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

Laura M. Sánchez-Galindo1, Dorothee Sandmann1, Franca Marian1, Tobias Lauermann1, Mark Maraun1 and Stefan Scheu1,2

1 JFB Institute of Zoology and Anthropology, University of Göttingen, Göttingen, Germany
2 Centre of Biodiversity and Sustainable Land Use, University of Göttingen, Göttingen, Germany

ABSTRACT

Background. Plant litter decomposition is a key process in carbon and nutrient cycling. Among the factors determining litter decomposition rates, the role of soil biota in the decomposition of different plant litter types and its modification by variations in climatic conditions is not well understood.

Methods. In this study, we used litterbags with different mesh sizes (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 tropical montane rainforests in Ecuador. We examined decomposition rates, litter C and N concentrations, microbial biomass and activity, as well as decomposer microarthropod abundance over one year of exposure at three different altitudes (1,000, 2,000 and 3,000 m).

Results. Leaf litter mass loss did not differ between the 1,000 and 2,000 m sites, while root litter mass loss decreased with increasing altitude. Changes in microbial biomass and activity paralleled the changes in litter decomposition rates. Access of microarthropods to litterbags only increased root litter mass loss significantly at 3,000 m. The results 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. The findings also highlight litter quality as the dominant force structuring detritivore communities. Overall, the results support the view that microorganisms mostly drive decomposition processes in tropical montane rainforests with soil microarthropods playing a more important role in decomposing low-quality litter material.

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 & McClaugherty,
Although the annual input of leaf and root litter in forests is typically equivalent in mass (Norby et al., 2004; Freschet et al., 2013), most studies investigating the 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 & Takeda, 2017). Therefore, integration of both root litter and leaf litter is needed for a comprehensive understanding of the role of soil organisms in element cycling and ecosystem functioning.

Leaf and root litter differ in structure and chemical composition (Berg & McClougherty, 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, Aerts & Cornelissen, 2012; García-Palacios et al., 2016; Jo, Fridley & Frank, 2016). Additionally, leaf and root litter are found at different positions on 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 varying microenvironments for soil organisms (Ostertag & Hobbie, 1999; Fujii & Takeda, 2010; Fujii & Takeda, 2017). Differences in quality and input pathways of litter types 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, Bottner & Berg, 1995; Aerts, 1997; Hättenschwiler, Tiunov & Scheu, 2005). In tropical Andean montane ecosystems climatic conditions change strongly with altitude (Myers et al., 2000; Beck & Ritcher, 2008). Increasing altitude is associated with a decline in litter nutrient concentrations and an increase in the thickness of soil organic layers and fine root biomass (diameter < 2 mm) (Tanner, Vltousek & Cuevas, 1998; Soethe, Lehmann & Engels, 2007; Graefe, Hertel & Leuschner, 2008). Notably, at higher altitudes, more organic material originates from fine root litter than from fallen leaves (Röderstein, Hertel & Leuschner, 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, Ruan & Han, 2010; Garcia-Palacios et al., 2016). Variations in climatic conditions may also induce changes in soil community composition resulting in well-adapted communities able to govern decomposition processes (Allison et al., 2013). 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 (Decaëns et al., 2006; Bradford et al., 2017), particularly in tropical montane rainforest ecosystems (Marian et al., 2017; Marian et al., 2018).

Decomposer communities in tropical montane rainforests are dominated by microorganisms and soil microarthropods, whereas large decomposer species are virtually lacking (Illig et al., 2008; Maraun et al., 2008; Scheu et al., 2008). Among soil microarthropods, oribatid mites (Oribatida, Acari) and springtails (Collembola) are the most abundant and diverse worldwide (Seastedt, 1984; Ruess & Lussenhop, 2005). These microarthropods increase litter decomposition rates and nutrient cycling in forest
ecosystems either via litter consumption or through stimulation of microbial activity
and transport of microbial propagules (Swift, Heal & Anderson, 1979; Seastedt, 1984;
Ruess & Lussenhop, 2005). However, the positive effect of decomposer microarthropods
on microbial growth has been reported to be density-dependent and restricted to low
density (Kaneda & Kaneko, 2008; Crowther & A’Bear, 2012; Crowther, Boddy & Jones, 2012;
Gergócs & Hufnagel, 2016). In tropical montane rainforests, the density of microarthropods
is low compared to e.g., temperate forests, suggesting that they may stimulate or little
affect microorganisms and decomposition processes (Illig et al., 2008; Marian et al., 2017;
Sánchez-Galindo et al., 2021). Nevertheless, the role of microarthropods in decomposition
processes is likely to vary with altitude and litter types, but this has been little studied.

The present study investigates the effects of microorganisms and decomposer
microarthropods on leaf and root litter decomposition and their variations along an
altitudinal gradient of tropical montane rainforests in Ecuador. Decomposition rates,
microbial biomass and respiration, as well as Collembola and Oribatida abundances and
Oribatida community composition, 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 decreases with increasing altitude, and this is mainly due to
less favourable abiotic conditions. We also hypothesized that (2) access of litter by soil
microarthropods increases decomposition as well as microbial biomass and activity in
both leaf and root litter. Further, we hypothesized that (3) the abundance of decomposer
microarthropods and Oribatida species richness increase with increasing microbial biomass
in both leaf and root litter. Lastly, we hypothesized that (4) increase in litter quality (as
indicated by litter C-to-N ratio) and microbial biomass during decomposition are key
factors structuring Oribatida communities in both leaf and root litter.

**MATERIALS & METHODS**

**Study area**
The study area is in the northern fringes of the Podocarpus National Park in the eastern
slopes of the Andean Cordillera, Southeast Ecuador. Three study sites, situated at 1,000,
2,000 and 3,000 m a.s.l. were selected to represent an altitudinal gradient with moderately
steep slopes of 26–31° (Moser, Hertel & Leuschner, 2007). The lower site at 1,000 m a.s.l.
($04°06’54”$, $78°58’02”$) is in the Río Bombuscaro valley and classified as evergreen
submontane rainforest dominated by tree species of Arecaceae, Combretaceae, Moraceae,
Monimiaceae, Rubiaceae and Sapotaceae (Homeier et al., 2008). The intermediate site at
2,000 m a.s.l. ($53°58’18”$, $79°4’45”$) is 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 Arecaceae, Clusiaceae, Ericaceae, Lauraceae,
Melastomataceae and Rubiaceae (Homeier et al., 2008). The highest site at 3,000 m a.s.l.
($04°06’711”$, $79°10’58”$) is near the upper Cajanuma mountain at the northwest gate
of Podocarpus National Park. The forest has been classified as an evergreen elfin forest
dominated by trees/shrubs of Aquifoliaceae, Bromeliaceae, Chloranthaceae, Clusiaceae,
Ericaceae and Melastomataceae (Homeier et al., 2008). The climate is semi-humid with
an average annual temperature of 14.9, 12.3 and 8.9 °C and annual precipitation of approximately 2,200, 3,500 and 4,500 mm at 1,000, 2,000 and 3,000 m a.s.l., respectively (Bendix et al., 2006; Homeier et al., 2010). Soil types of the study sites are alumic Acrisol (1,000 m), Gley Cambisol (2,000 m) and Podzol (3,000 m) (Soethe, Lehmann & Engels, 2006; Moser, Hertel & Leuschner, 2007). The thickness of the organic soil layers increases with altitude from 4.8 cm at 1,000 m to 30.5 cm at 2,000 m to 43.5 cm at 3,000 m (Leuschner et al., 2007; Graefe, Hertel & Leuschner, 2008). In parallel, fine root biomass increases from 2.7 to 6.2 to 10.8 t ha$^{-1}$ at the respective sites (Soethe, Lehmann & Engels, 2006).

**Experimental design**

Nylon litterbags (17 × 17 cm) with mesh sizes of 45 µm, 1 mm and 4 mm were filled with 10 g of leaf or root litter. The mesh sizes we used are typically used to evaluate the role of meso- and macrofauna in decomposition processes. The 45 µm mesh prevents access by even the smallest mites and springtails, the 1 mm mesh allows access by virtually all mesofauna species and the 4 mm mesh allows access by virtually all macrofauna species (Bradford et al., 2002; Kampichler & Bruckner, 2009; Bokhorst & Wardle, 2013). Leaf litter consisted of a mixture of freshly fallen leaves of three locally abundant tree species of each study site: *Pouteria* sp., *Cecropia andina* and *Mollinedia* sp. at 1,000 m, *Graffenrieda emarginata*, *Clusia* sp. and *Cavendishia zamorensis* at 2,000 m, *Clusia* sp. *Graffenrieda emarginata* and *Hedyosmum* sp. at 3,000 m. Root litter 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 SI 1). This was done to mimic close to natural conditions in the litterbags for the colonization by the local soil animal community. 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 analyzed 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, Lloyd & Ghelardi, 1963) and counted. Adult Oribatida were identified to species level or sorted into morphospecies (Balogh & Balogh, 1990; Balogh & Balogh, 2002), following the nomenclature of Subías (2018). All identified species are recorded in the Ecotaxonomy database (Potapov, Sandmann & Scheu, 2019).
Analytical procedures
Mass loss ($M_{\text{loss}}$) for both leaves and roots were calculated as $M_{\text{loss}} = ((m_0 - m_1/m_0)) \times 100$, where $m_0$ is 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 analyzed using a CN elemental analyzer (Vario EL III, Elementar, Hanau, Germany).

Microbial basal respiration (BR) and microbial biomass ($C_{\text{mic}}$) were measured using a computer-controlled O$_2$ micro-compensation apparatus (Scheu, 1992). BR ($\mu$l 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. $C_{\text{mic}}$ was calculated from the maximum initial respiratory response (MIRR; $\mu$l O$_2$ g$^{-1}$ h$^{-1}$) measured after glucose saturation following the substrate-induced respiration method (SIR) of Anderson & Domsch (1978). MIRR was calculated as the average of the lowest three readings within the first 10 h and $C_{\text{mic}}$ was calculated as $C_{\text{mic}} = 38 \times$ MIRR (mg g$^{-1}$ dry weight) (Beck et al., 1997; Joergensen & Scheu, 1999).

Statistical analyses
Analyses were performed using R version 3.6.0 (R Core Team, 2019). Linear mixed-effects models were used to analyze changes in $M_{\text{loss}}$, $C_{\text{mic}}$, BR, the abundance of Oribatida and Collembola, and Oribatida species richness data separately for leaf and root litter (hypotheses 1 and 2). Sampling date (6 and 12 months), mesh size (45 $\mu$m, 1 mm and 4 mm), altitude (1,000, 2,000 and 3,000 m a.s.l.) and all possible interactions were fitted as fixed factors, and block was fitted as a random factor with random intercept (R package “nlme”; Pinheiro et al., 2020). Data were log-transformed if necessary. Model residuals were checked for normality and homoscedasticity using Shapiro–Wilk test and Bartlett’s test (R package “stats” R Core Team, 2019). Differences between means were inspected using Tukey’s honestly significant difference test (R package “emmeans”; Lenth, 2020). Pearson correlation coefficients (package “stats”) were calculated to investigate relationships between $M_{\text{loss}}$, $C_{\text{mic}}$, BR, C-to-N ratio, and the abundance of Collembola and Oribatida, and Oribatida diversity separately for leaf and root litter (hypothesis 3).

Canonical correspondence analysis (CCA) performed in CANOCO 5.02 (Ter Braak & Smilauer, 2012) was used to explore the relationship between Oribatida community composition and litter characteristics ($M_{\text{loss}}$, C-to-N ratio) as well as microbial indicators (BR, $C_{\text{mic}}$) (hypothesis 4). Only species with more than three individuals in the samples were included. 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 $\mu$m, 1 mm and 4 mm) and altitude (1,000, 2,000 and 3,000 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 and $R^2 > 0.90$ (Legendre & Legendre, 1998; Blanchet, Legendre & Borcard, 2008).
RESULTS

Decomposition of leaves and roots
Generally, $M_{\text{loss}}$ significantly increased during the time of exposure in both leaf and root litter. Leaf litter $M_{\text{loss}}$ was not significantly affected by any interaction between the three factors studied, but it was higher at 1,000 and 2,000 m compared to 3,000 m at both sampling dates (Table 1, SI 2). By contrast, in root litter the interactions between altitude and date, as well as between altitude and mesh size significantly affected $M_{\text{loss}}$. After 12 months it decreased in a linear way with increasing altitude (Fig. 1, Table 1). Further, at 3,000 m root litter $M_{\text{loss}}$ in litterbags of 4 mm mesh size was higher than in litterbags of 45 $\mu$m and 1 mm mesh size (Table 1, SI 2). $M_{\text{loss}}$ positively correlated with $C_{\text{mic}}$, BR and negatively with litter C-to-N ratios in both leaf and root litter. In root litter, $M_{\text{loss}}$ also positively correlated with Collembola and Oribatida abundance and Oribatida richness (Table 2).

The C-to-N ratio of both leaf and root litter significantly increased with altitude from 1,000 m to similar values at 2,000 m and 3,000 m (Table 1, SI 2). In leaf litter the C-to-N ratio decreased with time, whereas the C-to-N ratio in root litter did not change significantly with time. 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 $\mu$m mesh size. C-to-N ratios negatively correlated with $M_{\text{loss}}$ and the abundance of Collembola and Oribatida, and Oribatida richness in leaf litter. In root litter, C-to-N ratios negatively correlated with $M_{\text{loss}}$, $C_{\text{mic}}$, BR and the abundance of Collembola and Oribatida, and Oribatida richness (Table 2).

Microorganisms
Generally, $C_{\text{mic}}$ and BR significantly increased with time of exposure and varied with altitude in both litter types (Table 1, SI 3). In leaf litter, $C_{\text{mic}}$ was higher at 1,000 and 2,000 m compared to 3,000 m, whereas in root litter, both $C_{\text{mic}}$ and BR were higher at 1,000 m compared to 2,000 and 3,000 m.

In leaf litter, variations in $C_{\text{mic}}$ and BR with altitude depended on time, but the effect of altitude also varied with mesh size (significant three factor interaction; Fig. 2, Table 1, SI 3). Similar to leaf litter, in root litter variations in $C_{\text{mic}}$ with altitude depended on time and mesh size while variations in BR in root litter with altitude depended on mesh size (Fig. 2, Table 1, SI 3). In both leaf and root litter, $C_{\text{mic}}$ and BR positively correlated with $M_{\text{loss}}$ (Table 2). In root litter, $C_{\text{mic}}$ and BR also positively correlated with Collembola and Oribatida abundances, and Oribatida richness, but negatively with litter C-to-N ratios.

Abundance of Collembola and Oribatida
Contrasting $C_{\text{mic}}$ and BR, time of exposure as main effect neither affected the abundance of Collembola nor that of Oribatida (Table 3). Rather, the abundance of Collembola and Oribatida in both litter types varied strongly with altitude and mesh size.

Generally, in both litter types, the abundance of Collembola decreased strongly with increasing altitude (Table 3, SI 5). In leaf litter the decrease in Collembola abundance with altitude also varied with sampling date. In root litter, the variation in the abundance of Collembola with altitude varied significantly with mesh size (Table 3, SI 5 and SI 6).
Table 1  Effects of time, mesh size and altitude on mass loss (\(M_{\text{loss}}\)), litter C-to-N ratio, microbial biomass (\(C_{\text{mic}}\)) and basal respiration (BR) in leaf and root litter. \(F\)- and \(P\)-values of linear mixed-effects models on the effect of time of exposure (6 and 12 months), mesh size (45 \(\mu\)m, 1 mm, 4 mm) and altitude (1,000, 2,000 and 3,000 m a.s.l.) on \(M_{\text{loss}}\), litter C-to-N ratio, \(C_{\text{mic}}\) and BR in leaf and root litter.

|                  | \(F\)-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       | 0.069       | 0.527       | 1.05        | 0.362       |
| 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       | 0.02        | 0.980       | 0.30        | 0.741       |
| 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      | 28.47       | <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   | <0.001       | 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       |

Notes. Significant effects are given in bold, \(p < 0.05\).

Generally, contrasting the pattern in Collembola, the abundance of Oribatida in leaf litter was similar at 1,000 and 2,000 m and significantly lower at 3,000 m, whereas in root litter the abundance at 1,000 m strongly exceeded that at 2,000 and 3,000 m (Table 3, SI 5). In contrast to Collembola, in both litter types, the abundance of Oribatida generally varied with mesh size. However, in root litter the effect varied with altitude (Table 3, SI 5 and SI 6).

In both leaf and root litter the abundance of Collembola and Oribatida correlated negatively with litter C-to-N ratios and positively with the Oribatid richness (Table 2). However, in root litter the abundance of Collembola and Oribatida also correlated positively with \(M_{\text{loss}}\), \(C_{\text{mic}}\) and BR.

**Oribatida species richness**
In both leaf and root litter the average Oribatida species richness per litterbag was significantly affected by mesh size and altitude (Table 3, SI 5). In leaf litter, Oribatida species richness was generally affected by the interaction between time, altitude and mesh size; whereas in root litter Oribatida species richness only varied with mesh size and altitude (Table 3, SI 5). In both leaf and root litter Oribatida species richness correlated negatively with litter C-to-N ratios and positively with the abundance of Collembola and Oribatida (Table 2). However, in root litter Oribatida richness correlated positively with \(M_{\text{loss}}\), \(C_{\text{mic}}\) and BR.
Figure 1  Effect of altitude on mass loss ($M_{\text{loss}}$) after 6 and 12 months. Variations in $M_{\text{loss}}$ of leaf and root litter exposed in litterbags at three different altitudes (1,000, 2,000 and 3,000 m a.s.l.) 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, $p < 0.05$).

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Table 2  Pearson correlation coefficients between mass loss ($M_{\text{loss}}$), microbial biomass ($C_{\text{mic}}$), basal respiration (BR), litter C-to-N ratio, the abundance of Collembola, and the abundance and richness of Oribatida in leaf and root litter.

|                  | $M_{\text{loss}}$ | $C_{\text{mic}}$ | BR     | Collembola abundance | Oribatida abundance | Oribatida richness |
|------------------|-------------------|------------------|--------|----------------------|---------------------|-------------------|
| **Leaf litter**  |                   |                  |        |                      |                     |                   |
| $C_{\text{mic}}$ | 0.45***           | 1                | –      | –                    | –                   | –                 |
| BR               | 0.32*             | 0.55***          | 1      | 1                    | –                   | –                 |
| Collembola abundance | 0.12             | 0.15             | –0.24  | 1                    | –                   | –                 |
| Oribatida abundance    | 0.11             | 0.11             | –0.16  | 0.50*                | 1                   | –                 |
| Oribatida richness   | 0.19              | 0.14             | –0.20  | 0.54**               | 0.92***             | 1                 |
| C-to-N              | –0.44***          | –0.11            | 0.18   | –0.60***             | –0.31*              | –0.45***          |
| **Root litter**    |                   |                  |        |                      |                     |                   |
| $C_{\text{mic}}$  | 0.75***           | 1                | –      | –                    | –                   | –                 |
| BR                | 0.74***           | 0.86***          | 1      | –                    | –                   | –                 |
| Collembola abundance | 0.35*            | 0.46***          | 0.35** | 1                    | –                   | –                 |
| Oribatida abundance    | 0.33              | 0.44***          | 0.33** | 0.67**               | 1                   | –                 |
| Oribatida richness   | 0.36              | 0.45***          | 0.35** | 0.68**               | 0.98***             | 1                 |
| C-to-N              | –0.47***          | –0.64***         | –0.41*** | –0.43***            | –0.49**             | –0.52***          |

**Notes.**  
Significant correlations are given in bold (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$).
Figure 2. Effect of mesh size and altitude on C\textsubscript{mic} and BR after 6 and 12 months. Variation in (A) microbial biomass (C\textsubscript{mic}) and (B) basal respiration (BR) in leaf litter (left panel) and root litter (right panel) at three altitudes (1,000, 2,000 and 3,000 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, \(p < 0.05\)).

Community structure of Oribatida

In total, 176 species of Oribatida were identified (see SI 7 for full list of species). CCA of Oribatida species in leaf litter with litter C-to-N ratio, M\textsubscript{loss}, BR and C\textsubscript{mic} included as environmental variables explained 12.7% of the variation of Oribatida community composition (Fig. 3A); litter C-to-N ratio accounted for 4.4% (pseudo-F = 1.9, \(P = 0.002\)), M\textsubscript{loss} for 4.3% (pseudo-F = 1.8, \(P = 0.002\)) and BR for 3.9% (pseudo-F = 1.6, \(P = 0.007\)). The community composition of Oribatida at 2,000 and 3,000 m correlated positively with increasing litter C-to-N ratio and BR; M\textsubscript{loss} correlated positively with the first sampling date and was associated with lower species abundance.

CCA of Oribatida species in root litter with litter C-to-N ratio, BR, M\textsubscript{loss} and C\textsubscript{mic} included as environmental variables explained 10.2% of the variation of Oribatida community composition (Fig. 3B); litter 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, Oribatida species at 2,000 and 3,000 m correlated positively with increasing litter 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 1,000 m site was separated from the 2,000 and 3,000 m sites along the first axis and the centroids of mesh size were close to the center of the ordination. As note of caution, however, most Oribatida species were rare and only occurred at certain altitudes and at specific sampling dates; for the abundance of species at each of the study sites see SI 7.
Table 3  Effects of time, mesh size and altitude on the abundance of Collembola, and the abundance and richness of Oribatida in leaf and root litter. 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.

|                      | 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   |

Notes.
Significant effects are given in bold, p < 0.05.

DISCUSSION

Variations in 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. For leaf litter, M_{loss} did not follow the expected linear decrease with altitude, rather, decomposition rates at 1,000 and 2,000 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; Marian et al., 2019) and indicates that leaf litter decomposition cannot be explained only by the linear decrease in temperature along the altitudinal gradient studied. Potentially, the decline in leaf litter decomposition with temperature was compensated by higher precipitation at 2,000 m compared to 1,000 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, Bottner & Berg, 1995; Aerts, 1997), the role of climatic factors might be overridden by the variability of litter traits at local scales (Scowcroft, Turner & Vitousek, 2000; Richardson, Richardson & Soto-Adames, 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 1,000
Figure 3  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 = 1,000 m, green = 2,000 m, blue = 3,000 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 SI 7.

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m site were of considerably higher quality than those from the 2,000 m site (as well as the 3,000 m site), suggesting that the high decomposition rates of leaf litter at 2,000 m also cannot be explained by litter quality. Nonetheless, caution is recommended in the interpretation of this result, as other litter chemical compounds were not measured and might have influenced litter decomposition rates. Further, leaf litter $M_{\text{loss}}$ was potentially 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 $C_{\text{mic}}$ and BR were higher in leaf litter at 2,000 m than at 1,000 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 \( C_{\text{mic}} \) and BR in leaf litter at 2,000 and 3,000 m, despite the very high litter C-to-N ratio, also suggest that microbial communities at these sites are well adapted to decompose litter of low quality (Gholz et al., 2000; Strickland et al., 2009; Milcu & 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, Vitousek & Cuevas, 1998; Kitayama et al., 2004). This is supported by the high C-to-N ratios and low \( C_{\text{mic}} \) and BR, as well as the abundance of decomposer microarthropods at 2,000 and 3,000 m (compared to 1,000 m). The contrasting results between leaf and root litter decomposition rates suggest that in the studied tropical montane rainforests differences in litter chemical composition and their association with nutrient limitations among the altitudinal sites are more critical factors for the decomposition of root litter than for leaf litter. Nonetheless, a complete litter chemical composition profile is needed to support this conclusion. 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 & Hobbie, 1999; Silver & Miya, 2001). However, as root litter generally decomposed slower than leaf litter at 2,000 and 3,000 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 1,000 m the more buffered climatic condition together with the proximity of the mineral soil layer might have favoured the faster decomposition rates of roots than leaf litter.

**Faunal contribution to leaf and root litter decomposition**

The abundance of both Collembola and Oribatida was higher in 1 and 4 mm mesh bags irrespective of the plant litter type indicating that, as intended, 45 \( \mu \)m mesh size restricted the access to the litterbags by mesofauna. Thus, the different mesh sizes are a useful tool to evaluate the effects of decomposer animals on decomposition processes. However, restricting the access of mesofauna in 45 \( \mu \)m litterbags 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 & Bruckner, 2009). Further, contrasting our second hypothesis, access by microarthropods to litterbags containing leaf litter did not vary the general decomposition rates, nor at any of the three altitudes. However, soil microarthropod access to root litter increased its mass loss at 3,000 m (4 mm mesh bags). Despite the widely assumed beneficial effects of soil microarthropods on litter decomposition, experimental evidence supporting this assumption is controversial; some studies indeed found positive effects on litter mass loss (Bradford et al., 2002; Carrillo et al., 2011; Bokhorst & Wardle, 2013), whereas others suggest their contribution to be minor or absent (Schinner, 1982;
Overall, our results for leaf litter support the latter and previous findings at our study sites also indicate that the decomposition of leaf litter is predominantly 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; Marian et al., 2019). This finding is supported by lack of correlation of Collembola and Oribatida abundances with \( \text{M}_{\text{loss}} \), \( C_{\text{mic}} \) and BR in leaf litter. Both decomposer groups may play a more important role at more advanced stages of decomposition when microorganisms have colonized leaf litter making it more palatable for arthropod consumers (Bardgett, 2005; Coulis et al., 2009; Das & Joy, 2009). However, the increase in root litter \( \text{M}_{\text{loss}} \) at 3,000 m in 4 mm mesh bags suggests that under unfavourable environmental conditions, the decomposition of low-quality litter is stimulated by soil arthropods. Several processes may have accelerated root litter decomposition including stimulation of microbial growth via nutrient mobilization, litter fragmentation and dispersal of microbial propagules (Verhoef & Brussaard, 1990; Ruess & Lussenhop, 2005; Scheu, Ruess & Bonkowski, 2005). The fact that at 3,000 m \( C_{\text{mic}} \) and BR in roots increased in 1 and 4 mm mesh bags supports these findings and reinforces that the contribution of microarthropods to decomposition of recalcitrant substrates is more pronounced than in readily decomposable materials (Joo, Yim & Nakane, 2006; Milcu & Manning, 2011; Gergős & Hufnagel, 2016).

Notably, \( C_{\text{mic}} \) 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, \( C_{\text{mic}} \) was higher in 1 and 4 mm mesh bags, while BR was higher in 45 \( \mu \text{m} \) mesh bags. Overall, this supports our expectation that decomposer microarthropods stimulate microorganisms, thereby enhancing their biomass. Potentially, grazing on microorganisms results in increased nutrient mobilization favouring microbial growth (Seastedt, 1984; Hättenschwiler, Tiunov & Scheu, 2005). Further, grazing may foster 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 (Dilly & Munch, 1996; Chapman et al., 2013). Indeed, it has been stressed earlier that the structure of microbial communities is an important determinant of litter decomposition rates particularly in forest ecosystems (Strickland et al., 2009).

Additionally, despite the general lack of effect of mesh size on root litter mass loss, the abundances of both Collembola and Oribatida, and Oribatida species richness positively correlated with \( \text{M}_{\text{loss}} \), \( C_{\text{mic}} \) and BR. These results support our third hypothesis and suggest that litter accumulation in nutrient-poor sites can provide more habitat space for soil decomposer microarthropods. Notably, the increase in animal abundance and diversity may enhance the faunal contribution to litter decomposition (Perez et al., 2013). Moreover, the close vicinity of roots to the mineral soil layer might have favored nutrient availability and thereby improved food resources for decomposer microarthropods (Marian et al., 2019). Further, 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 3,000 m, where the concentration of root biomass is at a maximum (Röderstein, Hertel &
Leuschner, 2005; Soethe, Lehmann & Engels, 2007), soil arthropods may benefit more from root-derived resources than at 1,000 and 2,000 m either by grazing on microorganisms or directly by feeding on roots.

Interestingly, the abundance of both decomposer microarthropods in leaf and root litter did not vary significantly with sampling date. Potentially, the nutritional value of the litter material for these detritivore microarthropods changed little during the exposure time. Substrate quality may also be related to the generally low effects of soil decomposer microarthropods on leaf and root litter decomposition. Litter of different quality may attract different faunal communities and this likely contributes to the varying effects of decomposer animals on decomposition processes (Fujii & Takeda, 2012; Fujii et al., 2017).

**Oribatida species richness and community structure in leaf and root litter**

Similar to Oribatida abundance, the higher Oribatida species richness 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. 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 such as temperature, precipitation, moisture and soil pH (Illig et al., 2008; Marian et al., 2018). By contrast, in root litter, the high number of Oribatida species at 1,000 m and the similarly low numbers at 2,000 and 3,000 m suggest that apart from abiotic conditions changing with altitude other factors modify Oribatida species richness. The fact that C-to-N ratios of root litter were similar at 2,000 and 3,000 m support this conclusion and suggests that root litter quality may be a regulator of Oribatida richness; the strong correlation of Oribatida species richness with litter C-to-N ratio supports this conclusion and suggests that increasing amounts of low-quality root litter material with altitude detrimentally affect Oribatida richness at 2,000 and 3,000 m (Röderstein, Hertel & Leuschner, 2005; Maraun et al., 2013). Indeed, Illig et al. (2010) also concluded that Oribatida species diversity at the studied montane rainforests is related to litter quality as important driving factor.

Similar to Oribatida species richness, Oribatida community assemblages varied mostly with altitude in both leaf and root litter. Most of the 176 species identified were registered on the 1,000 m site, only few species were only present at 2,000 and 3,000 m, presumably reflecting less favorable climatic conditions and poor resource quality at the highest altitudes (Marian et al., 2018). Interestingly, in leaf litter certain Oribatida species including *Sternoppia mirbilis*, *Lanceoppia* sp.1 and *Rostrozetes* sp.6 preferentially colonized litter after 12 months of exposure with the latter two species exclusively recorded at 2,000 m. This supports our fourth hypothesis indicating that certain Oribatida species rely on food resources associated with changes in leaf litter physicochemistry during 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 works as important factor structuring Oribatida communities in both leaf and root litter. Contrasting leaf litter, increase in root litter decomposition 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 in contrast to our expectations, Oribatida community structure in root litter is not principally linked with decomposition or the gross characteristics of microbial communities. However, potential effects of root litter decomposition on the general quality of the organic litter material may function as key factor structuring Oribatida communities as indicated by their relationship with C-to-N ratios. Additionally, as mentioned before, root exudates may also modify the general characteristics of the organic matter and become an important carbon source fuelling Oribatida communities (Pollierer et al., 2007; Dennis, Miller & Hirsch, 2010; Zieger et al., 2017). Overall, our results indicate that the environmental factors considered explained only little of the variation in Oribatida community composition in both leaf and root litter. Still, both leaf and root litter characteristics, such as C-to-N ratio, as well as $C_{mic}$, significantly correlated with Oribatida community composition and this is consistent with earlier findings (Fujii & Takeda, 2017; Marian et al., 2018).

**CONCLUSIONS**

The results of our study suggest that the decomposition of both leaf and root litter in montane rainforests is mainly due to microorganisms when compared to the role of microarthropods. However, soil microarthropods may contribute to the decomposition of low-quality litter such as root litter, particularly at very high altitude. Generally, the contrasting patterns of microbial biomass and the abundance of decomposer microarthropods and Oribatida species richness with the time of exposure highlight the minor importance of microorganism abundance as a food resource and structuring force of decomposer microarthropod communities. Rather, the results point to the dominance of litter characteristics, such as litter C-to-N ratio, as key factor structuring Oribatida communities in both leaf and root litter. Additionally, our findings highlight the main role of climatic factors driving root litter decomposition across altitudinal gradients, but their effects on leaf litter decomposition might be overridden at the local scale by litter traits and biotic factors. Further, at local scales differences in litter characteristics and the nutritional requirements of decomposer communities may modulate both leaf and root litter decomposition, and nutrient cycling in tropical montane rainforest ecosystem. Importantly, however, our 12 months study may not have been long enough to uncover the total contribution of soil microarthropods to litter decomposition. Due to general low quality of the litter material in this tropical rainforest, the functional role of soil microarthropods might become more significant in the long-term. Nonetheless, the study contributed to a better understanding of the role of decomposer microarthropods for litter decomposition in tropical rainforest ecosystems.

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**Author Contributions**
- Laura M. Sánchez-Galindo performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft.
- Dorothee Sandmann conceived and designed the experiments, performed the experiments, analyzed the data, authored or reviewed drafts of the article, and approved the final draft.
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REFERENCES

Aerts R. 1997. Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. Oikos 79:439–449 DOI 10.2307/3546886.

Allison SD, Lu Y, Weihe C, Goulden ML, Martiny AC, Treseder KK, Martiny JBH. 2013. Microbial abundance and composition influence litter decomposition response to environmental change. Ecology 94:714–725 DOI 10.1890/12-1243.1.

Anderson JPE, Domsch KH. 1978. A physiological method for the quantitative measurement of microbial biomass in soils. Soil Biology and Biochemistry 10:215–221 DOI 10.1016/0038-0717(78)90099-8.

Balogh J, Balogh P. 1990. Oribatid mites of the neotropical region II. Budapest: Elsevier Science Publishers.

Balogh J, Balogh P. 2002. Identification keys to the oribatid mites of the extra-holartic regions I. Hungary: Well-Press Publishing Limited.

Bardgett RD. 2005. The biology of soils: a community and ecosystem approach. Oxford: Oxford University Press.

Beck T, Joergensen RG, Kandeler E, Makeschin F, Nuss E, Oberholzer HR, Scheu S. 1997. An inter-laboratory comparison of ten different ways of measuring soil microbial biomass C. Soil Biology and Biochemistry 29:1023–1032 DOI 10.1016/S0038-0717(97)00030-8.

Beck E, Ritcher M. 2008. Ecological aspects of a biodiversity hotspot in the Andes of southern Ecuador. Society for Ecological Restoration 2:195–217.

Bendix J, Homeier J, Ortiz ECueva, Emck P, Breckle S-W, Richter M, Beck E. 2006. Seasonality of weather and tree phenology in a tropical evergreen mountain rain forest. International Journal of Biometeorology 50:370–384 DOI 10.1007/s00484-006-0029-8.

Berg B, McClougherty C. 2008. Plant litter. Second Edition. Berlin Heidelberg: Springer-Verlag.

Blanchet FG, Legendre P, Borcard D. 2008. Forward selection of explanatory variables. Ecology 89:2623–2632 DOI 10.1890/07-0986.1.

Bokhorst S, Wardle DA. 2013. Microclimate within litter bags of different mesh size: implications for the arthropod effect on litter decomposition. Soil Biology and Biochemistry 58:147–152 DOI 10.1016/j.soilbio.2012.12.001.

Bradford MA, Ciska GF, Bonis A, Bradford EM, Classen AT, Cornelissen JHC, Crowther TW, Long JRD, Freschet GT, Kardol P, Manrubia-Freixa M, Maynard DS, Newman GS, Logtestijn RSP, Viketof M, Wardle DA, Wieder WR, Wood SA, Van der Putten WH. 2017. A test of the hierarchical model of litter decomposition. Nature Ecology & Evolution 1:1836–1845 DOI 10.1038/s41559-017-0367-4.
Bradford MA, Tordoff GM, Eggers T, Jones TH, Newington JE. 2002. Microbiota, fauna, and mesh size interactions in litter decomposition. *Oikos* 99:317–323.

Carrillo Y, Ball BA, Bradford MA, Jordan CF, Molina M. 2011. Soil fauna alter the effects of litter composition on nitrogen cycling in a mineral soil. *Soil Biology and Biochemistry* 43:1440–1449 DOI 10.1016/j.soilbio.2011.03.011.

Chapman SK, Newman GS, Hart SC, Schweitzer JA, Koch GW. 2013. Leaf litter mixtures alter microbial community development: mechanisms for non-additive effects in litter decomposition. *PLOS ONE* 8(4):e62671 DOI 10.1371/journal.pone.0062671.

Coulis M, Hättenschwiler S, Rapior S, Coq S. 2009. The fate of condensed tannins during litter consumption by soil animals. *Soil Biology and Biochemistry* 41:2573–2578 DOI 10.1016/j.soilbio.2009.09.022.

Coûteaux MM, Bottner P, Berg B. 1995. Litter decomposition, climate and litter quality. *Tree* 10:63–66.

Crowther TW, A’Bear AD. 2012. Impacts of grazing soil fauna on decomposer fungi are species-specific and density-dependent. *Fungal Ecology* 5:277–281 DOI 10.1016/j.funeco.2011.07.006.

Crowther TW, Boddy L, Jones THefin. 2012. Functional and ecological consequences of saprotrophic fungus-grazer interactions. *The ISME Journal* 6:1992–2001 DOI 10.1038/ismej.2012.53.

Cusack DF, Chou WW, Yang WH, Harmon ME, Silver WL. 2009. Controls on long-term root and leaf litter decomposition in neotropical forests. *Global Change Biology* 15:1339–1355 DOI 10.1111/j.1365-2486.2008.01781.x.

Das S, Joy VC. 2009. Chemical quality impacts of tropical forest tree leaf litters on the growth and fecundity of soil Collembola. *European Journal of Soil Biology* 45:448–454 DOI 10.1016/j.ejsobi.2009.09.001.

Decaëns T, Jiménez JJ, Gioia C, Measey GJ, Lavelle P. 2006. The values of soil animals for conservation biology. *European Journal of Soil Biology* 42:S23–S38 DOI 10.1016/j.ejsobi.2006.07.001.

Dennis PG, Miller AJ, Hirsch PR. 2010. Are root exudates more important than other sources of rhizodeposits in structuring rhizosphere bacterial communities? *FEMS Microbiology Ecology* 72:313–327 DOI 10.1111/j.1574-6941.2010.00860.x.

Dilly O, Munch JC. 1996. Microbial biomass content, basal respiration and enzyme activities during the course of decomposition of leaf litter in a black alder (*Alnus glutinosa* (L.) Gaertn.) forest. *Soil Biology and Biochemistry* 28:1073–1081 DOI 10.1016/0038-0717(96)00075-2.

Freschet GT, Aerts R, Cornelissen JHC. 2012. A plant economics spectrum of litter decomposability. *Functional Ecology* 26:56–65 DOI 10.1111/j.1365-2435.2011.01913.x.

Freschet GT, Cornwell WK, Wardle DA, Elumeeva TG, Liu W, Jackson BG, Onipchenko VG, Soudzilovskaia NA, Tao J, Cornelissen JHC. 2013. Linking litter decomposition of above- and below-ground organs to plant-soil feedbacks worldwide. *Journal of Ecology* 101:943–952 DOI 10.1111/1365-2745.12092.
Fujii S, Cornelissen JHC, Berg MP, Mori AS. 2017. Tree leaf and root traits mediate soil faunal contribution to litter decomposition across an elevational gradient. *Functional Ecology* 32:840–852.

Fujii S, Takeda H. 2010. Dominant effects of litter substrate quality on the difference between leaf and root decomposition process above- and belowground. *Soil Biology and Biochemistry* 42:2224–2230 DOI 10.1016/j.soilbio.2010.08.022.

Fujii S, Takeda H. 2012. Succession of collembolan communities during decomposition of leaf and root litter: effects of litter type and position. *Soil Biology and Biochemistry* 54:77–85 DOI 10.1016/j.soilbio.2012.04.021.

Fujii S, Takeda H. 2017. Succession of soil microarthropod communities during the aboveground and belowground litter decomposition processes. *Soil Biology and Biochemistry* 110:95–102 DOI 10.1016/j.soilbio.2017.03.003.

García-Palacios P, Prieto I, Ourcival JM, Hättenschwiler S. 2016. Disentangling the litter quality and soil microbial contribution to leaf and fine root litter decomposition responses to reduced rainfall. *Ecosystems* 19:490–503 DOI 10.1007/s10021-015-9946-x.

Gergóc V, Hufnagel L. 2016. The effect of microarthropods on litter decomposition depends on litter quality. *European Journal of Soil Biology* 75:24–30 DOI 10.1016/j.ejsobi.2016.04.008.

Gholz HL, Wedin DA, Smitherman SM, Harmon ME, Parton WJ. 2000. Long-term dynamics of pine and hardwood litter in contrasting environments: toward a global model of decomposition. *Global Change Biology* 6:751–765 DOI 10.1046/j.1365-2486.2000.00349.x.

Graefe S, Hertel D, Leuschner C. 2008. Fine root dynamics along a 2000 m elevation transect in South Ecuadorian mountain rainforests. *Plant Soil* 313:155–166 DOI 10.1007/s11104-008-9688-z.

Hättenschwiler S, Tiunov AV, Scheu S. 2005. Biodiversity and litter decomposition in terrestrial ecosystems. *Annual Review of Ecology, Evolution, and Systematics* 36:191–218 DOI 10.1146/annurev.ecolsys.36.112904.151932.

Hobbie SE, Oleksyn J, Eissenstat DM, Reich PB. 2010. Fine root decomposition rates do not mirror those of leaf litter among temperate tree species. *Oecologia* 162:505–513 DOI 10.1007/s00442-009-1479-6.

Homeier J, Breckle S, Günter S, Rollenbeck RT, Leuschner C. 2010. Tree diversity. *forest structure and productivity along altitudinal and topographical gradients in a species-rich Ecuadorian montane rain forest*. *Biotropica* 42:140–148.

Homeier J, Werner FA, Gradstein SR, Breckle SW, Richter M. 2008. Potential vegetation and floristic composition of Andean forests in south Ecuador, with a focus on the RBFS. In: Beck E, Bendix J, Kottke I, Makeschin F, Mosandl R, eds. *Gradients in a tropical mountain ecosystem of Ecuador*. Berlin, Heidelberg: Springer, 87–100.

Illig J, Norton RA, Scheu S, Maraun M. 2010. Density and community structure of soil- and bark-dwelling microarthropods along an altitudinal gradient in a tropical montane rainforest. *Experimental and Applied Acarology* 52:49–62 DOI 10.1007/s10493-010-9348-x.
Illig J, Schatz H, Scheu S, Maraun M. 2008. Decomposition and colonization by microarthropods of two litter types in a tropical montane rain forest in southern Ecuador. *Journal of Tropical Ecology* 24:157–167 DOI 10.1017/S0266467407004750.

Jo I, Fridley JD, Frank DA. 2016. More of the same? *In situ* leaf and root decomposition rates do not vary between 80 native and nonnative deciduous forest species. *New Phytologist* 209:115–122 DOI 10.1111/nph.13619.

Joergensen RG, Scheu S. 1999. Response of soil microorganisms to the addition of carbon, nitrogen and phosphorus in a forest Rendzina. *Soil Biology and Biochemistry* 31:859–866 DOI 10.1016/S0038-0717(98)00185-0.

Joo SJ, Yim MH, Nakane K. 2003. Leaf litter decomposition in relation to dynamics of soil mesofaunain litter boxes with different mesh sizes in a Quercus serrata forest. *Soc Appl Forest Science* 12:109–116.

Joo SJ, Yim MH, Nakane K. 2006. Contribution of microarthropods to the decomposition of needle litter in a Japanese cedar (*Cryptomeria japonica* D. Don) plantation. *Forest Ecology and Management* 234:192–198 DOI 10.1016/j.foreco.2006.07.005.

Kampichler C, Bruckner A. 2009. The role of microarthropods in terrestrial decomposition: a meta-analysis of 40 years of litterbag studies. *Biological Reviews* 84:375–389 DOI 10.1111/j.1469-185X.2009.00078.x.

Kaneda S, Kaneko N. 2008. Collembolans feeding on soil affect carbon and nitrogen mineralization by their influence on microbial and nematode activities. *Biology and Fertility of Soils* 44:435–442 DOI 10.1007/s00374-007-0222-x.

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

Kitayama K, Suzuki S, Hori M, Takyu M, Aiba S-I, Majalap-Lee N, Kikuzawa K. 2004. On the relationships between leaf-litter lignin and net primary productivity in tropical rain forests. *Oecologia* 140:335–339 DOI 10.1007/s00442-004-1590-7.

Legendre L, Legendre P. 1998. *Numerical ecology*. Second edition. Amsterdam: Elsevier.

Lenth RV. 2020. emmeans: estimated marginal means, aka least-squares means..

Leuschner C, Moser G, Bertsch C, Roderstein M, Hertel D. 2007. Large altitudinal increase in tree root/shoot ratio in tropical mountain forests of Ecuador. *Basic and Applied Ecology* 8:219–230 DOI 10.1016/j.baae.2006.02.004.

Macfadyen A. 1961. Improved funnel-type extractors for soil arthropods. *Journal of Animal Ecology* 30:171–184 DOI 10.2307/2120.

Maraun M, Fronczek S, Marian F, Sandmann D. 2013. More sex at higher altitudes: changes in the frequency of parthenogenesis in oribatid mites in tropical montane rain forests. *Pedobiologia* 56:185–190 DOI 10.1016/j.pedobi.2013.07.001.

Maraun M, Illig J, Sandmann D, Krashevska V, Norton RA, Scheu S. 2008. Soil fauna. In: Beck E, Bendix J, Kottke I, Makeschin F, eds. *Gradients in a tropical mountain ecosystem of Ecuador*. Berlin, Heidelberg: Springer, 181–192.

Marian F, Brown L, Sandmann D, Maraun M, Scheu S. 2019. Roots, mycorrhizal fungi and altitude as determinants of litter decomposition and soil animal communities in...
tropical montane rainforests. *Plant Soil* 438:1–18 DOI 10.1007/s11104-019-03999-x.

Marian F, Sandmann D, Krashevskva V, Maraun M, Scheu S. 2017. Leaf and root litter decomposition is discontinued at high altitude tropical montane rainforests contributing to carbon sequestration. *Ecology and Evolution* 7:6432–6443 DOI 10.1002/ece3.3189.

Marian F, Sandmann D, Krashevskva V, Maraun M, Scheu S. 2018. Altitude and decomposition stage rather than litter origin structure soil microarthropod communities in tropical montane rainforests. *Soil Biology and Biochemistry* 125:263–274 DOI 10.1016/j.soilbio.2018.07.017.

Milcu A, Manning P. 2011. All size classes of soil fauna and litter quality control the acceleration of litter decay in its home environment. *Oikos* 120:1366–1370 DOI 10.1111/j.1600-0706.2010.19418.x.

Moser G, Hertel D, Leuschner C. 2007. Altitudinal change in LAI and stand leaf biomass in tropical montane forests: a transect study in ecuador and a pan-tropical meta-analysis. *Ecosystems* 10:924–935 DOI 10.1007/s10021-007-9063-6.

Myers N, Mittermeier R, Mittermeier C, Fonseca GABD, Kent J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403:853–858 DOI 10.1038/35002501.

Norby RJ, Ledford J, Reilly CD, Miller-Struttmann N, O’Neill EG. 2004. Fine-root production dominates response of a deciduous forest to atmospheric CO2 enrichment. *Proceedings of the National Academy of Sciences of the United States of America* 101:9689–9693 DOI 10.1073/pnas.0403491101.

Ostertag R, Hobbie SE. 1999. Early stages of root and leaf decomposition in Hawaiian forests: effects of nutrient availability. *Oecologia* 121:564–573 DOI 10.1007/s004420050963.

Perez G, Aubert M, Decaëns T, Trap J, Chauvat M. 2013. Home-field advantage: a matter of interaction between litter biochemistry and decomposer biota. *Soil Biology and Biochemistry* 67:245–254 DOI 10.1016/j.soilbio.2013.09.004.

Pinheiro J, Bates D, DebRoy S, Sarkar D. 2020. NLME-linear and nonlinear mixed effects models. Available at https://cran.r-project.org/web/packages/nlme/index.html.

Pollierer MM, Langel R, Körner C, Maraun M, Scheu S. 2007. The underestimated importance of belowground carbon input for forest soil animal food webs. *Ecology Letters* 10:729–736 DOI 10.1111/j.1461-0248.2007.01064.x.

Potapov A, Sandmann D, Scheu S. 2019. Ecotaxonomy database traits and species..

R Core Team. 2019. R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. Available at https://www.r-project.org/.

Richardson BA, Richardson MJ, Soto-Adames FN. 2005. Separating the effects of forest type and elevation on the diversity of litter invertebrate communities in a humid tropical forest in Puerto Rico. *Journal of Animal Ecology* 74:926–936 DOI 10.1111/j.1365-2656.2005.00990.x.
Röderstein M, Hertel D, Leuschner C. 2005. Above- and below-ground litter production in three tropical montane forests in southern Ecuador. *Journal of Tropical Ecology* 21:483–492 DOI 10.1017/S026646740500249X.

Ruess L, Lussenhop J. 2005. Trophic interactions of fungi and animals. In: Dighton J, Oudemans P, White J, eds. *The fungal community: its organization and role in the ecosystem*. Boca Raton: CRC, 581–598.

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. *Tropical Ecology* 60:350–361 DOI 10.1007/s42965-019-00038-9.

Sánchez-Galindo LM, Sandmann D, Marian F, Krashevska V, Maraun M, Scheu S. 2021. Leaf litter identity rather than diversity shapes microbial functions and microarthropod abundance in tropical montane rainforests. *Ecology and Evolution* 11:2360–2374 DOI 10.1002/ece3.7208.

Scheu S. 1992. Automated measurement of the respiratory response of soil microcompartments: active microbial biomass in earthworm faeces. *Soil Biology and Biochemistry* 24:1113–1118 DOI 10.1016/0038-0717(92)90061-2.

Scheu S, Illig J, Eissfeller V, Krashevska V, Sandmann D, Maraun M. 2008. The soil fauna of a tropical mountain rainforest in southern Ecuador: structure and functioning. In: Gradstein SR, Gansert D, Homeier J, eds. *The tropical mountain forest. Patterns and processes in a biodiversity hotspots*. Göttingen: Universitätsverlag Göttingen, 79–96.

Scheu S, Ruess L, Bonkowski M. 2005. Interactions and soil micro- and mesofauna. In: Varma A, Buscot F, eds. *Microorganisms in soils: roles in genesis and functions. Soil Biology*, vol. 3. Berlin: Springer Heidelberg.

Schinner F. 1982. Soil microbial activities and litter decomposition related to altitude. *Plant Soil* 65:87–94 DOI 10.1007/BF02376806.

Scowcroft PG, Turner DR, Vitousek PM. 2000. Decomposition of Metrosideros polymorpha leaf litter along elevational gradients in Hawaii. *Global Change Biology* 6:73–85 DOI 10.1046/j.1365-2486.2000.00282.x.

Seastedt TR. 1984. The role of microarthropods in decomposition and mineralization processes. *Annual Review of Entomology* 29:25–46 DOI 10.1146/annurev.en.29.010184.000325.

Silver WL, Miya RK. 2001. Global patterns in root decomposition: comparisons of climate and litter quality effects. *Oecologia* 129:407–419 DOI 10.1007/s004420100740.

Soethe N, Lehmann J, Engels C. 2006. The vertical pattern of rooting and nutrient uptake at different altitudes of a south Ecuadorian montane forest. *Plant Soil* 286:287–299 DOI 10.1007/s11104-006-9044-0.

Soethe N, Lehmann J, Engels C. 2007. Carbon and nutrient stocks in roots of forests at different altitudes in the Ecuadorian Andes. *Journal of Tropical Ecology* 23:319–328 DOI 10.1017/S0266467407004002.
Strickland MS, Osburn E, Lauber C, Fierer N, Bradford MA. 2009. Litter quality is in the eye of the beholder: initial decomposition rates as a function of inoculum characteristics. *Functional Ecology* 23:627–636 DOI 10.1111/j.1365-2435.2008.01515.x.

Subías LS. 2018. Listado sistemático, sinonímico y biogeográfico de los ácaros oribátidos (Acariformes: Oribatida) del mundo (Excepto fósiles) (13ª actualización). Available at [http://bba.bioucm.es/cont/docs/RO_1.pdf](http://bba.bioucm.es/cont/docs/RO_1.pdf).

Swift M, Heal O, Anderson J. 1979. *Decomposition in terrestrial ecosystems*. United Kingdom: Oxford University Press.

Tanner EVJ, Vltousek PM, Cuevas E. 1998. Experimental investigation of nutrient limitation of forest growth on wet tropical mountains. *Ecology* 79:10–22 DOI 10.1890/0012-9658(1998)079[0010:EIONLO]2.0.CO;2.

Ter Braak C, Smilauer P. 2012. Canoco reference manual and user’s guide: software for ordination. Available at [https://research.wur.nl/en/publications/canoco-reference-manual-and-users-guide-software-for-ordination-v](https://research.wur.nl/en/publications/canoco-reference-manual-and-users-guide-software-for-ordination-v).

Verhoef HA, Brussaard L. 1990. Decomposition and nitrogen mineralization in natural and agroecosystems: the contribution of soil animals. *Biogeochemistry* 11:175–211.

Vitousek PM, Turner DR, Parton WJ, Sanford RL. 1994. Litter decomposition on the Mauna Loa environmental, matrix, Hawai’i: patterns, mechanisms, and models. *Ecology* 75:418–429 DOI 10.2307/1939545.

Wang S, Ruan H, Han Y. 2010. Effects of microclimate, litter type, and mesh size on leaf litter decomposition along an elevation gradient in the Wuyi Mountains, China. *Ecological Research* 25:1113–1120 DOI 10.1007/s11284-010-0736-9.

Zieger SL, Ammerschubert S, Polle A, Scheu S. 2017. Root-derived carbon and nitrogen from beech and ash trees differentially fuel soil animal food webs of deciduous forests. *PLOS ONE* 12(12):e0189502 DOI 10.1371/journal.pone.0189502.