The use of plant litter and soil fauna traits in a mechanistic assessment of litter decomposition under global change

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Chapter III

Is the structure of micro-arthropod community in plant litter driven by litter quality?

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Abstract

Belowground biodiversity is vast, but which factors cause this large diversity, remains still poorly understood. An important part of the decomposer community that is fed by plant litter, is formed by soil micro-arthropods, of which Oribatida and Collembola are the two dominant groups. We set up a field experiment to test the relationship between the diversities of plant litter (1 to 4 species) and micro-arthropods, which inhabit the litter layer in the subarctic birch forest. We found that richness of species and functional types of plant litter did not affect the communities of the two soil micro-arthropod groups. In contrast, the micro-arthropods were found to be strongly affected by plant litter species identity and composition which was further assessed by litter traits. The densities of most species of Collembola and Oribatida followed a plant litter quality gradient of low ratios of litter carbon and cellulose to phosphorus and high SLA, leaf water saturation capacity and concentrations of Na, K and cellulose. Nevertheless, some species-specific relationships with different litter quality aspects were found indicating niche partitioning that partly contributes to the large diversity in soils.

Introduction

Belowground biodiversity is vast, but what is causing this large diversity remains still poorly understood (Wardle 2006). Unlike belowground biodiversity, the causes and consequences of aboveground biodiversity have been in the focus of biodiversity research for decades. The link between aboveground biodiversity and functioning of ecosystems has been debated for a long time, and the major results have been summarized in a recent review by Isbell *et al.* (2011). This review shows that 84% of all the studied grassland plant species in 17 biodiversity experiments promoted ecosystem functioning, thereby highlighting the role of biodiversity in maintaining ecosystem functioning. The alarming loss of biodiversity (Sala *et al.* 2000; Secretariat of the Convention on Biological Diversity 2010) has stimulated also research with a focus on belowground biodiversity, as it may i) similarly to its aboveground part, be connected to ecosystem function (Lavelle 1996; Brussaard *et al.* 1997) and ii) be linked to the aboveground biodiversity (Hooper *et al.* 2000).

Plant litter is one of the main food sources for belowground organisms (Berg & Bengtsson 2007), of which an important part is formed by the micro-arthropods (Lavelle & Spain 2001; Kampichler & Bruckner 2009). The two most abundant groups of soil micro-arthropods are Collembola and Oribatida that that are dominantly considered fungivorous, who, by feeding on fungi that are adhered to detritus, fragment litter and thus influence decomposition in various ways (Seastedt 1984). Recently a link between plant species richness and species richness in soil Collembola and Oribatida has been found in grassland (Sabais *et al.* 2011) and forest (Eisenhauer *et al.* 2011) ecosystems, thus supporting the link between above- and belowground diversity. The existance of a similar link between plant litter (i.e., substrate and habitat) diversity and soil fauna diversity is depated. As the diversity of living plants is not necessarily equal to plant litter diversity due to differences in tissue turnover rates among plant functional groups and species (e.g. Aerts & Chapin. 2000), expectations to find the link in diversities of plant litter and soil micro-arthropods are mixed. The few studies conducted so far are conflicting. The studies by Hansen & Coleman (1998) and Kaneko & Salamanca (1999) found that plant litter species

richness influenced Collembola and Oribatida diversity and abundance. In contrast, Wardle *et al.* (2006) found no evidence that litter diversity influences Collembola and Oribatida or any other assessed soil fauna group. Instead they found that litter species identity and composition affects the abundance and diversity of both fauna groups.

Therefore, we set up a field experiment to test the effects of both, plant litter species richness and composition, on micro-arthropod community structure in the litter layer of subarctic birch forest. We selected four plant species of different functional type, i.e., an N-fixer, an evergreen, and a slow- and a fast-decomposing broadleaf species. The possible effect of litter composition in litter monocultures and mixtures was not only assessed by the identity of the plant species but also by relating the micro-arthropod densities to litter chemical and physical traits. The aim of the trait assessment was to assess the connections among Oribatida and Collembola species and the plant litter characteristics. Especially we hypothesized that the structure of micro-arthropod community is: 1) independent from litter species richness but 2) affected by litter species identity and composition, through specific litter traits.

Materials & methods

Site description

The experiment was conducted in Abisko, subarctic Sweden (68°21' N, 18°49' E). The study area consists of mountain birch *Betula pubescens* ssp. *czerepanovii* [Orl.] Hämet-Ahti dominated open forest with an understorey of dwarf shrubs. The dominant understorey species were *Empetrum nigrum* ssp. *hermaphroditum* (Hagerup), *Vaccinium vitis-idaea* (L.), *Vaccinium myrtillus* (L.),*Vaccinium uliginosum* (L.) and *Lycopodium annotinum* L. and several bryophyte species. The experimental area locates at 400 m a.s.l. altitude, has a mean annual temperature of 1 °C and receives a mean annual precipitation of 300 mm (Abisko Scientific Research Station, Meteorological station). Soil pH is 4.63 ± 0.27 and the depth of the organic horizon is quite variable and ranges from 0 to 9 cm.

Plant litter treatments

Freshly senesced plant litter of four woody vascular species representing different functional types was collected by hand from the area in autumn 2006. The four selected plant species were: an N-fixer (*Alnus incana* (L.) Moench), a deciduous rapid-decomposing broad-leaf species (*Sorbus aucuparia* L.), a deciduous slow-decomposing broad-leaf species (*Populus tremula* L.) and an evergreen dwarfshrub (*Vaccinium vitis-idaea* L.). The litter was dried at 40 °C after collecting. We incubated monocultures of all species and all possible mixtures of two, three, and four litter species. Each litter treatment consisted of total 4 g of dried initial material and mixtures were made with even contribution of all component litter species on a weight basis. Litter was incubated in the field in circular cylindrical PVC microcosms (16 cm diameter, 9 cm height), of which top and bottom were closed with 50 μm mesh, which prohibited physical loss of litter particles or introduction of freshly fallen material. Additionally, the sides had two 100 cm^2 windows with 5 mm mesh to allow the access of the full decomposer community (including soil macrofauna) to the plant litter. Microcosms were placed directly on the forest floor, avoiding any vascular plants to be left underneath them. During the experiment, possible external litter was regularly removed from the lids of the microcosms and plant shoots growing into the microcosms were removed as well. Microcosms were placed in the field according to a randomized block design,

with a minimum of 50 cm distance between the microcosms. Five blocks were set up and they located at least 20 m apart from each other.

Plant litter traits were used to explain variation in micro-arthropod densities among litter treatments. 26 widely-used chemical and physical litter traits that are known to influence litter decomposition rates were used to characterize the litter species. The chemical traits were pH; the concentrations of nitrogen (N), carbon (C), cellulose, hemicellulose, lignin, total phenols, soluble phenols, condensed tannins, phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), sodium (Na), water soluble compounds (all concentrations expressed as % dry matter or d.m.); and the ratios of C/N, C/P, lignin/N, lignin/P, phenols/N and phenols/P. The physical traits were leaf toughness (g H_2O), specific leaf area (SLA: cm^2 g^{-1}), litter water saturation (% H_2O d.m.), three-dimensionality (total leaf surface area per volume: cm^2 cm^{-3}), and tensile strength (N cm1). The methods for trait measurements are given in Chapter V of this thesis.

Harvesting, fauna extraction and fauna determination

The experiment ran from the end of September 2006 until the beginning of September 2008 (altogether 714 days). The harvest of the experiment was conducted on two different days, with a seven day interval between them. This sampling interval was due to limited extraction capacity for the fauna samples. During the first and second harvest day, three and two blocks were harvested, respectively, and harvest was always carried out between 10 and 12 AM. In addition to microcosm litter samples, we collected three samples of natural litter around each block (altogether n = 15) so that the soil micro-arthropod densities in litter microcosms could be compared to the natural densities. The natural litter samples were collected from the surroundings of the blocks and each sample was taken from a circular area with a diameter of 16 cm (the area that corresponds to the area covered by a microcosm). Furthermore, only the litter on top of the moss layer was taken to avoid micro-arthropods escaping during the sampling. Natural litter samples were extracted in the same way and on the same time as the litter samples from the microcosms. During harvest, litter was swiftly moved from the microcosms to transporting boxes (11 x 11 x 7 cm). Immediately after the harvest and an acclimatization period of nine hours, soil fauna was extracted from the litter using a modified Berlese extractor for six consecutive days and stored in 70% ethanol. The extraction boxes were circulated under the heat source to ensure homogeneous temperature conditions. Collembola and Oribatida were determined to the species level using the keys of Fjellberg (1998, 2007) and Weigmann (2006) respectively. Only the total number of Oribatida juveniles, Prostigmata and Mesostigmata was recorded. Other fauna groups occurred only seldomly and were not counted. Plant litter was dried (40 °C) and weighed for calculating litter mass remaining.

Calculations and statistical analysis

The densities of micro-arthropods in decomposed litter samples of varying mass were standardized as individuals g^{-1} remaining litter on dry weight basis (Ind g^{-1} d.m.). Densities of micro-arthropods were given per taxon or as group total. Partly damaged specimens were pooled into a group named "unknown". Additionally, species richness and diversity were calculated only for Oribatida and Collembola. Species richness was calculated as the total number of species and species diversity was calculated using the Shannon's diversity index (*H*) (Magurran 1988):

$$H = -\sum_{i=1}^{S} p_i \ln p_i$$

where S = total number of species in the community and p_i = relative abundance of the i-th species. The difference in total densities of each micro-arthropod group between litter in microcosms and natural litter samples was tested by a t-test. The total densities were $\log_{10}$-transformed prior to analysis. Despite transformation, homogeneity of variance was still not always ensured. In these cases we used test statistics that do not assume equal variance (Welch's t test).

The effects of litter species richness and litter treatment (litter diversity and composition) on total densities of all micro-arthropod groups assessed in the study, additional community measures (species richness and diversity) of Oribatida and Collembola, and litter mass loss were tested by two-way nested ANOVA, where the effect of litter treatment was nested within litter species richness. Log_{10}-transformations ensured the homogeneity of variance for all dependent variables. As the effect of litter treatment within litter species richness had a significant effect on two dependent variables (Oribatida total density and litter mass loss), their interdependence was assessed by a linear regression. For this, averages per litter treatments were used and the variables were $\log_{10}$-transformed when it improved the linearity of the regression.

Additionally, we assessed whether total litter mass loss or the total densities in micro-arthropod groups differed between litter mixtures (observed) and their corresponding monocultures (average values from the monocultures: expected). The comparison in litter mass loss and fauna group total densities per litter mixture was done by paired t-tests as the observed values were given and the expected values were calculated separately for each of the five replicate blocks according to Wardle *et al.* (1997). Logarithmic- and rank-transformations ensured the homogeneity of variance for all dependent variables

The densities in Oribatida and Collembola species as a function of litter treatment and litter traits were assessed by a Principal Component Analysis (PCA) using Canoco for Windows version 4.5 (ter Braak & Šmilauer 2002). In addition to using species densities as response variables and litter treatments as samples, we used litter traits as the supplementary variables. Litter traits were projected passively and thus did not affect the ordination of micro-arthropod densities, but allowed us to assess the relationship between litter traits and species densities. We used only the averages of species densities per litter treatment as we were solely interested to explain variation among litter treatments, and not the natural variation occurring within a given litter treatment. The micro-arthropod species that were present in at least two litter treatments were included in the assessment. The supplementary variables, i.e., the 26 litter traits, were given as community-weighted mean trait scores (T_m) and were calculated according to Garnier *et al.* (2004) as:

$$T_m = \sum_i p_i x_i$$

where x = the trait attribute of the i-th species and p_i = the relative initial proportion of the i-th species in the litter mixture. No direct gradient analyses were performed due to high collinearity among the mean trait scores and number of explanatory variables. All analyses were performed with SPSS for Windows version 17.0 (SPSS Inc., Chicago, IL, USA), unless stated otherwise.

Results

Micro-arthropod community structure versus litter species richness

Micro-arthropod groups were, in descending order of density, Oribatida, Collembola, Prostigmata and Mesostigmata (Table 1). Altogether we found 18 Oribatida and 13 Collembola species. The total densities of Collembola, adults and juveniles of Oribatida were 4.3, 2.3 and 4.7 fold higher, respectively, in litter microcosms compared to the surrounding (natural) litter at the experimental site (Table 2).

Table 1. Average ± standard error of mean (SEM) of total micro-arthropod group and species densities in litter microcosms (Ind g^{-1} d.m. of remaining litter), n=75. The total group densities are also given per surface area (Ind m^{-2}) to aid comparison with other studies. Species are listed in the descending order of their average density.

	Ind g^{-1} d.m.	Ind m^{-2}
Collembola		
Total	4.58±0.31	495±35
Lepidocyrtus lignorum	1.10±0.15	
Parisotoma notabilis	0.76±0.11	
Pogonognathellus flavescens	0.42±0.07	
Dicyrtoma fusca	0.30±0.05	
Folsomia quadrioculata	0.14±0.03	
Desoria hiemalis	0.10±0.03	
Megalothorax minimus	0.07±0.03	
Entomobrya nivalis	0.07±0.03	
Dicyrtomina minuta	0.02±0.01	
Arrhopalites principalis	0.02±0.01	
Poduromorpha juv.	0.01±0.01	
Sminthurus nigromaculatus	0.01±0.01	
Sminthuridae spec.	0.01±0.01	
unknown	0.06±0.02	
Oribatida		
Total adults	7.78±0.47	840±50
Total juv.	1.64±0.12	180±14
Oribatella quadricornuta	3.86±0.33	
Hemileius initialis	0.92±0.12	
Belba bartosi	0.78±0.10	
Diapterobates humeralis	0.52±0.08	
Eupelops torulosus	0.50±0.08	
Adoristes ovatus	0.40±0.07	
Ceratoppia bipilis	0.28±0.05	
Phthiracarus globosus	0.14±0.04	
Chamobates borealis	0.14±0.03	
Eupelops strenzkei	0.08±0.02	
Eueremaeus silvestris	0.04±0.02	
Carabodes marginatus	0.03±0.01	
Camisia biurus	0.02±0.01	
Edwardzetes edwardsi	0.02±0.01	
Platynothrus peltifer	0.01±0.01	
Camisia spinifer	0.01±0.01	
Neonothrus humicolus	0.01±0.01	
Porobelba spinosa	0.01±0.01	
Prostigmata		
Total	1.33±0.16	145±18
Mesostigmata		
Total	0.65±0.06	71±6

None of the community structure measures of any of the micro-arthropod groups in litter microcosms were affected by litter species richness (Appendix S1). Additionally, litter mass loss and fauna densities in the litter mixtures were in general within the range of that of the component litter species in monocultures (Fig. 1). Only the observed densities of Oribatida adults were higher in *Vaccinium-Anthriscus* (t = 5.75, *P* = 0.005) and *Populus-Sorbus-Alnus* (t = 5.90, *P* = 0.004) mixtures when they were compared to the densities in the corresponding monocultures (i.e., expected). In contrast, the densities of Collembola were lower in *Vaccinium-Populus-Alnus* mixtures compared to their densities in monocultures (t = -3.55, *P* = 0.024).

Table 2. Mean ± SEM total densities (Ind g^{-1} d.m.) of Collembola, Oribatida, Prostigmata and Mesostigmata in surrounding litter in the in the experimental blocks (n=15) and *t*-test statics (T) and significance (*P*) of the comparison between total fauna densities in surrounding litter and litter in microcosms shown in Table 1. The mean dry weight of the litter in natural litter samples where fauna was extracted from was 5.65 ± 0.32 g.

	Densities	T	*P*
Collembola	0.86 ± 0.15	7.05	< 0.001
Oribatida adult	2.35 ± 1.16	7.08	< 0.001
Oribatida juv.	0.29 ± 0.04	8.93	< 0.001
Prostigmata	0.90 ± 0.23	0.96	0.338
Mesostigmata	0.42 ± 0.13	1.70	0.092

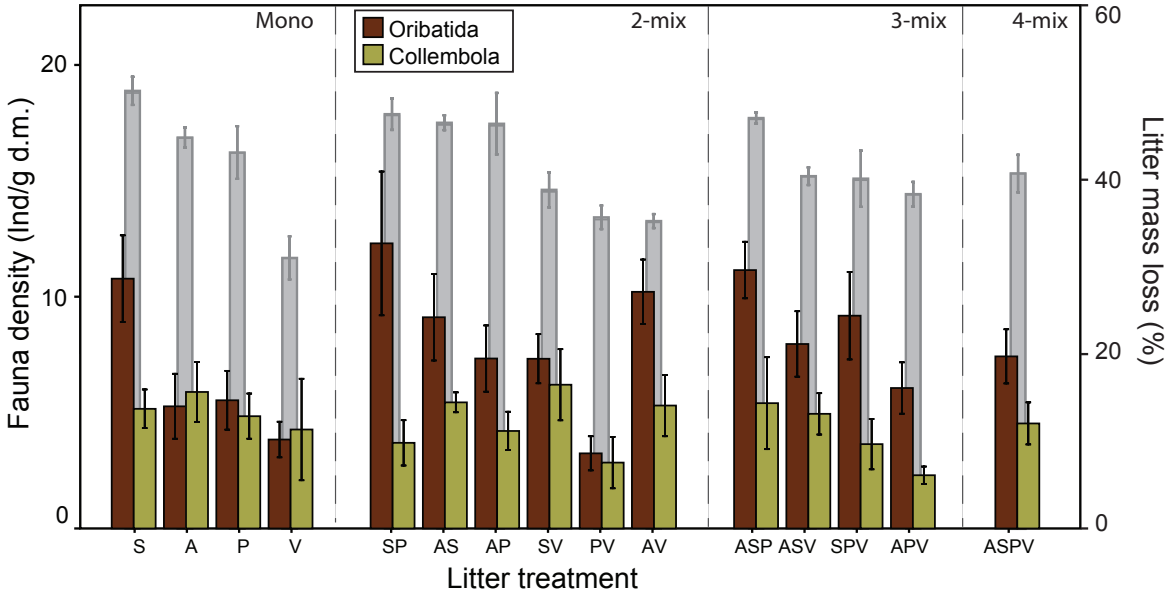

Figure 1. Average ± SEM of total densities (left y-axis; Ind g^{-1} d.m.) of Oribatida and Collembola, and litter mass loss (%) (right y-axis; narrower light grey bars) per litter treatment of litter monocultures (mono) and mixtures of two (2-mix), three (3-mix) and four (4-mix) species. Litter treatments are abbreviated according to their component litter species as: S = *Sorbus*, A = *Alnus*, P = *Populus* and V = *Vaccinium*.

Densities of micro-arthropod species versus plant litter quality

Unlike litter species richness, litter treatment (i.e., identity and composition) strongly affected Oribatida total density ($F_{11,75}$= 3.12, P = 0.002) and the litter mass loss ($F_{11,75}$= 9.62, P < 0.001) (Appendix S1). Moreover, a significant positive relation between mean Oribatida total densities and litter mass loss (including all litter treatments) was found (Fig. 1, Appendix S2) (linear regression: r^2 = 0.374, P = 0.015). Despite that fauna densities are calculated by litter mass remaining, the linear regression between Oribatida density and litter mass loss was biologically valid. The validity was assured by a positive trend in relation between total abundance of Oribatida and litter mass loss, i.e., the higher the litter mass loss, the higher the Oribatida abundance (Appendix S2).

The relationship between litter traits and the densities of Oribatida and Collembola species was assessed by a PCA, of which the two first axes together explained 57.1% of all the variation in the species densities (Fig. 2). Plant litter traits (supplementary variables in the PCA) would have been able to explain 43.4% of all the variation in the species densities and they correlated strongly with both the first and second PCA axis (r^2 = 0.781 and r^2 = 0.775, respectively). The densities of Oribatida and Collembola species that were well presented by the two first PCA axes were found to both correlate and be independent from each other. In the same line the major similarities and dissimilarities among the taxa were found in their relation to litter traits. More specifically, the densities of 12 out of 15 Oribatida and Collembola species which were well presented by the two first PCA axes followed the same aspects of litter quality. These aspects of litter quality were

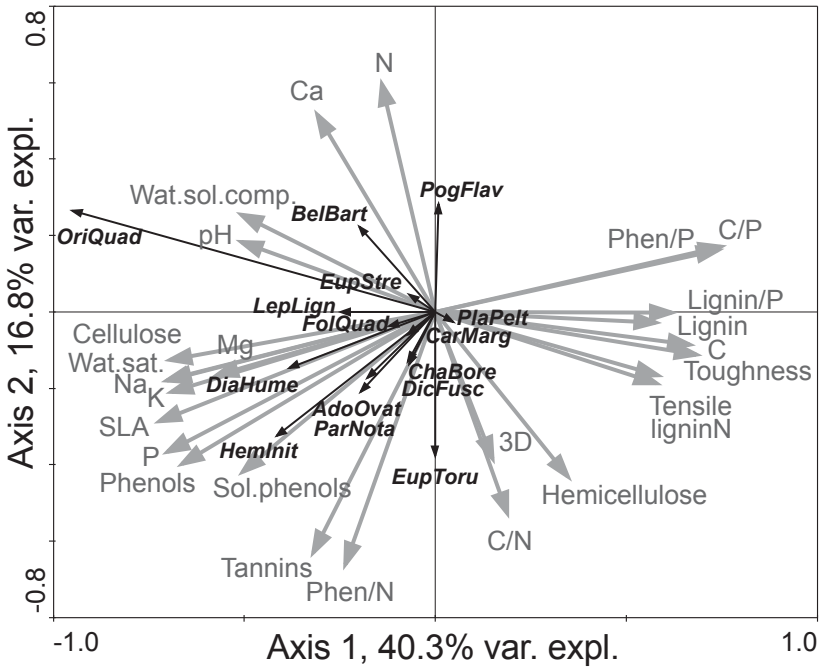

Figure 2. Principal component analysis (PCA) ordination of Collembola and Oribatida species densities (black arrows). Only species that were present in at least two litter treatments were included in the analysis and only species with the highest fit are shown in ordination. Collembola and Oribatida densities were log transformed prior to analysis. Scaling is centered by species. Passive supplementary variables, i.e., plant litter traits, are trait mean scores (T_m) (grey arrows) that were centered and standardized prior to ordination. Oribatida and Collembola taxa are abbreviated according to their taxonomic names (see Table 1) and litter traits are given in full or by their chemical symbol except: Wat sat = water saturation, SLA= specific leaf area, 3D = three-dimensionality, Wat. sol. comp. = water soluble compounds.

well characterized by litter C/P ratio when assessed by the t-value biplot rule according to Lepš & Šmilauer (2003) (Fig. 2, Appendix S4). The litter C/P ratio, had the highest correlation with the first PCA axis. Furthermore, the densities of 11 species were negatively correlated with the C/P ratio, and only the density of *Platynothrus peltifer* was positively correlated with the C/P ratio. In contrast, the density of the most abundant species *Oribatella quadricornuta* was not correlated with any of the 26 litter traits. Instead the density of *O. quadricornuta* correlated strongly with the first PCA axis, which in addition to the ratio of C/P, had highest positive correlation with the ratios of phenols/P and lignin/P; leaf litter toughness and C concentration. The highest negative correlations with the first axis were found with SLA, leaf water saturation capacity, and concentrations of P, Na, cellulose and K. The densities of the two remaining species, *Eupelops torulosus* and *Pogonognathellus flavescens*, correlated well with the second PCA axis and were strongly correlated with the phenols/N ratio, which presented best the second axis (Fig. 2, Appendix S4). The correlation between the densities of both *E. torulosus* and *P. flavescens* and the ratio of phenols/N were positive and negative, respectively. In addition to low phenols/N ratio, the second PCA axis was characterized by low ratio of C/N, and concentration of tannins; and high concentrations of N and Ca.

Discussion

In this paper we ask whether the structure of micro-arthropod community living in plant litter is driven by the quality of plant litter. The answer is yes; as we found that plant litter species identity and composition strongly affected micro-arthropod communities. However, there was no relation between plant litter species richness and the micro-arthropod community structures. In general the densities of both, Collembola and Oribatida were related to plant litter quality proxies. Despite the overall similar relationship for species of both soil fauna groups with certain litter traits, we also found strongly varying species-specific relationships. The effect of litter species diversity, identity and composition on micro-arthropod community structures are further discussed below after discussing the higher micro-arthropod densities found in litter microcosms compared to the surrounding natural litter.

Several explanations can be given for the differences in fauna densities found in the microcosm and surrounding litter. As the surrounding litter was collected exclusively from the top of the moss layer, it presents only the freshly senesced litter, whereas litter harvested from microcosms had been decaying already nearly two years. Additionally, higher resource quality and litter diversity can explain higher fauna densities in microcosm litter compared to the upper part of the surrounding litter layer. The higher densities could also be caused by side-effects, such as altered micro-climatic conditions (Witkamp & Olson 1963) and loss of fragmented litter (Parker *et al.* 1984), that are reported in litterbag studies although the microcosm design aims to decrease these. However, when we compare the fauna densities in microcosm litter to previous litterbag studies, the results fall in the same range (Appendix S3). More specifically we were able to compare our results to two previous studies (Hansen & Coleman 1998; Kaneko & Salamanca 1999) that have, in addition to data of fauna abundances, also given remaining litter mass, and thus allow a calculation of fauna densities. Consequently, the micro-arthropod densities in the microcosms present either naturally prevailing densities in further decomposed plant litter or, higher than the natural densities. Furthermore, whether or not the densities in microcosms are in the same range as in the surrounding litter, our mechanistic assessment is valid as we study the effect of litter diversity only in microcosms.

Micro-arthropod communities are not affected by plant litter species richness

In support of our first hypothesis, we found that plant litter species richness did not affect the density of any assessed micro-arthropod group, nor the species diversity or richness of Oribatida or Collembola. In addition, none of the total densities of micro-arthropod groups showed consistent differences between litter mixtures and their corresponding monocultures. We found a change in micro-arthropod density for only three (out of 11) litter mixtures in total, when the densities in litter mixtures were compared to densities in monocultures (observed versus expected). This supports the study by Wardle *et al.* (2006), who observed that instead of litter species richness, litter identity had strong effects on soil fauna. However, our results are in contrast with the studies by Hansen & Coleman (1998) and Kaneko & Salamanca (1999) that found higher abundances of soil fauna in mixed litters compared to litter monocultures. Although we might expect that the probability to find a link between litter species richness and micro-arthropod community would increase by increasing the number of litter species used in the assessed mixtures, it does not seem to be a reasonable expectation. The most recent study by Wardle *et al.* (2006) used eight litter species, yet found no link between the litter species richness and micro-arthropod community, whereas the link was found in the two previous studies, which were both conducted with only three litter species.

Furthermore, we used litter of four different plant functional types and found that it is not the richness of litter species or plant functional types, but merely the litter identity and community that drives the micro-arthropod communities. This is in line with other observations that it is the plant identity and community composition that controls the fauna communities (Wardle *et al.* 2003; De Deyn *et al.* 2004). The effect of plant litter identity and composition on micro-arthropod species densities is discussed below.

Litter quality driving the micro-arthropod communities

Although the total density of only Oribatida was found to depend on the decomposition rate of plant litter, also the densities of several Collembola species similarly to Oribatida species were well characterized by the litter traits. Thus in agreement with our second hypothesis, both Oribatida and Collembola communities were controlled by litter quality. More specifically, the total density of Oribatida was higher in further decomposed litter, i.e., in higher litter quality. The positive correlation between fauna abundances and decomposition stage has been reported previously for litter monocultures (Anderson 1975; Reddy 1989; Wang *et al.* 2009). Additionally, Kaneko and Salamanca (1999) reported that the densities of micro-arthropods followed mass loss but only in litter mixtures and not in monocultures. Thus, our study is the first that shows that litter decomposition rates are related to differences in fauna communities when comparing litter monocultures and mixtures. The reason that total Collembola density did not follow mass loss may indicate that in general Oribatida are more involved in litter decomposition or their relation to decaying plant litter is more direct compared to Collembola. The difference between oribatids and collembolans in their relation to litter quality was further assessed at the taxon level.

Species densities of Collembola and Oribatida correlated both positively and negatively with each other, or were independent from each other. For instance the densities of the oribatid *Eupelops torulosus* and the collembolan *Pogonognathellus flavescens* correlated well with litter N concentration, yet their densities increased in opposite directions. Furthermore the density of the collembolan *Lepidocyrtus lignorum* was independent from litter N concentration and the densities of *P. flavescens*

and *E. torulosus*. In contrast the density of *L. lignorum* correlated well with the densities of the collembolan *Folsomia quadrioculata* and the oribatid *Oribatella quadricornuta* and was most abundant on litters with low ratios of carbon, lignin and phenols to phosphorus. The interdependence and the negative correlation between the densities of representatives of both taxonomical groups in relation to litter quality proxies indicates specialization among Collembola and Oribatida species in their responses to varying litter quality. The specialization was not observed specifically between Collembola and Oribatida in general but among certain species within both groups (cf. also Fig. 2).

The species-specific relationships with different litter quality aspects indicate niche partitioning among the micro-arthropods. Litter species may differ in resource quality for both microbes and micro-arthropod detritivores, and may affect the activity and community composition of soil fauna and flora due to differences in moisture conditions. We have tried to find patterns in the reactions of micro-arthropod species to litter quality traits especially with a focus on food preferences. However, no clear patterns were observed. Our results ask for additional analyses including traits of mouthpart morphology, or information obtained from stable isotopes or fatty acid composition. Finding niche partitioning among the oribatids and collembolans is not surprising as even trophic niche differentiation has been found within both of these groups (Schneider *et al.* 2004; Chahartaghi *et al.* 2005). Importantly, niche partitioning is one mechanisms allowing coexistence of species (Schoener 1974; Chesson 2000) and thus helps explaining the high biodiversity in soils (Giller 1996).

Conclusions

Plant litter species and functional type richness did not affect the community structure of micro-arthropod groups inhabiting plant litter. In contrast, the micro-arthropods were strongly affected by plant litter species identity and composition. The densities of most species of Collembola and Oribatida followed a plant litter quality gradient of low ratios of litter carbon and cellulose to phosphorus, and high SLA, leaf water saturation capacity and concentrations of Na, K and cellulose. Moreover, some species of Collembola and Oribatida showed species-specific reactions to litter quality traits that indicate some degree of niche differentiation.

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Supplementary material: Appendices 1–4

Appendix 1 The effect of litter species richness and litter treatment on litter mass loss and micro-arthropods

Table S1. Results nested ANOVAs for the effects of plant litter species richness and plant litter treatment nested within the plant litter species richness on litter mass loss (%) total density (Ind g^{-1} d.m.) of Collembola, Oribatida adults and juveniles, Prostigmata and Mesostigmata, and other community indices of Collembola and Oribatida (total df = 75).

	Litter species richness				Litter treatment (Rich)			
	df	MS	*F*	*P*	df	MS	*F*	*P*
Litter mass loss (%)	3	0.00	0.04	ns	11	0.02	9.62	**<0.001**
Collembola								
Total density (Ind/g d.m.)	3	0.02	0.32	ns	11	0.07	1.27	ns
Species richness (no of species)	3	0.02	0.69	ns	11	0.03	1.11	ns
Diversity (*H'*)	3	0.02	1.94	ns	11	0.01	1.07	ns
Oribatida adults								
Total density (Ind/g d.m.)	3	0.08	2.09	ns	11	0.12	3.12	**0.002**
Species richness (no of species)	3	0.01	0.27	ns	11	0.03	1.34	ns
Diversity (*H'*)	3	0.00	0.41	ns	11	0.01	1.18	ns
Oribatida juveniles								
Total density (Ind/g d.m.)	3	0.05	1.60	ns	11	0.03	0.89	ns
Prostigmata								
Total density (Ind/g d.m.)	3	0.01	0.25	ns	11	0.0	0.18	ns
Mesostigmata								
Total density (Ind/g d.m.)	3	0.02	1.10	ns	11	0.0	1.18	ns

Appendix 2 Relations of both, density and abundance of Oribatida and Collembola to mass loss

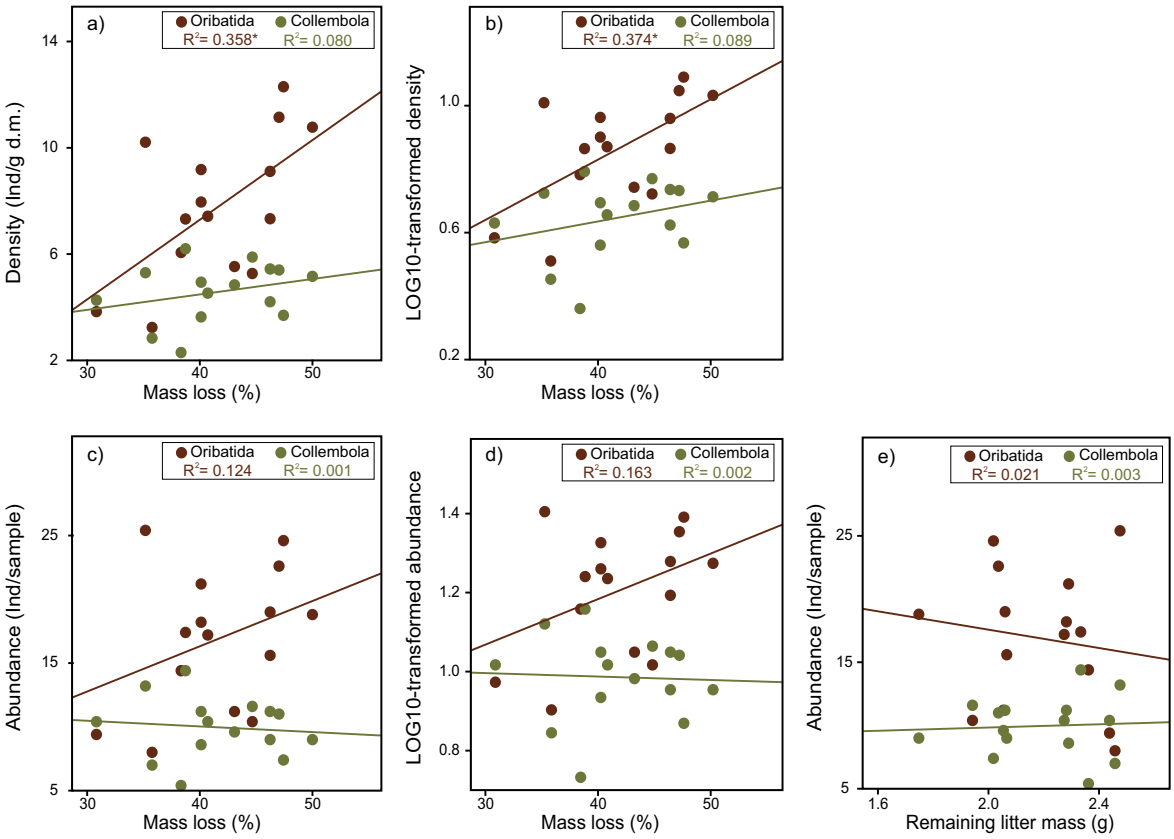

Figure S2. Linear regressions of Oribatida and Collembola a-b) density and c-e) abundance to either a-d) mass loss(%) or e) remaining litter mass (g). Significance in the regressions is indicated with asterisks (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$). Values are averages per litter treatment, thus n=15.

Appendix 3 Calculated micro-arthropod densities in previous studies

Table S3.1. Calculated micro-arthropod densities based on the litter mass loss and microarthropod abundances reported by Kaneko & Salamanca (1999).

				Abundance					Density (Ind/g)				
litter treatment	Mass remaining (%)	Mass initial (g)	Mass remaining (g)	Collembola	Mesostigmata	Prostigmata	Astigmata	Oribatida	Collembola	Mesostigmata	Prostigmata	Astigmata	Oribatida
1st year													
Quercus	65.8	11.2	7.3696	14.3	7	20	0	58.5	1.9	0.9	2.7	0.0	7.9
Pinus	71.1	11.2	7.9632	15	2.8	23.5	0.8	64	1.9	0.4	3.0	0.1	8.0
Sasa	77	11.2	8.624	21.3	15	55.8	0	65.3	2.5	1.7	6.5	0.0	7.6
QP	68.1	11.2	7.6272	17.5	7.5	17	0	77.3	2.3	1.0	2.2	0.0	10.1
PS	73	11.2	8.176	23.5	12	66	1.8	79	2.9	1.5	8.1	0.2	9.7
SQ	70.8	11.2	7.9296	37.8	9.5	102	0.3	98	4.8	1.2	12.9	0.0	12.4
QPS	68.4	11.2	7.6608	30.3	9.5	49	1	103.3	4.0	1.2	6.4	0.1	13.5
2nd year													
Quercus	48.3	11.2	5.4096	12.5	10.3	13	0	66	2.3	1.9	2.4	0.0	12.2
Pinus	55.9	11.2	6.2608	7.3	3.3	4.8	0	20.8	1.2	0.5	0.8	0.0	3.3
Sasa	69.3	11.2	7.7616	18.8	7.5	5.8	0.3	43	2.4	1.0	0.7	0.0	5.5
QP	52	11.2	5.824	21.5	15.8	9.5	0.5	54.5	3.7	2.7	1.6	0.1	9.4
PS	62.9	11.2	7.0448	19.3	6.3	4.3	0.3	51	2.7	0.9	0.6	0.0	7.2
SQ	58.6	11.2	6.5632	8	10.5	5	0	45.5	1.2	1.6	0.8	0.0	6.9
QPS	54.6	11.2	6.1152	28.8	13.3	7	1.3	70.3	4.7	2.2	1.1	0.2	11.5

Table S3.2. Calculated Oribatida densities based on the litter mass loss and Oribatida abundances reported by Hansen & Coleman (1998).

				Abundance Oribatida				Density Oribatida (Ind/g)			
Species	Mass remaining %)	Mass initial (g)	Mass remaining (g)	day 302	day 353	day 251	day 306	day 302	day 353	day 251	day 306
Birch	71.1	8	5.688	25	20	24	35	4.4	3.5	4.2	6.2
Oak	68.5	8	5.48	39	29	38	38	7.1	5.3	6.9	6.9
Maple	62.1	8	4.968	46	59	39	39	9.3	11.9	7.9	7.9
3-mix	62.4	8	4.992	40	31	36	42	8.0	6.2	7.2	8.4
7-mix	60.2	8	4.816	46	46	41	47	9.6	9.6	8.5	9.8

Appendix 4 Collembola and Oribatida species densities characterised by litter C/P and phenols/N ratios

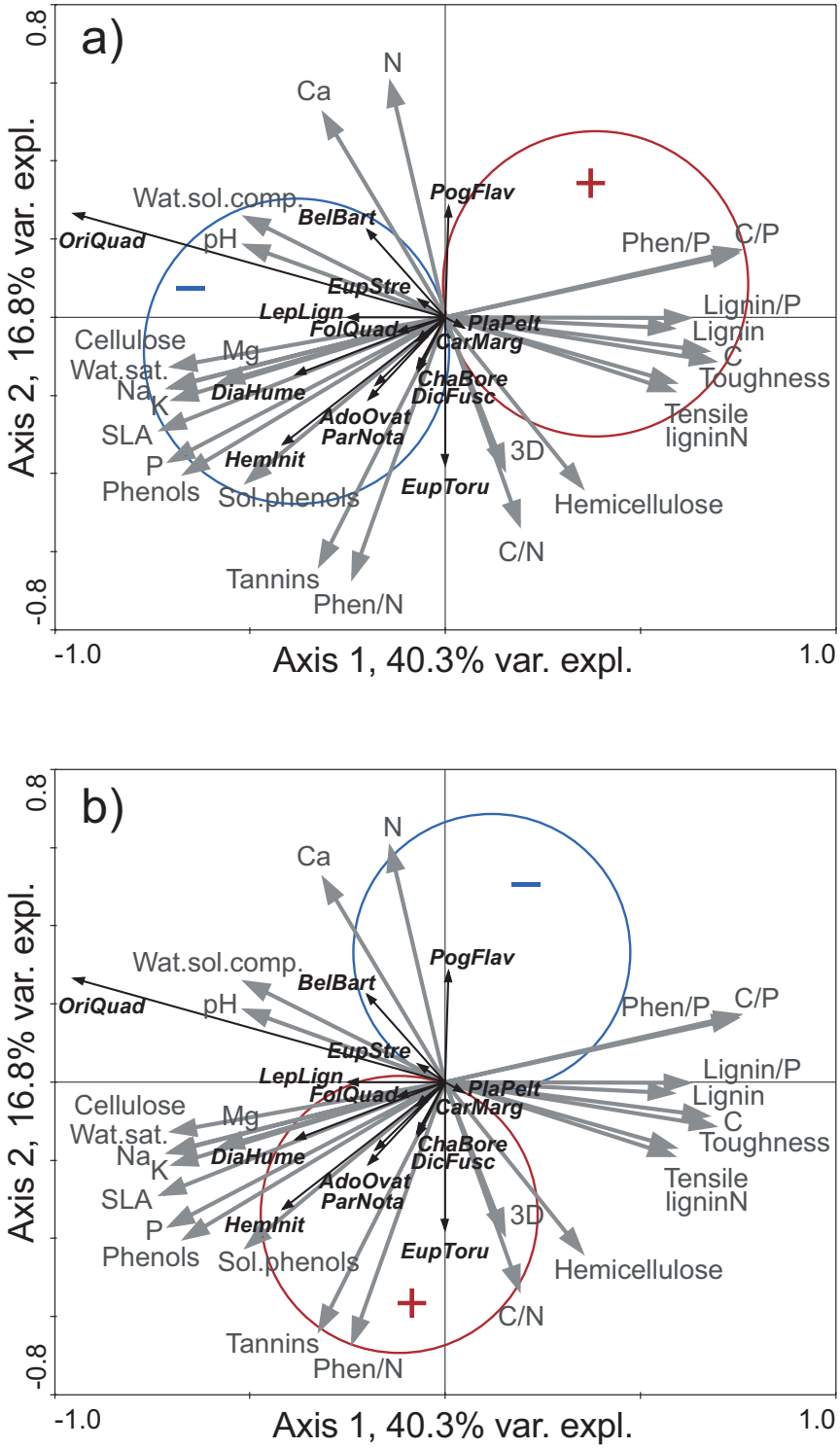

Figure S4. The densities of collembolans and oribatids characterised by litter ratios of a) carbon to phosphorus (C/P) and b) phenols to nitrogen (phen/N) in a PCA ordination assessed by the *t*-value biplot rule. The circles with either a plus (+) or a minus sign (-) indicate positive and negative correlation respectively. For further explanation of the PCA ordination see Figure 2 in the main text.