaf litter diversity on soil decomposer communities in different ecosystems (Gartner and Cardon 2004; Nadrowski et al. 2010; Handa et al. 2014). In fact, recent studies have shown that leaf species identity, which encompasses all specific litter chemical and physical characteristics of a single species, has a higher explanatory power for litter decomposition rates and appears to be a better predictor of the interaction effects among litter types and decomposer-driven processes than leaf litter species diversity (Hoorens et al. 2010; Makkonen et al. 2012; Cesarz et al. 2013; Korboulewsky et al. 2016). Thus, it remains controversial whether the positive effect of leaf litter mixtures on decomposition is due to the increase in species diversity or whether it is driven by the identity of the species present in mixtures.

Traditionally, most litter decomposition studies linking plant species diversity to decomposition have focused on leaf litter traits (Freschet et al. 2012). However, plant-specific litter traits that influence decomposition also vary between the resources provided, i.e. plant organs such as leaves, stems and roots (McLaren and Turkington 2010; Freschet et al. 2013). In fact, the input of root resources may be almost as high as that of leaf litter (Norby et al. 2004; Hobbie et al. 2010) and the different physical and biochemical traits modify not only the characteristics of the resulting soil organic matter, but could also change the structure of soil decomposer communities, and thereby decomposition rates.

Rhizodeposits and mycorrhizal fungi

Plant roots modify the physical and chemical characteristics of soil organic matter through rhizodeposition, i.e. the release of carbon compounds into the surrounding soil (Hütsch et al. 2002; Dennis et al. 2010). Rhizodeposits, which include root exudates (e.g., sugars, amino acids and organic acids), mucilage, border cells, dead fine roots and gases, modify nutrient availability in soil, thereby affecting the interaction between roots and soil organisms in the rhizosphere (Jones et al. 2004; Bais et al. 2006; Dennis et al. 2010). Particularly, root exudates and fine root litter sustain soil microbial communities at the root surface, where microbial biomass is significantly higher compared to the bulk soil (Bais et al. 2006; Jones et al. 2009; Dennis et al. 2010) providing ample resources for microarthropod communities (Pollierer et al. 2007; Zieger et al. 2017).

A large proportion of carbon released by plant roots is translocated into the soil by mycorrhizal fungi (Brundrett 1991; Hobbie 1992). Mycorrhizal fungi are ubiquitous soil organisms that form symbiotic associations in which the host plant receives mineral nutrients and the fungus obtains photosynthetically fixed carbon compounds (van der Heijden and Sanders 2002; Smith and Read 2008). Seven different categories of mycorrhizal symbiosis have been distinguished on the basis of morphological characteristics, and the fungal and plant species involved (Finlay 2008; Smith and Read 2008). However, the most abundant types of mycorrhizae are arbuscular mycorrhizal (AM), ectomycorrhizal (EM) and ericoid mycorrhizal fungi (ERM) (Brundrett 1991; Johnson and Gehring 2007).

AM symbiosis is the most widespread type of mycorrhizal association involving fungi from the Glomeromycota phylum associated with a wide range of plant species including grasses, herbs, crops and trees (Johnson and Gehring 2007; Finlay 2008). The symbiosis is characterized by the development of highly branched fungal structures within the cortical cell of the roots forming arbuscules or coils (Bever et al. 2001; Smith and Read 2008). EM is most abundant plant – fungal symbiosis in temperate and boreal forest ecosystems where fungi predominantly from the Basidiomycota and Ascomycota phylum form associations with shrubs and trees, especially conifers. In contrast to AM fungi, EM fungi do not penetrate their hosts cells but rather form a fungal mantle or a network of intercellular hyphae known as Hartig net that is connected to the epidermal and cortical cells and covers the entire host root (Brundrett 2002; Smith and Read 2008). ERM only form associations between various fungi from the Ascomycota phylum and plants belonging to the Ericales order. ERM typically grow in dwarf shrubs in acid and nutrient poor areas, mainly of the tundra regions (Brundrett 1991; Johnson and Gehring 2007) and are characterized by the formation of extensive hyphal coils within root cells during establishment (Perotto et al. 1995; Smith and Read 2008).

EM and ERM fungi are biotrophs with saprotrophic abilities able to take up simple carbon compounds and produce extracellular enzymes that decompose complex organic substrates (Read and Perez-Moreno 2003). By contrast, AM fungi are obligate biotrophs without saprotrophic capabilities (Smith and Read 2008). However, recent studies suggest that AM fungi contribute indirectly to decomposition of complex compounds by influencing the saprotrophic microbial community that decompose complex organic sources and release simple substances for AM hyphal capture (Hodge et al. 2001; Talbot et al. 2008; Nuccio et al. 2013; Leifheit et al. 2015). AM fungi also interact with a wide array of organisms, including bacteria, other fungi, protozoa, nematodes, arthropods and even large animals. These complex interactions among communities of mycorrhizal fungi and other soil organisms can mediate rhizosphere processes and thereby nutrient dynamics and decomposition processes (Fitter and Garbaye 1994; Gryndler 2000).

Decomposer microarthropods

Bacteria and fungi are considered the main drivers of soil organic matter breakdown. Nonetheless, feeding activities of the diverse community of soil-dwelling invertebrates also influence decomposition processes (Seastedt 1984; Bardgett 2005; Scheu et al. 2005). Soil microarthropods are a highly diverse and abundant component of invertebrates in soil of virtually any ecosystem (Bardgett 2005). Among soil microarthropods, mites (Acari) and springtails (Collembola) are the most abundant and diverse organisms (Seastedt 1984; Ruess and Lussenhop 2005). Acari and Collembola regulate organic matter turnover and nutrient cycling directly by litter fragmentation or indirectly via trophic interactions with fungal and bacterial communities (Swift et al. 1979; Seastedt 1984; Ruess and Lussenhop 2005). Although the two groups of decomposer microarthropods are considered to occupy similar niches and affect litter decomposition in similar ways, they comprise different trophic levels and differ in a variety of ecological traits (Siepel 1994; Scheu 2002; Schneider et al. 2004; Illig et al. 2005). Differences in the diversity and abundance of Acari and Collembola between ecosystems and their variation even within few centimeters of soil are still little understood, but are likely related to variations in biotic and abiotic factors, such as local climatic conditions and litter quality (Hättenschwiler et al. 2005; Wardle et al. 2006; Gergócs and Hufnagel 2016).

Oribatid mites (Oribatida) are the most species rich Acari subgroup with more than 11,000 described species in 163 families (Subías 2018). Oribatid mites are very common in soils rich in organic matter, reaching densities >100,000 individuals per square meter (Maraun and Scheu 2000; Dhooria 2016). Feeding behavior of oribatid mites is diverse and they can be divided into three different trophic groups: microphytophages (species that feed on plant litter material), macrophytophages (species that feed on fungi, pollen, algae, mosses and lichens) and panphytophages (non-specialized species) (Maraun et al. 2003; Dhooria 2016). However, oribatid mites are also known to switch feeding habits when the preferred food is scarce (Maraun et al. 2003; Schneider and Maraun 2005). Oribatid mites typically are characterized by low fecundity and long immature and adult life span (Norton 1994), and have developed strong defense mechanisms, such as protective structures, strong

sclerotization and defensive glands to be protected themselves from predators (Peschel et al. 2006).

Tropical Andean montane rainforest: the study sites

Tropical Andean montane rainforest ecosystems are considered one of the hotspots of biodiversity on earth and harbor a particularly high number of endemic vascular plant and animal species (Myers et al. 2000; Beck and Ritcher 2008; Homeier et al. 2008). The vast diversity of plants and animals in these ecosystems is favored by changes in abiotic conditions along the altitudinal gradient (Myers et al. 2000; Beck and Ritcher 2008). In spite of the huge diversity of plants and animals in these ecosystems, few studies investigated the effect of plant litter diversity and root resources on the composition and activity of soil communities and thereby their impacts on litter decomposition processes (Butenschoen et al. 2014; Krashevska et al. 2017; Marian et al. 2017). Previous work on decomposer microarthropods documented that the decomposer fauna in Andean rainforest ecosystems is dominated by small soil invertebrates, such as oribatid mites, collembolans and testate amoebae (Illig et al. 2005; Krashevska et al. 2007; Maraun et al. 2008), and consequently, these groups may play an important role in litter decomposition processes. Litter decomposition rates in tropical montane rainforests are reported to be slower than in lowland tropical rainforests (Heneghan et al. 1998) with the early phase lasting for about 12 months (Marian et al. 2017). One of the reasons for slow decomposition rates may be the general low quality of the litter material. The food quality may limit the abundance and activity of soil decomposer, particularly at higher elevations (Illig et al. 2008; Scheu et al. 2008; Marian et al. 2017).

In Andean topical montane ecosystems roots of plants are in intimate association with litter and may grow towards and throughout litter (Aristizábal et al. 2004). The great majority of tree roots are colonized by AM fungi (Kottke et al. 2004; Camenzind and Rillig 2013) and form pronounced extra-radical mycelia growing even into decomposing litter material (Camenzind and Rillig 2013) stimulating plant nutrients uptake (Delavaux et al. 2017) and likely affecting decomposition by interacting with the microbial community. However, interactions between AM fungi and other organisms have been little studied in Andean

tropical ecosystems, but may be of significant importance for understanding the role of AM fungi in decomposition processes and nutrient cycling.

Studies presented in this thesis were conducted on the eastern slope of the tropical Andes in southern Ecuador within the northern fringes of the Podocarpus National Park. In this area, three study sites were located at 1000, 2000, and 3000 m a.s.l. representing an altitudinal gradient with moderately steep slopes of typically 26–31° (Moser et al. 2007). The lower site at 1000 m a.s.l. (S04°06′54′′, W78°58′02′′) is located in the Río Bombuscaro valley and is classified as evergreen submontane rainforest dominated by Arecaceae, Combretaceae, Moraceae, Monimiaceae, Rubiaceae and Sapotaceae (Homeier et al. 2008). The intermediate site at 2000 m a.s.l. (S3°58′18′′, W79°4′45′′) is part of the Reserva Biológica San Francisco located between the cities of Loja and Zamora on the north facing flank of the Río San Francisco valley, and consists of an evergreen lower montane rainforest, with Arecaceae, Clusiaceae, Ericaceae, Lauraceae, Melastomataceae and Rubiaceae being the most widespread tree families (Homeier et al. 2008). The highest site at 3000 m a.s.l. (S04°06′711′′, W79°10′58′′) is located in the south of the city of Loja close to the Cajanuma mountain at the northwest gate of the Podocarpus National Park. The site is characterized by evergreen elfin-forest with the vegetation largely dominated by shrubs and trees of the families Aquifoliaceae, Bromeliaceae, Chloranthaceae, Clusiaceae, Ericaceae and Melastomataceae (Homeier et al. 2008).

The study area has a semi-humid climate with an average annual temperature of 14.9 °C, 12.3 °C and 8.9 °C, and annual precipitation of approximately 2200, 3500 and 4500 mm at 1000, 2000 and 3000 m a.s.l., respectively (Bendix et al. 2006; Homeier et al. 2010). Soil types of the study sites are alumic Acrisol (1000 m), Gley Cambisol (2000 m) and Podzol (3000 m) (Soethe et al. 2006; Moser et al. 2007). The organic soil layer increases with elevation from 4.8 cm at 1000 m to 30.5 cm at 2000 m to 43.5 cm at 3000 m (Leuschner et al. 2007; Graefe et al. 2008). Fine roots are concentrated in organic layers (Wilcke et al. 2002) and its biomass increase in parallel with the soil organic layer from 2.7 t ha^{-1} at 1000 m to 6.2 t ha^{-1} at 2000 m to 10.8 t ha^{-1} at 3000 m (Soethe et al. 2006).

Objectives and hypotheses

This thesis aims to deepen our understanding of the role of leaf litter diversity and root resources on microorganisms and decomposer microarthropods during early stages of litter decomposition in tropical montane rainforest ecosystems.

The main hypotheses of this thesis are the following:

1. Higher leaf litter diversity results in faster decomposition rates, and an increase in the abundance and diversity of decomposer communities.

2. The abundance and diversity of the soil decomposer organisms is regulated by litter quality and differ between plant organs (leaf and fine root litter).

3. Decomposer microarthropods are similarly involved in the decomposition of leaf and root litter during early stages of decomposition in tropical montane rainforests.

4. Root-derived resources and carbon inputs via AM fungi increase the abundance, activity and diversity of soil microorganisms and microarthropods within the organic layer, indirectly altering litter decomposition rates. These effects vary with the nutrient status of the ecosystem being lower at higher nutrient availability.

The study presented in **Chapter 2** aims at quantifying the impact of leaf litter identity and diversity on the abundance and activity of microorganisms and decomposer microarthropods. I hypothesized microbial growth and activity to increase with litter diversity, but the abundance of decomposer microarthropods to rely more on litter identity than litter diversity. Further, I hypothesized that nutrient availability increases with time reducing microbial stress conditions. I also hypothesized that the abundance of decomposer microarthropods increases as decomposition proceeds. Lastly, I hypothesized that the presence of high-quality litter benefits microorganisms, as well as the abundance of decomposer microarthropods.

The study presented in **Chapter 3** investigates how microorganisms and soil decomposer microarthropods affect leaf and root decomposition along an altitudinal gradient of the tropical montane rainforests studied. The access of soil fauna to the litter was controlled by using litterbags of different mesh size. Due to less favorable abiotic conditions with increasing altitude. I hypothesized that the decomposition of litter, regardless of litter tissue, decreases with increasing altitude. I further hypothesized that limiting the access of litter by microarthropods accelerates decomposition by increasing microbial biomass and activity in both leaf and root litter, with the effect being stronger at higher altitudes where nutrients are more limited. Further, I hypothesized that the abundance of decomposer microarthropods and the diversity of oribatid mites is higher in leaf than in root litter irrespective of altitude, and increase with increasing microbial biomass. Lastly, I hypothesized that the role of litter quality in structuring oribatid mite communities declines with time, with the effect being less pronounced in root than in leaf litter.

The study presented in **Chapter 4** investigates the response of AM fungi, microorganisms and microarthropods to the rotation of hyphal-ingrowth cores, defaunation and nitrogen addition. I hypothesized that the colonization of the cores by AM fungi is reduced by regular rotation of the cores and that the reduction of mycorrhizal hyphae results in an increased activity of saprotrophic microorganisms, thereby accelerating decomposition processes. I further hypothesized that the increase in saprotrophic organisms, particularly fungi, in rotated cores benefit oribatid mites. In addition, I hypothesized that the addition of N reduces the concentration of AM fungi, but fosters the activity of saprotrophic microorganisms and thereby increases litter decomposition.

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Chapter 2

Leaf litter identity rather than litter diversity shapes microbial functions and microarthropod abundance in tropical montane rainforests

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Abstract

In tropical forest ecosystems leaf litter from a large variety of species enters the decomposer system, however, the impact of leaf litter diversity on the abundance and activity of soil organisms during decomposition is little known. We investigated the effect of leaf litter diversity and identity on microbial functions and the abundance of microarthropods in Ecuadorian tropical montane rainforests. We used litterbags filled with leaves of six native tree species (*Cecropia andina*, *Dictyocaryum lamarckianum*, *Myrcia pubescens*, *Cavendishia zamorensis*, *Graffenrieda emarginata* and *Clusia* spp.) and incubated monocultures and all possible two and four species combinations in the field for 6 and 12 months. Mass loss, microbial biomass, basal respiration, metabolic quotient and the slope of microbial growth after glucose addition, as well as the abundance of microarthropods (Acari and Collembola) were measured at both sampling dates. Leaf litter diversity significantly increased mass loss after 6 months of exposure, but reduced microbial biomass after 12 months of exposure. Leaf litter species identity significantly changed both microbial activity and microarthropod abundance with species of high quality (low C-to-N ratio), such as *C. andina*, improving resource quality as indicated by lower metabolic quotient and higher abundance of microarthropods. Nonetheless, species of low quality, such as *Clusia* spp., also increased the abundance of Oribatida suggesting that leaf litter chemical composition alone is insufficient to explain variation in the abundances of soil microarthropods. Overall, the results provide evidence that decomposition and microbial biomass in litter respond to leaf litter diversity as well as litter identity (chemical and physical characteristics), while microarthropods respond only to litter identity but not litter diversity.

Keywords: Acari; Collembola; decomposition; litterbags; litter quality; microorganisms; metabolic quotient.

Introduction

The great majority of plant material enters the soil as litter, in the form of leaves, stems and roots. Decomposition of these materials is an essential process for nutrient cycling and provides the basal resources of the soil food web (Berg et al. 1993; Berg and McClaugherty 2008). In addition to providing food resources, leaf litter accumulating on the soil surface forms a variety of microhabitats for soil organisms, with more diverse litter materials increasing habitat variability, but also providing the opportunity for enhanced nutrient acquisition (Bardgett 2005; Gessner et al. 2010). Therefore, high diversity of leaf litter in mixtures is expected to be an important determinant of the diversity and structure of decomposer communities and, consequently, litter decomposition (Hättenschwiler et al. 2005; Gessner et al. 2010; Trogisch et al. 2016).

Tropical montane rainforest ecosystems harbor an exceptional diversity of plant species (Myers et al. 2000; Beck and Ritcher 2008; Homeier et al. 2008) and are associated with high numbers of animal species above- and belowground (Brehm et al. 2008; Maraun et al. 2008; Paulsch and Müller-Hohenstein 2008). However, the effect of plant litter diversity on decomposer communities and decomposition of litter in this ecosystems is little studied (Illig et al. 2008; Krashevska et al. 2017). Controlled experiments are needed to assess the effect of diversity and composition of litter species in mixtures on litter decomposition and microarthropod abundance.

Differences in leaf-litter chemical composition are recognized as the main drivers of decomposition rates at the ecosystem level (Coûteaux et al. 1995; Hättenschwiler et al. 2005). Studies have reported positive, negative, but also no effects of litter mixtures on decomposition, with mixture effects typically related to variations in litter nutrient concentrations (Gartner and Cardon 2004; Makkonen et al. 2012; Handa et al. 2014). However, differences in litter chemistry are not the only factors contributing to variations in litter decomposition in mixtures (Hoorens et al. 2003; Hättenschwiler 2005). Physical leaf litter traits, such as toughness, surface structure and shape, also contribute to microhabitat diversity and modify micro-environmental conditions of decomposer organisms, resulting either in accelerated or decelerated litter decomposition (Hansen and Coleman 1998; Kaneko and Salamanca 1999). Therefore, species identity, which

encompasses chemical and physical characteristics, may well explain diversity effects on decomposition. Indeed, the effect of litter species identity has been found to be more powerful in explaining colonization of litter by invertebrates than litter diversity (Schädler and Brandl 2005; Wardle et al. 2006; Vos et al. 2011; Eissfeller et al. 2013; Korboulewsky et al. 2016).

Commonly, studies investigating effects of litter diversity on litter decomposition focused on microorganisms and detritivore invertebrates (Gessner et al. 2010). Microorganisms are assumed to respond more sensitively to litter diversity than invertebrates as they directly depend on the variety of litter chemical compounds needed for metabolism and growth (Bardgett and Shine 1999; Chapman et al. 2013). By contrast, the response of invertebrate detritivores, particularly the key decomposer groups Acari and Collembola, more strongly depends on the identity rather than diversity of leaf litter species and varies with the stage of litter decomposition (Kaneko and Salamanca 1999; González and Seastedt 2001; Wardle et al. 2006; Illig et al. 2008; Korboulewsky et al. 2016). Indeed, many decomposer microarthropods have the ability to select among co-occurring leaf litter species according to litter palatability and/or the microorganisms colonizing the litter (Klironomos et al. 1992; Schneider and Maraun 2005; Korboulewsky et al. 2016). Studies linking microbial-dominated litter decomposition processes and colonization of litter by detritivore invertebrates are needed to uncover the mechanisms responsible for litter diversity effects on the structure and functioning of the decomposer system, particularly in tropical ecosystems characterized by high diversity of plant (tree) species.

In the present study, we investigated the effect of leaf litter diversity and identity on the colonization of litter by microorganisms and microarthropods including Acari and Collembola after 6 and 12 months of incubation in Ecuadorian montane rainforests. We hypothesized that (1) microbial growth and activity increase with litter diversity, but that the abundance of both Acari and Collembola relies more on litter identity. Additionally, assuming that microorganisms are limited by multiple nutrients (Demoling et al. 2007; Krashevska et al. 2010), we hypothesized that (2) nutrient availability increases and microbial stress conditions decrease with time, and that (3) the presence of high-quality litter benefits microorganisms. Further, assuming that Acari and Collembola prefer similar food resources and consume both leaf litter tissue and microorganisms (Seastedt 1984;

Ruess and Lussenhop 2005; Dhooria 2016), we hypothesized that (4) the abundance of Acari and Collembola increases as decomposition proceeds, particularly in presence of high-quality litter.

Materials and methods

Study site

The study area is located in southern Ecuador on the eastern slopes of the Andean Cordillera. The site forms part of the Reserva Biológia San Francisco located on the northern borders of the Podocarpus National Park at 2000 m a.s.l. (3°58′S, 79°04′W). The region is characterized by a semi-humid climate with annual precipitation of about 2200 mm and average annual temperature of 15.2°C (Bendix et al. 2006; Wullaert et al. 2009). The soil is Gley Cambisol with a soil pH of ~3.5 and a thick organic layer up to 35 cm comprised of mainly fermentation/humus material overlaid by litter material (Moser et al. 2007). The tropical rainforest is mostly undisturbed and holds an exceptionally high diversity of fauna and flora with *Rubiaceae, Melastomataceae* and *Piperaceae* as dominant plant families (Brehm and Fiedler 2005; Beck and Ritcher 2008; Maraun et al. 2008; Homeier et al. 2010)

Experimental design

In September 2008, freshly fallen leaves of six common plant species at the study sites [*Cecropia andina* (Cuatrec.) (CA), *Dictyocaryum lamarckianum* (H. Wendl.) (DL), *Myrcia pubescens* (Humb. & Bonpl. ex Willd.) (MP), *Cavendishia zamorensis* (A. C. Sm.) (CZ), *Graffenrieda emarginata* (Ruiz & Pav.) (GE) and *Clusia* spp. (L.) (Cs); ordered by increasing C-to-N ratio, see Appendix 1], were collected, dried (60°C for 72 h) and used to fill 20 × 20 cm and 4 mm nylon mesh litterbags. Initial chemical composition of the litter species is given in Appendix 1. The leaves used had no signs of herbivory, fungal infection or atypical texture or color. Large leaves exceeding the size of the litter bags, were cut into ~5 x 5 cm pieces. Single-species litterbags (12 g each) and mixtures with all possible two- (6 g per species) and four-species combinations (3 g per species) were prepared, resulting in a total of 36 litterbag types with three levels of species diversity (1, 2, and 4 leaf litter

species). Litterbags were randomly placed in the field on top of the undisturbed litter layer and fixed with nails in four blocks. Minimum distance between the blocks was 20 m. One replicate of each treatment was harvested after 6 and 12 months.

Analytical procedures

After harvest, material in each litterbag was separated into two subsamples of equal weight, disturbing the fauna as little as possible but ensuring that all litter types were present in both halves. One half was used for microarthropod extraction and the other for analysis of microbial parameters. Microarthropods were extracted by heat over one week using a modified high gradient extractor and then stored in 70% ethanol (Macfadyen 1961; Kempson et al. 1963). Microarthropods were determined to group level [Collembola (Insecta), Oribatida, Mesostigmata and Prostigmata (Acari)] using Schaefer (2018). The dry litter was sorted to species, weighed and used to measure litter chemical composition.

Microbial basal respiration (BR) and microbial biomass (C_{mic}) were determined using an automated respirometer system (Scheu 1992). BR (µl O_2 g^{-1} dry weight h^{-1}) was measured at 22 ºC and calculated as mean of O_2 consumption rates 10 to 20 h after attachment of the samples to the respirometer system. C_{mic} was measured by the substrate-induced respiration method (SIR; Anderson and Domsch, 1978; Beck et al., 1997). The maximum initial respiratory response (MIRR; µl O_2 g^{-1} dry weight h^{-1}) was measured at 22 ºC after the addition of glucose to saturate the catabolic activity of microorganisms. MIRR was calculated as the average of the lowest three readings within the first 10 h and C_{mic} was calculated as C_{mic} = 38 × MIRR (mg g^{-1} dry weight). Respiration rates between the lowest (usually 3–6 h after glucose addition) and highest reading were taken to calculate the slope of microbial growth ($+C_{Slope}$). Data were ln-transformed and the slope determined by linear regression. The microbial metabolic quotient (qO_2; µl O_2 mg^{-1} C_{mic} h^{-1}) was calculated by dividing BR by C_{mic}.

Leaf litter mass loss (M_{loss}) was calculated as M_{loss} (%) $= ((m_0 - m_1/m_0)) \times 100$, where m_0 is the initial dry weight and m_1 the dry weight of leaf litter at harvest. To measure chemical composition, leaves from each of the six species were dried (65 °C for 72 h) and milled to particles <1 mm. Carbon (C) and nitrogen (N) were measured using a CN

elemental analyzer (Vario EL III, Elementar, Hanau, Germany). Total element analysis was measured by an ICP-OES system (ICP-OES, Optima 5300 DV, Perkin Elmer, USA). Lignin and cellulose concentration were measured based on the methanol-chloroform-water (2:2:1) extraction method detailed in Allen et al. (1974). For litter mixtures, the proportion of elements per litterbag was calculated by proportionally summing the amount of the respective elements in the individual litter species. The chemical concentrations of elements, lignin and cellulose was expressed as milligram per gram litter dry weight (dw).

Statistical analyses

Analyses were performed using R version 3.6.0 (R Core Team 2014). Data was checked for normality and homoscedasticity using Shapiro–Wilk test and Bartlett's test (package "stats"). To improve normality and homoscedasticity, data were transformed using the "bestNormalize" function (package "CRAN"). Changes in M_{loss}, C_{mic}, BR, qO_2, $+C_{Slope}$ and the abundance of microarthropod taxa (Collembola, Oribatida, Mesostigmata and Prostigmata) were analyzed using individual linear mixed-effects models (package "nlme"). In each model the fixed factors litter diversity (LD; 1, 2 and 4 litter species), time of exposure (6 and 12 months) and the presence/absence all leaf litter species (litter identity; 1,0; CA, DL, MP, CZ, GE and Cs), as well as the interactions (time × LD and time × litter identity) were fitted in a hierarchical design. Block was fitted first as random factor followed by the fixed factors litter diversity, time, interaction between litter diversity and time, and litter identity. To assess the relative importance of the six leaf litter species, analyses were repeated changing the order of fitting individual litter species and their interactions. F- and P-values for individual litter species in the text and tables refer to those when fitted first (Schmid et al. 2002, 2017). Differences between means were inspected using Tukey's honestly significant difference test (package "emmeans"). Values presented in text are means ± SD of non-transformed data. Pearson correlation coefficients were calculated to investigate relationships between C-to-N ratio, C_{mic}, qO_2 and M_{loss}, and the abundance of Collembola and Acari (package "stats").

Results

Initial litter chemistry

Initial N concentrations were highest in *C. andina*, followed by *D. lamarckianum*, *M. pubescens*, *C. zamorensis*, *G. emarginata* and *Clusia* spp. (1.08%, 0.73%, 0.60%, 0.50%, 0.40% and 0.40%, respectively), resulting in C-to-N ratios between 36.3 in *C. andina* and 107.2 in *Clusia* spp. (see Appendix 1 for details on litter chemistry). Lignin concentrations were generally high and varied between 63.9% in *Clusia* spp. to 42.6% in *G. emarginata*. By contrast, concentrations of cellulose were lowest in *Clusia* spp. (13.0%), low in *C. andina* (29.6%), but similar in the other four litter species varying between 35.8% and 40.7%. Concentrations of P and other litter elements also varied markedly between leaf litter species with P, Ca, Mg, K and Fe being highest in *C. andina*, and P and Ca being lowest in *G. emarginata*.

Mass loss

Generally, M_{loss} was higher after 12 than after 6 months of incubation with averages of 52.6% ± 7.1% and 41.8% ± 6.9% of initial, respectively (Table 1). M_{loss} varied significantly with species diversity but the effect depended on time (Figure 1A; Table 1); after 6 months M_{loss} was lower in single species (average of 29.6% ± 6.9%) compared to the two and four litter species treatments (43.1% ± 3.8 and 44.9% ± 3.6%, respectively), while after 12 months decomposition was similar in each of the litter diversity treatments. Further, M_{loss} varied significantly with litter species identity, however, this depended on time, with the effect generally being restricted to the first sampling date and to four of the six litter species (Table 1). At the first sampling date, M_{loss} increased in presence of *C. andina* from 39.7% ± 7.4% to 44.4% ± 5.1%, in presence of *C. zamorensis* from 40.5% ± 7.9% to 43.2% ± 5.3%, in presence of *G. emarginata* from 39.4% ± 7.6% to 44.8% ± 4.2% and in presence of *Clusia* spp. from 39.6% ± 7.3% to 44.6% ± 5.1%. M_{loss} positively correlated with C_{mic}, BR, qO_2, $+C_{Slope}$ and the abundance of Collembola and Oribatida, but negatively with the litter C-to-N ratio (Pearson correlation coefficients; Table 2).

	df	M_{loss}	C_{mic}	BR	qO_2	$+C_{Slope}$
LD	2, 239	**26.32*****	**3.01***	1.12	2.01	2.03
Time	1, 239	**244.03*****	**31.48*****	**78.10*****	**21.15*****	**24.61*****
CA	1, 239	0.51	1.63	1.04	**7.76****	1.21
DL	1, 239	1.09	<0.01	1.78	1.93	**4.59***
MP	1, 239	2.09	<0.01	**3.91***	0.46	0.70
CZ	1, 239	0.02	0.53	<0.01	**4.49***	**4.33***
GE	1, 239	0.43	0.11	0.04	<0.01	0.05
Cs	1, 239	0.97	0.05	0.02	<0.01	0.01
Time × LD	2, 239	**43.44*****	**4.37****	1.43	1.27	1.73
Time × CA	1, 239	**23.01*****	0.12	0.01	<0.01	2.30
Time × DL	1, 239	0.91	0.47	0.11	0.66	**3.89***
Time × MP	1, 239	1.76	0.60	3.13	0.60	0.59
Time × CZ	1, 239	**7.25****	0.71	0.80	**3.76***	2.48
Time × GE	1, 239	**35.12*****	**6.76****	2.29	0.60	<0.01
Time × Cs	1, 239	**21.73*****	1.77	0.07	0.02	2.72

Table 1. F-values of linear mixed effects models on the effect of litter species diversity (LD), time of exposure (Time) and leaf litter species identity [*Cecropia andina* (CA), *Dictyocaryum lamarckianum* (DL), *Myrcia pubescens* (MP), *Cavendishia zamorensis* (CZ), *Graffenrieda emarginata* (GE) *and Clusia* spp. (Cs)] on mass loss (M_{loss}), microbial biomass (C_{mic}), basal respiration (BR), microbial metabolic quotient (qO_2) and the slopes of microbial growth after C addition ($+C_{Slope}$). F-values represent those where the respective factor was fitted first. Significant effects are given in bold (*P< 0.05; **P< 0.01; ***P< 0.001); df, degrees of freedom.

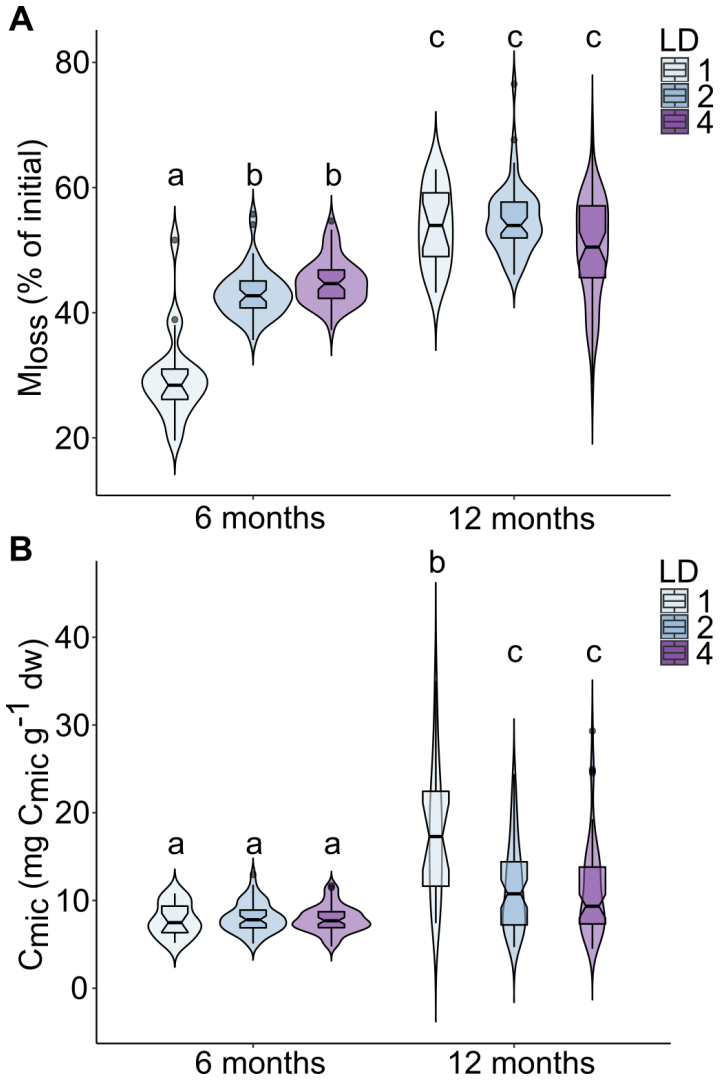

Figure 1. Effect of litter species diversity (LD; 1, 2 and 4 species) on (**A**) litter mass loss (M_{loss}) and (**B**) litter microbial biomass (C_{mic}) after 6 and 12 months of incubation in the field. Boxplots show medians and quantiles for each LD level. Violin plot illustrate kernel probability density. Different letters indicate significant differences (Tukey's HSD test, $P < 0.05$

	M_{loss}	C_{mic}	BR	qCO_2	$+C_{Slope}$	Collembola	Oribatida	Mesostigmata	Prostigmata
M_{loss}	1	-	-	-	-	-	-	-	-
C_{mic}	**0.30*****	1	-	-	-	-	-	-	-
BR	**0.42*****	**0.53*****	1	-	-	-	-	-	-
qO_2	**0.20****	**-0.16** ***	**0.50*****	1	-	-	-	-	-
$+C_{slope}$	**0.20****	**0.23*****	**0.38*****	0.07	1	-	-	-	-
Collembola	**0.16****	0.09	0.04	-0.10	0.12	1	-	-	-
Oribatida	**0.25*****	0.08	**0.13***	0.04	0.12	**0.50*****	1	-	-
Mesostigmata	-0.05	-0.07	**-0.15***	**-0.16***	-0.05	**0.40*****	**0.40*****	1	**-**
Prostigmata	0.05	0.02	<0.01	-0.11	0.07	**0.37*****	**0.39*****	**0.48*****	1
C-to-N	**-0.24*****	**-0.16***	**-0.19****	0.05	**-0.15***	**-0.15***	-0.01	-0.07	**-0.19*****

Table 2. Pearson correlation coefficients between mass loss (M_{loss}), microbial biomass (C_{mic}), basal respiration (BR), microbial growth after C addition ($+C_{slope}$), metabolic quotient (qO_2), the abundance of Collembola, Oribatida, Mesostigmata and Prostigmata and litter C-to-N ratio. Significant correlations are given in bold (*P< 0.05; **P< 0.01; ***P< 0.001).

Microbial parameters

Parallel to M_{loss}, the microbial parameters C_{mic}, BR, qO_2 and $+C_{Slope}$ significantly increased from 6 to 12 months (Table 1; for means see Appendix 2). Among microbial parameters, only C_{mic} varied with litter diversity. Unlike M_{loss}, the effect of litter diversity was restricted to the second sampling date, decreasing in the order one > two > four litter species (Figure 1B). Further, C_{mic} also varied with litter species identity, but the effect was restricted to treatments with *G. emarginata* and depended on time. At the second sampling date C_{mic} decreased from 15.23 ± 11.74 to 11.58 ± 7.37 mg C_{mic} g^{-1} dw in litterbags without and with *G. emarginata*, respectively. The other microbial parameters only were significantly affected by litter species identity, with the effects in part varying with time (Table 1). BR decreased significantly in presence of *M. pubescens* from an average of 157.3 ± 107.7 to 133.1 ± 69.40 µl O_2 mg^{-1} C_{mic} h^{-1} in litterbags without and with *M. pubescens*, respectively. qO_2 decreased from 14.90 ± 5.65 to 13.50 ± 4.18 µl O_2 mg^{-1} C_{mic} h^{-1} in presence of *C. andina*, irrespective of sampling date, but it increased from 14.44 ± 5.37 to 16.91 ± 7.45 45 µl O_2 mg^{-1} C_{mic} h^{-1} in presence of *C. zamorensis* at the second sampling date. $+C_{Slope}$ decreased significantly from 0.0097 ± 0.0149 to 0.0061 ± 0.0131 in presence of *C. zamorensis* irrespective of sampling date, but in presence of *D. lamarckianum* it increased from 0.0086 ± 0.0195 to 0.0151 ± 0.0180 after the second sampling.

Pearson correlation coefficients indicated that C_{mic} positively correlated with M_{loss}, BR and $+C_{Slope}$, but negatively with qO_2 and the litter C-to-N ratio. BR positively correlated with M_{loss}, C_{mic}, qO_2, $+C_{Slope}$ and the abundance of Oribatida, but negatively with the abundance of Mesostigmata and the litter C-to-N ratio. qO_2 positively correlated with M_{loss} and BR, but negatively with C_{mic} and the abundance of Mesostigmata. $+C_{Slope}$ positively correlated with M_{loss}, C_{mic}, BR, but negatively with the litter C-to-N ratio (Table 2).

Microarthropods

The number of Collembola, Oribatida and Prostigmata significantly increased from 6 to 12 months, but the abundance of Mesostigmata decreased (Figure 2; Table 3; for means see Appendix 3). None of the soil microarthropod taxa investigated varied with litter diversity,

although they did vary significantly with litter species identity (Table 3). Collembola abundance (25.3% of total microarthropods; overall mean of 70 ± 80 ind. 10 g^{-1} litter dw) increased significantly in presence of *C. andina* by 43.4% and in presence of *G. emarginata* by 29.2%, but decreased in presence of *D. lamarckianum* and *C. zamorensis* by 39.1% and 38.1%, respectively (Appendix 3 and 4). However, the effect varied with time for *D. lamarckianum* and *C. zamorensis* (Table 3); in the presence of these species the reduction was most pronounced after 12 months (from 60 ± 42 to 123 ± 132 and from 62 ± 38 to 124 ± 135 ind. 10 g^{-1} litter dw, respectively). The abundance of Oribatida (53.7% of total microarthropods; overall mean 146 ± 119 ind. 10 g^{-1} litter dw) increased significantly in litterbags containing *G. emarginata* or *Clusia* spp. from 133 ± 119 to 162 ± 118 and from 131 ± 99 to 163 ± 138 ind. 10 g^{-1} litter dw, respectively. Further, Mesostigmata abundance (11.1% of total microarthropods; overall mean of 30 ± 27 ind. 10 g^{-1} litter dw) decreased significantly by 24.5% from 34 ± 31 to 26 ± 21 ind. 10 g^{-1} litter dw in the presence of *C. zamorensis*. Prostigmata abundance (9.5% of total microarthropods; overall mean of 26 ± 22 ind. 10 g^{-1} litter dw) increased significantly in litterbags where *C. andina* or *Clusia* spp. were present. With the former, it increased by 28.1% from 23 ± 22 to 29 ± 22 ind. 10 g^{-1} litter dw, while in the presence of the latter the effect was restricted to the second sampling date, increasing by 23.1% from 27 ± 25 to 33 ± 26 ind. 10 g^{-1} litter dw.

Pearson correlation coefficients indicated that Collembola abundance positively correlated with M_{loss} and the abundance of Oribatida, Mesostigmata and Prostigmata, but negatively with the litter C-to-N ratio. Oribatida abundance positively correlated with M_{loss}, BR and the abundance of Collembola, Mesostigmata and Prostigmata. Mesostigmata abundance positively correlated with the abundance of Collembola, Oribatida and Prostigmata, but negatively with BR and qO_2. Prostigmata abundance positively correlated with the abundance of Collembola, Oribatida and Mesostigmata, but negatively with litter C-to-N ratio (Table 2).

	df	Collembola	Oribatida	Mesostigmata	Prostigmata
LD	2, 239	0.15	1.41	0.75	0.74
Time	1, 239	**28.08*****	**78.95*****	**4.93***	**4.22***
CA	1, 239	**15.83*****	1.50	2.86	**7.92****
DL	1, 239	**13.34*****	0.34	0.05	0.66
MP	1, 239	<0.01	0.85	0.37	2.74
CZ	1, 239	**8.80****	2.73	**4.61***	2.06
GE	1, 239	**7.59****	**5.98****	2.43	1.56
Cs	1, 239	<0.01	**4.24***	0.07	0.02
Time × LD	2, 239	2.80	0.61	0.71	0.39
Time × CA	1, 239	0.14	0.59	2.26	3.08
Time × DL	1, 239	**8.04****	0.02	1.01	0.42
Time × MP	1, 239	0.85	0.30	0.23	0.03
Time × CZ	1, 239	**4.52***	0.01	0.01	<0.01
Time × GE	1, 239	0.22	0.03	0.14	0.33
Time × Cs	1, 239	0.44	0.02	0.04	**4.25***

Table 3. F-values of linear mixed effects models on the effect of litter species diversity (LD), time of exposure (Time) and leaf litter species identity [*Cecropia andina* (CA), *Dictyocaryum lamarckianum* (DL), *Myrcia pubescens* (MP), *Cavendishia zamorensis* (CZ), *Graffenrieda emarginata* (GE) *and Clusia* spp. (Cs)] on the abundance of Collembola, Oribatida, Mesostigmata and Prostigmata. F-values represent those where the respective factor was fitted first. Significant effects are given in bold (*P< 0.05; **P< 0.01; ***P< 0.001); df, degrees of freedom.

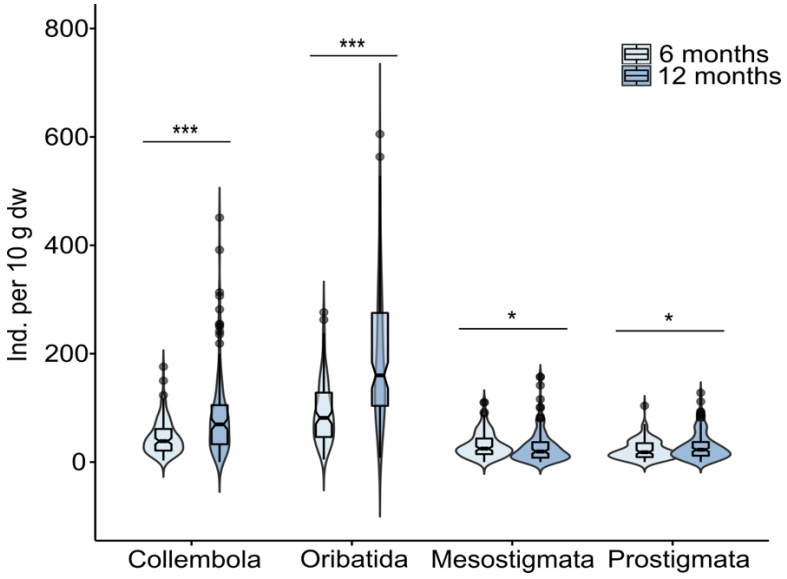

Figure 2. Abundance of Collembola, Oribatida, Mesostigmata and Prostigmata in litterbags after 6 and 12 months of incubation in the field**.** Boxplots show medians and quantiles for each date of exposure. Violin plots illustrate kernel probability density. ***P < 0.001; *P < 0.05.

Discussion

Litter diversity

Contrary to our first hypothesis, C_{mic} decreased rather than increased with increasing litter diversity after one year of exposure in the field (Figure 1). Leaves of tropical forest trees are of low nutritional quality and contain high concentrations of structural compounds and secondary metabolites, typically higher than those in trees of temperate forests (Coley and Barone 1996; Hallam and Read 2006; Cárdenas et al. 2015). Secondary metabolites, particularly polyphenols known to suppress microorganisms by inhibiting enzyme activity (Hättenschwiler and Vitousek 2000; Hoorens et al. 2003), are important drivers of decomposition processes particularly in tropical rainforests (Coq et al. 2010). Potentially, secondary compounds, such as polyphenols, detrimentally affected litter microorganisms in a systemic way resulting in a decrease in C_{mic}, thereby resulting in a negative complementarity effect in leaf litter mixtures (Chomel et al. 2016; Ristok et al. 2019). The fact that BR, qO_2 and $+C_{Slope}$ were not significantly affected by litter diversity suggests that higher leaf litter diversity does not necessarily result in an increase in the availability of nutrient and carbon resources in this tropical rainforest. Rather, the results suggest that litter diversity increases the exposure of microorganisms to secondary leaf litter compounds, detrimentally affecting their activity. Due to the preferential decay of labile litter compounds, the concentration of secondary compounds as well as recalcitrant structural compounds, such as lignin, may increase during litter decomposition, thereby reducing litter decomposition at later stages of litter decay, as has previously been suggested for litter at our study sites (Butenschoen et al. 2014; Marian et al. 2017).

Similar to C_{mic}, M_{loss} significantly increased in single litter species treatments after one year of exposure underscoring the correlation between (Table 2). Changes in the chemical composition of litter material throughout the decomposition process alter the structure and functioning of microbial communities and thus affect the rate at which litter material is decomposed (Berg and McClaugherty 2008). Notably, M_{loss} increased with litter diversity after 6 months of exposure, however, the effect was no longer present after 12 months. Presumably, this reflects reliance of the early microbial community on labile litter

compounds, which were more abundant in leaf litter mixtures (Pérez Harguindeguy et al. 2008; Rinkes et al. 2014). However, as decomposition proceeded, the remaining more recalcitrant compounds accumulated and their decomposition was independent of litter diversity.

In contrast to C_{mic} and M_{loss}, the abundance of microarthropods was not affected by litter diversity (Table 3). Some previous studies found mixtures to promote the abundance of microarthropods (Migge et al. 1998; Hansen 2000; Hättenschwiler and Gasser 2005; Schädler and Brandl 2005), while others did not find evidence that litter diversity beneficially affects microarthropods (Scheu et al. 2003; Ilieva-Makulec et al. 2006; Korboulewsky et al. 2016; Bluhm et al. 2019; Patoine et al. 2020). Our results agree with the latter findings and support the results of Marian et al. (2018) suggesting that litter diversity in this tropical rainforest neither improves habitat conditions nor the availability of resources for microarthropods, at least during early stages of decomposition. Indeed, detritivore microarthropods are considered to comprise predominantly generalist feeders colonizing a range of forest types and therefore are rather insensitive to changes caused by litter mixing (Wardle et al. 2006; Ball et al. 2014; Gergócs and Hufnagel 2016; Patoine et al. 2020). However, even though litter diversity did not affect microarthropod abundance, it may still have fostered the diversity of microarthropods, as has been shown for other soil organisms, such as testate amoebae at our study site (Krashevska et al. 2017).

Exposure time

Generally, M_{loss} increased with time parallel to microbial parameters. Litter decomposition at our study site can be divided into three phases, with the early phase lasting for about 12 months (Marian et al. 2017). This early phase of decomposition is characterized by the loss of labile C compounds via leaching and by the growth of opportunistic microorganisms that form new soluble compounds (Berg and McClaugherty 2008), and this likely explains the close link between M_{loss} and microbial activity and growth (Table 2). However, contrary to our second hypothesis, the increase in qO_2 values between 6 and 12 months of exposure indicates that microorganisms increasingly suffered from stress conditions later during

exposure. Stress conditions result in less efficient use of C compounds and increased investment into maintenance metabolism (Yan et al. 2003; Ndaw et al. 2009). Presumably, toward the end of the early litter decomposition stage microorganisms increasingly competed for resources as easily decomposable leaf litter compounds vanished (Fontaine et al. 2003; Poll et al. 2008; Rinkes et al. 2011). The parallel increase in the $+C_{Slope}$ with time suggests that this was associated with less efficient nutrient capture by microorganisms pointing towards a switch from predominant limitation by nutrients early during exposure to the limitation by easily available carbon resources later (Sall et al. 2003; Laganière et al. 2010). Early stages of litter decay in the studied tropical montane rainforest might be associated with high abundance of mycorrhizal fungi (Marian et al. 2017). The C input that mycorrhizal fungi obtain from plants may allow them to efficiently compete with saprotrophic fungi for nutrients, even though their enzymatic capability is typically inferior to that of saprotrophic fungi (Hodge et al. 2001; Camenzind and Rillig 2013). Indeed, the assumption that mycorrhizal and saprotrophic fungi interact antagonistically early during litter decomposition at our study site is supported by earlier studies (Marian et al. 2019; Sánchez-Galindo et al. 2019).

Parallel to microbial parameters, the abundance of all microarthropod taxa studied increased with time, with the exception of Mesostigmata. Mesostigmata commonly hunt in the litter for other microarthropods, particularly Collembola, Astigmata and weakly sclerotized Oribatida (Koehler 1997; Schneider and Maraun 2009). Although variations in the abundance of Mesostigmata were closely linked to the abundance of Collembola and Oribatida (Table 2), the fact that their abundance decreased with time likely reflect that Mesostigmata in the litterbags were not only feeding on microarthropods, but also on other organisms, presumably Nematoda, insect larvae and eggs. Indeed, some species of Mesostigmata may preferentially colonize certain microhabitats to hunt for prey such as Nematoda (Klarner et al. 2013; Heidemann et al. 2014).

The increase in the abundance of the microarthropod decomposers Collembola and Oribatida with time indicates that changes during the initial stages of decomposition influence both groups in a similar way. Surprisingly, Collembola and Oribatida abundance

was not closely associated with microbial biomass (Table 2) even though microorganisms are their major food resource (Maraun et al. 2003; Scheu et al. 2005; Dhooria 2016). Rather, the stage of litter decomposition within the early decomposition phase (i.e., 6 *vs* 12 months), appears to be the more important driver of the abundance of microarthropod decomposers. Indeed, litter material that is highly colonized by microorganisms becomes more palatable for microarthropods (Bardgett 2005; Das and Joy 2009), which at least in part is due to the reduction in plant secondary compounds such as phenols (Coulis et al. 2009; Asplund et al. 2013). Overall, our results support earlier findings at this study site in that the role of litter resources for the nutrition of decomposer microarthropods increases with litter decomposition (Marian et al. 2018). Moreover, the parallel increase in the abundance of Prostigmata suggests that the increase in the abundance of decomposer microarthropod prey benefitted higher trophic levels.

Leaf litter identity

The presence of specific plant leaf litter species in mixtures might increase or decrease the rate at which the litter decomposes (Hector et al. 2000; Hoorens et al. 2003, 2010). Variation can be attributed predominantly to differences in litter quality among the component species in mixtures (Gartner and Cardon 2004; Hättenschwiler et al. 2005). Indeed, litter decomposition and colonization of the litter by microarthropods in our study were related to the initial chemical composition of the litter species. Our third hypothesis was supported by the beneficial effects of high-quality *C. andina* litter. Presence of this litter species significantly decreased qO_2 values and increased the abundance of Collembola and Prostigmata. *C. andina* had high initial N and P concentrations, and low lignin content (see Appendix 1), providing readily available nutrients, reducing nutrient stress for microorganisms and thereby contributing to an increase in C_{mic}. Increased microbial C use efficiency may also have resulted from a shift in microbial community composition toward high-energy-efficient species (Dilly and Munch 1996), e.g. from opportunistic bacteria to fungi able to break down complex litter compounds (Chapman et al. 2013). Changes in microbial community composition probably were driven by increasing concentrations of recalcitrant litter compounds favoring saprotrophic fungi able to degrade these compounds,

which in turn beneficially affected decomposers, such as Collembola and Oribatida, feeding on these fungi and the litter materials degraded by them.

The high qO_2 and the $+C_{Slope}$ values after 12 months of exposure reflected the low quality of *D. lamarckianum*, *C. zamorensis* and *G. emarginata* litter, and presumable scarcity of easily accessible C resources to microorganisms. All these litter species were characterized by low initial N and P concentrations, and high concentrations of lignin and cellulose (Appendix 1). The concentrations of lignin and cellulose serve as indicator of litter quality and as predictor of litter decomposition (Fioretto et al. 2005; Berg 2014). Cellulose not entrapped in lignin degrades rapidly during early stages of decomposition and this contributes to the release of N and P, typical elements limiting microbial growth (Berg and McClaugherty 2008; Hobbie et al. 2012; Berg 2014). However, during this stage, labile compounds are commonly used by opportunistic microorganisms (Cornelissen et al. 1999; Fioretto et al. 2005), impeding the growth of microorganism able to degrade recalcitrant litter compounds (Ilieva-Makulec et al. 2006). Therefore, by the end of the early stage of litter decomposition, structural compounds become relatively more abundant and reduce resource quality, which differentially affects microorganisms and microarthropods, as indicated by the lower abundance of Collembola in litter of *C. zamorensis* and *D. lamarckianum*. Interestingly, the decrease in C_{mic} after 12 months in litterbags containing *G. emarginata* was associated with high abundance of decomposer microarthropods, suggesting that there is no close relationship between decomposer microarthropods and bulk microbial biomass in litter. This conclusion is also supported by the lack of significant correlations between C_{mic} and decomposer microarthropod abundances (Table 2).

The correlation between the abundance of Collembola and Oribatida and litter M_{loss} presumably reflects that these microarthropods benefited from both higher quality litter and by microorganisms colonizing the litter at later stages of decay. The significant negative correlation between Collembola abundance and litter C-to-N ratio (Table 2) indicates that Collembola heavily rely on litter quality. However, contrary to our fourth hypothesis, the differential responses of microarthropods to litter species suggests that leaf litter chemical composition alone is insufficient to explain variations in the abundance of soil

microarthropods, as has been suggested in earlier studies (Kaneko and Salamanca 1999; González and Seastedt 2001; Hoorens et al. 2010). This is most strongly supported by the greater abundance of Oribatida in litterbags containing *Clusia* spp. litter, which was of particular low quality. This indicates that physical litter characteristics such as toughness and structure, might play a more important role in driving soil microarthropod abundance than litter chemistry and the degree of microbial colonization.

Conclusions

The results of our study showed that higher levels of litter diversity may negatively affect soil microbial biomass and mass loss in the studied tropical montane rainforest, presumably due to the accumulation of recalcitrant compounds and the generally low quality of the leaf litter material. Notably, the response of microbial parameters and microarthropod abundance to litter identity was more pronounced than to litter diversity, with the differential responses of soil biota to litter identity in part being due to differences in the initial chemical composition of litter species. Generally, the results indicate that both microarthropods and microorganisms benefit from larger amounts of easily available litter resources during early stages of decomposition, highlighting the importance of litter quality as driver of the abundance and activity of decomposer organisms. However, the results also indicate that litter traits, related to the physical structure of litter may be more important to decomposer invertebrates than litter chemistry and gross microbial characteristics of litter such as microbial biomass. Overall, our findings indicate that litter species identity functions as major driver of the abundance and activity of soil organisms, and thereby exert distinct effects on ecosystem processes such as decomposition and nutrient mobilization.

Acknowledgments

We thank the Deutsche Forschungsgemeinschaft (DFG; FOR816) for financial support. Further, we thank the Ministerio de Ambiente del Ecuador and the Universidad Técnico Particular de Loja (UTPL) for the research permits and the center Naturaleza y Cultura Internacional (NCI) for access to the San Francisco reserve. We thank student helpers for

the establishment of the experiment in the field and Christina Lucas for her help in the laboratory.

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Appendix

Appendix 1. Initial chemical composition of the litter species used in the experiment. The analyses were performed in triplicate using bulk samples. Data are given in percentages of dry mass; nd = not detected.

	Cecropia andina	*Dictyocaryum lamarckianum*	*Myrcia pubescens*	*Cavendishia zamorensis*	*Graffenrieda emarginata*	*Clusia* spp.
C	39.30 ± 3.65	41.25 ± 1.70	39.61 ± 3.65	41.74 ± 0.01	40.28 ± 1.68	42.80 ± 3.65
N	1.08 ± 0.02	0.73 ± 0.01	0.60 ± 0.02	0.50 ± 0.01	0.40 ± 0.16	0.40 ± 0.02
C-to-N	36.29 ± 2.91	58.59 ± 1.25	65.64 ± 4.62	84.64 ± 0.01	91.29 ± 1.68	107.21 ± 6.00
Lignin	46.67 ± 6.37	52.40 ± 9.83	50.53 ± 9.07	51.73 ± 13.95	42.60 ± 8.40	63.93 ± 10.10
Cellulose	29.60 ± 6.28	40.73 ± 4.29	35.80 ± 7.27	39.53 ± 3.33	40.40 ± 6.73	13.00 ± 3.37
Al	1.88 ± 0.65	0.14 ± 0.08	0.18 ± 0.06	0.23 ± 0.02	2.41 ± 0.33	0.13 ± 0.01
Ca	17.32 ± 0.82	1.13 ± 0.08	1.07 ± 0.02	6.11 ± 0.83	1.07 ± 0.02	3.07 ± 0.82
Fe	2.03 ± 0.05	1.18 ± 0.02	0.29 ± 0.08	0.09 ± 0.03	0.30 ± 0.03	0.06 ± 0.02
K	3.05 ± 0.01	0.37 ± 0.09	1.23 ± 0.09	1.08 ± 0.01	1.08 ± 0.03	1.65 ± 0.09
Mg	3.22 ± 0.73	1.25 ± 0.09	1.22 ± 0.09	1.72 ± 0.09	1.72 ± 0.09	1.55 ± 0.09
Mn	0.11 ± 0.01	0.31 ± 0.03	0.14 ± 0.09	0.06 ± 0.01	0.26 ± 0.09	0.48 ± 0.09
Na	nd	0.03 ± 0.02	0.30 ± 0.02	nd	nd	nd
P	0.48 ± 0.08	0.21 ± 0.08	0.22 ± 0.10	0.27 ± 0.10	0.12 ± 0.08	0.25 ± 0.08

Appendix 2. Means of microbial parameters (C_{mic}, microbial biomass carbon; BR, basal respiration, qO_2, microbial specific respiration; $+C_{Slope}$, the slopes of microbial growth after C addition). LD, litter diversity (LD1, one species; LD2, two species; LD4, four species); CA, *Cecropia andina*; DL, *Dictyocaryum lamarckianum*; MP, *Myrcia pubescens*; CZ, *Cavendishia zamorensis*; GE, *Graffenrieda emarginata*; Cs, *Clusia* spp. Values are means ± SD.

			C_{mic} [mg C_{mic} g^{-1} dw]	BR [µl O_2 mg^{-1} C_{mic} h^{-1}]	qO_2 [µl O_2 mg^{-1} C_{mic} h^{-1}]	$+C_{Slope}$
LD	1		13.30 ± 8.99	154.57 ± 97.62	12.97 ± 5.55	0.0113 ± 0.0208
	2		11.01 ± 9.74	152.42 ± 105.28	14.78 ± 5.71	0.0066 ± 0.0111
	4		10.10 ± 6.12	138.35 ± 79.27	14.27 ± 4.22	0.0084 ± 0.0121
Time	6 months		8.28 ± 4.19	101.7± 19.5	12.90 ± 2.21	0.0042 ± 0.0035
	12 months		13.62 ± 10.18	191.1 ± 114.0	15.65 ± 6.56	0.0117 ± 0.0190
CA	Presence		11.12 ± 6.22	148.50 ± 94.82	13.50 ± 4.18	0.0089 ± 0.0157
	Absence		10.81 ± 9.56	144.73 ± 91.97	14.90 ± 5.65	0.0075 ± 0.0114
DL	Presence		10.58 ± 6.98	150.09 ± 89.94	14.74 ± 4.06	0.0097 ± 0.0140
	Absence		11.28 ± 9.20	143.14 ± 96.06	13.85 ± 5.82	0.0067 ± 0.0130
MP	Presence		10.53 ± 9.53	133.07 ± 69.40	14.15 ± 4.14	0.0074 ± 0.0104
	Absence		11.29 ± 6.97	157.33 ± 107.72	14.37 ± 5.75	0.0088 ± 0.0156
CZ	Presence		10.33 ± 8.53	143.71 ± 89.58	14.94 ± 5.75	0.0065 ± 0.0117
	Absence		11.54 ± 7.89	149.02 ± 96.61	13.63 ± 4.27	0.0097 ± 0.0149
GE	Presence		10.31 ± 6.80	141.93 ± 94.72	14.34 ± 5.10	0.0079 ± 0.0121
	Absence		11.46 ± 9.17	149.98 ± 91.98	14.21 ± 5.08	0.0084 ± 0.0146
Cs	Presence		10.36 ± 6.53	142.19 ± 90.71	14.32 ± 5.05	0.0080 ± 0.0101
	Absence		11.42 ± 9.33	149.78 ± 95.13	14.24 ± 5.12	0.0083 ± 0.0157
Time × LD						
LD1	6 months		7.79 ± 1.85	96.07 ± 18.97	12.65 ± 2.50	0.0045 ± 0.0031
	12 months		18.81 ± 9.92	213.06 ± 109.53	13.29 ± 7.53	0.0182 ± 0.0280
LD 2	6 months		8.03 ± 1.71	103.05 ± 19.08	13.03 ± 1.91	0.0041 ± 0.0036
	12 months		13.97 ± 13.06	201.79 ± 130.59	16.53 ± 7.48	0.0091 ± 0.0149
LD 4	6 months		8.67 ± 5.94	102.47 ± 20.01	12.86 ± 2.38	0.0043 ± 0.0036
	12 months		11.52 ± 6.01	174.23 ± 98.28	15.69 ± 5.11	0.0126 ± 0.0158
Time × Litter identity						
CA	Presence	6 months	8.64 ± 1.66	103.19 ± 19.44	12.12 ± 2.00	0.0037 ± 0.0044
	Absence	6 months	7.99 ± 5.44	100.50 ± 19.58	13.53 ± 2.20	0.0047 ± 0.0026
	Presence	12 months	13.61 ± 7.91	193.81 ± 116.56	14.89 ± 5.23	0.0142 ± 0.0206
	Absence	12 months	13.63 ± 11.76	188.97 ± 112.63	16.27 ± 7.46	0.0104 ± 0.0155
DL	Presence	6 months	8.25 ± 5.81	103.55 ± 19.70	13.62 ± 2.31	0.0044 ± 0.0034
	Absence	6 months	8.31 ± 1.79	100.05 ± 19.29	12.24 ± 1.92	0.0041 ± 0.0037
	Presence	12 months	12.90 ± 7.31	196.63 ± 107.35	15.86 ± 5.04	0.0151 ± 0.0180
	Absence	12 months	14.29 ± 12.21	186.23 ± 120.22	15.45 ± 7.71	0.0094 ± 0.017
MP	Presence	6 months	8.27± 5.94	98.27 ± 16.49	13.03 ± 2.36	0.0041 ± 0.0033
	Absence	6 months	8.29 ± 1.74	104.52 ± 21.33	12.79 ± 2.10	0.0043 ± 0.0038

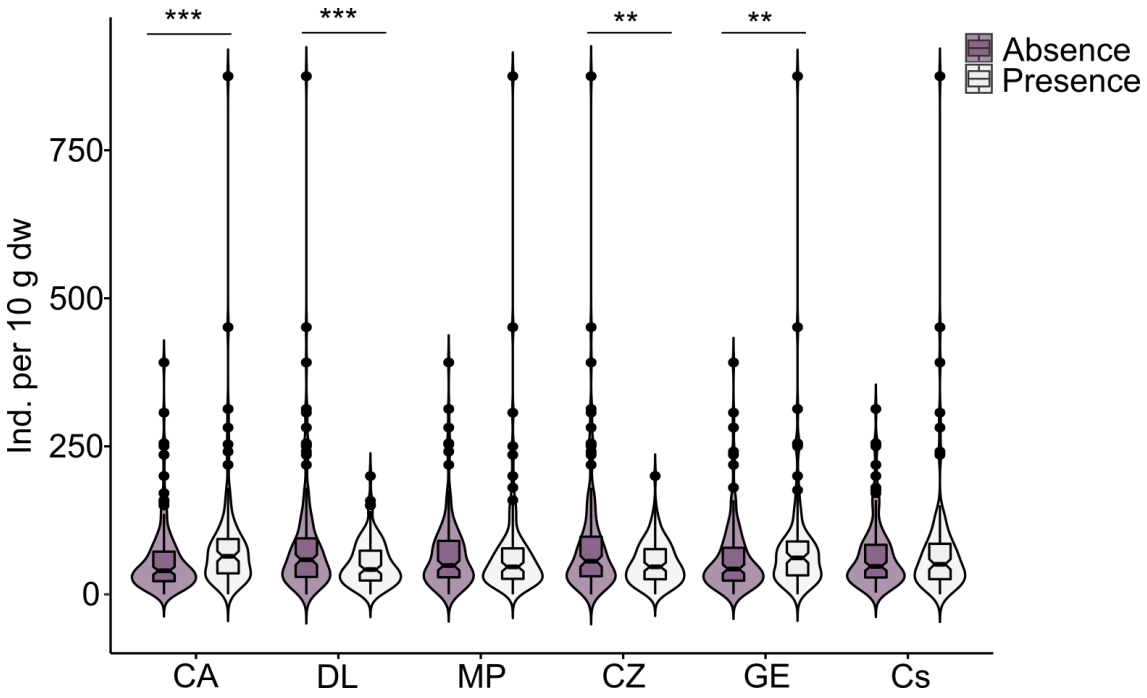
	Presence	12 months	12.80 ± 11.71	167.88 ± 83.56	15.27 ± 5.14	0.0106 ± 0.0136
	Absence	12 months	14.30 ± 8.76	210.15 ± 131.38	15.96 ± 7.56	0.0133 ± 0.0209
CZ	Presence	6 months	8.07 ± 1.52	103.63 ± 18.99	12.98 ± 1.81	0.0039 ± 0.0028
	Absence	6 months	8.48 ± 5.68	99.88 ± 19.92	12.82 ± 2.56	0.0046 ± 0.0041
	Presence	12 months	12.59 ± 11.57	183.80 ± 112.03	16.91 ± 7.45	0.0092 ± 0.0160
	Absence	12 months	14.60 ± 8.61	198.16 ± 116.24	14.44 ± 5.38	0.0149 ± 0.0194
GE	Presence	6 months	9.03 ± 5.98	105.82 ± 20.97	12.71 ± 2.31	0.0039 ± 0.0031
	Absence	6 months	7.69 ± 1.62	98.45 ± 17.71	13.04 ± 2.14	0.0045 ± 0.0038
	Presence	12 months	11.58 ± 7.37	178.04 ± 122.51	15.98 ± 6.45	0.0119 ± 0.0159
	Absence	12 months	15.23 ± 11.74	201.52 ± 106.48	15.39 ± 6.68	0.0122 ± 0.0196
Cs	Presence	6 months	8.40 ± 6.07	99.02 ± 21.32	12.88 ± 2.48	0.0056 ± 0.0042
	Absence	12 months	8.18 ± 1.60	103.83 ± 17.76	12.91 ± 1.99	0.0032 ± 0.0026
	Presence	6 months	12.32 ± 6.44	185.36 ± 111.16	15.75 ± 6.41	0.0105 ± 0.0133
	Absence	12 months	14.65 ± 12.31	195.73 ± 116.75	15.57 ± 6.72	0.0133 ± 0.0210

Appendix 3. Means of microarthropod abundance. Values are means ± SD. For legend see Appendix 2.

			Collembola [ind. 10 g^{-1}]	Oribatida [ind. 10 g^{-1}]	Mesostigmata [ind. 10 g^{-1}]	Prostigmata [ind. 10 g^{-1}]
LD	1		73 ± 79	132 ± 116	26 ± 24	22 ± 18
	2		71 ± 67	150 ± 128	32 ± 29	26 ± 23
	4		67 ± 91	147 ± 113	30 ± 26	27 ± 23
Time	6 months		46 ± 31	90 ± 55	32 ± 23	22 ± 17
	12 months		93 ± 104	201 ± 137	29 ± 30	29 ± 26
CA	Presence		83 ± 99	141 ± 117	33 ± 27	29 ± 22
	Absence		58 ± 59	150 ± 121	28 ± 27	23 ± 22
DL	Presence		52 ± 37	141 ± 106	30 ± 27	25 ± 23
	Absence		85 ± 103	150 ± 130	30 ± 27	27 ± 22
MP	Presence		71 ± 98	144 ± 125	30 ± 28	24 ± 22
	Absence		69 ± 63	147 ± 114	30 ± 26	27 ± 22
CZ	Presence		53 ± 35	132 ± 95	26 ± 21	25 ± 23
	Absence		85 ± 105	159 ± 137	34 ± 31	27 ± 22
GE	Presence		80 ± 99	162 ± 118	34 ± 29	28 ± 24
	Absence		62 ± 61	133 ± 119	27 ± 25	24 ± 20
Cs	Presence		75 ± 104	163 ± 138	30 ± 28	27 ± 23
	Absence		65 ± 56	131 ± 99	30 ± 26	25 ± 22
Time × LD						
LD1	6 months		35 ± 24	76 ± 59	27 ± 23	18 ± 13
	12 months		111 ± 96	189 ± 132	25 ± 25	26 ± 22
LD 2	6 months		47 ± 35	93 ± 53	32 ± 26	21 ± 14
	12 months		94 ± 82	207 ± 154	32 ± 32	32 ± 28
LD 4	6 months		48 ± 29	93 ± 57	33 ± 21	25 ± 21
	12 months		87 ± 123	200 ± 128	27 ± 31	28 ± 25
Time × Litter identity						
CA	Presence	6 months	56 ± 34	88 ± 54	37 ± 26	28 ± 20
	Absence	6 months	37 ± 26	92 ± 57	27 ± 20	17 ± 15
	Presence	12 months	111 ± 131	193 ± 137	28 ± 28	30 ± 24
	Absence	12 months	78 ± 74	208 ± 140	29 ± 32	28 ± 27
DL	Presence	6 months	44 ± 30	90 ± 56	33 ± 25	23 ± 20
	Absence	6 months	47 ± 32	91 ± 55	30 ± 21	21 ± 15
	Presence	12 months	60 ± 42	192 ± 119	27 ± 28	26 ± 25
	Absence	12 months	123 ± 132	209 ± 154	30 ± 33	32 ± 27
MP	Presence	6 months	43 ± 27	87 ± 48	30 ± 20	22 ± 20
	Absence	6 months	48 ± 34	93 ± 61	33 ± 25	22 ± 15
	Presence	12 months	98 ± 131	201 ± 151	31 ± 35	26 ± 24
	Absence	12 months	89 ± 77	201 ± 129	27 ± 27	32 ± 27
CZ	Presence	6 months	44 ± 30	85 ± 54	28 ± 20	21 ± 16
	Absence	6 months	47 ± 32	96 ± 57	34 ± 26	23 ± 19
	Presence	12 months	62 ± 38	179 ± 103	23 ± 22	28 ± 27
	Absence	12 months	124 ± 135	222 ±163	34 ± 37	30 ± 24
GE	Presence	6 months	50 ± 34	102 ± 61	35 ± 22	25 ± 20

	Absence	6 months	42 ± 29	81 ± 49	29 ± 23	20 ± 15
	Presence	12 months	109 ± 131	221 ± 130	33 ±35	32 ± 28
	Absence	12 months	81 ± 76	185 ± 144	25 ± 26	27 ± 24
Cs	Presence	6 months	45 ± 27	100 ± 57	30 ± 19	21 ± 17
	Absence	6 months	46 ± 34	82 ± 53	33 ± 26	23 ± 18
	Presence	12 months	106 ± 138	226 ± 165	31 ± 33	33 ± 26
	Absence	12 months	84 ± 66	181 ± 111	27 ± 27	27 ± 25

Appendix 4. Abundance of Collembola as affected by the presence of leaf litter species [*Cecropia andina* (CA), *Dictyocaryum lamarckianum* (DL), *Myrcia pubescens* (MP), *Graffenrieda emarginata* (GE), *Cavendishia zamorensis* (CZ) and *Clusia spp.* (Cs)]. Boxplots show medians and quantiles of Collembola abundance for presence and absence of each leaf litter species. Violin plots illustrate kernel probability density. ***P < 0.001; **P < 0.01.



Chapter 3

Differences in leaf and root litter decomposition are mediated by soil microorganisms not decomposer microarthropods in tropical montane rainforests

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Abstract

Plant litter decomposition is a key process in carbon and nutrient cycling. Among the factors determining litter decomposition rates, the role of soil biota for the decomposition of different plant litter types and its modification by variations in climatic conditions is not well understood. In this study we used litterbags with different mesh size (45 µm, 1 mm and 4 mm) to investigate the effect of microorganisms and decomposer microarthropods on leaf and root litter decomposition along an altitudinal gradient of a tropical montane rainforest in Ecuador. We examined decomposition rates, litter C and N concentrations, microbial biomass and activity, as well as decomposer microarthropod abundance, with a focus on oribatid mites (Oribatida, Acari) over one year of exposure at three different altitudes (1000, 2000 and 3000 m). Leaf litter mass loss did not differ between the 1000 and 2000 m sites, while root litter mass loss decreased with increasing altitude. These changes in litter decomposition rates were paralleled by changes in microbial biomass and activity. Access of the litterbags by microarthropods (1 and 4 mm mesh size) did not affect leaf litter mass loss, whereas in root litter mass loss increased significantly at 3000 m with the access of soil microarthropods (4 mm mesh size). In both leaf and root litter Oribatida community composition varied with altitude and litter C-to-N ratio. The result suggest that the impacts of climatic conditions differentially affect the decomposition of leaf and root litter and these modifications are modulated by the quality of the local litter material. These findings also highlight the dominance of litter quality as dominant force structuring Oribatida communities. Overall, the results support the view that decomposition processes in montane rainforests are mostly driven by microorganisms with soil microarthropods playing a more important role for the decomposition of litter material of low-quality.

Keywords: Acari; Collembola; Litterbags; Mesh size; Microbial biomass.

Introduction

Dead leaves and roots comprise the major plant litter material that enters the belowground system and represent the main energy resource for soil organisms (Berg and McClaugherty 2008). Although the annual input of leaf and root litter in forests are typically equivalent in mass (Norby et al. 2004; Freschet et al. 2013), most studies investigating effects of soil organisms on plant litter decay focus on leaves, overlooking the potential of roots as a food resource and regulator of carbon and nutrient cycling (García-Palacios et al. 2016; Fujii and Takeda 2017). Therefore, integration of both root litter and leaf litter is needed for a comprehensive understanding of the role of soil animals in element cycling and ecosystem functioning.

Leaf and root litter material differ in structure and chemical composition (Berg and McClaugherty 2008). Generally, roots contain higher concentrations of recalcitrant compounds compared to leaves, which inhibits degradation by soil organisms and this is assumed to be the reason for the slower decay rates of roots compared to leaves (Hobbie et al. 2010; Freschet et al. 2012; García-Palacios et al. 2016; Jo et al. 2016). Additionally, leaf and root litter are located at different positions in the forest floor. Leaf litter is deposited on top of the soil, while root litter enters the decomposer system directly within the soil. These different locations generate different input pathways of nutrients and are associated with different microenvironments for soil organisms (Ostertag and Hobbie 1999; Fujii and Takeda 2010, 2017). Differences in quality and input pathways of litter type are likely to affect the abundance, composition and activity of soil organisms, with knock-on effects for decomposition rates and soil nutrient dynamics.

Effects of soil organisms on litter decomposition not only change with litter traits, but also with climatic conditions (Coûteaux et al. 1995; Aerts 1997; Hättenschwiler et al. 2005). In tropical Andean montane ecosystems, considered a biodiversity hotspot, climatic conditions change strongly with altitude (Myers et al. 2000; Beck and Ritcher 2008). Increasing altitude is associated with a decline in litter nutrient concentrations and increase in the thickness of organic layers and fine root biomass (diameter < 2 mm) (Tanner et al. 1998; Soethe et al. 2007; Graefe et al. 2008). Notably, at higher altitudes, more organic material originates from fine root litter than from fallen leaves (Röderstein et al. 2005).

Such changes in litter traits with environmental conditions affect the nutrient supply for decomposer organisms and thereby likely control the abundance and diversity of soil decomposer species (Wang et al. 2010; García-Palacios et al. 2016). However, few studies have investigated the impacts of litter traits and altitudinal changes in climate on soil animal communities and their role in leaf and root litter decomposition in tropical montane rainforest ecosystems (Marian et al. 2017, 2018).

Decomposer communities in tropical montane rainforests are dominated by microorganisms and soil microarthropods (Illig et al. 2008; Maraun et al. 2008; Scheu et al. 2008). Among soil microarthropods, oribatid mites (Oribatida, Acari) and springtails (Collembola, Insecta) are the most abundant and diverse organisms (Seastedt 1984; Ruess and Lussenhop 2005). These microarthropods increase rates of litter decomposition and nutrient cycling in forest ecosystems either via the consumption of litter or through stimulation of microbial activity and transport of microbial propagules (Swift et al. 1979; Seastedt 1984; Ruess and Lussenhop 2005). However, interactions between microorganisms, microarthropods and litter type are not well understood. Nonetheless, the exclusion of specific faunal size classes from litter has demonstrated the importance of particular groups of soil organisms on litter decomposition rates (Bradford et al. 2002; Joo et al. 2006; Kampichler and Bruckner 2009). Such experiments are crucial for identifying the role of different animal communities for litter decomposition.

The present study investigates how the effects of microorganisms and decomposer microarthropods on leaf and root litter decomposition vary along an altitudinal gradient of tropical montane rainforests in Ecuador. Decomposition rates, microbial biomass and respiration, as well as decomposer microarthropod abundance, with focus on Oribatida, were studied over one year using litterbags with different mesh sizes to control access by soil fauna to the litter. We hypothesized that (1) the decomposition of litter, regardless of litter type, decreases with increasing altitude due to less favourable abiotic conditions with increasing altitude. Since litter decomposition in the study area is mainly due to the action of microorganisms (Illig et al. 2008; Marian et al. 2017), we hypothesized that (2) limiting the access of litter by microarthropods accelerates decomposition by increasing microbial biomass and activity in both leaf and root litter, with the effect being stronger at higher

altitudes where nutrients are more limited. Further, we hypothesized that (3) the abundance of decomposer microarthropods and the diversity of Oribatida is higher in leaf than in root litter irrespective of altitude and increase with increasing microbial biomass. Lastly, we hypothesized that (4) the role of litter quality in structuring Oribatida communities declines with time, with the effect being less pronounced in root than in leaf litter.

Materials and methods

Study area

The study area is located in the northern fringes of the Podocarpus National Park in the eastern slopes of the Andean Cordillera, Southeast Ecuador. Three study sites at 1000, 2000, and 3000 m a.s.l. represent an altitudinal gradient with moderately steep slopes of 26–31° (Moser et al. 2007). The lower site at 1000 m a.s.l. (S04°06′54′′, W78°58′02′′) is located in the Río Bombuscaro valley and classified as evergreen submontane rainforest dominated by tree species of the families *Arecaceae*, *Combretaceae*, *Moraceae*, *Monimiaceae*, *Rubiaceae*, and *Sapotaceae* (Homeier et al. 2008). The intermediate site at 2000 m a.s.l. (S3°58′18′′, W79°4′45′′) is located in the Reserva Biológica San Francisco on the north-facing flank of the Río San Francisco valley and consists of an evergreen lower montane rainforest dominated by trees of the families *Arecaceae*, *Clusiaceae*, *Ericaceae*, *Lauraceae*, *Melastomataceae* and *Rubiaceae* (Homeier et al. 2008). The highest site at 3000 m a.s.l. (S04°06′711′′, W79°10′58′′) is located near the upper Cajanuma mountain at the northwest gate of Podocarpus National Park. The forest has been classified as evergreen elfin forest dominated by trees / shrubs of the families *Aquifoliaceae*, *Bromeliaceae*, *Chloranthaceae*, *Clusiaceae*, *Ericaceae* and *Melastomataceae* (Homeier et al. 2008). The climate is semi-humid with an average annual temperature of 14.9 °C, 12.3 °C and 8.9 °C and annual precipitation of approximately 2200, 3500 and 4500 mm at 1000, 2000 and 3000 m a.s.l., respectively (Bendix et al. 2006; Homeier et al. 2010). Soil types of the study sites are alumic Acrisol (1000 m), Gley Cambisol (2000 m) and Podzol (3000 m) (Soethe et al. 2006; Moser et al. 2007). The thickness of organic soil layers increases with altitude from 4.8 cm at 1000 m to 30.5 cm at 2000 m to 43.5 cm at 3000 m (Leuschner et al. 2007;

Graefe et al. 2008). In parallel, fine root biomass increases from 2.7 to 6.2 to 10.8 t ha^{-1} at the respective sites (Soethe et al. 2006).

Experimental design

Nylon litterbags (17 x 17 cm) of mesh sizes of 45 µm, 1 mm and 4 mm were filled with 10 g of leaf or root litter. Leaf litterbags consisted of a mixture of freshly fallen leaves of three local abundant tree species of each study site: *Pouteria* sp., *Cecropia andina* and *Mollinedia* sp. at 1000 m, *Graffenrieda emarginata*, *Clusia* sp. and *Cavendishia zamorensis* at 2000 m, *Clusia* sp. *Graffenrieda emarginata* and *Hedyosmum* sp. at 3000 m. For root litterbags, the roots were collected by hand from the upper 20 - 30 cm of the soil/organic layer of respective sites and consisted of a mixture of three size classes: Small (< 1 mm diameter), medium (1-2 mm diameter) and large (> 3 mm diameter). The amount of individual leaf species and root size classes placed in the litterbags was chosen to resemble their amount in the litter layer and soil, respectively (see Appendix 1). The collected leaves and roots were gently rinsed with tap water to clear them from adhering soil and dried at 60°C.

Litterbags were placed in the field in October 2008 (end of the rainy season). Bags containing leaf litter were randomly placed on top of the litter layer and fixed with nails, while those containing root litter were placed approximately 5 cm below the litter layer. Three blocks were established at each of the three altitudes with a minimum distance between blocks of 20 m. Two replicates of each treatment were placed in each block, with one replicate retrieved after 6 months and the other after 12 months.

After retrieval, the litter material in each litterbag was divided into two parts of equal mass. The first half was analysed for dry mass, microbial biomass, basal respiration, and C and N concentrations. From the second half, Oribatida and Collembola were extracted using a modified high-gradient heat extractor (Macfadyen 1961; Kempson et al. 1963) and counted. Adult Oribatida were identified to species level or sorted into morphospecies (Balogh and Balogh 1990, 2002), following the nomenclature of Subías (2018). All identified species are recorded in Ecotaxonomy database (Potapov et al. 2019).

Analytical procedures

Mass loss (M_{loss}) for both leaves and roots was calculated as $M_{loss} = ((m_0 - m_1/m_0)) \times 100$, with m_0 the dry weight of the initial litter placed in the litterbags and m_1 the dry weight of litter at harvest. To measure carbon (C) and nitrogen (N) concentrations, dried (60°C, 72 h) leaves and roots were milled to powder (<1 mm) and analysed using a CN elemental analyser (Vario EL III, Elementar, Hanau, Germany).

Microbial basal respiration (BR) and microbial biomass (C_{mic}) were measured using a computer-controlled O_2 micro-compensation apparatus (Scheu 1992). BR (µl O_2 g^{-1} dry weight h^{-1}) was determined as mean O_2 consumption rates 10 to 20 h after attachment of the samples to the respirometer. C_{mic} was calculated from the maximum initial respiratory response (MIRR; µl O_2 g^{-1} h^{-1}) measured after glucose saturation following the SIR method of Anderson and Domsch (1978). MIRR was calculated as the average of the lowest three readings within the first 10 h and C_{mic} was calculated as C_{mic} = 38 × MIRR (mg g^{-1} dry weight) (Beck et al. 1997; Joergensen and Scheu 1999).

Statistical analyses

Analyses were performed using R version 3.6.0 (R Core Team 2019). Each data set was checked for normality and homoscedasticity using Shapiro–Wilk test and Bartlett's test (package "stats"). Data was log-transformed if necessary. Changes in M_{loss}, C_{mic}, BR and abundance of Oribatida and Collembola, as well as Oribatida richness were analyzed separately for leaf and root litter using linear mixed-effects models (package "nlme") with sampling date (6 and 12 months), mesh size (45 µm, 1 mm and 4 mm), altitude (1000, 2000 and 3000 m a.s.l.) and all possible interactions fitted as fixed factors, and block fitted as random factor. Differences between means were inspected using Tukey's honestly significant difference test (package "emmeans"). Means presented in text and figures are based on non-transformed data.

Oribatida species with more than three individuals across all samples were used for non-metric multidimensional scaling (stress = 0.04, k = 6; package "vegan"). Multivariate analysis of variance (MANOVA; package "stats") and linear discriminant analyses (LDA;

package "MASS") were used to assess differences on Oribatida community composition among altitudes and mesh sizes in both leaf and root litter. Significant differences between group centroids were identified using Squared Mahalanobis Distances (MD^2).

Canonical correspondence analysis (CCA) performed in CANOCO (Ter Braak and Smilauer 2012) was used to explore the relationship between Oribatida community composition and litter characteristics (M_{loss}, C-to-N ratio) as well as microbial indicators (BR, C_{mic}). Monte Carlo randomization tests using 999 simulations were used to determine the significance of the axes. Sampling date (6 and 12 months), mesh sizes (45 µm, 1 mm and 4 mm) and altitude (1000, 2000 and 3000 m a.s.l.) were coded as supplementary variables not affecting the ordination. Since the global test with all litter and microbial indicators was significant, we used forward selection to identify the most important variables structuring Oribatida communities. This was done to reduce the number of explanatory variables entering the analysis while keeping the variation explained caused by them at a maximum. The forward selection procedure was stopped if a variable reached a level of significance > 0.05.

Results

Decomposition of leaves and roots

Generally, M_{loss} significantly increased during the time of exposure reaching averages of 46.6% ± 10.1% and 46.6% ± 10.7% for leaf and root litter after 12 months, respectively. M_{loss} of leaf litter was not significantly affected by any interaction between the three factors studied, but at both sampling dates it was higher at 1000 and 2000 m compared to 3000 m (Figure 1, Table 1). By contrast, in root litter the interactions between altitude and date, as well as between altitude and mesh size significantly affected M_{loss}. After 6 months root litter M_{loss} was at a maximum at 1000 m and similar in 2000 and 3000 m, whereas after 12 months it decreased in a linear way with increasing altitude. Further, at 3000 m root litter M_{loss} in litterbags of 4 mm mesh size (37.6% ± 5.9%) was higher than in litterbags of 45 µm and 1 mm mesh size (averages of 29.7% ± 8.7% and 26.2% ± 9.5%, respectively),

whereas at 1000 and 2000 m M_{loss} was not affected by mesh size (averages of 46.6% ± 12.7% and 35.8% ± 13.7).

	M_{loss}		C-to-N		C_{mic}		BR	
	F-value	*p*-value	*F*-value	*p*-value	*F*-value	*p*-value	*F*-value	*p*-value
Leaf litter								
Time	**152.01**	**< 0.001**	**21.41**	**< 0.001**	**21.82**	**< 0.001**	**39.37**	**< 0.001**
Mesh size	0.069	0.527	1.05	0.362	**20.21**	**< 0.001**	**6.98**	**0.003**
Altitude	**24.33**	**< 0.001**	**233.30**	**< 0.001**	**16.74**	**< 0.001**	**12.82**	**< 0.001**
Time × mesh size	1.42	0.255	0.02	0.980	0.30	0.741	**5.47**	**0.009**
Time × altitude	2.84	0.072	2.74	0.078	**8.17**	**0.001**	2.46	0.104
Mesh size × altitude	0.55	0.697	0.29	0.882	1.58	0.201	0.76	0.561
Time × mesh size × Altitude	1.13	0.360	0.24	0.911	**3.67**	**0.013**	**8.16**	**< 0.001**
Root litter								
Time	**110.09**	**< 0.001**	0.06	0.806	**167.86**	**< 0.001**	**226.11**	**< 0.001**
Mesh size	0.79	0.461	**4.46**	**0.019**	1.62	0.213	0.96	0.391
Altitude	**30.19**	**< 0.001**	**106.07**	**< 0.001**	**128.27**	**< 0.001**	**32.67**	**< 0.001**
Time × mesh size	0.21	0.808	0.97	0.388	0.90	0.416	2.17	0.129
Time × altitude	**8.01**	**0.001**	0.99	0.382	**18.33**	**< 0.001**	1.14	0.332
Mesh size × altitude	**3.26**	**0.023**	1.61	0.193	**6.81**	**< 0.001**	**6.19**	**< 0.001**
Time × mesh size × Altitude	1.67	0.179	2.42	0.067	**5.47**	**0.001**	1.16	0.343

Table 1. *F*- and *P*-values of linear mixed-effects models on the effect of time of exposure (6 and 12 months), mesh size (45 µm, 1 mm, 4 mm) and altitude (1,000, 2,000 and 3,000 m a.s.l.) on mass loss (M_{loss}), litter C-to-N ratio, microbial biomass (C_{mic}) and basal respiration (BR) in leaf and root litter. Significant effects are given in bold, $p \leq 0.05$.

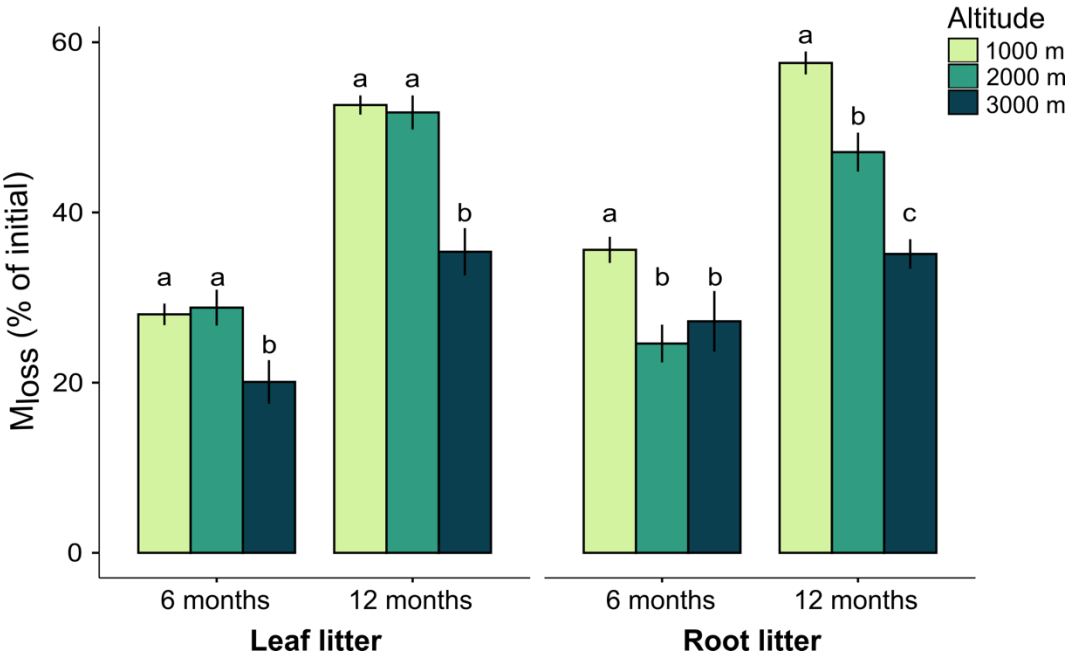

Figure 1. Effect of altitude on mass loss (M_{loss}) after 6 and 12 months. Variations in M_{loss} of leaf and root litter exposed in litterbags at three different altitudes (1000 m, 2000 m, 3000 m) for 6 and 12 months. Values are means ± SE. For each litter type, bars marked with different letters within each time of exposure differ significantly (Tukey's HSD tests, $p < 0.05$).

The C-to-N ratio of both leaf and root litter significantly increased with altitude from 1000 m (23.7 ± 2.9 and 39.6 ± 4.2, respectively) to similar values at 2000 m (59.5 ± 11.7 and 65.1 ± 9.0, respectively) and 3000 m (63.7 ± 7.0 and 69.0 ± 9.6, respectively) (Table 1). In leaf litter the C-to-N ratio decreased from 53.9 ± 22.3 after 6 months to 44.9 ± 17.5 after 12 months, whereas the C-to-N ratio in root litter did not change with the time (overall mean 57.4 ± 14.9). In leaf litter mesh size did not affect the C-to-N ratio, whereas the C-to-N ratio in root litter was lower in litterbags with 45 µm mesh size (53.7 ± 13.1) compared to litterbags with 1 and 4 mm mesh size (59.0 ± 16.0 and 59.5 ± 15.3, respectively).

Microorganisms

Generally, C_{mic} and BR significantly increased from 6 to 12 months of exposure with averages after 12 months of 7.50 ± 1.41 mg C_{mic} g^{-1} dw and 94.31 ± 18.08 µl O_2 g^{-1} dw h^{-1} for leaf litter, respectively, and 8.40 ± 2.66 mg C_{mic} g^{-1} dw and 104.32 ± 23.16 µl O_2 g^{-1} dw

h^{-1} for root litter, respectively. C_{mic} and BR also varied with altitude in both litter types. In leaf litter, C_{mic} was higher at 1000 and 2000 m compared to 3000 m, whereas BR significantly increased in the order 1000 m < 3000 m < 2000 m. In root litter, C_{mic} was higher at 1000 m compared to 2000 and 3000 m, whereas BR was higher at 1000 m compared to 2000 and 3000 m (for means of treatments see Appendix 2).

In leaf litter, variations in C_{mic} and BR with time depended on altitude; both generally were higher at 2000 m compared to 1000 and 3000 m after 6 months of exposure, while after 12 months C_{mic} was higher at 1000 and 2000 m compared to 3000 m and BR did not vary between altitudes (Figure 2, Table 1; for means pooled for mesh size see Appendix 3). However, the effect of altitude also varied with mesh size (significant three factor interaction). In leaf litter at 1000 m C_{mic} and BR were lowest in bags with 1 mm mesh size after 6 months, whereas after 12 months C_{mic} was highest and BR was lowest in 4 mm mesh bags. At 2000 m, C_{mic} and BR were highest in 4 mm mesh bags, whereas after 12 months C_{mic} did not vary with mesh size and BR was highest in 4 mm mesh bags. At 3000 m, C_{mic} and BR were not affected by mesh size after 6 months, whereas after 12 months C_{mic} and BR were lowest in 1 mm mesh bags.

Similar to leaf litter, in root litter variations in C_{mic} with time depended on altitude and mesh size (Figure 2, Table 1; for means of treatments see Appendix 2). At 1000 m, C_{mic} was highest in 45 µm mesh bags after both 6 and 12 months, whereas at 2000 m it was highest in 4 mm mesh bags and did not vary with mesh size after 12 months. At 3000 m, C_{mic} was not affected by mesh size after 6 months, whereas after 12 months it was highest in 1 and 4 mm mesh bags. Also, variations in BR in root litter with altitude depended on mesh size, but the effect was restricted to 1000 and 2000 m where BR was highest in litterbags with 45 µm and 4 mm mesh size (Table 1, Figure 2; for means of treatments see Appendix 2).

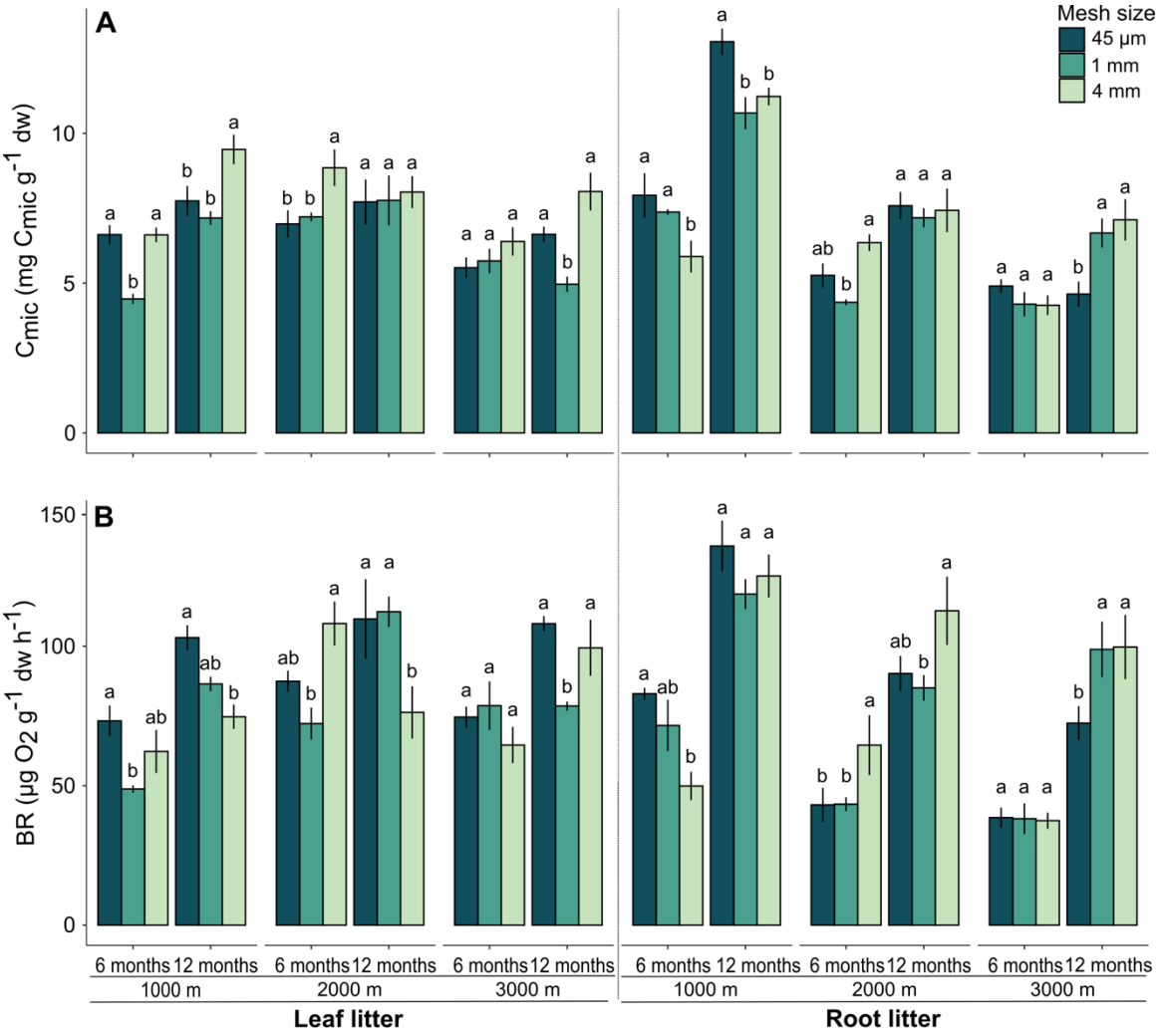

Figure 2. Effect of mesh size and altitude on Cmic and BR after 6 and 12 months of incubation. Variation in (**A**) microbial biomass (C_{mic}) and (**B**) basal respiration (BR) in leaf litter (left panel) and root litter (right panel) at three altitudes (1000, 2000 3000 m a.s.l.) after 6 and 12 months of incubation. Values are means ± SE. For each litter type, altitude and sampling date, bars marked with different letters differ significantly among mesh sizes (Tukey's HSD tests, $p < 0.05$).

Abundance of Collembola and Oribatida

Contrasting C_{mic} and BR, time of exposure as main effect neither affected the abundance of Collembola nor that of Oribatida (Table 2). Rather, the abundance of Collembola and Oribatida in both litter types varied strongly with altitude and mesh size. The most

important factor affecting the abundance of Collembola in both litter types was altitude, whereas the most important factor affecting the abundance of Oribatida was mesh size.

	Collembola		Oribatida			
	Abundance		Abundance		Richness	
	F-value	*p*-value	*F*-value	*p*-value	*F*-value	*p*-value
Leaf litter						
Time	0.09	0.756	0.07	0.783	0.04	0.841
Mesh size	**5.77**	**0.007**	**29.41**	**< 0.001**	**32.13**	**< 0.001**
Altitude	**26.22**	**< 0.001**	**11.80**	**< 0.001**	**21.21**	**< 0.001**
Time × mesh size	0.15	0.857	2.64	0.085	**4.63**	**0.016**
Time × altitude	**3.25**	**0.051**	0.07	0.933	0.48	0.61
Mesh size × altitude	0.34	0.849	0.519	0.722	0.79	0.541
Time × mesh size × Altitude	2.14	0.097	2.41	0.068	**2.82**	**0.039**
Root litter						
Time	0.01	0.895	0.25	0.618	0.01	0.921
Mesh size	2.61	0.088	**33.47**	**< 0.001**	**37.86**	**< 0.001**
Altitude	**53.07**	**< 0.001**	**64.88**	**< 0.001**	**70.23**	**< 0.001**
Time × mesh size	0.14	0.870	0.34	0.71	0.75	0.481
Time × altitude	1.59	0.217	1.78	0.18	2.25	0.121
Mesh size × altitude	**3.81**	**0.011**	**6.01**	**< 0.001**	**3.57**	**0.015**
Time × mesh size × Altitude	1.92	0.129	0.73	0.57	0.77	0.553

Table 2. F- and P-values of linear mixed-effects models on the effect of time of exposure (6 and 12 months), mesh size (45 µm, 1 mm, 4 mm) and altitude (1,000, 2,000 and 3,000 m a.s.l.) on the abundance of Collembola, and the abundance and richness of Oribatida in leaf and root litter. Significant effects are given in bold, $p \leq 0.05$.

Overall, the abundance of Collembola in root litter (60 ± 58 ind. 10 g^{-1} litter dw) exceeded that in leaf litter (31 ± 38 ind. 10 g^{-1} litter dw). Generally, in both litter types the abundance decreased strongly with increasing altitude (Figure 3A, Table 2; for means of treatments see Appendix 4). However, in leaf litter the decrease varied with sampling date and was

restricted to the second sampling where Collembola abundance was higher at 1000 m (41 ± 26 ind. 10 g^{-1} litter dw) compared to 2000 and 3000 m (18 ± 19 and 13 ± 11 ind. 10 g^{-1} litter dw). Further, in leaf litter Collembola abundance was significantly higher in 1 and 4 mm mesh bags compared to 45 µm mesh bags, however, the differences were not pronounced (averages of 32 ± 27, 33 ± 43 and 28 ± 44 ind. 10 g^{-1} litter dw, respectively). In root litter, the abundance of Collembola did not vary significantly with mesh size as main factor but the effect of mesh size depended on altitude; Collembola abundance did not vary with mesh size at 1000 and 2000 m, but at 3000 m it was higher in 1 and 4 mm mesh bags than in 45 µm mesh bags. Generally, high abundance of Collembola in 45 µm mesh bags reflects that Collembola also effectively colonized leaf and root litterbags of this small mesh size.

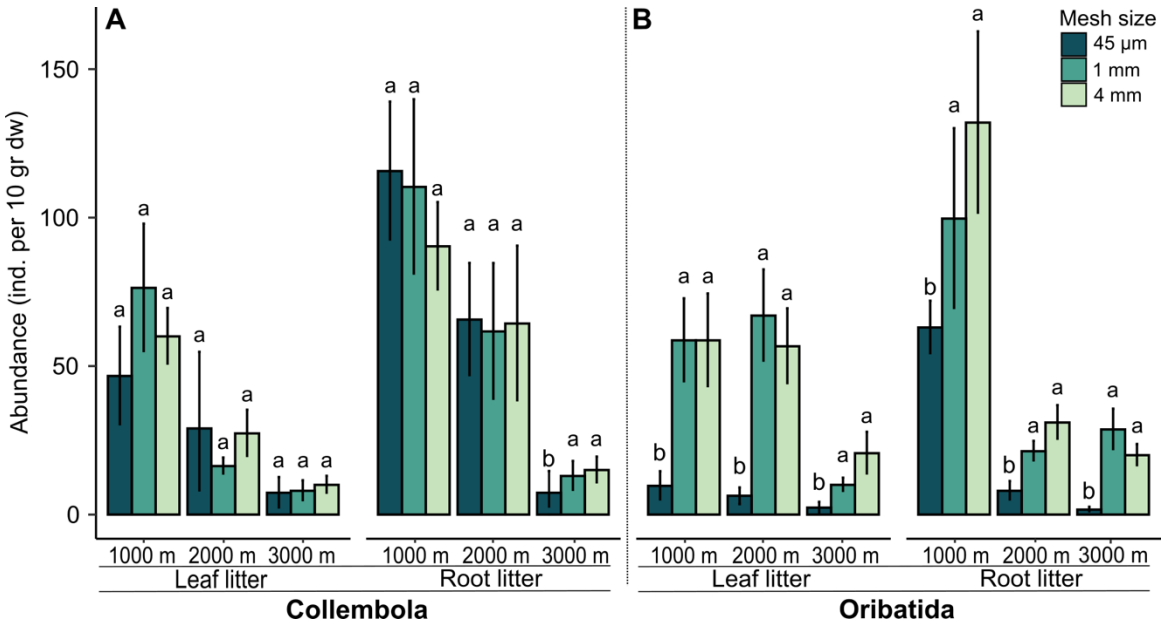

Figure 3. Effect of mesh size and altitude on Collembola and Oribatida abundance in leaf and root litter. Variations in (**A**) Collembola and (**B**) Oribatida abundance in leaf and root litter in litterbags of different mesh size (45 µm, 1 mm and 4 mm) at three altitudes (1000, 2000 and 3000 m). Values are means ± SE. Bars marked with different letters within each altitude differ significantly (Tukey's HSD tests, $p < 0.05$).

Generally, across altitude, sampling time and mesh size the abundance of Oribatida (37 ± 45 ind. 10 g^{-1} litter dw) was similar to that of Collembola (45 ± 51 ind. 10 g^{-1} litter dw).

However, in contrast to Collembola, the overall abundance of Oribatida in leaf and root litter was similar (32 ± 35 and 45 ± 54 ind. 10 g^{-1} litter dw, respectively). Further, contrasting the pattern in Collembola, the abundance of Oribatida in leaf litter was similar at 1000 and 2000 m and significantly lower at 3000 m, whereas in root litter the abundance at 1000 m strongly exceeded that at 2000 and 3000 m (Figure 3B, Table 2; for means of treatments see Appendix 4). Further, in contrast to Collembola, in both litter types the abundance of Oribatida was generally low in litterbags of 45 µm mesh size and similar in litterbags of 1 and 4 mm mesh size. However, in root litter the effect varied with altitude with the abundance of Oribatida in litterbags of 45 µm mesh size being considerably higher at 1000 m than at 2000 and 3000 m.

Species richness of Oribatida

In both leaf and root litter the average Oribatida species richness per litterbag was significantly affected by mesh size and altitude (Table 2). In leaf litter the number of species significantly declined with altitude from 11 ± 8 to 5 ± 1 to 3 ± 2 species 10 g^{-1} at 1000, 2000 and 3000 m, respectively. By contrast, in root litter Oribatida species richness was highest at 1000 m (19 ± 9 species 10 g^{-1} litter) and similarly low at 2000 and 3000 m (6 ± 3 and 5 ± 4 species 10 g^{-1} litter, respectively). In leaf litter, Oribatida species richness was generally higher in litterbags with 1 and 4 mm than in those with 45 µm mesh size at all three altitudes, but at 1000 and 3000 m after 12 months it did not vary between litterbags of different mesh size (significant interaction between time, altitude and mesh size; for means of treatments see Appendix 4). Similar to leaf litter, in root litter Oribatida species richness was higher in litterbags with 1 and 4 mm compared to those with 45 µm mesh size, but the variation depended on altitude with the effect being restricted to 1000 m where mesh size did not affect Oribatida richness.

Community structure of Oribatida

In total, 176 species of Oribatida were identified (see Appendix 5 for full list of species). MANOVA performed with NMDS axis scores indicated that altitude was the most

important factor affecting Oribatida community composition in both leaf and root litter ($F_{2,24}$ = 18.96, P < 0.001 and $F_{2,24}$ = 22.14, P < 0.001, respectively). Sampling date also affected Oribatida community composition in leaf litter ($F_{1,24}$ = 3.62, P = 0.014) but not in root litter. In in both litter types the effect of altitude varied with time ($F_{2,24}$ = 2.72, P = 0.008 for leaf litter and $F_{2,24}$ = 6.20, P < 0.001 for root litter). Mesh size did not affect Oribatida community composition neither in leaf nor in root litter. LDA separated Oribatida communities of the three altitudes in both leaf (Wilks' lambda = 0.08, approx. F = 44.89, p < 0.001; Figure 4A) and root litter (Wilks' lambda = 0.11, approx. F = 47.59, p < 0.001; Figure 4B). In both litter types Oribatida communities at 1000 m were separated from those at 2000 and at 3000 m along the first axis, and Oribatida communities at 2000 m and 3000 m along the second axis (for Mahalanobis distances see Appendix 6).

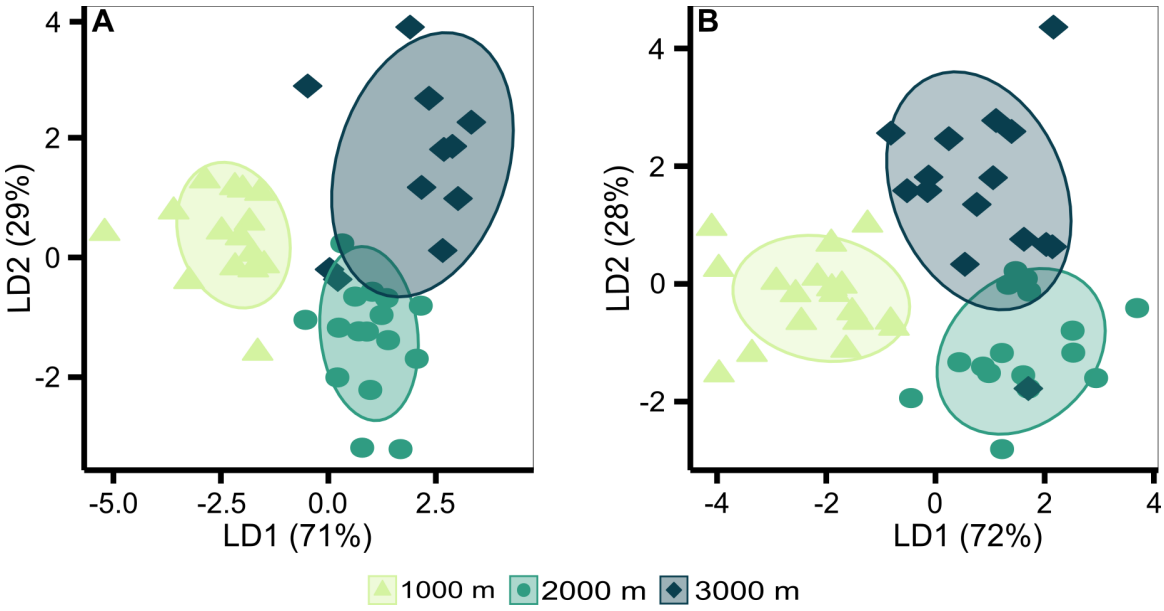

Figure 4. Linear discriminant function analyses (LDA) of Oribatida community composition in litterbags with (**A**) leaf litter and (**B**) root litter exposed at three altitudes (1000, 2000 and 3000 m) (pooled for 6 and 12 months of exposure). Ellipses represent 75% confidence ranges.

CCA of Oribatida species in leaf litter with C-to-N ratio, M_{loss}, BR and C_{mic} included as environmental variables explained 12.7% of the variation of Oribatida community composition (Figure 5A); C-to-N ratio accounted for 4.4% (pseudo F = 1.9, P = 0.002),

M_{loss} for 4.3 % (pseudo F = 1.8, P = 0.002) and BR for 3.9% (pseudo F = 1.6, P = 0.007). Similar to LDA, the 1000 m site was separated from the 2000 and 3000 m sites along the first axis, and the second axis separated the 2000 and 3000 m sites as well as the sampling dates. The community composition of Oribatida at 2000 and 3000 m correlated positively with increasing C-to-N ratio and BR; M_{loss} correlated positively with the first sampling date and was associated with lower species abundance.

CCA of Oribatida species in root litter with C-to-N ratio, BR, M_{loss} and C_{mic} included as environmental variables explained 10.2% of the variation of Oribatida community composition (Figure 5B); C-to-N ratio accounted for 7.0% of the variation (pseudo F = 3.7, P < 0.001) and BR for 3.2 % (pseudo F = 1.6, P = 0.004). As in leaf litter, the 1000 m site was separated from the 2000 and 3000 m sites along the first axis, and the second axis separated the 2000 and 3000 m sites as well as the sampling dates. As in leaf litter, Oribatida species at 2000 and 3000 m correlated positively with increasing C-to-N ratio, but BR correlated positively with the sampling date after 12 months. In both the CCA of leaf and root litter, the centroids of mesh size were close to the center of the ordination reflecting that Oribatida communities in litterbags of different mesh size were similar.

Rostrozetes ovulum ovulum was the only species occurring in leaf and root litter across the three altitudes (Figure 5). From the species occurring in both litter types *Cosmozetes reticulatus*, N*eoamerioppia longiclava*, *Rostrozetes carinatus* and *Hemileius hemileiformis* were most abundant, with the *Cosmozetes reticulatus* and *Hemileius hemileiformis* occurring predominately at 1000 m and 3000 m, respectively. N*eoamerioppia longiclava* and *Rostrozetes carinatus* were especially abundant in leaf litter at 2000 m (in total >100 and > 40 individuals sampled, respectively). Most other species were rare and only occurred at certain altitudes; for the abundance of species at each of the study sites see Appendix 5.

Of the species present only in leaf litter, *Neoamerioppia rotunda*, *Microtegeus borhidii*, *Sellnickochthonius elsosneadensis*, *Epieremulus* sp.1 and *Neoamerioppia longicoma* were most abundant (in total 24, 12, 11, 10 and 8 individuals sampled, respectively) (Figure 5A). *Sellnickochthonius elsosneadensis* only occurred at 1000 m and *Neoamerioppia rotunda* and *Epieremulus* sp.1 only occurred at 2000 m. *Microtegeus borhidii* occurred at 1000 and 3000 m, whereas *Neoamerioppia longicoma* only occurred at 2000 and 3000 m, but both

were especially abundant at 3000 m. *Rostrozetes* sp.6 and *Lanceoppia* sp.1 were associated with the second sampling date and were only present at 2000 m.

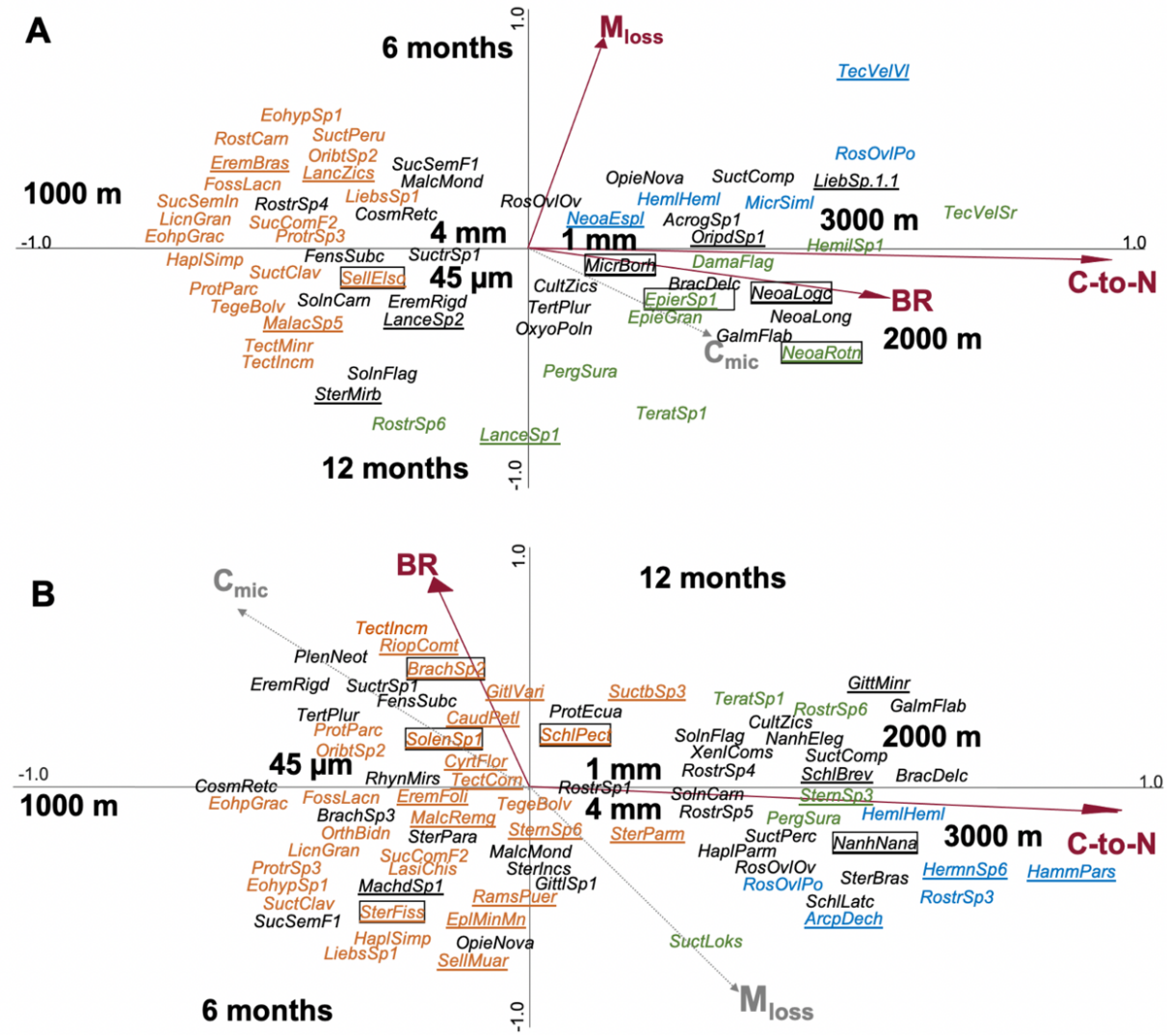

Figure 5. Canonical correspondence analysis (CCA) of Oribatida species in litterbags with (**A**) leaf and (**B**) root litter and their relationship with environmental variables (forward selection). Arrows in red represent significant environmental variables. Species present only at one of the three altitudes are marked in color (orange = 1000 m, green = 2000 m, blue = 3000 m); others are given in black. Species present in only one litter type are underlined and of them the most abundant species (>10 individual across the samples) are framed; for full species names see Appendix 5.

In root litter, *Solenozetes* sp.1, *Brachioppiella sp.2*, *Schalleria pectinata*, *Sternoppia fissurata* and *Nanhermannia nana* form.1 were most abundant (in total 52, 46, 22, 14 and 13 individuals sampled, respectively) with the first two being especially abundant at 1000 m (Figure 5B). *Nanhermannia nana* form.1 was only present at 2000 and 3000 m.

Discussion

Variations of leaf and root litter decomposition with altitude

In contrast to our first hypothesis, M_{loss} of both leaf and root litter showed different patterns of decomposition along the altitudinal gradient. In leaf litter, M_{loss} did not follow the expected linear decrease with altitude, rather, decomposition rates at 1000 and 2000 m were similar after the 12 months of exposure. This contrasts previous studies at our study sites (Illig et al. 2008; Marian et al. 2017, 2019) and indicates that leaf litter decomposition cannot be explained only by the linear decrease of temperature along the altitudinal gradient studied. Potentially, the decline in leaf litter decomposition with temperature was compensated by higher precipitation at 2000 m compared to 1000 m (see Methods). High rainfall facilitates decomposition especially at early stages by increasing leaching of soluble compounds (Cusack et al. 2009). However, although climate is considered the primary driver of litter decomposition at large scales (Coûteaux et al. 1995; Aerts 1997), the role of climatic factors might be overridden by the variability of litter traits at local scales (Scowcroft et al. 2000; Richardson et al. 2005; Fujii et al. 2017). In our study, litter characteristics such as C-to-N ratio differed strongly between the leaf litter materials exposed at the three altitudes. However, as indicated by the C-to-N ratio, leaf litter materials from the 1000 m site were of considerably higher quality than those from the 2000 m site (as well as the 3000 m site), suggesting that the high decomposition rates of leaf litter at 2000 m also cannot be explained by litter quality. Potentially, leaf litter M_{loss} was modified by physicochemical interactions among the three leaf litter species placed in the litterbags and biotic factors such as microbial community composition. The fact that C_{mic} and BR were higher in leaf litter at 2000 m than at 1000 m after 6 months of exposure supports this conclusion and suggests that the leaf litter mixtures favoured the activity and abundance of

microbial communities early after exposure. The generally high values of C_{mic} and BR in leaf litter at 2000 and 3000 m, despite the very high litter C-to-N ratio, also suggests that microbial communities at these sites are well adapted to decompose litter of low quality (Gholz et al. 2000; Strickland et al. 2009; Milcu and Manning 2011; Marian et al. 2017).

In contrast to leaf litter, root litter showed the expected linear decrease in litter decomposition with increasing altitude after 12 months. Less favorable abiotic conditions, such as those at higher altitude, might affect root litter decomposition by reducing the quality of the litter material and thereby nutrient availability as reported for tropical rainforests (Vitousek et al. 1994; Tanner et al. 1998; Kitayama et al. 2004). This is supported by the high C-to-N ratios and low C_{mic} and BR, as well as abundance of decomposer microarthropods at 2000 and 3000 m (compared to 1000 m). This contrasting results between leaf and root litter decomposition rates suggest that in the studied tropical montane rainforest ecosystems, differences in the availability of nutrients and associated nutrient limitations among the altitudinal sites appear to be more important factors for the decomposition of root litter than for leaf litter. Moreover, leaf litter might be more susceptible than roots to effects of climatic variations as leaf litter is located on top of the soil and thereby exposed to more variable microclimatic conditions than root litter in soil (Ostertag and Hobbie 1999; Silver and Miya 2001). However, as root litter generally decomposed slower than leaf litter at 2000 and 3000 m, more buffered conditions in soil do not implicate an override of the primacy of nutrient limitations as driving factor of litter decomposition. Nonetheless, at 1000 m the more buffered climatic condition together with the close proximity of the mineral soil layer at 1000 m might have favoured the faster decomposition rates of roots than leaf litter.

Faunal contribution to leaf and root litter decomposition along the altitudinal gradient

The abundance of both Collembola and Oribatida were higher in 1 and 4 mm mesh bags irrespective of the plant litter type indicating that, as intended, 45 µm mesh size restricted the access of the litterbags by mesofauna. Thus, the different mesh sizes are a useful tool to evaluate the effects of microarthropods on decomposition processes. However,

restricting the access of the litterbags by 45 µm mesh size was more effective in Oribatida than in Collembola indicating that the mesh size approach is limited for evaluating the role of mesofauna for decomposition processes and suggesting that it likely underestimates their effects on litter decomposition as discussed earlier (Bradford et al. 2002; Kampichler and Bruckner 2009). Further, contrasting our second hypothesis, access of microarthropods to litterbags containing leaf litter did not result in different decomposition rates at any of the three altitudes, however, arthropod access to root litter increased root litter mass loss at 3000 m (4 mm mesh bags). Despite the widely assumed beneficial effects of soil microarthropods on litter decomposition, experimental evidence supporting this assumption is mixed; some studies indeed found positive effects on litter mass loss (Bradford et al. 2002; Carrillo et al. 2011; Bokhorst and Wardle 2013), while others suggest their contribution to be minor or lacking entirely (Schinner 1982; Joo et al. 2003; Kampichler and Bruckner 2009; Marian et al. 2019). Overall, our results support the latter and previous findings at our study sites also indicating that the decomposition of leaf litter predominantly is due to microorganisms, with the contribution of microarthropods being minor, in particular at early stages of litter decomposition (Illig et al. 2008; Marian et al. 2017, 2019). Both decomposer groups, Oribatida and Collembola, might play a more important role at more advanced stages of decomposition when the litter has been colonized by microorganisms thereby making it more palatable for arthropod consumers (Bardgett 2005; Coulis et al. 2009; Das and Joy 2009). However, the fact that the abundance of both decomposer microarthropods did not vary significantly with sampling date indicates that the nutritional value of the litter material for decomposer microarthropods changed little during the 12 months of exposure.

Notably, contrasting M_{loss}, C_{mic} and BR varied with mesh size in both leaf and root litter with the effect in root but not in leaf litter varying with altitude. Generally, C_{mic} was higher in 1 and 4 mm mesh bags, while BR was higher in 45 µm mesh bags. Overall, this contrasts our expectation that decomposer microarthropods are grazing on microorganisms thereby reducing their biomass. However, as suggested earlier this view might be oversimplistic as grazing on microorganisms may also result in increased mobilization of nutrients, thereby facilitating microbial growth (Seastedt 1984; Hättenschwiler et al. 2005). Further, grazing may result in changes in microbial community composition resulting in more effective use

of resources by microorganisms and this may explain the reduced BR in litterbags with coarse mesh size. Indeed, it has been stressed earlier that the structure of microbial communities is an important determinant of litter decomposition rates in particular in forest ecosystems (Strickland et al. 2009).

Increased M_{loss} of root litter at 3000 m in 4 mm compared to 1 mm and 45 µm mesh bags suggests that under unfavourable environmental conditions the decomposition of low-quality litter is stimulated by soil arthropods. A number of processes may have accelerated litter decomposition including stimulation of microbial growth via nutrient mobilization, litter fragmentation and dispersal of microbial propagules (Verhoef and Brussaard 1990; Ruess and Lussenhop 2005; Scheu et al. 2005). The fact that at 3000 m C_{mic} and BR in roots increased in 1 and 4 mm mesh bags supports this conclusion and suggests that the contribution of arthropods to decomposition of recalcitrant substrates is more pronounced than in readily decomposable materials (Joo et al. 2006; Milcu and Manning 2011; Gergócs and Hufnagel 2016). Additionally, at our study sites, the role of root exudates and mycorrhizal fungi are increasingly recognized as drivers of litter decomposition, mineralization processes and determinants of soil food webs (Marian et al. 2019; Sánchez-Galindo et al. 2019). Therefore, at 3000 m, where the concentration of root biomass is at a maximum (Röderstein et al. 2005; Soethe et al. 2007), soil arthropods may benefit more from root-derived resources than at 1000 and 2000 m either by grazing on microorganisms or directly by feeding on roots.

Oribatida diversity and community structure in leaf and root litter

Similar to Oribatida abundance, the higher number of Oribatida species in litterbags of 1 and 4 mm mesh size in both litter types might be attributed to restricted access of microarthropods to the 45 µm mesh litterbags. However, Oribatida species richness mostly varied with altitude in both leaf and root litter. The significant decrease in Oribatida species richness with increasing altitude in leaf litter supports results of previous studies at our study sites in that species richness of Oribatida in leaf litter is driven predominantly by factors linked to altitude (Illig et al. 2008; Marian et al. 2018). By contrast, in root litter the high number of Oribatida species at 1000 m and the similarly low numbers at 2000 and

3000 m suggests that apart from abiotic conditions changing with altitude other factors modify Oribatid species richness. The fact that C-to-N ratios of root litter were similar at 2000 and 3000 m support this conclusion and suggests that root litter quality may function as regulator of Oribatida richness; potentially, high amounts of slightly decomposed low quality root litter material detrimentally affect Oribatida richness at 2000 and 3000 m (Röderstein et al. 2005; Maraun et al. 2013). Contrasting our third hypothesis, higher Oribatida species richness at 1000 m in roots compared to leaves might be related to the placement of the litterbags with more stable environmental conditions in roots favouring Oribatida richness (Fujii and Takeda 2010). Moreover, the close vicinity of the mineral soil layer to root litter at 1000 m might have favoured nutrient availability and decomposition of roots, and thereby improved food resources of Oribatida (Marian et al. 2019). Indeed, Illig et al. (2010) also concluded that Oribatida species richness at the studied montane rainforests is related to litter quality as important driving factor.

Contrasting Oribatida abundance and richness, Oribatida community structure did not differ between litterbags of different mesh size. Rather, Oribatida community assemblages varied mostly with altitude in both leaf and root litter. Most of the 176 species identified were associated with the 1000 m site, only few species were only present at 2000 and 3000 m, presumably reflecting less favorable climatic conditions and poor resource quality at the high altitude sites (Marian et al. 2018). Interestingly, in leaf litter certain Oribatida species including *Sternoppia mirbilis*, *Lanceoppia* sp.1 and *Rostrozetes* sp.6 preferentially colonized litter at later stages of decomposition (12 months) with the latter two species exclusively recorded at 2000 m. This contrast our fourth hypothesis indicating that certain Oribatida species rely on food resources associated with litter at later stages of decomposition particularly at higher elevations, suggesting that Oribatida species diversity at least in part is due to resource partitioning (Marian et al. 2018). This is supported by our finding that litter C-to-N ratio functions as important factor structuring Oribatida communities in both leaf and root litter. Contrasting leaf litter, changes in root litter with time did not affect Oribatida community structure, despite changes in C_{mic} and BR with time were more pronounced in root than in leaf litter. This suggests that Oribatida community structure is not closely linked with gross characteristics of microbial communities such as C_{mic} and BR, which is also supported by the fact that both C_{mic} and

BR varied strongly with time of exposure of the litter, whereas Oribatida community characteristics did not or only little (and the same was true for Collembola abundance). Overall, this indicates that the community structure of Oribatida is driven mainly by food quality, i.e. litter C-to-N ratio, as well as microbial community composition, rather than the amount of microorganisms as food resource (Fujii and Takeda 2017; Marian et al. 2018).

Conclusion

The results of our study suggest that the decomposition of both leaf and root litter in montane rainforests is mainly due to microorganisms, whereas the effect of microarthropods is minor across a wide altitudinal gradient. However, at high altitude soil microarthropods may accelerate the decomposition of low-quality litter such as root litter. Generally, abundance of both Collembola and Oribatida, and community composition of Oribatida varied not or little with time of exposure of leaf and root litter, contrasting the patterns of microbial biomass and highlighting that the abundance of microorganisms as food is of minor importance as structuring force of decomposer microarthropod communities. Rather, the results point to the dominance of litter quality, i.e. litter C-to-N ratio, as dominant force structuring Oribatida communities. Overall, our findings highlight that the role of climatic factors for decomposition of leaf and root litter might be overridden at the local scale by litter traits suggesting that differences in litter quality and the nutritional requirements of decomposer communities are important drivers of litter decomposition and nutrient cycling in tropical montane rainforest ecosystem.

Acknowledgements

We thank the Deutsche Forschungsgemeinschaft (DFG; FOR816) for financial support. Further, we thank the Ministerio de Ambiente del Ecuador and the Universidad Técnico Particular de Loja (UTPL) for the research permits and the center Naturaleza y Cultura Internacional (NCI) to allow us to work in the San Francisco reserve. We thank student helpers for the collaboration during the field work, Kristina Barnes and Stephan Töppich for their work in the laboratory and Tamara Hartke and Jingzhong Lu for helpful comments.

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Appendix

Appendix 1. Leaf and root litter mixtures per litterbags at the three altitudes (1000, 2000 and 3000 m).

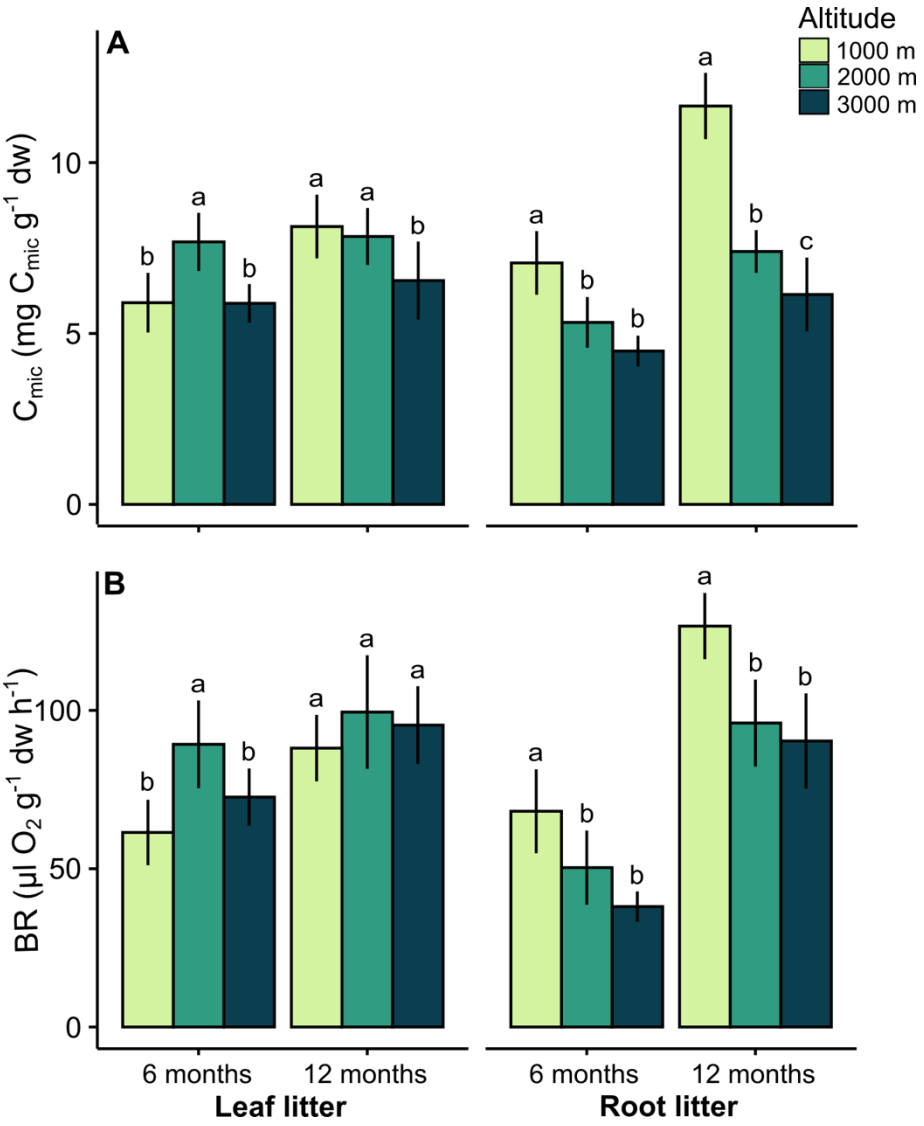
Site	Litter type	Species	Mass (g)	Total (g)
1000 m	Leaves	*Pouteria* sp.	5.0	10
		Cecropia sp.	3.0	
		Mollinedia sp.	2.0	
	Roots	Small	2.7	10
		Medium	4.8	
		Large	2.5	
2000 m	Leaves	*Graffenrieda emarginata*	5.0	10
		Clusia sp.	4.0	
		Cavendishia zamorensis	1.0	
	Roots	Small	4.4	10
		Medium	2.1	
		Large	3.5	
3000 m	Leaves	*Clusia* sp.	5.0	10
		Graffenrieda emarginata	4.0	
		Hedyosmum sp.	1.0	
	Roots	Small	3.4	10
		Medium	2.5	
		Large	4.1	

Appendix 2. Microbial biomass (C_{mic}) and basal respiration (BR) in leaf and root litter in litterbags of 45 µm, 1 mm and 4 mm mesh exposed at 1000, 2000 and 3000 m for 6 and 12 months. Values are means ± SD.

			Leaf litter		Root litter	
			C_{mic} [mg C_{mic} g^{-1} dw]	BR [µl O_2 g^{-1} dw h^{-1}]	C_{mic} [mg C_{mic} g^{-1} dw]	BR [µl O_2 g^{-1} dw h^{-1}]
Time						
6 months			6.48 ± 1.29	74.46 ± 18.28	5.63 ± 1.43	52.18 ± 18.26
12 months			7.50 ± 1.41	94.31 ± 18.08	8.40 ± 2.66	104.33 ± 23.16
Mesh size						
45 µm			6.89 ± 1.03	92.71 ± 18.55	7.23 ± 3.07	77.21 ± 34.54
1 mm			6.22 ± 1.40	79.53 ± 20.68	6.76 ± 2.27	75.97 ± 31.12
4 mm			7.90 ± 1.36	80.91 ± 21.01	7.05 ± 2.31	81.58 ± 36.20
Altitude						
1000 m			7.01 ± 1.61	74.77 ± 18.99	9.36 ± 2.65	97.39 ± 33.65
2000 m			7.76 ± 1.06	94.39 ± 20.90	6.36 ± 1.37	73.18 ± 28.48
3000 m			6.22 ± 1.18	83.99 ± 17.96	5.31 ± 1.35	64.20 ± 30.37
Time × mesh size						
6 months	45 µm		6.37 ± 0.87	78.43 ± 9.49	6.03 ± 1.62	54.89 ± 22.10
	1 mm		5.81 ± 1.25	66.60 ± 16.37	5.34 ± 1.57	51.04 ± 18.26
	4 mm		7.28 ± 1.37	78.34 ± 24.96	5.50 ± 1.12	50.63 ± 15.81
12 months	45 µm		7.36 ± 0.97	106.98 ± 13.51	8.43 ± 3.76	99.54 ± 30.40
	1 mm		6.63 ± 1.50	92.47 ± 16.25	8.18 ± 2.01	100.89 ± 18.05
	4 mm		8.52 ± 1.09	83.48 ± 17.31	8.59 ± 2.18	112.54 ± 19.45
Time × altitude						
6 months	1000 m		5.90 ± 1.13	61.45 ± 13.44	7.07 ± 1.21	68.15 ± 17.25
	2000 m		7.68 ± 1.11	89.29 ± 18.02	5.33 ± 0.97	50.35 ± 15.24
	3000 m		5.88 ± 0.73	72.62 ± 11.77	4.49 ± 0.59	38.05 ± 6.22
12 months	1000 m		8.13 ± 1.21	88.10 ± 13.65	11.65 ± 1.26	126.62 ± 13.60
	2000 m		7.84 ± 1.08	99.48 ± 23.35	7.40 ± 0.81	96.01 ± 17.87
	3000 m		6. 55 ± 1.48	95.35 ± 16.01	6.14 ± 1.41	90.35 ± 19.55
Mesh size × altitude						
45 µm	1000 m		7.18 ± 0.89	88.15 ± 18.09	10.50 ± 2.96	109.46 ± 30.77
	2000 m		7.34 ± 1.03	98.62 ± 20.28	6.42 ± 1.44	66.68 ± 27.52
	3000 m		6.07 ± 0.77	91.35 ± 19.04	4.77 ± 0.54	55.50 ± 20.10
1 mm	1000 m		5.83 ± 1.51	67.66 ± 20.88	9.02 ± 1.90	95.16 ± 28.32
	2000 m		7.49 ± 0.97	92.33 ± 23.60	5.77 ± 1.59	64.23 ± 23.55
	3000 m		5.35 ± 0.68	78.62 ± 9.70	5.49 ± 1.47	68.51 ± 35.51
4 mm	1000 m		8.04 ± 1.67	68.51 ± 11.83	8.56 ± 3.00	87.54 ± 42.46
	2000 m		8.45 ± 0.99	92.21 ± 22.02	6.89 ± 1.04	88.63 ± 31.83
	3000 m		7.22 ± 1.26	82.01 ± 23.15	5.69 ± 1.77	68.58 ± 36.52
Time × mesh size × Altitude						
6 months	45 µm	1000 m	6.62 ± 0.55	73.23 ± 9.53	7.93 ± 1.28	82.97 ± 3.69
		2000 m	6.98 ± 0.78	87.46 ± 6.52	5.26 ± 0.69	43.13 ± 10.54
		3000 m	5.52 ± 0.60	74.60 ± 6.51	4.90 ± 0.40	38.55 ± 6.15
	1 mm	1000 m	4.47 ± 0.29	48.82 ± 2.23	7.37 ± 0.16	71.59 ± 15.91

		2000 m	7.21 ± 0.25	72.29 ± 9.90	4.36 ± 0.18	43.37 ± 4.33
		3000 m	5.74 ± 0.71	78.69 ± 15.08	4.30 ± 0.70	38.15 ± 9.50
	4 mm	1000 m	6.61 ± 0.42	62.30 ± 13.34	5.89 ± 0.92	49.89 ± 8.71
		2000 m	8.85 ± 1.06	108.13 ± 13.68	6.35 ± 0.49	64.55 ± 18.58
		3000 m	6.39 ± 0.82	64.58 ± 11.24	4.26 ± 0.57	37.44 ± 5.05
12 months	45 µm	1000 m	7.75 ± 0.86	103.08 ± 7.71	13.06 ± 0.76	135.95 ± 15.77
		2000 m	7.71 ± 1.29	109.78 ± 24.73	7.59 ± 0.80	90.23 ± 10.89
		3000 m	6.63 ± 1.45	108.09 ± 4.75	4.64 ± 0.72	72.45 ± 10.52
	1 mm	1000 m	7.18 ± 0.40	86.49 ± 4.51	10.68 ± 0.93	118.72 ± 9.24
		2000 m	7.76 ± 1.44	112.37 ± 9.46	7.18 ± 0.55	85.09 ± 7.89
		3000 m	4.96 ± 0.44	78.54 ± 2.82	6.67 ± 0.84	98.87 ± 17.27
	4 mm	1000 m	9.46 ± 0.85	74.71 ± 7.50	11.23 ± 0.51	125.19 ± 13.35
		2000 m	8.04 ± 0.92	76.29 ± 16.28	7.43 ± 1.26	112.70 ± 21.19
		3000 m	8.06 ± 1.09	99.43 ± 17.40	7.11 ± 1.20	99.73 ± 19.98

Appendix 3. Effect of altitude on **(A)** microbial biomass (C_{mic}) and **(B)** basal respiration (BR) after 6 and 12 months. Values are means ± SE. For each litter type, bars marked with different letters within each harvesting time differ significantly (Tukey's HSD tests, $p < 0.05$).



Appendix 4. Collembola and Oribatida abundance and Oribatida species richness in leaf and root litter in litterbags of 45 µm, 1 mm and 4 mm mesh exposed at 1000, 2000 and 3000 m for 6 and 12 months. Values are means ± SD.

			Leaf litter			Root litter		
			Collembola [ind. 10 g^{-1}]	**Oribatida [ind. 10 g^{-1}]**	**Oribatida richness**	**Collembola [ind. 10 g^{-1}]**	**Oribatida [ind. 10 g^{-1}]**	**Oribatida richness**
Time								
6 months			38 ± 49	37 ± 40	7 ± 8	65 ± 66	53 ± 70	11 ± 11
12 months			24 ± 23	27 ± 28	6 ± 5	55 ± 51	37 ± 33	9 ± 7
Mesh size								
45 µm			28 ± 45	6 ± 9	2 ± 3	63 ± 61	24 ± 31	5 ± 5
1 mm			34 ± 43	45 ± 38	9 ± 7	62 ± 65	50 ± 55	12 ± 8
4 mm			32 ± 27	45 ± 34	7 ± 7	57 ± 52	61 ± 67	13 ± 10
Altitude								
1000 m			61 ± 40	42 ± 37	11 ± 8	105 ± 55	98 ± 66	19 ± 9
2000 m			24 ± 37	43 ± 38	7 ± 5	64 ± 53	20 ± 14	6 ± 3
3000 m			8 ± 9	11 ± 13	2 ± 2	13 ± 14	17 ± 16	5 ± 4
Time × mesh size								
6 months	45 µm		41 ± 60	4 ± 6	1 ± 1	80 ± 76	24 ± 29	5 ± 5
	1 mm		41 ± 56	58 ±44	11 ± 8	67 ± 80	58 ± 74	12 ± 10
	4 mm		33 ± 30	49 ± 36	10 ± 8	48 ± 35	78 ± 88	15 ± 13
12 months	45 µm		14 ± 15	9 ± 10	3 ± 4	45 ± 39	24 ± 35	5 ± 5
	1 mm		26 ± 26	32 ± 27	8 ± 5	56 ± 49	42 ± 30	11 ± 7
	4 mm		32 ± 26	42 ± 33	8 ± 6	65 ± 66	44 ± 32	11 ± 7
Time × altitude								
6 months	1000 m		80 ± 44	58 ± 46	13 ± 11	122 ±67	124 ± 83	22 ± 11
	2000 m		30 ± 49	44 ± 40	6 ± 4	66 ± 47	21 ± 13	6 ± 3
	3000 m		4 ± 4	9 ± 7	2 ± 2	8 ± 11	15 ± 14	4 ± 3
12 months	1000 m		42 ± 26	26 ± 16	9 ± 5	89 ± 36	72 ± 28	16 ± 6
	2000 m		18 ± 20	43 ± 39	7 ± 6	62 ± 61	20 ± 16	6 ± 4
	3000 m		13 ± 11	13 ± 17	2 ± 2	15 ± 16	19 ± 18	5 ± 5
Mesh size × altitude								
45 µm	1000 m		47 ± 41	10 ± 12	4 ± 4	116 ± 57	63 ± 22	12 ± 3
	2000 m		29 ± 63	6 ± 7	2 ± 2	66 ± 47	8 ± 8	3 ± 1
	3000 m		7 ± 13	2 ± 5	1 ± 1	7 ± 18	2 ± 2	1 ± 1
1 mm	1000 m		76 ± 53	59 ± 35	15 ± 7	110 ± 72	100 ± 75	20 ± 10
	2000 m		16 ± 7	67 ± 38	9 ± 4	62 ± 56	21 ± 9	7 ± 1
	3000 m		8 ± 9	10 ± 6	3 ± 2	13 ± 12	29 ± 17	8 ± 4
4 mm	1000 m		60 ± 23	59 ± 39	15 ± 8	90 ± 37	132 ± 75	25 ± 8
	2000 m		27 ± 20	57 ± 31	9 ± 3	64 ± 64	31 ± 14	9 ± 4
	3000 m		10 ± 7	21 ± 18	3 ± 2	15 ± 11	20 ± 9	5 ± 2
Time × mesh size × Altitude								
6 months	45 µm	1000 m	68 ± 50	1 ± 1	0 ± 1	149 ± 59	61 ± 5	11 ± 4
		2000 m	55 ± 89	9 ± 9	2 ± 2	92 ± 52	11 ± 12	3 ± 2
		3000 m	0 ± 0	1 ± 1	0 ± 1	0 ± 0	1 ± 1	0 ± 1
	1 mm	1000 m	101 ± 64	88 ± 19	20 ± 8	129 ± 103	128 ± 102	24 ± 11

		2000 m	17 ± 6	75 ± 50	8 ± 3	68 ± 61	23 ± 10	7 ± 2
		3000 m	5 ± 3	11 ± 5	4 ± 1	5 ± 3	23 ± 17	5 ± 2
	4 mm	1000 m	72 ± 8	86 ± 28	19 ± 6	87 ± 21	184 ± 74	32 ± 6
		2000 m	18 ± 9	47 ± 24	8 ± 1	37 ± 9	28 ± 14	8 ± 4
		3000 m	8 ± 4	14 ± 6	3 ± 1	20 ± 14	21 ± 7	5 ± 2
12 months	45 µm	1000 m	25 ± 16	19 ± 11	7 ± 4	82 ± 37	65 ± 34	12 ± 3
		2000 m	3 ± 3	3 ± 3	2 ± 2	39 ± 26	5 ± 3	3 ± 2
		3000 m	15 ± 16	4 ± 7	1 ± 2	15 ± 25	3 ± 3	1 ± 2
	1 mm	1000 m	51 ± 32	29 ± 8	11 ± 2	92 ± 38	71 ± 33	17 ± 8
		2000 m	15 ± 9	59 ± 31	10 ± 5	55 ± 65	19 ± 8	6 ± 2
		3000 m	11 ± 12	9 ± 8	2 ± 2	21 ± 14	34 ± 19	10 ± 4
	4 mm	1000 m	48 ± 30	31 ± 27	10 ± 8	93 ± 48	80 ± 24	19 ± 2
		2000 m	37 ± 25	66 ± 40	10 ± 5	91 ± 90	34 ± 17	9 ± 4
		3000 m	12 ± 11	27 ± 25	3 ± 3	10 ± 6	19 ± 13	5 ± 3

Appendix 5. List of Oribatida species, abbreviations used in Figure 5 and their abundance in leaf and root litter.

No.	Species	Abbreviation	Leaves	Included in CCA leaves	Abundance in leaves	Roots	Included in CCA roots	Abundance in roots
1	*Acrogalumna cubana*		x	-	2	-	-	0
2	*Acrogalumna n sp 1*	*AcrogSp1*	x	x	6	x	-	2
3	*Amazoppia tricuspidata*		-	-	0	x	-	2
4	*Arceremaeus incaensis*		x	-	2	-	-	0
5	*Arcoppia dechambrierorum*	*ArcpDech*	-	-	0	x	x	3
6	*Arcoppia tripartita*		-	-	0	x	-	1
7	*Beckiella elongata*		x	-	1	-	-	0
8	*Brachioppia deliciosa*	*BracDelc*	x	x	6	x	x	13
9	*Brachioppia n sp 2*		-	-	0	x	-	1
10	*Brachioppia sp 3*	*BrachSp3*	x	-	2	x	x	22
11	*Brachioppiella n sp 2*	*BrachSp2*	-	-	0	x	x	46
12	*Campachipteria brevisetosa*		x	-	1	-	-	0
13	*Caudamaeolus petalus*	*CaudPetl*	-	-	0	x	x	3
14	*Ceratorchestes globosus*		x	-	2	-	-	0
15	*Ceratorchestes sp 1*		x	-	1	-	-	0
16	*Ceratozetes n sp 1*		x	-	1	-	-	0
17	*Cosmozetes n sp 2*		x	-	1	-	-	0
18	*Cosmozetes n sp 3*		x	-	1	-	-	0
19	*Cosmozetes reticulatus*	*CosmRetc*	x	x	35	x	x	37
20	*Crotonia reticulata*		x	-	1	-	-	0
21	*Cultroribula zicsii*	*CultZics*	x	x	7	x	x	6
22	*Cyrthermannia florence*	*CyrtFlor*	-	-	0	x	x	12
23	*Damaeus flagellatus*	*DamaFlag*	x	x	5	x	-	1
24	*Dynatozetes n sp 1*		-	-	0	x	-	2
25	*Enarthronota n sp 1*		x	-	1	x	-	2
26	*Eohypochthonius gracilis*	*EohpGrac*	x	x	5	x	x	39
27	*Eohypochthonius n sp 1*	*EohypSp1*	x	x	3	x	x	11
28	*Epidamaeus meridianus*		-	-	0	x	-	1
29	*Epieremulus granulatus*	*EpieGran*	x	x	7	x	-	1
30	*Epieremulus longiseta*		x	-	2	-	-	0
31	*Epieremulus n sp 1*	*EpierSp1*	x	x	10	-	-	0

No.	Species	Abbreviation	Leaves	Included in CCA leaves	Abundance in leaves	Roots	Included in CCA roots	Abundance in roots
32	*Epilohmannia minuta minuta*	*EplMinMn*	-	-	0	x	x	6
33	*Eremobelba foliata*	*EremFoli*	-	-	0	x	x	5
34	*Eremulus brasiliensis*	*EremBras*	x	-	3	-	-	0
35	*Eremulus rigidisetosus*	*EremRigd*	x	x	7	x	x	5
36	*Fenestrobelba subcomplexa*	*FensSubc*	x	x	8	x	x	6
37	*Fosseremus laciniatus*	*FossLacn*	x	x	3	x	x	8
38	*Galumna flabellifera*	*GalmFlab*	x	x	10	x	x	5
39	*Galumna n sp 1*		-	-	0	x	-	1
40	*Gehypochthonius n sp 1*		x	-	1	x	-	2
41	*Gitella variabilis*	*GitlVari*	-	-	0	x	x	6
42	*Gittella maxima*		-	-	0	x	-	2
43	*Gittella minor*	*GittMinr*	-	-	0	x	x	3
44	*Gittella n sp 1*	*GittlSp1*	x	-	1	x	x	9
45	*Hammerella parasufflata*	*HammPars*	-	-	0	x	x	5
46	*Haplobelba n sp 1*		-	-	0	x	-	1
47	*Haplobelba simplex*	*HaplSimp*	x	x	4	x	x	9
48	*Haplozetes paraminimicoma*	*HaplParm*	x	-	1	x	x	10
49	*Hemileius hemileiformis*	*HemlHeml*	x	x	18	x	x	6
50	*Hemileius n sp 1*	*HemilSp1*	x	x	28	x	-	2
51	*Hemileius parvus*		x	-	1	x	-	2
52	*Heminothrus castaneus*		x	-	1	-	-	0
53	*Hermannobates bifurcatus*		x	-	1	x	-	1
54	*Hermannobates monstruosus*		-	-	0	x	-	1
55	*Hermannobates n sp 6*	*HermnSp6*	-	-	0	x	x	3
56	*Kokoppia dudichi*		x	-	1	x	-	2
57	*Kokoppia euramosa*		-	-	0	x	-	2
58	*Lanceoppia n sp 1*	*LanceSp1*	x	x	3	-	-	0
59	*Lanceoppia n sp 2*	*LanceSp2*	x	x	6	-	-	0
60	*Lanceoppia zicsica*	*LancZics*	x	x	3	-	-	0
61	*Lasiobelba chistyakovi*	*LasiChis*	x	-	1	x	x	41
62	*Lichochthonius mollis*		-	-	0	x	-	1
63	*Licnozetes granulatus*	*LicnGran*	x	x	10	x	x	15
64	*Liebstadia n sp 1*	*LiebsSp1*	x	x	9	x	x	3
65	*Liebstadia n sp 1.1*	*LiebSp.1a*	x	x	5	-	-	0

No.	Species	Abbreviation	Leaves	Included in CCA leaves	Abundance in leaves	Roots	Included in CCA roots	Abundance in roots
66	*Liebstadia n sp 2*		x	-	2	-	-	0
67	*Machadobelba n sp 1*	*MachdSp1*	-	-	0	x	x	5
68	*Malacoangelia remigera*	*MalcRemg*	-	-	0	x	x	7
69	*Malaconothrus monodactylus*	*MalcMond*	x	x	5	x	x	5
70	*Malaconothrus n sp 3*		x	-	1	x	-	2
71	*Malaconothrus n sp 4*		-	-	0	x	-	2
72	*Malaconothrus n sp 5*	*MalacSp5*	x	x	6	-	-	0
73	*Microtegeus borhidii*	*MicrBorh*	x	x	12	-	-	0
74	*Microtegeus similis*	*MicrSiml*	x	x	5	x	-	1
75	*Nanhermannia elegantissima*	*NanhEleg*	x	-	2	x	x	12
76	*Nanhermannia nana form 1*	*NanhNana*	-	-	0	x	x	13
77	*Neoamerioppia longiclava*	*NeoaLong*	x	x	132	x	-	1
78	*Neoamerioppia longicoma*	*NeoaLogc*	x	x	8	-	-	0
79	*Neoamerioppia rotunda*	*NeoaRotn*	x	x	24	-	-	0
80	*Neoamrioppia espelatiarum*	*NeoaEspl*	x	x	3	-	-	0
81	*Neoctenogalumna longiciliata*		x	-	1	-	-	0
82	*Neosuctobelba transitoria*		x	-	2	-	-	0
83	*Opiella nova*	*OpieNova*	x	x	27	x	x	36
84	*Oribatella n sp 2*	*OribtSp2*	x	x	10	x	x	4
85	*Oripoda n sp 1*	*OripdSp1*	x	x	3	-	-	0
86	*Orthozetes bidentatus*	*OrthBidn*	x	-	2	x	x	20
87	*Oxyoppia polynesia*	*OxyoPoln*	x	x	7	-	-	0
88	*Parhypochthonius n sp 1*		x	-	1	-	-	0
89	*Pergalumna australis*		-	-	0	x	-	1
90	*Pergalumna sura*	*PergSura*	x	x	4	x	x	5
91	*Perscheloribates luminosus*		x	-	2	x	-	2
92	*Perscheloribates paratzitzikamaensis*		-	-	0	x	-	2
93	*Plenotocepheus neotropicus*	*PlenNeot*	x	-	2	x	x	8
94	*Protoribates ecuadoriensis*	*ProtEcua*	x	-	2	x	x	13
95	*Protoribates n sp 3*	*ProtrSp3*	x	x	4	x	x	25
96	*Protoribates n sp 4*		-	-	0	x	-	1

No.	Species	Abbreviation	Leaves	Included in CCA leaves	Abundance in leaves	Roots	Included in CCA roots	Abundance in roots
97	*Protoribates paracapucinus*	*ProtParc*	x	x	8	x	x	29
98	*Pulchroppia n sp 1*		x	-	1	-	-	0
99	*Ramusella puertomonttensis*	*RamsPuer*	-	-	0	x	x	3
100	*Rhynchoribates mirus*	*RhynMirs*	x	-	2	x	x	7
101	*Rhynchoribates n sp 1*		x	-	1	x	-	1
102	*Rioppia comteae*	*RiopComt*	x	-	2	x	x	6
103	*Rostrozetes carinatus*	*RostCarn*	x	x	41	x	-	1
104	*Rostrozetes glaber*		x	-	1	x	-	1
105	*Rostrozetes ovulum ovulum*	*RosOvlOv*	x	x	11	x	x	39
106	*Rostrozetes ovulum poensis*	*RosOvlPo*	x	x	7	x	x	16
107	*Rostrozetes sp 1*	*RostrSp1*	x	-	2	x	x	3
108	*Rostrozetes sp 3*	*RostrSp3*	x	-	1	x	x	6
109	*Rostrozetes sp 4*	*RostrSp4*	x	x	5	x	x	6
110	*Rostrozetes sp 5*	*RostrSp5*	x	-	2	x	x	6
111	*Rostrozetes sp 6*	*RostrSp6*	x	x	21	x	x	16
112	*Scapheremaeus bicornutus*		-	-	0	x	-	1
113	*Scapheremaeus fungisetosus*		x	-	2	-	-	0
114	*Schalleria brevisetosa*	*SchlBrev*	-	-	0	x	x	5
115	*Schalleria pectinata*	*SchlPect*	-	-	0	x	x	22
116	*Scheloribates laticlava*	*SchlLatc*	x	-	1	x	x	3
117	*Scheloribates artigasi*		-	-	0	x	-	1
118	*Scheloribates diversidactylus*		x	-	1	-	-	0
119	*Scheloribates elegans*		x	-	1	-	-	0
120	*Scheloribates huancayensis sp*		-	-	0	x	-	1
121	*Scheloribates n sp 1*		x	-	1	x	-	1
122	*Scheloribates n sp 1.1*		-	-	0	x	-	1
123	*Sellnickochthonius elsosneadensis sp*	*SellElso*	x	x	11	-	-	0
124	*Sellnickochthonius muara sp*	*SellMuar*	-	-	0	x	x	5
125	*Sellnickochthonius tropic*		x	-	2	-	-	0
126	*Solenozetes carinatus*	*SolnCarn*	x	x	6	x	x	39
127	*Solenozetes flagellatus*	*SolnFlag*	x	x	4	x	x	9
128	*Solenozetes n sp 1*	*SolenSp1*	-	-	0	x	x	52

No.	Species	Abbreviation	Leaves	Included in CCA leaves	Abundance in leaves	Roots	Included in CCA roots	Abundance in roots
129	*Sternoppia brasiliensis*	*SterBras*	x	-	2	x	x	3
130	*Sternoppia fissurata*	*SterFiss*	-	-	0	x	x	14
131	*Sternoppia incisa*	*SterIncs*	x	-	1	x	x	10
132	*Sternoppia mirabilis*	*SterMirb*	x	x	5	-	-	0
133	*Sternoppia n sp 1*		-	-	0	x	-	1
134	*Sternoppia n sp 3*	*SternSp3*	-	-	0	x	x	5
135	*Sternoppia n sp 6*	*SternSp6*	-	-	0	x	x	4
136	*Sternoppia n sp 8*		-	-	0	x	-	1
137	*Sternoppia paraincisa*	*SterPara*	x	-	1	x	x	22
138	*Sternoppia paramirabilis*	*SterParm*	-	-	0	x	x	5
139	*Striatoppia opuntiseta*		-	-	0	x	-	1
140	*Striatoppia silvicola*		-	-	0	x	-	1
141	*Suctobelba compacta*		x	-	1	-	-	0
142	*Suctobelbella andrassyi*		-	-	0	x	-	1
143	*Suctobelbella baculifera*		-	-	0	x	-	1
144	*Suctobelbella claviseta*	*SuctClav*	x	x	7	x	x	19
145	*Suctobelbella complexa*	*SuctComp*	x	x	16	x	x	4
146	*Suctobelbella complexa sp Form2*	*SucComF2*	x	x	14	x	x	34
147	*Suctobelbella loksai*	*SuctLoks*	x	-	1	x	x	4
148	*Suctobelbella macrodentata*		x	-	1	x	-	2
149	*Suctobelbella n sp 1*		-	-	0	x	-	1
150	*Suctobelbella n sp 3*	*SuctbSp3*	-	-	0	x	x	3
151	*Suctobelbella peracuta*	*SuctPerc*	x	-	1	x	x	4
152	*Suctobelbella perdentata*		x	-	2	x	-	1
153	*Suctobelbella semiplumosa indica*	*SucSemIn*	x	x	5	x	-	2
154	*Suctobelbella semiplumosa sp Form1*	*SucSemF1*	x	x	13	x	x	15
155	*Suctobelbella variosetosa*		x	-	2	-	-	0
156	*Suctobelbila n sp 1*		-	-	0	x	-	1
157	*Suctobelbila n sp 2*		x	-	1	x	-	1
158	*Suctobelbila n sp 3*	*SuctbSp3*	-	-	0	x	-	2
159	*Suctobelbila n sp 5*		-	-	0	x	-	1
160	*Suctobelbila peruensis*	*SuctPeru*	x	x	7	x	-	2
161	*Suctoribates n sp 1*	*SuctrSp1*	x	x	4	x	x	4
162	*Suctoribates Oxyamerus*		x	-	1	-	-	0

No.	Species	Abbreviation	Leaves	Included in CCA leaves	Abundance in leaves	Roots	Included in CCA roots	Abundance in roots
163	*Tecteremaeus cornutus*	*TectCorn*	x	-	2	x	x	23
164	*Tecteremaeus incompletus*	*TectIncm*	x	x	4	x	x	13
165	*Tectocepheus minor*	*TectMinr*	x	x	5	x	-	1
166	*Tectocepheus velatus sarekensis*	*TecVelSr*	x	x	3	-	-	0
167	*Tectocepheus velatus velatus*	*TecVelVl*	x	x	3	-	-	0
168	*Tegeocranellus bolivianus*	*TegeBolv*	x	x	14	x	x	3
169	*Teratoppia n sp 1*	*TeratSp1*	x	x	3	x	x	5
170	*Teratoppia pluripectinata*	*TertPlur*	x	x	17	x	x	16
171	*Xenillus n sp 2*		-	-	0	x	-	1
172	*Xenillus setiger*		-	-	0	x	-	1
173	*Xenolohmannia comosa*	*XenlComs*	x	-	1	x	x	3
174	*Yoshiobodes n sp 1*		-	-	0	x	-	1
175	*Yoshiobodes n sp 2*		-	-	0	x	-	1
176	*Zetomimus polpaicoensis*		x	-	1	-	-	0

Appendix 6. Mahalanobis Distances (MD^2) of discriminant function analysis (DFA) based on Oribatida community composition in leaf and root litter exposed at 1000, 2000 and 3000 m for 12 months.

Litter type	From	F-value	df1	df2	p-value	MD^2
Leaf	1000 m – 2000 m	63.45	2	28	<0.001	3.76
	1000 m – 3000 m	45.10	2	23	<0.001	4.85
	2000 m – 3000 m	23.27	2	24	<0.001	3.80
Root	1000 m – 2000 m	74.21	2	32	<0.001	4.14
	1000 m – 3000 m	53.69	2	30	<0.001	3.99
	2000 m – 3000 m	23.62	2	29	<0.001	3.43

Chapter 4

Impacts of core rotation, defaunation and nitrogen addition on arbuscular mycorrhizal fungi, microorganisms and microarthropods in a tropical montane rainforest

Laura M. Sánchez Galindo, Tessa Camenzind, Mark Maraun & Stefan Scheu

Abstract

In tropical ecosystems interactions between arbuscular mycorrhizal fungi (AMF) and other organisms have been little studied, but may be of significant importance for understanding the role of AMF in decomposition processes and nutrient cycling. In this study, we used ingrowth cores to investigate the impacts of regular rotation of the cores, defaunation and nitrogen addition on AMF, microbial biomass and microarthropods in the fermentation/humus (F/H) and litter (L) layers of an Ecuadorian montane tropical rainforest. AMF were substantially reduced in the F/H layer (to 34% of initial), while in the L layer they remained constant during the experiment. Overall, microorganisms and microarthropods were largely independent of AMF hyphae and their exudates, however, defaunation strongly affected the recovery of their communities. Nitrogen addition increased the quality of litter material and beneficially affected microbial communities thereby increasing decomposition rates, but did not impact AMF abundance and microarthropod communities. These findings suggest that the cutoff of the carbon supply from the plant to the fungal mycelium was not compensated by switching resources in the F/H layer, underlining strong association of AMF and living roots. While in the L layer, AMF likely competed with saprotrophic microorganisms for litter-derived resources at intermediate stages of decomposition pointing to indirect contributions of AMF to decomposition processes. Overall, the results support the view that root-derived resources are important in fueling soil food webs, but also indicate that in the studied montane rainforest these resources are only available close to roots and not channeled distant to roots via AMF.

Keywords: Acari, Collembola, Organic layer, Oribatid mites, Root-derived resources, Saprotrophic fungi.

Introduction

Mycorrhizal fungi are key components of microorganisms in soil influencing plant nutrient uptake and growth (Johansson et al. 2004; Brundrett and Tedersoo 2018). In tropical forest ecosystems, arbuscular mycorrhiza fungi (AMF; Glomeromycotina) represent the dominant mycorrhizal form (Kottke et al. 2004; Öpik et al. 2006). These obligate biotrophs facilitate the mobilization and uptake of mineral by plants released from decomposition of organic matter in exchange for photosynthetic carbon (Read and Perez-Moreno 2003; Smith and Read 2008; Johnson 2010; Bagyaraj 2014). Factors that affect the abundance and effectiveness of AMF include climatic changes, soil fertility, disturbances and changes in nutrient availability (Gryndler 2000; Cardoso and Kuyper 2006; Camenzind et al. 2014; Lehmann et al. 2017). Elevated nutrient availability – mainly P and N – decreases the formation of fine roots and mycorrhizal structures, reducing the benefit provided by these symbionts (Treseder and Allen 2002; Johnson 2010). Therefore, changes following nutrient additions might strongly affect tropical forests where P and N are limiting and plants rely on AMF symbionts (Cardoso and Kuyper 2006; Dalling et al. 2016; Sheldrake et al. 2018).

In addition to roots, AMF interact with other organisms including bacteria, saprotrophic fungi, protozoa, nematodes, arthropods and even large animals (Ruess and Lussenhop 2005; Miransari 2011; Lehmann et al. 2017). These interactions may be synergistic, competitive or antagonistic and may affect all stages of the mycorrhizal fungal life cycle (Finlay 2004; Johansson et al. 2004; Miransari 2011). Interacting mechanisms which are of particular importance for the functioning of the symbiosis include mycorrhiza associated bacteria promoting or inhibiting mycorrhiza formation (Toljander et al. 2007; Svenningsen et al. 2018), potential restriction of saprotrophic fungal activity due to competition for substrate (Bödeker et al. 2016; Marian et al. 2019), and grazing of external mycelium by soil microarthropods (Ruess and Lussenhop 2005; A'Bear et al. 2014). The most abundant and frequent groups of soil microarthropods are mites (Acari) and springtails (Collembola) (Maraun et al. 2003; Franklin et al. 2004). Particularly oribatid mites (Oribatida) are rich in species and colonize virtually any soil reaching maximum diversity and density in forest ecosystems, where they participate in the decomposition of organic matter (Franklin et al. 2004). Oribatid mites feed on a variety of fungal species and contribute to the dispersion of

fungal structures (Renker et al. 2005; Vašutová et al. 2019). However, AMF presumably are not the preferred food resource of oribatid mites, but might be consumed to some extent (Gange and Brown 2002; Schneider et al. 2005).

Typically, interactions between soil microarthropods and AMF are studied using sterilized soil re-inoculated with microorganisms and microarthropods (Toljander et al. 2007; Nuccio et al. 2013; Ngosong et al. 2014). For quantifying AMF biomass, as well as their contribution to nutrient translocation, plant growth and their interactions with microbial communities, ingrowth cores are increasingly used (Nottingham et al. 2013; Leifheit et al. 2014). Ingrowth cores comprise compartments separated by mesh barriers for excluding roots, but allowing access of extraradical mycorrhizal hyphae, with soil physical and chemical conditions inside the cores resembling those outside the cores (Wallander et al. 2013). Rotating these cores detaches fungal ingrowth and thereby, the comparison of rotated and non-rotated cores provides insight into the role of mycorrhizal fungi for element cycling and decomposition (Johnson et al. 2001).

To explore the role of AMF in soil nutrient dynamics and their interactions with soil organisms in tropical montane rainforests, we evaluated the impact of rotation of ingrowth cores in combination with soil defaunation and N addition on AMF abundance, microorganisms and soil microarthropods, with focus on oribatid mites. We hypothesized that (1) the colonization of soil inside the cores by AMF is reduced by regular rotation. Assuming that mycorrhiza indirectly alter decomposition processes by restraining the activity of saprotrophic fungi we furthermore hypothesized that (2) the exclusion of mycorrhiza results in increased activity of saprotrophic microorganisms, accelerating decomposition processes. Further, we hypothesized that (3) oribatid mites benefit from the increased dominance of saprotrophic fungi in rotated cores. Also, we hypothesized that (4) the reduction of microarthropod abundance in defaunated cores promotes fast recovery of AMF mycelium and soil microorganisms. Finally, we hypothesized that (5) the addition of N reduces the concentration of AMF, but fosters the activity of saprotrophic microorganisms and thereby increases litter decomposition.

Material and methods

Study site

The study site is located in Southern Ecuador within the Podocarpus National Park near the research station San Francisco at 2000 m a.s.l. (3°58′S, 79°04′W) (for location details see Richter et al. 2009). The climate is warm humid with an average annual temperature of 15.2°C and an annual precipitation of approximately 2000 mm. Precipitation is high from April to September, and lower between October and March, but there is no pronounced dry season (Bendix et al. 2006). The soil is stagnic cambisol with a thick organic layer ranging between 8 and 40 cm (Wilcke et al. 2002; Wullaert et al. 2010). The area is characterized by high diversity of organisms and a particular high number of endemic vascular plant species, with *Melastomataceae, Lauraceae* and *Rubiaceae* being the dominant plant families (Bendix et al. 2006; Beck and Ritcher 2008; Homeier et al. 2010). Roots of trees in the forests are colonized predominantly by AMF and are characterized by high rates of AMF colonization suggesting high contribution of AMF hyphae to soil fungal biomass (Kottke et al. 2004; Camenzind and Rillig 2013).

Ingrowth core

Ingrowth cores were constructed using 15 cm (diameter) x 20 cm (length) plastic tubes. Two rectangular holes (10 x 15 cm) opposite to each other were cut into the tubes and covered with 45 µm nylon mesh. Two layers of 45 µm nylon mesh, separated by 5 cm, were glued inside the tubes to allow drainage of leaching water but block ingrowth of roots and mycorrhizal hyphae from the bottom. The ingrowth cores were closed with a lid of 4 mm nylon mesh to allow mesofauna access (Figure 1A).

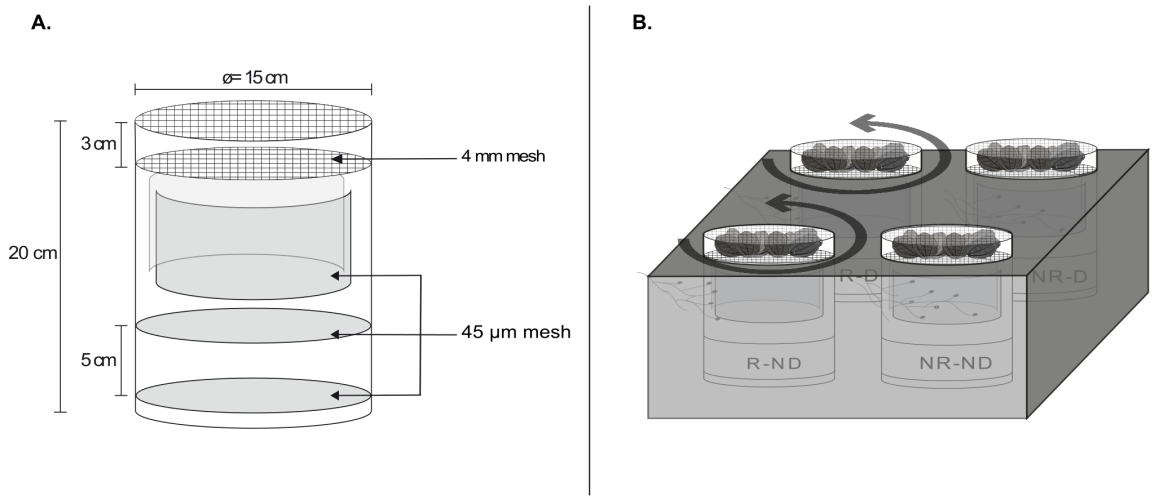


Figure 1. Scheme of the ingrowth cores and representation of experimental design. (**A**) Scheme of the ingrowth cores; see text for details. (**B**). Representation of the experimental design per subplot with the ingrowth cores inserted in the soil and litter material placed on top of the soil inside the cores separated from the soil by 4 mm mesh; four ingrowth cores were placed per subplot; R-ND= rotated and non-defaunated, R-D= rotated and defaunated, NR-ND= non-rotated and non-defaunated, NR-D= non-rotated and defaunated; arrows indicate rotation by 45° every second day.

Experimental design

The experiment started in June 2015 and was conducted in the framework of the Nutrient Manipulation Experiment (NUMEX) (Homeier et al. 2012). Briefly, NUMEX is an altitudinal fertilization experiment that was set up in a complete randomized block design with four blocks, each containing one plot (20 x 20 m) of four different treatments: addition of N (+N), addition of P (+P), addition of N and P (+N+P) and unfertilized control plots (Ctr) (Wullaert et al. 2010; Homeier et al. 2012). For the present experiment soil samples (~15 cm deep) were taken from two subplots (2 x 2 m) marked randomly inside the +N and Ctr plots of NUMEX at 2000 m with a stainless-steel corer (14.5 cm inner diameter). The soil samples comprised the fermentation/humus (F/H) and litter (L) layers and were inserted intact into the ingrowth cores and placed into the same holes from which the soil sample were excavated. Prior to placement in the field, half of the prospective rotated and non-rotated cores were frozen at -20°C for one week to kill soil living animals. Once in the field, the soil sample was covered by 4 mm mesh on top of which 2 g of dry (60°C, 48 h) *Graffenrieda emarginata* leaves, the most abundant tree species in the study area, were placed as standard litter material allowing to investigate the decomposition of leaf litter

inside the cores (Figure 1B). Decomposition of the added *Graffenrieda* litter was calculated as $mass\ loss\ (\%) = ((m_0 - m_1/m_0)) \times 100$, with m_0 as the initial dry weight of the leaves and m_1 as the dry weight of the leaves at harvest.

The cores were rotated every second day by 45º during 5 months. After removal of the cores by the end of the experiment, L and F/H layer materials were sampled separately. Half of each sample was used for the analysis of soil properties, the other half for extraction of microarthropods. Microarthropods were extracted by heat using a modified high gradient extractor (Macfadyen 1961; Kempson et al. 1963). Thereafter, they were determined to group level (Oribatida, Collembola, Prostigmata, Gamasina, Uropodina), with the exception of adult Oribatida which were identified to species level. For identification, the keys of Hammer (1958, 1961) and Balogh and Balogh (1990, 2002) were used and nomenclature followed Subías (2018).

Microbial respiration and microbial biomass

Microbial basal respiration (BR) and microbial biomass (C_{mic}) were determined by measuring O_2 consumption using an automated respirometer system (Scheu 1992). The O_2 consumption was measured every hour during 24 h at 22°C. BR (µl O_2 g^{-1} dry weight h^{-1}) was calculated as mean of O_2 consumption rates from 10 to 20 h after attachment of the samples to the respirometer system.

C_{mic} (µg g^{-1} dry weight) was determined by measuring the maximum initial respiratory response (MIRR; µl O_2 g^{-1} h^{-1}). Moist samples equivalent to 0.2 g dry weight were supplemented with D-glucose (80 mg g^{-1} and 40 mg g^{-1} dry weight for L and F/H layers, respectively). The average of the lowest three readings within the first 10 h was used as MIRR. Microbial biomass was calculated as $C_{mic} = 38 \times MIRR$ (SIR-method;Anderson and Domsch 1978; Beck et al. 1997).

Fatty acid analysis

Phospholipid fatty acids (PLFAs) and neutral lipid fatty acids (NFLAs) were extracted from L and F/H layer material, as well as from initial soil samples taken from each subplot following the protocol of Frostegård et al. (1993). Fatty acid methyl esters (FAMEs) were identified by chromatographic retention time based on a standard mixture composed of 37 different FAMEs ranging from C11 to C24 (Sigma–Aldrich, St Louis, USA). The analysis was performed by gas chromatography using a GC-FID Clarus 500 (PerkinElmer Corporation, Norwalk, USA) equipped with HP-5 capillary column (30 m x 0.32 mm id, film thickness 0.25 μm).

PLFAs and NLFAs were expressed in nmol g^{-1} dry weight. PLFAs were used as indicator of the microbial community structure. The sum of i15:0, a15:0, 15:0, i16:0, 16:1w7, i17:0, 17:0, cy17:0, 18:1ω7 and cy19:0 was used as indicator of bacterial biomass (Frostegård et al. 1993; Frostegård and Bååth 1996). The sum of 16:1ω7, cy17:0, 18:1ω7 and cy19:0 as indicator of Gram-negative and the sum of i15:0, a15:0, i16:0, i17:0 and a17:0 as indicator of Gram-positive bacteria (Zelles 1997, 1999). The PLFAs 18:2ω6,9 and 18:1ω9 were used as markers for saprotrophic fungi (Frostegård and Bååth 1996; Ruess and Chamberlain 2010). The NLFA 16:1ω5 was used as marker for AMF (Olsson et al. 1995; Olsson 1999).

Carbon and nitrogen analyses

Soil pH was determined based on a 1:5 (v:v) suspension of soil in deionized water. Total C and N contents in soil and litter were determined from milled samples using an elemental analyzer (EuroEA, HekaTech, Germany). The fraction of Bray-extractable inorganic phosphorus (P) in soil was determined based on protocols described by Bray and Kurtz (1945). Available P was extracted from 2 g dry soil adding a solution containing hydrochloric acid (HCl) and ammonium fluoride (NH_4F). The resulting P content in the solution filtered through phosphorus-free filter paper was analyzed by ICP-OES analyses (Optima 2100 DV, Perkin Elmer, Germany).

Statistical analyses

Prior to statistical analysis, the data were inspected for normality and homogeneity of variance using Shaphiro wilks and Breush-Pagan test, respectively. If necessary, data were log- or arcsine-transformed to improve homogeneity of variances. Soil characteristics (concentration of C, N, PO_4^{3-}, P and pH), microbial activity (BR and C_{mic}), fatty acids (NLFAs and PLFAs) and microarthropod groups (Oribatida, Gamasina, Uropodina, Astigmata and Prostigmata (all Acari) and Collembola) were analyzed using separated three-way linear mixed-effects models (LMM) with rotation, N addition and defaunation fitted as fixed effects and block fitted as random effect. Oribatid mite community data were compressed using non-metric multidimensional scaling (NMDS). Only species with more than three individuals in the samples were included. The stress value obtained reduced the number of meaningful dimensions to six axes. Afterwards, multivariate analysis of variance (MANOVA) was used to inspect effects of treatments on oribatid mite community composition. Additionally, using the same data set principal components analysis (PCA) was used to analyze and present graphically the response of oribatid mite species to rotation, N addition and defaunation in the L and F/H layer. The soil layer (L and F/H layer) and the three treatments (Rotation, N addition and defaunation) were coded as supplementary variables not affecting the ordination. Only species that were present in more than three samples were included in the analysis. PCA was carried out using CANOCO 5 (Ter Braak and Smilauer 2012). LMM, MANOVA and NMDS were conducted in R version 3.2.1 (R Core Team 2014) using the functions lme() in the package "nlme", manova() in the package "stats" and metaMDS() in the package "vegan", respectively.

Results

Litter decomposition

On average, 70% of the initial dry mass of the leaf litter placed in the upper part of the cores remained at the end of the experiment. Rotation and defaunation did not significantly

affect litter decomposition, however, the leaves decomposed faster in the cores of the +N than in those of the Ctr treatment (31.8% *vs.* 26.9%, $F_{1,57} = 6.69$, $p = 0.01$).

In general, the C/N ratio was higher in the cores of the Ctr than in those of the +N treatment with averages of 38.33 ± 0.22 *vs*. 33.74 ± 0.23 ($F_{1,57} = 8.22$, $p = 0.005$) for the L layer and 27.67 ± 0.26 *vs*. 25.39 ± 0.25 ($F_{1,57} = 4.16$, $p = 0.04$) for the F/H layer. Further, the C/N ratio of the L layer in defaunated cores exceeded that of the F/H layer with an average of 38.38 ± 0.29 *vs*. 33.69 ± 0.18 ($F_{1,57} = 7.22$, $p = 0.009$). Rotation of the cores did not significantly affect the C/N ratio of the L and F/H layer.

Concentrations of PO_4^{3-} and available P (only measured in the F/H layer) did not differ significantly between treatments with averages of 0.21 ± 0.09 and 0.06 ± 0.02 mg g^{-1}, respectively. However, the pH (only measured in F/H layer) in the +N treatment exceeded that in the Ctr treatment (3.94 *vs*. 3.79; $F_{1, 57} = 7.62$, $p = 0.007$).

Arbuscular mycorrhizal fungi

Generally, the concentration of NLFA 16:1ω5 in the F/H layer declined during the experiment from an overall mean of 33.38 ± 10.83 to 21.83 ± 5.11 nmol g^{-1} by the end of the experiment ($F_{1,22} = 12.39$, $p = 0.001$; Figure 2A). By contrast, it stayed at the same level in the L layer (overall mean 16.08 ± 6.10 nmol g^{-1}). Defaunation significantly reduced the concentration of NLFA 16:1ω5 in the F/H layer ($F_{1,56} = 10.44$, $p = 0.002$; Figure 2B) but not in the L layer. Neither rotation nor N addition affected the concentrations of NLFA 16:1ω5 in the L and F/H layer.

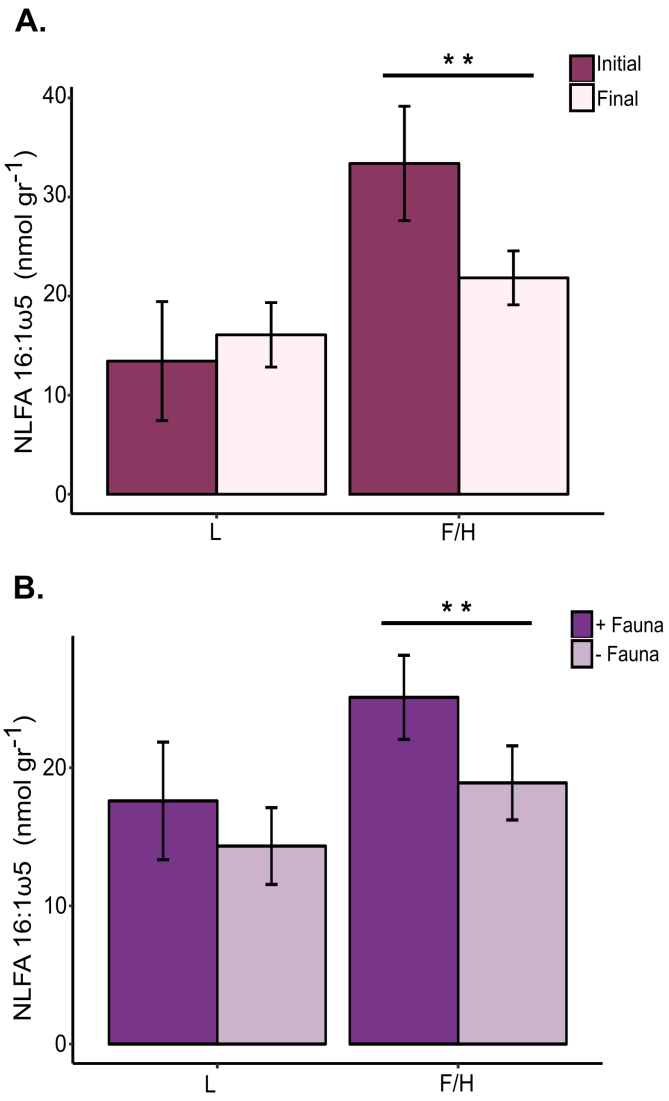


Figure 2. Concentration of the AMF marker fatty acid in the L and F/H layer. Variations in the concentration of the AMF marker fatty acid 16:1ω5 in the L and F/H layer. (**A**) During exposure for five months in the field (Initial = before exposure, Final = at the end of experiment). (**B**) In defaunated (-Fauna) and non-defaunated cores (+Fauna). Values are means ± SE. ** $P < 0.01$.

Microbial biomass and respiration

In general, C_{mic} and BR in the L layer (overall means of 9,308 ± 4,031 µg C_{mic} g^{-1} dry weight (dw) and 47.63 ± 20.62 µl O_2 g^{-1} dw h^{-1}, respectively) exceeded that in the F/H layer (respective values of 4,4394 ± 1,685 µg C_{mic} g^{-1} dw and 43.42 ± 17.80 µl O_2 g^{-1} dw h^{-1}). In defaunated cores C_{mic} in both the L and F/H layer was significantly reduced as compared to non-defaunated cores ($F_{1,52} = 10.05$, $p = 0.002$ and $F_{1,52} = 20.81$, $p < 0.0001$, respectively;

Figure 3A). BR also was significantly reduced in defaunated cores in the L layer ($F_{1,52}$ = 7.61, p = 0.008; Figure 3B), while in the F/H layer it was not significantly affected (overall mean of 39.92 ± 19.05 µl O_2 g^{-1} dw h^{-1}). Further, BR in the L layer in the +N treatment significantly exceeded that in the Ctr treatment ($F_{1,52}$ = 6.52, p = 0.01), but this was not the case in the F/H layer (overall mean of 44.11 ± 15.70 µl O_2 g^{-1} dw h^{-1}). Also, C_{mic} was not significantly affected by N addition, neither in the L layer nor in the F/H layer (overall means of 9,937 ± 4,578 and 4,555 ± 1,607 µg C_{mic} g^{-1} dw, respectively). Further, rotation neither significantly affected C_{mic} (overall means of 9,096 ± 4,035 and 4,346 ± 1,699 µg C_{mic} g^{-1} dw in the L and F/H layer, respectively) nor BR (overall means of 47.48 ± 21.12 and 43.52 ± 21.77 µl O_2 g^{-1} dw h^{-1} in the L and F/H layer, respectively).

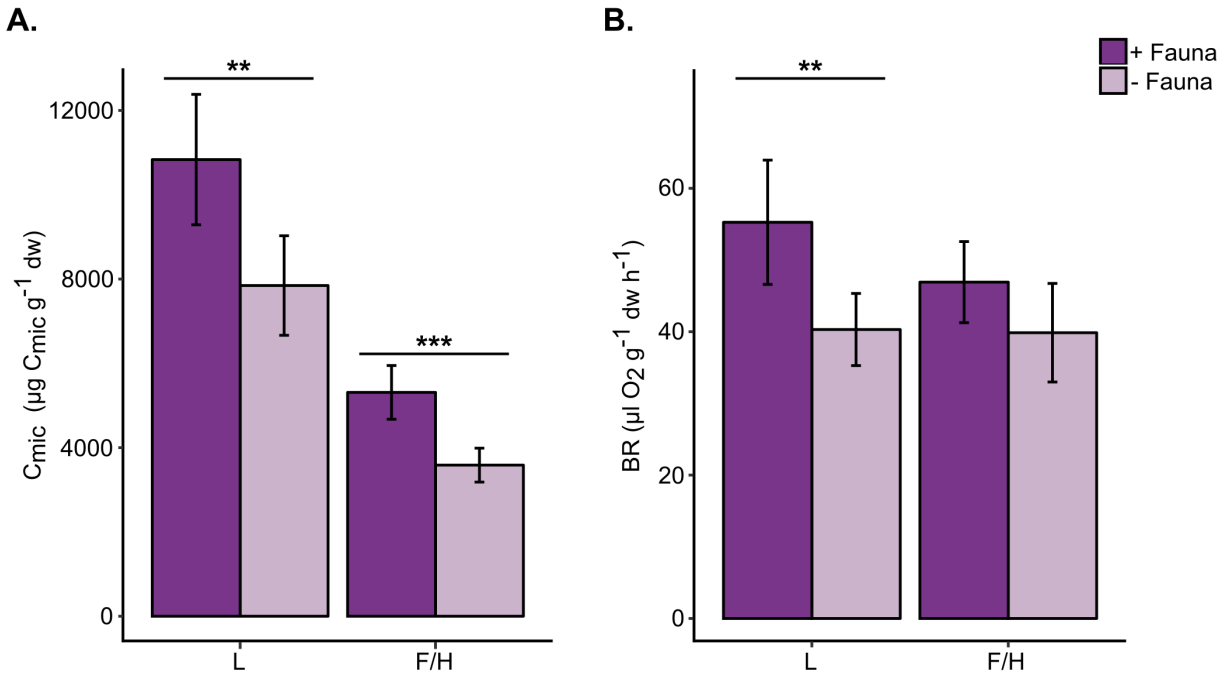


Figure 3. Effect of defaunation on microbial biomass and basal respiration in the L and F/H layer. Variations in (**A**) microbial biomass (C_{mic}) and (**B**) basal respiration (BR) in the L and F/H layer of defaunated (-Fauna) and non-defaunated cores (+Fauna). Values are means ± SE. ***P < 0.001; ** P < 0.01.

Microbial community structure

The concentration of Gram-positive bacteria and saprotrophic fungi significantly changed during the experiment; Gram-positive bacteria significantly increased in the L layer from an overall mean of 80.80 ± 36.14 to 111.01 ± 32.13 nmol g^{-1} by the end of the experiment ($F_{1,26}$ = 8.07, p = 0.008) and saprotrophic fungi significantly decreased in the F/H layer from an overall mean of 61.33 ± 12.23 to 52.31 ± 7.05 nmol g^{-1} by the end of the experiment ($F_{1,26}$ = 6.42, p = 0.01).

The concentration of Gram-positive, Gram-negative and saprotrophic fungi markers in the L layer (overall means of 111.01 ± 39.59, 158.47 ± 59.74 and 200.54 ± 77.79 nmol g^{-1}, respectively) exceeded that in the F/H layer (respective values of 76.77 ± 14.36, 94.38 ± 22.24 and 52.31 ± 13.93 nmol g^{-1}). Gram-positive, Gram-negative and total bacterial PLFA markers were not significantly affected by any of the treatments, neither in the L nor in the F/H layer (Table 1). By contrast, in the L layer the concentration of the saprotrophic fungal markers 18:2ω6,9 and 18:1ω9 in non-rotated cores exceeded those in rotated cores (averages of 219.61 ± 78.33 and 181.48 ± 66.94 nmol g^{-1}, respectively) while in the F/H layer the concentration did not differ significantly between rotated and non-rotated cores (overall mean of 54.21 ± 15.49 nmol g^{-1}). Neither defaunation nor N addition affected the concentrations of the fungal markers in the L and F/H layer.

	Gram$^+$		Gam$^-$		Total bacteria		Saprotrophic fungi	
	***F*-value**	***p*-value**	***F*-value**	***p*-value**	***F*-value**	***p*-value**	***F*-value**	***p*-value**
Litter								
+N	2.25	0.14	0.35	0.56	0.94	0.34	0.03	0.87
Rotation	0.58	0.45	0.04	0.84	0.02	0.87	**4.40**	**0.04**
Defaunation	2.46	0.12	0.08	0.78	0.17	0.68	0.46	0.49
F/H								
+N	0.005	0.94	0.24	0.62	0.09	0.77	0.53	0.47
Rotation	0.54	0.47	0.59	0.44	0.65	0.42	0.80	0.31
Defaunation	2.71	0.11	0.66	0.42	1.48	0.23	2.04	0.16

Table 1. Nitrogen addition, rotation and defaunation effects on PLFA for Gram-positive, Gram-negative and total bacteria, and saprotrophic fungi. F- and p-values of linear mixed effects models on the effect of nitrogen addition (+N), rotation and defaunation on PLFA for Gram-positive, Gram-negative and total bacteria, and saprotrophic fungi in the L and F/H layer of the ingrowth cores exposed in the field for five months. Significant effects are given in bold.

Microarthropods

Generally, microarthropods were more abundant in the F/H than in the L layer (Oribatida 17.85 ± 25.84 *vs*. 12.98 ± 12.62, Gamasina 3.32 ± 5.28 *vs*. 2.85 ± 3.21, Uropodina 4.07 ± 11.65 *vs*. 1.60 ± 3.01, Prostigmata 2.17 ± 2.91 *vs*. 1.28 ± 1.82, Astigmata 3.90 ± 12.66 *vs*. 0.98 ± 2.45, Collembola 6.70 ± 9.24 *vs*. 5.92 ± 7.01 ind. core^{-1}). Overall, microarthropod numbers were lower in defaunated than in non-defaunated cores (Oribatida 3.82 ± 3.49 *vs*. 27.01 ± 23.53, Gamasina 2.81 ± 4.58 *vs*. 3.38 ± 4.16, Uropodina 0.56 ± 1.35 *vs*. 5.17 ± 11.72, Prostigmata 1.17 ± 1.86 *vs*. 2.30 ± 2.86, Astigmata 1.40 ± 3.17 *vs*. 3.52 ± 12.68, Collembola 4.48 ± 6.45 *vs*. 8.17 ± 9.32 ind. core^{-1}). The number of Uropodina and Prostigmata were lower in both the L (averages of 0.65 ± 1.73 and 1.01 ± 1.79 ind. core^{-1}, respectively) and the F/H layer of defaunated cores (averages of 0.46 ± 0.84 and 1.34 ± 1.94 ind. core^{-1}, respectively). Further, in the L layer of non-defaunated cores the number of Astigmata exceeded that in defaunated cores with 1.67 ± 3.28 and 0.31 ± 0.82 ind. core$^{-1,}$ respectively. Also, in the F/H layer the number of Collembola in non-defaunated cores exceeded that in defaunated cores with 9.90 ± 11.17 and 3.50 ± 5.23 ind. core^{-1}, respectively. Rotation generally little affected the number of microarthropods with the exception of Gamasina in the F/H layer of rotated cores which exceeded that in non-rotated cores with averages of 4.81 ± 6.86 and 1.84 ± 2.25 ind. core^{-1}, respectively (Table 2).

	Collembola		**Gamasina**		**Uropodina**		**Astigmata**		**Prostigmata**	
	***F*-value**	***p*-value**	***F*-value**	***p*-value**	***F*-value**	***p*-value**	***F*-value**	***p*-value**	***F*-value**	***p*-value**
Litter										
+N	0.43	0.51	0.58	0.45	0.30	0.58	1.39	0.24	0.77	0.38
Rotation	0.03	0.85	0.68	0.41	2.40	0.12	1.27	0.26	0.98	0.32
Defaunation	1.01	0.32	1.06	0.31	**12.25**	**<0.01**	**12.49**	**<0.01**	**4.61**	**0.03**
F/H										
+N	0.64	0.43	1.90	0.17	0.08	0.78	0.43	0.51	0.50	0.48
Rotation	0.02	0.87	**4.71**	**0.03**	0.11	0.74	0.06	0.81	0.03	0.85
Defaunation	**13.51**	**<0.01**	0.44	0.51	**25.58**	**<0.01**	1.05	0.31	**7.46**	**<0.01**

Table 2. Nitrogen addition, rotation and defaunation effects on the abundance of Collembola, Gamasina, Uropodina, Astigmata and Prostigmata. F- and p-values of linear mixed effects models on the effect of nitrogen addition (+N), rotation and defaunation on the abundance of Collembola, Gamasina, Uropodina, Astigmata and Prostigmata in the L and F/H layer of ingrowth cores exposed in the field for five months. Significant effects are given in bold.

In total, 60 species of Oribatida were identified (see S1 Table for full list of species). The three most common species of Oribatida associated with the L layer were *Neoamerioppia rotunda, Cultroribula zicsii* and *Epieremulus granulatus,* whereas in the F/H layer the three most common associated species were *Rostrozetes faveolatus*, *Nanhermannia elegantissima* and *Scheloribates elegans*. No Oribatida species exclusively occurred in any of the treatments. The PCA defined two main gradients of variation of the Oribatida communities, separating defaunated and non-defaunated cores and differentiating litter and soil layer, which together accounted for 57.8% of the total variation (Figure 4).

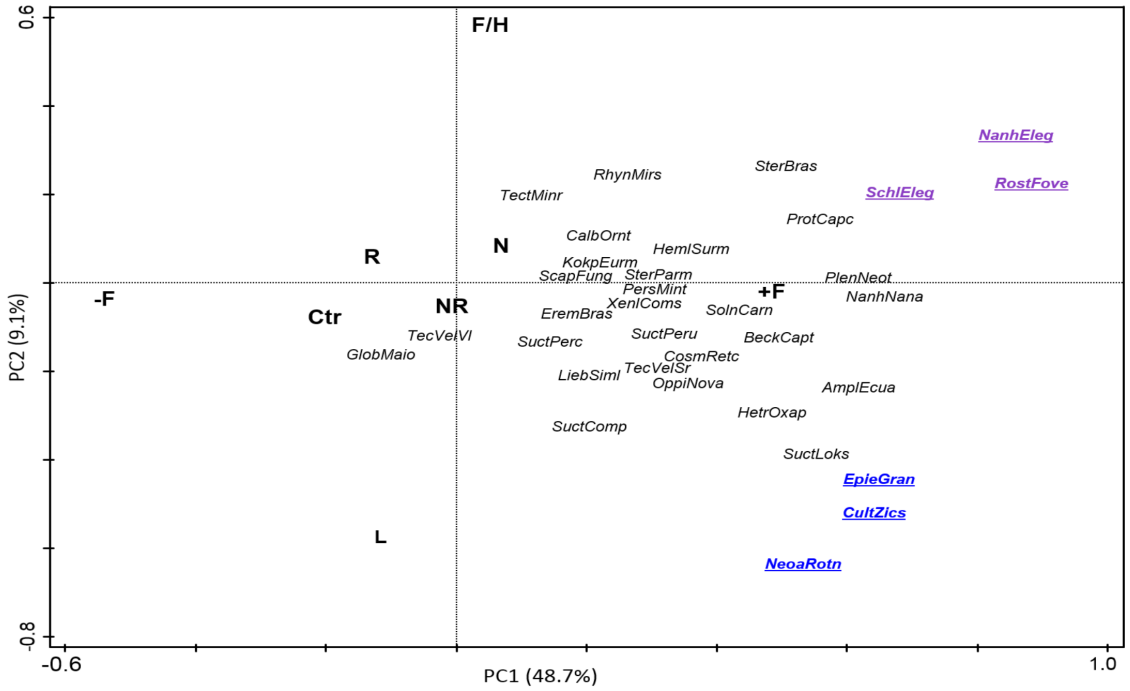


Figure 4. Principal components analysis of oribatid mite species. Principal components analysis (PCA) of oribatid mite species in control (Ctr), nitrogen addition (N), rotated (R), non-rotated (NR) defaunated (-F) and non-defaunated cores (+F) in the L and F/H layer after five months of exposure in the field. The three most abundant species in the L layer are underlined and given in blue and the three most abundant species in the F/H layer are underlined and given in purple. Full species names are given in S1 Table.

The first principal component axis (PC1) explained the majority of variability (48.7%) and was positively associated with non-defaunated soil cores, while the second principal component axis (PC2) explained only 9.1% and was associated with the soil layer. MANOVA performed with NMDS axes scores confirmed that defaunation strongly

affected the Oribatida community in both the L and F/H layer ($F_{6,49}$ = 6,61, p = 0.02; $F_{6,47}$ =6.52, p< 0.0001, respectively).

In general, both the richness and abundance of Oribatida were strongly affected by defaunation (Table 3), being lower in defaunated cores (2.90 ± 2.27 species core^{-1} and 4.50 ± 4.10 ind. core^{-1} in the L layer, and 2.21 ± 1.71 species core^{-1} and 3.15 ± 2.66 ind. core^{-1} in the F/H layer) than in non-defaunated cores (7.765 ± 3.01 species core^{-1} and 21.46 ± 12.58 ind. core^{-1} in the L layer, and 7.56 ± 4.03 species core^{-1} and 32.56 ± 30.06 ind. core^{-1} in the F/H layer). Neither rotation nor N addition affected the abundance or richness of microarthropods.

	Richness		Abundance	
	F-value	**p-value**	**F-value**	**p-value**
Litter				
+N	<0.01	0.97	0.53	0.47
Rotation	<0.01	0.95	<0.01	0.99
Defaunation	**45.80**	**<0.01**	**67.48**	**<0.01**
F/H				
+N	0.13	0.71	0.22	0.64
Rotation	0.18	0.67	0.05	0.82
Defaunation	**86.10**	**<0.01**	**159.09**	**<0.01**

Table 3. Nitrogen addition, rotation and defaunation effects on the richness and abundance of Oribatida. F- and p-values of linear mixed effects models on the effect of nitrogen addition (+N), rotation and defaunation on the richness and abundance of Oribatida in the L and F/H layer of ingrowth cores exposed in the field for five months. Significant effects are given in bold.

Discussion

Rotation of cores

Our findings do not provide evidence that AMF mycelia were reduced by regular rotation of the ingrowth cores. However, the AMF fatty acid marker inside the cores decreased during the experiment in the F/H layer. Kottke et al. (2004) observed extensive root development in the organic layer of the study sites and this likely favors the exploitation of nutrients by root associated AMF. The soil inside ingrowth cores was separated from roots

and the reduction in AMF marker concentration in the F/H layer material likely reflects the cutoff from the carbon supply from the plant to the fungal mycelium (Rillig 2004). The fact that the AMF marker fatty acid was not reduced by rotation of the ingrowth cores indicates that the AMF hyphae are only functioning in close association with roots without forming extensive extraradical mycelium. Further studies at the study site based on both fatty acids and microscopic inspection of AMF mycelia support this conclusion (Camenzind and Rillig 2013; Camenzind et al. 2014). Still, AMF may have affected the periphery of the non-rotated cores which are closer to living roots, with subtle effects to be detected when analyzing mixed samples from the complete core.

The reduced concentration of the AMF marker in the F/H layer neither was associated with a decline in C_{mic} nor in BR, indicating that microorganisms and microbial activity inside the cores were largely independent of AMF hyphae and their exudates based on plant carbon. Obviously, microorganisms in the F/H layer almost exclusively exploited dead organic matter resources comprising leaf litter and dead roots at later stages of decay. Notably, the reduction of AMF concentration also did not affect the abundance of soil microarthropods with the exception of Gamasina which significantly increased in the F/H layer of rotated cores. Gamasina typically live as predators hunting for other microarthropods, predominantly Collembola, as well as Nematoda (Koehler 1997; Dhooria 2016). Since Collembola were not affected by rotation of the cores the increase in Gamasina due to rotation might have been due to increased nematode density in rotated cores. Interactions between nematodes and mycorrhiza have been assumed to be mutually inhibitory due to competition for space and food sources (Francl 1993; Pinochet et al. 1996; Borowicz 2001; Schouteden et al. 2015). However, the interactions are complex and as yet little understood in particular in tropical ecosystems (Hol and Cook 2005).

Oribatida richness, abundance and community composition were not significantly affected by rotation of the ingrowth cores. This indicates that they exclusively exploited resources inside the cores and this was independent of interruptions of fungal hyphae colonizing the cores. By contrast, Oribatida richness and abundance varied between soil horizons with both being considerably higher in the F/H than the L layer. The L layer was colonized by species typically occurring in the litter layer of the study site such as *Cultroribula zicsii*

(Illig et al. 2005), whereas the F/H layer was colonized mostly by individuals of the genera *Nanhermannia*, *Rostrozetes* and *Scheloribates* typical inhabitants of F and H layers (Mitchell and Parkinson 1976; Illig et al. 2005). Unfortunately, little is known on food sources of tropical Oribatida species, but presumably they comprise predominantly secondary decomposers feeding on microorganisms and microbial residues, with only few primary decomposers feeding on litter (Illig et al. 2005); this may explain the dominance of Oribatida in F/H material in the present study.

In contrast to the F/H layer, the concentration of AMF markers in the L layer did not significantly change during the experiment. In litter of an intermediate stage of decomposition, AMF are likely to compete for resources with saprotrophic fungi. Although the enzymatic capability of AMF typically is inferior to that of saprotrophic fungi, they effectively capture nutrients from decomposing litter material (Hodge et al. 2001; Camenzind and Rillig 2013), and this is most effective after saprotrophic microorganisms have started to decompose the litter (Posada et al. 2012). Previous work at our study site (Marian et al. 2019) also provided evidence that the presence of mycorrhiza suppresses the activity of saprotrophic microorganisms, thereby affecting the density of microarthropods such as Collembola. In our study, however, the abundance of microarthropods did not decline with the reduction of the AMF marker. Nevertheless, we assume that antagonistic interactions between AMF and saprotrophic fungi in the L layer persisted as colonization of litter by AMF did not decline during the experiment and this may have impacted other soil microorganisms (Krashevska et al. 2010). This conclusion is supported by the fact that saprotrophic fungi in the L layer in the non-rotated cores exceeded those in rotated cores pointing to stronger competition between saprotrophic fungi and AMF in non-rotated cores. However, part of the AMF marker might have originated from spores of AMF containing high amounts of AMF marker fatty acids (Olsson 1999), but this does not explain why AMF marker fatty acids declined in the F/H but not in the L layer during the experiment.

Defaunation

Arbuscular mycorrhizal fungi did not recover from defaunation in the F/H layer and this likely is related to excluding colonization of the cores by roots (see above). Similarly, C_{mic} did not recover from defaunation in the L and F/H layer during the experiment. Potentially, grazing by microarthropods contributed to the slow recovery. However, the abundances of all soil faunal groups investigated were strongly reduced in both the L and F/H layer of defaunated cores, pointing to restricted colonization of microarthropods from outside the ingrowth cores. This also indicates that the role of microarthropods in fragmenting organic material was reduced and thereby their contribution to the formation of new surface area facilitating microbial colonization (Seastedt 1984; Moore et al. 1988; Lussenhop 1992; Ruess and Lussenhop 2005). The restricted colonization by microarthropods together with the reduced C_{mic} in defaunated cores also might have been related to a decline in food availability due to a reduced input of root derived resources in the cores. At our study sites roots are concentrated in organic layers (Wilcke et al. 2002) and root-derived resources are increasingly recognized as being of fundamental importance in fueling soil food webs (Pollierer et al. 2007, 2012; Scheunemann et al. 2016; Zieger et al. 2017; Marian et al. 2019).

The slow recovery of C_{mic} and BR in both the L and F/H layer might have been due to low quality of litter. Nitrogen concentration in litter and litter decomposition are very low at our study site and this likely is responsible for the pronounced accumulation of organic matter in organic layers (Butenschoen et al. 2014; Marian et al. 2017). Low litter quality is associated with low nutrient mobilization during decomposition and therefore, to low supply of nutrients from the L to the F/H layer, and this is reflected by the decline in C_{mic} from the L layer to the F/H layer. Microbial biomass typically follows the stratified distribution of organic matter in the soil profile of forest ecosystems (Yang and Insam 1991; Wardle 1993). Presumably, both poor mineralization of nutrients from decomposing litter, and exclusion of roots and root-derived resources contributed to the restricted recovery of C_{mic} in defaunated soil cores. This is supported by the fact that BR stayed constant in the L and F/H layer in defaunated cores suggesting that microorganisms did not recover from the disturbance caused by defaunation.

Defaunation also significantly affected the community composition of Oribatida in both the L and F/H layers. Domes et al. (2007) showed that the eggs present in soil are sufficient to ensure establishment of a diverse community of Oribatida in organic layers, although Oribatida species differ in the speed they recover from disturbance. Therefore, the reduced diversity and abundance of Oribatida in defaunated cores might have been due to both reduced availability of resources as well as limited recovery and colonization of the cores by Oribatida from the surrounding soil, suggesting that colonization by Oribatida did not reach equilibrium during the five months of the experiment.

Nitrogen addition

The concentration of the AMF marker fatty acid was not significantly affected by N addition, neither in the L nor in the F/H layer. This contrasts results of previous studies (Camenzind et al. 2014) that AMF root colonization decreased due to N fertilization. The different findings are difficult to explain, but varying effects of N fertilization on AMF have been reported previously (reviewed in Treseder and Allen 2000; Rillig et al. 2003; Treseder 2004).

Earlier studies at our study site reported evidence that microorganisms benefited from N fertilization (Krashevska et al. 2010). Results of the present study support these findings, although the addition of N did not alter microbial biomass. However, the addition of N increased leaf litter decomposition rates and BR in the L layer suggesting that the availability of N limited microbial activity. This is supported by the lower C/N ratio in the L layer in the N addition treatment, reflecting that the addition of N improved litter quality for decomposer organisms. Overall, however, this suggests that nutrient dynamics inside the cores were largely independent of AMF hyphae and exudates.

The addition of N increased the pH in the F/H layer. Increase in pH may stimulate nutrient mobilization and this may result in increased microbial activity and microbial biomass (Thirukkumaran and Parkinson 2000; Vance and Chapin 2001). However, in our study N fertilization did not affect the microbial biomass levels and only little affected microbial activity in the F/H layer. Presumably, microorganisms in the F/H layer are not only limited by N but also by other nutrients. In fact, although increased pH may stimulate the

mobilization of N, it may aggravate the limitation of P (Gallardo and Schlesinger 1994), and P supply is very low in the studied tropical montane rainforest (Krashevska et al. 2010; Homeier et al. 2012).

Conclusions

Results of this study suggest that in nutrient limited tropical montane rainforests AMF hyphae are in close association with roots and do not form extensive extraradical mycelia, indicating that interactions of AMF with other soil biota are restricted to the close vicinity of roots. In contrast to the F/H layer, AMF did not decline in the L layer during the experiment suggesting that interactions with other soil biota are concentrated in the L layer where AMF likely compete with saprotrophic microorganisms for litter-derived resources. The restricted recovery of microorganisms and microarthropods after defaunation inside the cores points to the importance of root-derived resources for fueling soil food webs. Unexpectedly, N addition did not affect AMF suggesting that N dynamics inside the cores were independent of mycorrhiza, despite litter N concentrations were increased and this likely was responsible for the increase in microbial respiration and decomposition due to N addition. Further research on interactions between AMF and other soil biota under field conditions is needed to improve our understanding of their role in structuring microbial and animal communities as well as their importance for decomposition processes in tropical forest ecosystems. The concentration of these interactions in the vicinity of roots and the litter layer, as suggested by results of the present study, pose particular challenges.

Acknowledgements

We would like to thank the Deutsche Forschungsgemeinschaft (DFG FOR816) for financial support. Further, we thank the Ministerio de Ambiente del Ecuador and the Universidad Técnico Particular de Loja (UTPL) for the research permits and the center Naturaleza y Cultura Internacional (NCI) to allow us to work in the San Francisco reserve. We thank Miguel Velez Espinoza for his collaboration during the field work and Odette Gonzalez Macé for helpful comments.

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Supplementary Material

S1 Table. List of Oribatida species, abbreviations used in Fig 4 and the soil layer in which where found.

Family	Species name	Abbreviation	Used in PCA	L	F/H
Hermanniellidae	*Ampullobates ecuadoriensis* (Ermilov, 2013)	*AmplEcua*	x	x	x
Oppiidae	*Arcoppia dechambrierorum* (Mahunka, 1983)				x
Dampfiellidae	*Beckiella capitulum* (Balogh & Mahunka, 1978)	*BeckCapt*	x	x	x
Oppiidae	*Brachioppia cuscensis* (Hammer, 1961)				x
Oripodidae	*Calobates ornatus* (Mahunka, 1986)	*CalbOrnt*	x	x	x
Carabodidae	*Carabodes nigrosetosus* (Mahunka, 1979)			x	x
Damaeolidae	*Caudamaeolus petalus* (P. Balogh, 1988)				x
Ceratoppiidae	*Ceratorchestes cornutus* (Mahunka, 1982)				x
Ceratoppiidae	*Ceratorchestes globosus* (Balogh & Mahunka, 1969)			x	
Microzetidae	*Cosmozetes reticulatus* (Balogh, 1962)	*CosmRetc*	x	x	x
Astegistidae	*Cultroribula zicsii* (Balogh & Mahunka, 1981)	*CultZics*	x	x	x
Damaeidae	*Damaeus flagellatus* (Wang, 1994)			x	
Caleremaeidae	*Epieremulus granulatus* (Balogh & Mahunka, 1979)	*EpieGran*	x	x	x
Eremulidae	*Eremulus brasiliensis* (Pére-Íñigo & Baggio, 1985)	*EremBras*	x	x	x
Eremulidae	*Eremulus rigidisetus* (Balogh & Mahunka, 1969)				x
Oppiidae	*Gittella flagellata* (Mahunka, 1983)				x
Oppiidae	*Globoppia maior* (Hammer, 1962)	*GlobMaio*	x	x	x
Granuloppiidae	*Hammerella parasufflata* (Ermilov, 2013)				x
Hemileiidae	*Hemileius suramericanus* (Hammer, 1958)	*HemlSurm*	x	x	x
Heterobelbidae	*Heterobelba oxapampensis* (Beck, 1962)	*HetrOxap*	x	x	x

Family	Species name	Abbreviation	Used in PCA	L	F/H
Oppiidae	*Kokoppia euramosa* (Balogh & Mahunka, 1969)	*KokpEurm*	x		x
Oppiidae	*Lanceoppia zicsica* (Mahunka, 1988)			x	
Microzetidae	*Licnozetes granulatus* (Balogh & Mahunka, 1969)				x
Liebstadiidae	*Liebstadia pannonica* (Willmann, 1951)			x	x
Liebstadiidae	*Liebstadia similis* (Michael, 1888)	*LiebSiml*	x	x	x
Nanhermammiidae	*Nanhermannia elegantissima* (Hammer, 1958)	*NanhEleg*	x	x	x
Nanhermammiidae	*Nanhermannia nana* (Nicolet, 1855)	*NanhNana*	x	x	x
Oppiidae	*Neoamerioppia rotunda* (Hammer, 1958)	*NeoaRotn*	x	x	x
Galumnidae	*Neoctenogalumna longiciliata* (Ermilov 2013)				x
Oppiidae	*Oppiella nova* (Oudemans, 1902)	*OppiNova*	x	x	x
Microzetidae	*Orthozetes bidentatus* (Ermilov, 2013)			x	
Oppiidae	*Oxyoppia polynesia* (Hammer, 1972)				x
Scheloribatidae	*Perscheloribates minutus* (Pletzen, 1965)	*PersMint*	x	x	x
Pheroliodidae	*Pheroliodes intermedius* (Hammer, 1961)				x
Plasmobatidae	*Plasmobates pagoda* (Grandjean, 1929)				x
Tetracondylidae	*Plenotocepheus neotropicus* (Ermilov, 2013)	*PlenNeot*	x	x	x
Protoribatidae	*Protoribates capucinus* (Mihelcic, 1958)	*ProtCapc*	x	x	x
Oripodidae	*Pteroripoda minutissima* (Balogh & Mahunka, 1974)			x	x
Rhynchoribatidae	*Rhynchoribates grandis* (Hammer, 1961)			x	x
Rhynchoribatidae	*Rhynchoribates mirus* (Beck, 1961)	*RhynMirs*	x	x	x
Haplozetidae	*Rostrozetes foveolatus* (Sellnick, 1925)	*RostFove*	x	x	x
Cymbaeremaeidae	*Scapheremaeus fungisetosus* (Ríos & Palacios-Vargas, 1998)	*ScapFung*	x	x	x
Microzetidae	*Schalleria brevisetosa* (Ermilov, 2013)				x

Family	Species name	Abbreviation	Used in PCA	L	F/H
Scheloribatidae	*Scheloribates elegans* (Hammer, 1958)	*SchlEleg*	x	x	x
Plasmobatidae	*Solenozetes carinatus* (Hammer, 1961)	*SolnCarn*	x	x	x
Plasmobatidae	*Solenozetes flagellifer* (Mahunka, 1983)			x	x
Sternoppiidae	*Sternoppia brasiliensis* (Franklin & Woas, 1992)	*SterBras*	x		x
Sternoppiidae	*Sternoppia mirabilis* (Balogh & Mahunka, 1968)				x
Sternoppiidae	*Sternoppia paramirabilis* (Balogh & Mahunka, 1968)	*SterParm*	x		x
Suctobelbidae	*Suctobelbella complexa* (Hammer, 1958)	*SuctComp*	x	x	x
Suctobelbidae	*Suctobelbella loksai* (Balogh & Mahunka, 1981)	*SuctLoks*	x	x	x
Suctobelbidae	*Suctobelbella peracuta* (Balogh & Mahunka, 1980)	*SuctPerc*	x	x	x
Suctobelbidae	*Suctobelbila peruensis* (Woas, 1986)	*SuctPeru*	x	x	x
Suctobelbidae	*Suctobelbella semiplumosa* (Balogh & Mahunka, 1967)				x
Tectocepheidae	*Tectocepheus minor* (Berlese, 1903)	*TectMinr*	x	x	x
Tectocepheidae	*Tectocepheus velatus sarekensis* (Trägårdh, 1910)	*TecVelSr*	x	x	x
Tectocepheidae	*Tectocepheus velatus velatus* (Michael, 1880)	*TecVelVl*	x	x	x
Teratoppiidae	*Teratoppia pluripectinata* (Balogh & Mahunka, 1978)			x	
Liebstadiidae	*Totobates discifer* (Hammer, 1961)				x
Lohmanniidae	*Xenolohmannia comosa* (P. Balogh, 1984)	*XenlComs*	x	x	x

Chapter 5

General discussion

Belowground communities are assumed to be fueled principally by plant litter- and root-derived resources (Hättenschwiler et al. 2005). Diversity in quantity and quality of resources provided by plants strongly modifies decomposer organisms and thereby influence litter decomposition and nutrient mineralization processes. Higher plant diversity is generally assumed to improve habitat conditions and availability of resources, thereby improving the abundance and activity of decomposer organisms. Nonetheless, the debate on how plant species diversity influences decomposer organism is still open, and plant litter identity, which encompasses all specific litter chemical and physical characteristics of a single species, increasingly is considered as a major driver of decomposer abundance and diversity. In spite of the huge diversity of plant and animals in the Andean tropical montane rainforest ecosystems, little is known on the impact of plant litter diversity and root resources on the abundance, activity and diversity of soil communities and thereby litter decomposition processes, particularly during early stages of decomposition (Krashevska et al. 2017; Marian et al. 2017, 2019).

In this thesis I investigated the impacts of leaf litter diversity and root resources on microorganisms and decomposer microarthropods during the early stages of litter decomposition in tropical montane rainforest ecosystems. Using leaf litter mixtures the study presented in Chapter 2 investigated whether higher leaf litter diversity favors the abundance and activity of soil decomposers during early stages of decomposition. Further, comparing leaf and root litter along an altitudinal gradient, the study reported in Chapter 3 evaluated the effect of plant litter quality as structuring force of the abundance and activity of soil decomposer organisms. The study presented in Chapter 3 further evaluated the contribution of decomposer microarthropods to leaf and root litter decomposer during early stages of litter decomposition. In the studied tropical montane rainforests, the high concentration of roots in organic layers and the abundance of AM fungi (Wilcke et al. 2002; Kottke et al. 2004; Camenzind and Rillig 2013) might favor the abundance and activity of soil microorganisms and microarthropods. Using rotated ingrowth cores, the study presented in Chapter 4 assessed the impact of root-derived resources and AM fungi colonization on soil microorganisms and microarthropods within the organic layer and their responses with nutrient additions

Litter identity drives decomposer organisms and decomposition rates during early stages of decomposition

The results presented in Chapter 2 showed that leaf litter diversity partially explained changes in the abundance and activity of soil microorganisms, but was a poor predictor of the abundance of soil microarthropods in the studied tropical montane rainforests. Notably, however, the decrease in the abundance of microorganisms with higher litter diversity by the end of early stages of decomposition indicates an accumulation of recalcitrant compounds. This reflects the preferential exploitation of labile carbon compounds by opportunistic microorganisms during early stages of decomposition (Berg and McClaugherty 2008; Berg 2014), and the general low quality of the leaf litter material (high C-to-N ratio) in this tropical rainforest ecosystem (Butenschoen et al. 2014).

Contrasting leaf litter diversity, leaf litter identity explained the majority of variation in the abundance and activity of soil organisms during early stages of decomposition. The differential responses of soil biota to litter identity were closely associated with differences in the initial chemical composition of the litter species studied. However, the initial chemical composition of leaf litter was insufficient to explain variations in the abundance of soil microarthropods, suggesting that physical traits might play an important role driving their abundances as has been demonstrated in earlier studies in temperate forest ecosystems (Kaneko and Salamanca 1999; Hoorens et al. 2010). The results also suggest that traits associated with the identity of litter species determine the quality of litter resources and function as key driver of the response of soil biota during early stages of decomposition in the studied tropical montane rainforest.

The results presented in Chapters 2 and 4 also indicate that changes in litter quality during decomposition are directly related to changes in microbial community functions, and are thereby reflected in decomposition rates. These findings support results of previous studies in the region (Illig et al. 2008, 2010; Marian et al. 2017) indicating that variations in decomposition rates during early stages of litter decomposition in montane rainforests strongly depend on the impact of litter quality on decomposer organisms.

Quality of plant litter resources has been shown to decrease with increasing altitude in the study region (Maraun et al. 2008; Rillig et al. 2013; Marian et al. 2017), and decomposition rates were previously found to follow this pattern during early stages of litter decomposition (Marian et al. 2017). However, the results presented in Chapter 3 indicate that this may only be the case in root litter material. Contrasting the findings of Marian et al. (2017), leaf litter decomposition rates presented in Chapter 3 were highest at 2000 m, and these changes were not linked to a higher litter quality (as compared to 1000 and 3000 m). The results suggest that in the studied tropical montane rainforests, differences in the availability of nutrients associated with local litter quality appear to be more important factors for the decomposition of root litter than leaf litter. Presumably, buffered environmental conditions in the soil favor litter quality as the primary driving factor for root litter decomposition. Notably, leaf litter decomposition patterns presented in Chapter 3 were similar to those reported by Marian et al. (2019). Interestingly, both studies took place during low-rainfall periods in the study area (Bendix et al. 2006), suggesting that seasonal variations, particularly drought, might override the primacy of litter quality as major driver of decomposer organisms during early stages of decomposition along the altitudinal gradient investigated here. However, virtually nothing is known about seasonal changes in the soil fauna community of tropical montane rainforests.

Decomposer microarthropods play a minor role during early stages of litter decomposition

The results presented in Chapters 2, 3 and 4 indicate that decomposer microarthropod abundance little affects decomposition processes at early stages of litter decomposition in the studied tropical montane rainforests. This supports previous findings in the study region (Illig et al. 2008; Marian et al. 2018) indicating that decomposition of litter material during early stages of decomposition is driven predominantly by microorganisms, while microarthropods are of little importance. However, both decomposer groups studied in more detail, Oribatida and Collembola, may play a more important role at more advanced stages of decomposition when the litter palatability has been improved by intensive microbial action (Bardgett 2005; Das and Joy 2009; Marian et al. 2018). Indeed, results of

the study presented in Chapter 2 indicated a stronger relationship between the abundance of decomposer microarthropods and the degree of litter decomposition, with the abundance of both Collembola and Oribatida increasing towards the end of the early decomposition stage. Nonetheless, as indicated by the results presented in Chapter 3, microarthropods facilitate litter decomposition at high altitude by grazing on microorganisms or fragmentation of the litter material. Presumably, this stimulation of litter decomposition by microarthropods is related to unfavorable climatic conditions and low quality of the litter material, hampering the attack of the litter by microorganisms.

The studies presented in Chapters 2 and 3 showed that the abundance of Collembola and Oribatida, as well as Oribatida community structure, were not closely associated with microbial biomass, even though microorganisms are known to be their major food resources (Maraun et al. 2003; Scheu et al. 2005; Dhooria 2016). In the studied tropical montane rainforests roots grow into and throughout the organic layer (Wilcke et al. 2002; Kottke et al. 2004), and root-derived resources are increasingly recognized as being of fundamental importance in fueling soil food webs (Pollierer et al. 2007, 2012; Zieger et al. 2017; Marian et al. 2019). The fact that the abundance of decomposer microarthropods was not closely related to bulk microbial biomass (Chapter 2), and microarthropod abundance did not recover after defaunation in cores that were detached from living roots (Chapter 3) indicates that decomposer microarthropod communities in tropical montane rainforests are fueled predominantly by root-derived resources and litter materials at later stages of decay.

The results presented in Chapter 3 also demonstrate that the abundance of Oribatida and Collembola varies between leaf and root litter. The higher density of Oribatida and Collembola in root litter compared to leaf litter suggests that roots provide more resources for decomposer microarthropods during early stages of decay than litter does. However, the higher densities of Oribatida and Collembola may also be related to the position of the litter material in the soil, with root litter in the soil providing more stable microclimatic conditions than leaf litter exposed in the litter layer (Fujii and Takeda 2017). The results further suggest that, even though Oribatida and Collembola comprise different trophic levels and differ in various ecological traits (Siepel 1994; Scheu 2002; Schneider et al.

2004), they contribute in similar ways to early-stage litter decomposition in tropical montane rainforests.

AM fungi: an important actor for determining the abundance and activity of microbial communities during early stages of decomposition

The results presented in Chapter 4 indicate that the colonization of soil cores by AM fungi, and thereby also their impact on soil organisms differs with the depth of the soil organic layer. Vertical stratification of AM fungi colonization has been previously reported in tropical Andean montane rainforests (Aristizábal et al. 2004; Camenzind and Rillig 2013). In the litter layer of the studied tropical montane rainforest, the results suggest antagonistic interactions between AM fungi and saprotrophic microorganisms, presumably because both compete for the same nutrient resources. This result not only supports the view that AM fungi capture nutrients from decomposing litter material in spite of their lack of degradative capability (Hodge et al. 2001; Talbot et al. 2008; Camenzind and Rillig 2013; Nuccio et al. 2013), but also indicates that AM fungi exert an important role during the early stages of leaf-litter decomposition in the studied tropical montane rainforests. Indeed, the results presented in Chapter 4 indicated that nutrient exploitation by AM fungi likely suppresses the activity of saprotrophic fungi in the litter layer. Further, the dominance of AM fungi during early stages of decomposition may contribute to the low abundance of microarthropods in the litter layer, since AM fungi are little consumed by microarthropods (Potapov et al. 2019). This might contribute to the lack of relationship between microarthropod abundance and microorganisms discussed above.

Unlike the litter layer, AM fungi significantly decreased during the experiment in the fermentation/humus (F/H) layer. This was unexpected since AM fungi were anticipated to favor the exploitation of nutrients in the heavily rooted organic layers of the study sites (Wilcke et al. 2002; Kottke et al. 2004), and thereby affect the abundance and activity of soil microorganisms and microarthropods. Presumably, contrasting previous findings in the studied rainforest (Camenzind and Rillig 2013), AM fungi do not form pronounced extraradical mycelia in organic layers that can be cut by rotation of ingrowth cores. Rather,

AM fungi only function in close association with living roots and the carbon supplied by plants to fungi is not or minimally translocated by extraradical hyphae outside the root. Potentially, low litter quality and strong nutrient limitation of decomposition processes enforce confinement of AM fungi near the root surface. This also suggests that in the F/H layer of the studied tropical montane rainforests, interactions between AM fungi and other soil biota are restricted to the close vicinity of roots and cannot be effectively manipulated by using rotation of hyphal ingrowth cores.

The tropical montane rainforests investigated have been shown to be co-limited by both N and P (Homeier et al. 2012), and the addition of both nutrients has been documented to decrease AM fungi abundance and diversity (Camenzind et al. 2014) as well as microbial biomass (Krashevska et al. 2008). However, as presented in Chapter 4, the addition of N did not change the abundance of AM fungi nor the saprotrophic microbial communities. This suggests that increased N availability might aggravate the limitation of other nutrients such as P (Gallardo and Schlesinger 1994; Li et al. 2016), resulting in a lack of effect on the activity of saprotrophic communities or in a change in the dominant role of AM fungi. Overall, the results presented in Chapter 4 indicate that investigating interactions of arbuscular mycorrhiza with soil microarthropods in tropical montane rainforests is more complex than assumed previously and requires improvement of existing methodologies for excluding arbuscular mycorrhiza, as well as long-term experiments to investigate soil fauna – mycorrhiza interactions in these forests.

Conclusion

The findings presented in this thesis indicate that soil biota communities in Andean tropical montane rainforests are structured by leaf-litter identity rather than leaf-litter diversity during early stages of litter decomposition. The results further suggest that litter decomposition processes during early stages of decomposition are mainly driven by microorganisms, with the contribution of microarthropods relevant only at high altitudes, where litter quality is particularly low and climatic conditions are unfavorable. Generally, microarthropod abundance and diversity were not closely associated with changes in microbial characteristics. Rather, the results suggest that the stage of litter decomposition and availability of root-derived resources function as major drivers of the structure of microarthropod communities. Further, the results suggest that colonization of litter materials by AM fungi and their impact on soil decomposer biota varies with soil depth. AM fungi in the litter layer likely compete with saprotrophic microorganisms for litter-derived nutrients and capture nutrients predominantly from litter at early stages of decomposition, while in the F/H layer remain in immediate vicinity of living roots. This highlights that the role of AM fungi in affecting the abundance and activity of microbial communities in the studied tropical montane rainforests is likely to be restricted to the close vicinity of roots at least during early stages of litter decomposition.

Overall, the studies presented in this thesis contributed to a better understanding of key drivers of decomposer communities in Andean tropical rainforest ecosystems. The results improved our understanding of the role of plant species diversity as a key driver of decomposer communities, and indicated that in tropical montane rainforest ecosystems litter identity outweighs litter diversity in determining decomposer community structure and functioning. More detailed studies are required to identify the plant litter traits responsible for litter identity effects on soil decomposer communities and to investigate the role of root-derived resources in structuring decomposer communities and thereby the functioning of tropical montane rainforest ecosystems.

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Acknowledgements

First I would like to thank Stefan Scheu for giving me the opportunity to be his Ph.D. student and for all the support that I always received from him. I have got nothing but words of gratitude. I could not have had a better thesis supervisor!

Thanks also to Christoph Bleidorn for being always open to help. Thanks also to Mark Maraun for being super enthusiastic and positive with all the results. Was always nice to talk with you both.

I especially would like to thank Franca for all her help and patience. I really enjoyed our discussions about results! I will never forget that I started in the AG-Scheu as her Hiwi, we went to Ecuador and she trained me for the fieldwork. Thanks for all Franca!

I would also like to thank Tamara for her helpful comments and for spending her time reading and correcting the redaction and English of my papers and the thesis. Was really nice to count on you! Thanks a lot Tamara.

Thanks also to Doro, Anton, and Melanie for all their helpful comments, to Logos for his help with statistics and R, to Jochen and Yako for being my friendly office colleagues, to Winda for been always super positive and share her good vibes, and to my favorite TA: Guido, I am pretty sure he will forever remember my 20 samples of Fatty acids in a row. I had a really nice time in the lab and also talking with him

And finally, thanks to all the AG-Scheu members…
I enjoy all the trips, parties and barbecues…
Was very nice to be part of this working group and
have colleagues like you all!

Before to switch the language, I would like to thank Marcel for his unconditional support, for helped me always with Teo and the endless German translations. Is nice to know that you have been part of my life during some years of this adventure. Thank you Klattcito! And of course, thanks to all the Klatt members for being like a second family for me.

Cambiando el idioma, primero quiero dar las gracias a mis padres y a mi hermano por haberme apoyado con mi idea loca de venir a Alemania sin algo fijo, sin ellos no habría llegado hasta acá. Muchas gracias, los amo con el alma. Al final el tiempo que he pasado lejos de ustedes ha valido la pena.

También le quiero dar las gracias a mis dos grandes amigas Odette y Magda. Son lo mejor que me ha dejado mi estancia en Göttingen. Han sido mi apoyo en muchas situaciones. Siempre recordaré todas las cosas que hemos vivido, buenas y malas. Hemos pasado por muchas chicas ¡Las quiero chicas!

Me gustaría también las gracias a todos los amigos que he tenido durante esta etapa en Göttingen, en especial a Pablinchis, Fabito, Juanito, Naty y a Dani Ramos. Gracias por las fiestas, los almuerzos, las charlas de la vida y de tonterías… ¡Muchas Gracias chicos! hicieron mi vida mas agradable y ha sido genial haberles conocido. Espero la vida nos cruce en algún momento de nuevo.

Quiero darle un agradecimiento especial a Arturo, porque sin él no habría considerado venir a Göttingen. Gracias por haberme ayudado a empezar en Alemania y por haberme apoyado durante los primeros años del doctorado. Indiscutiblemente ha sido mi locura mas grande, pero me trajo muy buenos resultados ¡Gracias Vera!

Aprovecho también para dale las gracias al Encantor, por su compañía y su apoyo durante las últimas etapas de este largo proceso. Y en general gracias a todas las personas que en algún momento hicieron parte de una charla, una fiesta, una cena, hasta de un chisme, me he divertido y lo agradezco.

Por último y no menos importante, quiero darle las gracias a Teo, él ha sido mi compañía y mi apoyo incondicional, el que me aguanta en las buenas y malas, es ese ángel que me motiva cuando me siento agotada. ¡Te amo Teito, gracias por se mi perrito y estar ahí siempre!

Gracias Dios por esta oportunidad es algo que siempre llevaré en mi corazón ☺

List of publications

Published in peer-reviewed journals

- Sánchez-Galindo LM, Camenzind T, Maraun M, Scheu S (2019) Impacts of core rotation, defaunation and nitrogen addition on arbuscular mycorrhizal fungi, microorganisms and microarthropods in a tropical montane rainforest. Trop Ecol 60:350–361

- Sánchez-Galindo LM, Sandmann D, Marian F, Krashevska V, Maraun M, Scheu S (2021) Leaf litter identity rather than litter diversity shapes microbial functions and microarthropod abundance in tropical montane rainforests**.** Ecology and Evolution. DOI: 10.1002/ece3.7208

Submitted

- Sánchez-Galindo LM, Sandmann D, Marian F, Lauermann T, Maraun M, Scheu S (2020) Differences in leaf and root litter decomposition are mediated by soil microorganisms not decomposer microarthropods in tropical montane rainforests**.** Biotropica.

Thesis declarations

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

The study presented in Chapter 4 was set up by me with additional help of Tessa Camenzind and Ecuadorian helpers (see acknowledges). The resulting manuscript is published in Tropical Ecology (60:350–361). The study presented in chapter 2 was set up and collected by Dorothee Sandmann and Franca Marian. The resulting manuscript is currently submitted in Ecology and Evolution. The study presented in chapter 3 was set up and collected by Dorothee Sandmann and Franca Marian. Samples of the different sampling dates were sorted with the help of Tobias Lauermann and is submitted in Biotropica.

I am the first author of all chapters; I have developed the main ideas, analyzed the data, written the manuscripts and created tables, figures and supplementary materials. The study design of each study was developed in the framework of the DFG Research Unit "Biodiversity and Sustainable Management of a Megadiverse Mountain Ecosystem in South Ecuador" with the financial support of Deutsche Forschungsgemeinschaft (DFG; FOR816). All persons contributing to the manuscripts have been named. All co-authors contributed to finalizing the manuscripts.

The cover-photographs were all taken by me, Franca Marian and Dorothee Sandmann (see acknowledgements).

Plagiarism declaration

I declare that I have written this doctoral thesis 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 also declare that I have not submitted this thesis in any form for another degree at any university or institution.

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Laura Margarita Sánchez Galindo
Göttingen, 22 December 2020