



Altitude and decomposition stage rather than litter origin structure soil microarthropod communities in tropical montane rainforests



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ABSTRACT

Microarthropods impact organic matter turnover and nutrient cycling via processing of organic matter entering the soil as litter and root exudates. Variations in the structure of soil microarthropod communities are due to both biotic and abiotic factors such as local climatic conditions and litter quality. However, in particular in tropical ecosystems the relative importance of these factors for structuring soil microarthropod communities are little understood. We investigated variations in the structure of soil microarthropod communities in leaf and root litter from three altitudes exposed in three tropical montane rainforests at different altitude in southern Ecuador for three years. Leaf litter from three abundant tree species and roots of different diameter were collected from three sites at different altitude (ca. 1000, 2000, 3000 m). Litter and roots were placed in litterbags at the three altitudes, and after 6, 12, 24 and 36 months soil microarthropods in the litterbags were analysed. Density of Acari and Collembola, and diversity of Oribatida decreased with increasing altitude and varied with the degree the litter was decomposed rather than with litter origin and therefore quality of the litter material. Densities fluctuated during litter decomposition generally being lowest after 24 months but higher after 36 months. Species composition of Oribatida varied strongly with altitude; only few species overlapped between altitudes. The percentage of parthenogenetic Oribatida species decreased with increasing altitude. The results suggest that the origin and therefore quality of litter material is of little importance as driving factor for the composition of microarthropod communities of tropical montane rainforests. Factors changing between rainforest sites at different altitude, as well as decomposition stage of litter and associated changes in the microbial community are much more important.

1. Introduction

Microarthropods are important drivers of decomposition processes in a wide range of terrestrial ecosystems (Castanho et al., 2012; Handa et al., 2014; Heneghan et al., 1999; Seastedt, 1984). Especially in highly diverse tropical forests, high diversity and abundance of soil microarthropods are closely related to increased decomposition rates (Castanho et al., 2012; Heneghan et al., 1999). However, most studies assessing soil microarthropod communities and their role in decomposition processes in tropical forests have been carried out in lowland rainforests where soils are old, climatic conditions are favourable and the diversity and abundance of microarthropods is high (Castanho et al., 2012; Heneghan et al., 1999; Palacios-Vargas et al., 2007). In contrast, little is known on interrelationships between litter decomposition and the structure of soil microarthropod communities in

tropical montane rainforests, where soils are younger, climatic conditions are less favourable and leaf litter quality might be very low (Beck et al., 2008).

In tropical montane rainforests strong variations in biotic and abiotic conditions occur on small local scales due to strong changes in climatic conditions, plant community composition as well as soil structure and pH along altitudinal gradients (Homeier et al., 2010; Leuschner et al., 2007; Moser et al., 2007). The thickness of organic layers, of great importance for soil animal communities, increases with increasing altitude (Leuschner et al., 2007; Röderstein et al., 2005; Wilcke et al., 2008), as a direct consequence of differences in the decomposition processes between different altitudes (Marian et al., 2017). The two most abundant soil microarthropod groups regulating decomposition processes in tropical montane rainforests are Oribatida and Collembola, while larger macro-decomposers are lacking (Illig et al.,

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2005; Maraun et al., 2008). Both microarthropod groups not only influence decomposition processes directly by feeding on dead organic material, but also indirectly through structuring of the litter material and their influence on the microbial, faunal and fungal community (Heneghan et al., 1998; Kampichler and Bruckner, 2009). They both comprise primary decomposers, as well as species feeding on lichens and algae, nematodes and root-derived resources, therefore ranging over three to four trophic levels (Chahartaghi et al., 2005; Pollierer et al., 2012, 2007; Schneider et al., 2004). Despite the increasing thickness of the litter layer Illig et al. (2010) found the abundance and diversity of Oribatida in the tropical Andes to decrease towards higher altitudes. Maraun et al. (2013) additionally reported the reproductive mode in Oribatida communities to shift towards a lower percentage of parthenogenetic species at higher elevations. It is still unknown whether these changes in the dominant soil microarthropod groups are driven by altitude dependant factors, e.g. temperature, precipitation and soil pH, or resource availability, i.e. litter quality.

The importance of decomposing litter material as resource for microarthropods has been suggested to change over the course of decomposition, with microarthropods influencing decomposition processes more during later stages of decomposition due to increased palatability of the resource (Bardgett, 2005; Coulis et al., 2009). Considering this, it is surprising that the majority of decomposition studies assessing interrelationships between litter decomposition and microarthropod communities focused on early stages of decomposition (Castanho et al., 2012; Heneghan et al., 1999; Kampichler and Bruckner, 2009; Scheu, 2002), whereas, with few exceptions (Takeda, 1995, 1987), changes in the structure of microarthropod communities during later stages of decomposition received little attention. This is especially relevant in tropical montane ecosystems at high elevation, where decomposition processes are exceptionally slow as compared to tropical lowland rainforests (Butenschoen et al., 2014; Heneghan et al., 1999; Marian et al., 2017; Post et al., 1982). In the tropical montane rainforest of the Andes less than 50% of the litter material decomposes within the first year and in later phases litter decomposition at higher altitudes slows down resulting in about 40% of the litter material remaining after 4 years (Butenschoen et al., 2014; Marian et al., 2017). Whether these patterns in decomposition rates over time are paralleled by changes in the abundance and diversity of soil microarthropods as major drivers of decomposition processes, however, remains unknown.

This study aims to relate the abundance of major microarthropod groups (Collembola and Acari) as well as the diversity of Oribatida to changes occurring in the litter layer of tropical montane rainforests at different altitude over the course of decomposition. Litterbags were filled with litter material from three tropical montane rainforest sites at different altitudes to investigate the influence of decomposition stage, altitude, i.e. site-specific conditions, and litter origin, i.e. initial litter quality, on colonization of leaf and root litter by microarthropods over the course of three years in three tropical montane rainforests in the Andes of southern Ecuador. Data on decomposition stage, litter quality and the microbial community in the litterbags has been published in a parallel study (Marian et al., 2017) and are referred to in the present study to explain changes in microarthropod abundance and diversity.

We hypothesized that (1) the abundance of soil microarthropods as well as Oribatida diversity and the percentage of parthenogenetic species decreases with increasing altitude in both leaf and root litter, due to the increasing harshness of environmental conditions. We further hypothesized that (2) the abundance of soil microarthropods and diversity of Oribatida are related to litter origin, i.e. initial litter quality, with litter of lower initial quality leading to both lower abundance and diversity. Lastly we hypothesized that (3) microarthropod abundance and Oribatida diversity varies over the course of decomposition, initially declining parallel to the depletion of litter resources and in later stages increasing due to increased palatability of the litter material.

2. Material and methods

2.1. Study sites

The three rainforest sites were located at ca. 1000, 2000 and 3000 m a.s.l. on the eastern slope of the Andes in southern Ecuador. All study sites are in the northern part of the Podocarpus National Park facing northeast to northwest. The slopes are moderately steep with 26°–31° (Moser et al., 2007) and covered with mostly undisturbed montane rainforest (Homeier et al., 2002). The lowest site between 990 and 1100 m a.s.l. (referred to as 1000 m; Bombuscaro, S04°06'54'', W78°58'02'') is located south of the city Zamora in the valley of the Rio Bombuscaro and has been classified as premontane rainforest (Homeier et al., 2008). The intermediate site between 1950 and 2100 m a.s.l. (referred to as 2000 m; San Francisco, S3°58'18'', W79°4'45''), classified as lower montane rainforest (Homeier et al., 2008), is part of a private reserve, the Reserva Biologica San Francisco, which includes an area of 9 ha on the flank of the valley of the Rio San Francisco on the northern border of the Podocarpus National Park. The third and highest site between 2900 and 3500 m a.s.l. (referred to as 3000 m; Cajanuma, S04°06'711'', W79°10'58'') is located south of the city Loja at the north-west gate of the Podocarpus National Park and has been classified as evergreen elfin-rainforest (Homeier et al., 2008). With 8–10 humid months per year the region has a semi humid climate. The rainy period lasts from late April to July alternating with a dryer period from September to March, however, rainfall is generally high throughout the year (Ortiz et al., 2006), with precipitation per month always exceeding 100 mm (Bendix et al., 2008; Homeier et al., 2010; Wolf et al., 2011). Mean annual rainfall increases from 2230 to 1950 mm at 1000 and 2000 m, respectively, to 4500 mm at 3000 m (Moser et al., 2007), while the mean annual air temperature gradually decreases with increasing altitude with little inter-annual fluctuation from 19.4 to 15.7 to 9.4 °C at 1000, 2000 and 3000 m, respectively (Bendix et al., 2008; Ortiz et al., 2006). Soil pH also gradually decreases with increasing altitude from 3.94 to 3.52 to 2.86 at 1000, 2000 and 3000 m, respectively (Moser et al., 2007). With increasing altitude the mean soil moisture in the organic layer increases to 45.3 vol% at 3000 m as compared to 9.9 and 11.6 vol% at 1000 and 2000 m, respectively (Leuschner et al., 2007). Biotic conditions also change between the altitudes. Mean tree height decreases from 15.6 to 10.1 to 5.2 m at 1000, 2000 and 3000 m, respectively, while thickness of organic layers as well as fine root biomass increases from 48 mm and 2.7 t ha⁻¹ to 305 mm and 6.2 t ha⁻¹ to 435 mm and 10.8 t ha⁻¹ at the respective sites (Graefe et al., 2008; Leuschner et al., 2007; Moser et al., 2007). Soil types at 1000, 2000 and 3000 m are predominantly Aluic Acrisols, Gley Cambisols and Podzols, respectively (Moser et al., 2007). At 1000 m the litter layer overlays the mineral soil (Ah horizon), i.e. F and H layers are lacking; in contrast, at 2000 and 3000 m the leaf litter overlays organic layers comprising predominantly of F material.

2.2. Experimental setup

Nylon bags (litterbags, 4 mm mesh) were used to investigate the influence of litter origin on soil microarthropod community composition and colonization of leaf and root litter by microarthropods. At each of the three study sites ('origins') freshly fallen leaf litter of the three most abundant tree taxa (i.e., *Puteria* sp., *Cavendishia zamorensis* and *Mollinedia* sp. from 1000 m; *Graffenrieda emarginata*, *Clusia* spp. and *Cavendishia zamorensis* from 2000 m; *Clusia* spp. *Graffenrieda emarginata* and *Hediosmum* sp. from 3000 m) was collected from the forest floor within the study sites. Roots were collected by digging up the upper 20–30 cm of organic material and soil, and removing all roots from this layer by hand. To clear from adhering soil, the roots were washed by gentle rinsing with tap water in the laboratory. Roots were separated into three size classes, small (< 2 mm diameter), medium (2–5 mm diameter) and large (> 5 mm diameter). Both litter and roots were

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