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Soil fauna alter the effects of litter composition on nitrogen cycling in a mineral soil

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ABSTRACT

Plant chemical composition and the soil community are known to influence litter and soil organic matter decomposition. Although these two factors are likely to interact, their mechanisms and outcomes of interaction are not well understood. Studies of their interactive effects are rare and usually focus on carbon dynamics of litter, while nutrient dynamics in the underlying soil have been ignored. A potential mechanism of interaction stems from the role fauna plays in regulating availability of litter-derived materials in the mineral soil. We investigated the role of soil fauna (meso, macro) in determining the effect of surface-litter chemical composition on nitrogen mineralization and on the micro-food web in mineral soils. In a field setting we exposed mineral soil to six types of surface-applied litter spanning wide ranges of multiple quality parameters and restricted the access of larger soil animals to the soils underlying these litters. Over six months we assessed litter mass and nitrogen loss, nitrogen mineralization rates in the mineral soils, and soil microbes and microfauna. We found evidence that the structure of the soil community can alter the effect of surface-litter chemical composition on nitrogen dynamics in the mineral soil. In particular, we found that the presence of members of the meso- and macrofauna can magnify the control of nitrogen mineralization by litter quality and that this effect is time dependent. While fauna were able to affect the size of the micro-food web they did not impact the effect of litter composition on the abundance of the members of the micro-food web. By enhancing the strength of the impact of litter quality on nitrogen dynamics, the larger fauna can alter nitrogen availability and its temporal dynamics which, in turn, can have important implications for ecosystem productivity. These findings contribute to evidence demonstrating that soil fauna shape plant litter effects on ecosystem function.

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1. Introduction

Although the process of decomposition in terrestrial systems is thought to be regulated by a suite of interactive factors (Aerts, 1997; Couteaux et al., 1995; Wall et al., 2008), there are still many gaps in our understanding of the mechanisms and importance of such interactions. This is especially true for the interaction between resource quality and the structure of the soil community, which tend to be strong controlling factors of decomposition at finer spatial and temporal scales (Lavelle et al., 1993) and which are highly susceptible to environmental change (Wolters et al., 2000). Control of decomposition by plant litter quality has been demonstrated with strong relationships found between plant quality parameters and rates of decomposition and nutrient mineralization (Aerts, 1997; Cornwell et al., 2008; Melillo et al., 1982; Parton et al., 2007). Quality indices, however, act only as surrogates for the actual regulators of the decomposition process (Meentemeyer, 1978). Wardle (2002) suggested that the effects of plant chemical composition on decomposition may be indirect and result from its effects on the decomposer organisms that drive decay – a potential form of interplay between resource quality and the soil community. Direct demonstrations of this mechanism are difficult to obtain. Yet, the chemical composition of plant inputs can affect the structure of the microbial community (Ndaw et al., 2009; Schutter and Dick, 2001) and faunal community (Hansen and Coleman, 1998; Parmelee et al., 1989) in litter and mineral soil. There is also evidence that such effects on the biota can then influence the

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decomposition dynamics of substrates added to soils (Ayres et al., 2009; Chigineva et al., 2009; Orwin et al., 2006).

An additional mechanism of interplay between resource quality and the soil community may involve the role that the faunal members of the soil community play in regulating the availability of litter materials. Fauna are well known to influence the decomposition and mineralization of litter and soil organic matter (Bradford et al., 2002; Brussaard, 1998; Edwards, 2000; Kampichler and Bruckner, 2009). Much of the influence of fauna on decomposition may occur through their impact on soil microbes, the ultimate actors in the decomposition process. It has been suggested that fauna can make litter and the products of its physical and chemical degradation more available to soil microbes (Edwards, 2000; Heal et al., 1997; Petersen and Luxton, 1982). Pieper and Weigmann (2008) showed greater mobilization of various nutrients as well as litter-derived dissolved organic carbon (C) in the presence of isopods. Chamberlain et al. (2006) demonstrated that the activity of Collembola produced greater availability of litter-derived C to the soil microbial community. If fauna can make litter more available to soil microbes, fauna could magnify the effect of litter chemical composition on soil N dynamics. In other words, soil animals could alter the control that litter quality exerts on decomposition, which represents a mechanism of interaction between litter composition and the soil community with significance for site fertility.

Interactive effects of soil fauna and litter chemical composition on litter decomposition have been documented, but the evidence is limited and contradictory. For example, fauna not only have been shown to increase decomposition of "low quality" litters (slowly decomposing) (Couteaux et al., 1991; Tian et al., 1997; Yang and Chen, 2009), but also can enhance the decomposition of "high quality" litter (Schadler and Brandl, 2005). Other studies have observed no interactive effects (González and Seastedt, 2001; Powers et al., 2009). The discrepancy among these results might reflect the fact that there are multiple mechanisms by which fauna can affect function, which might be, in turn, dependent on specific taxa, environmental factors and time (Smith and Bradford, 2003). However, these studies used very different approaches to manipulate litter chemical composition and most contrasted only two litter species (slowly decomposing vs. faster decomposing). Not having true chemical composition gradients might limit the power of their conclusions as results could be attributed to more than one quality parameter and/or to differences other than chemical composition (e.g. surface area or physical structure). In addition, studies investigating interactions between soil fauna and litter chemical composition have focused on their influence on dynamics of surface litters, ignoring nutrient dynamics in the underlying soil. Notably, recent modeling approaches (Adair et al., 2008), analyses of global data sets (Parton et al., 2007) and field observations (Garten, 2009) show that aboveground and belowground decomposition processes are potentially regulated by different factors and thus warrant separate study.

Here, we tested the hypothesis that the structure of the soil community alters litter composition effects on N dynamics in the mineral soil. Specifically we hypothesized that the presence of larger body-size fauna in soils would alter litter composition effects by magnifying the control by litter quality parameters on net N mineralization, as the fauna's role in increasing availability of litter materials to microbes would allow greater realization of the chemical differences among surface litters. Using a factorial arrangement, we exposed soils to six types of surface-applied litter spanning wide ranges of multiple quality parameters and restricted the access of larger soil animals (larger micro >40 μm body width, meso and macrofauna) to the soils underlying these litters. Over the course of six months we measured litter mass and N loss and mineral N release (net mineralization rates) in the mineral soils. We also assessed soil microbes and microfauna to examine whether impacts on N processes were associated with consistent responses of these groups.

2. Materials and methods

2.1. Study site and experimental design

The field study was conducted in experimental plots in a previously abandoned conventional farm in the Piedmont region of Georgia, USA (33°57′N, 83°19′W). Mean annual precipitation is 1400 mm and minimum and maximum annual mean temperatures are 8.9 °C and 18.4 °C with a long growing season and winter temperatures generally remain above freezing. The soil type is classified as a Pacolet sandy clay loam (kaolinitic, thermic typic hapludult). Top soils contain 0.7% C, 0.1% N and have a pH of 4.9. In June 2005, standing vegetation (consisting of grasses and forbs) was pulled from a 100-m^2 site. The site was kept vegetation-free throughout the duration of the study by periodically weeding all sprouting plants. The site was divided into 24 plots of 4 m^2 and sheets of aluminum flashing were buried to 4–5 cm around each plot. Soil from the top 5 cm of two areas of 25 × 50 cm within each plot was collected, mixed and sieved to 4 mm. Care was taken to allow at least 20-cm distance between these two areas and between their edges and the edge of the plot. Collected soil was frozen at −80 °C for 72 h to kill soil-dwelling fauna. Post thawing, soil was placed back in the field in metallic wire frames (25 cm × 50 cm × 5 cm, henceforth referred to as 'boxes') that fit into the previously dug collection areas, with the outer rim of the box remaining 1–2 cm above the surrounding soil surface. Soil under and around the sides of the boxes was relocated as necessary to ensure that there was contact between soil inside and outside the box. The bottom and the sides of the boxes were lined with mesh of either 40-μm or 5-mm diameter; the smaller mesh was to restrict re-colonization of larger-bodied fauna into the boxes. Soil was added to boxes to a depth of approx. 4 cm to allow room for the addition of litter. The boxes were open on top so that the mesh restricted access to mineral soil dwellers but not mobile (jumping) litter fauna. Soil was left bare for 6 weeks to permit re-colonization by fauna and to dissipate the nutrient flush associated with disturbance. According to the categories by Swift et al. (1979), the 40-μm mesh would exclude the larger members of the microfauna

Table 1
Initial chemical composition of five litter species and an equal mixture of all. Litters are presented in order of increasing C/N ratio. Values are means (±1 S.E.); $n = 4$.

	%N	%C	C/N	% P	% cellulose	% hemicellulose	% lignin
Amorpha fruticosa	2.4 (0.04)	47.1 (0.17)	20.2 (0.36)	0.61 (0.02)	26.9 (0.60)	13.9 (0.20)	10.0 (0.17)
Clover	2.0 (0.10)	43.3 (0.33)	22.4 (1.46)	0.50 (0.04)	33.4 (0.75)	12.1 (0.23)	8.0 (0.34)
Mixture	1.1 (0.06)	46.1 (0.93)	46.2 (4.25)	0.28 (0.08)	35.7 (0.63)	19.5 (0.48)	10.3 (0.44)
Rye	0.7 (0.06)	45.0 (0.95)	70.3 (5.72)	0.19 (0.02)	38.0 (1.16)	28.0 (0.35)	4.0 (0.51)
Wheat straw	0.5 (0.04)	47.1 (0.12)	102.5 (5.35)	0.16 (0.01)	40.4 (0.47)	30.1 (0.44)	4.6 (0.19)
Pine	0.4 (0.05)	51.0 (0.28)	127.9 (6.88)	0.05 (0.02)	30.5 (0.47)	11.9 (0.47)	19.2 (0.62)

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(<100 μm) and the meso (100 μm–2 mm) and macrofauna. Larger microarthropods, diplurans, insect larvae, enchytraeids, centipedes and earthworms are soil-dwelling groups that are present at the site and would be excluded with a 40-μm mesh. Members of these groups were observed either in Tullgren or Baermann funnel extractions of the 5-mm mesh soils, or *in situ* when excavating and preparing the soils.

Litter treatments consisting of leaf litter from five different plant species and an equal mixture of them (six litter types) were randomly assigned to four of the 4-m^2 plots and were surface applied at a rate of 327 g m^{-2} (air dry weight) both to the inside and to the outside of the boxes within each plot. Substrates applied were green litter of cereal rye (*Secale cereale* L.), crimson clover (*Trifolium incarnatum* L.) and false indigo (*Amorpha fruticosa* L.); wheat straw (*Triticum aestivum* L.), pine needles (*Pinus taeda* L.), and an even mixture of all the above by mass. These litter species were selected to provide strong gradients in the quality parameters assessed (Table 1). We used a litter mix to obtain an intermediate point along the quality parameters gradients. The litter species chosen are commonly used as amendments or mulch in agroecosystems in the southeastern USA.

Sampling for litter mass loss, and soil N dynamics was carried out 21, 91 and 165 days (August, October and February from here on) following litter application. The total duration of the experiment was determined by the rapid rate of decomposition of clover, the most labile substrate used, under the warm and moist conditions of the experimental site. After six months clover had lost about 80% of its biomass, at which point we terminated the experiment in order to avoid unintended effects related to differences in the abiotic environment due to reduced litter coverage. Nematode, microarthropod, protozoan and microbial community analyses of the mineral soils underlying the litters were carried out in August and February only. Soil gravimetric moisture content was measured at all sampling dates, by drying soils at 105 °C to constant mass. Analytical methods are described in detail below. Overall, our design provided a factorial design of litter mesh size (two levels: restricted and full soil community) by litter type (six levels: see Table 1). Each treatment was replicated 4 times and sampled at three time points for ecosystem processes (mass loss and N dynamics) and twice for biota. This gives 2 mesh sizes × 6 litters × 4 replicates × 3 or 2 sampling points = 144 observations for process variables and 96 for biotic variables.

2.2. Chemical composition and mass loss of litter substrates

Dry samples of the initial litter were ground to fine powder prior to chemical analyses. C and N were analyzed on a Carlo Erba Elemental Analyzer and are reported as %C and %N by dry mass. Phosphorus (P) was measured from 0.5 g of sample that was ashed, extracted in aqua regia acid and analyzed on an automated Alpkem Analyzer and is reported as %P by dry mass. Cellulose, hemicellulose, and lignin concentrations were measured from 0.5 g of each sample using sequential neutral detergent/acid detergent digestion on an Ankom A200 fiber analyzer. Percentage N and C were also determined for remaining mass at the final sampling date.

Litter mass loss dynamics were assessed using the litterbag approach. Nylon mesh litterbags, 13 cm × 15 cm in size and consisting of 2-mm mesh, were filled with 3 g of the same litter type assigned to the plot. During the packaging of the litter, care was taken to avoid breaking the material. For the mixed litter treatment, component litter species were equally represented by mass to total 3-g litter. To ensure that larger fauna could access litter in the bags placed in the 5-cm mesh sub-plots, ten 4-mm diameter holes were added to the litterbags. Three litterbags were placed in each box at the same time litter species were added to the 4 m^2 plots, and were placed in the litter layer, atop the soil and surrounded by litter on all remaining sides. Following field exposure for 21, 91 or 165 days, one litterbag was removed per time point from each box and picked-free of foreign material adhering to the decomposing litter. Following air-drying, litter sub-samples were placed for 3 h at 500 °C to determine ash-free dry mass (AFDM).

2.3. Net nitrogen mineralization rates

We determined net N mineralization (or immobilization) rates from the litters and soils in the boxes by summing two separate measurements. The first measurement was based on the accumulation of inorganic N in resin bags (see below) buried beneath the soil boxes. The second measurement estimated the net release or immobilization of inorganic N within the soils of the litter boxes by assessing changes in their extractable inorganic N values across

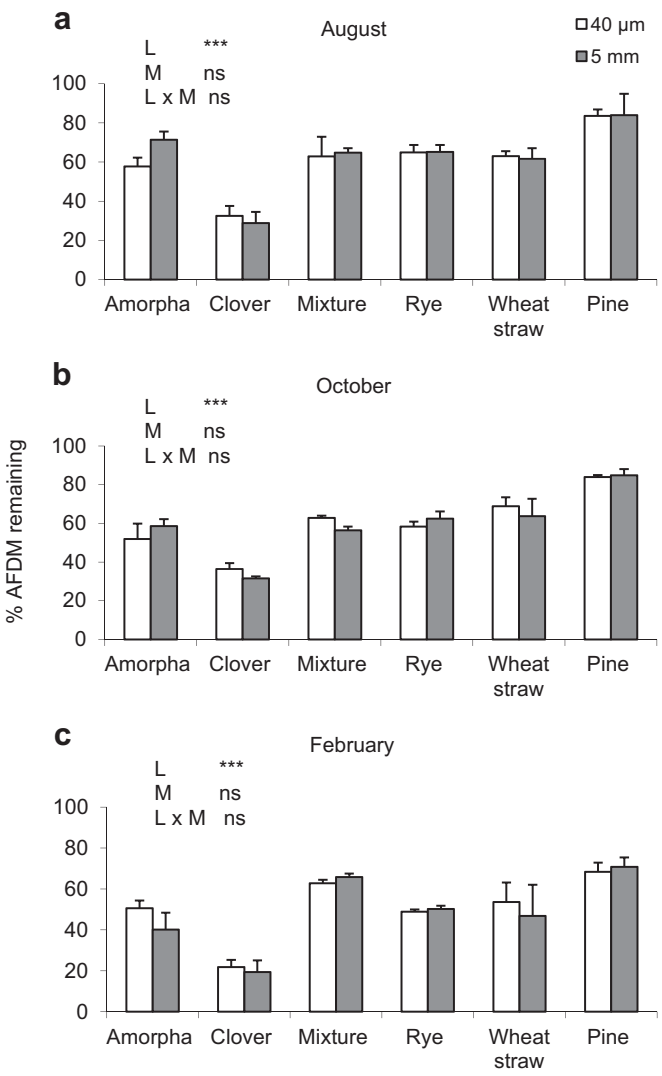

Fig. 1. Percentage of litter ash-free dry mass (AFDM) remaining in litter bags after 21 days (August; Fig. 1a), 95 days (October; Fig. 1b) and 165 days (February, Fig. 1c) of decomposition. Litter bags were placed on the soil surface in 0.125 m^2 plots bordered with mesh of 40 μm or 5 mm in diameter to manipulate soil faunal communities. Litters are ordered on the *x*-axis from low to high C/N ratios. Significance of the factors and their interactions (L = litter type, M = mesh size, LxM = the interaction) are shown for each plate as *, **, ***, † and ns, which denote $P < 0.05$, <0.01, <0.001, <0.1 and >0.1 respectively. Values are means ± 1 S.E. ($n = 4$).

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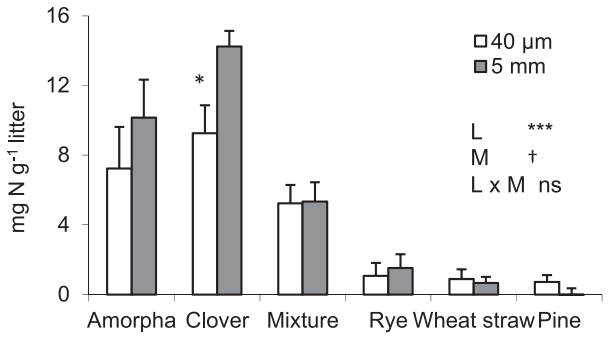

Fig. 2. Total nitrogen released per gram of ash-free dry litter mass after six months of decomposition. Values are means ± 1 S.E. ($n = 4$). Asterisks associated with a pair of bars indicate a significant ($P < 0.05$) mesh effect for that litter. See Fig. 1 legend for further details on design and statistical results.

measurement periods. For the resin bag approach, nylon bags containing anion and cation exchange resins were buried immediately beneath the boxes to retain NO_3^- and NH_4^+ leached from the litter and soil above (Binkley and Matson, 1983). Each nylon bag measured 4.5-cm diameter by 1-cm tall and contained 24 g of an even mixture of Na-saturated cation and Cl-saturated anion exchange resins (Sybron Ionac C-250 and ASB-1P, Sybron Chemicals, Birmingham, USA). Only one nylon bag was buried beneath each box immediately before litter application to the plots. The bag was removed on the first sampling date (July–August incubation period) and replaced by a new one for the next incubation period (August–October). The procedure was repeated for the final incubation period (October–February). Resins were extracted in 2 M KCl for 1 h (20 ml for the soils and 60 ml for the resin bags). Extracts were analyzed for NO_3^- and NH_4^+ using an Alpkem Continuous Flow Analyzer. It was assumed that the ions collected in each resin bag were derived from the soils and litter directly above as there is no slope associated with the site. Thus the soil volume above was approximately 64 cm^3 (diameter of the resin bag was 4.5 cm and the depth of the soil above each resin bag was 4 cm). Using this volume, the NO_3^- and NH_4^+ that accumulated in the resin over each incubation period was converted to $\mu g\ N\ g^{-1}$ soil using an average bulk density value of 1.1 $g\ cm^{-3}$ for the site. At each sampling time, soil was sampled from each box for determination of NO_3^- and NH_4^+. Initial soil concentrations of NO_3^- and NH_4^+ were estimated from six soil samples collected from randomly selected plots immediately before litter application. The concentration of mineral N at the end of one sampling period was used to estimate the starting mineral N concentration for the next sampling period. Soils (4 g) were extracted and analyzed in the same manner as resins and concentrations of mineral N in extracts were brought to $\mu g\ N\ g^{-1}$ soil. To determine the mean daily rates of net mineralization or immobilization for each box and time period, we added the N collected in the resin bags to the net amount of N mineralized or immobilized in the soils within the boxes, and then divided this value by the number of days in each incubation period (Kolberg et al., 1997).

2.4. Microbial and faunal analyses

Microbial and faunal analyses were performed in soils collected in August and February only. Soil samples (approximately 50 g) were obtained by collecting and compositing three sub-samples. To assess abundance of total live microbial, fungal, bacterial and protozoan biomass, we used a phospholipid fatty acid (PLFA) approach. PLFA were extracted from 5 g of 2-mm sieved and freeze-dried soils from each box. Samples were shaken for 2 h in a mixture of methanol–chloroform–phosphate buffer (2:1:0.8 in volume) (Bligh and Dyer, 1959). The organic phase was fractionated (Zelles and Bai, 1993) with an activated silica gel column (BondElut; Varian, Palo Alto, USA). Mild alkaline methanolysis was used to produce fatty acid methyl esters (FAMEs) (White et al., 1979). FAMEs were purified with NH_2 aminopropyl columns (BondElut; Varian, Palo Alto, USA) and analyzed with a Hewlett-Packard (HP, Palo Alto, USA) 6890 series GC with a flame ionization detector and a 30 m DB-5 (film thickness = 0.25 µm, internal diameter 0.32 mm; Agilent, Santa Clara, USA). Individual PLFAs were quantified in relation to an internal standard (20:0 ethyl ester). Compounds were identified by comparison of their retention times with those of a prepared mixture standard containing 36 FAMES (Matreya, USA; Sigma-Aldrich, USA; Nu-Chek, USA). Fatty acid notation used follows that in Frostegard and Baath (1996). Microbial groups PLFA markers were: cy17:0, cy19:0, 18:1ω7c and 18:1ω9c for Gram-negative bacteria; 14:0, i15:0, a15:0, 15:0, i16:0, i17:0 and a17:0 for Gram-positive bacteria; i15:0, a15:0, 15:0, i16:0, cy17:0, 17:0, 18:1ω7c and cy19:0 for all bacteria; 18:2ω6,9c for fungi and 10Me16:0, 10Me17:0 and 10Me18:0 for the actinobacteria.

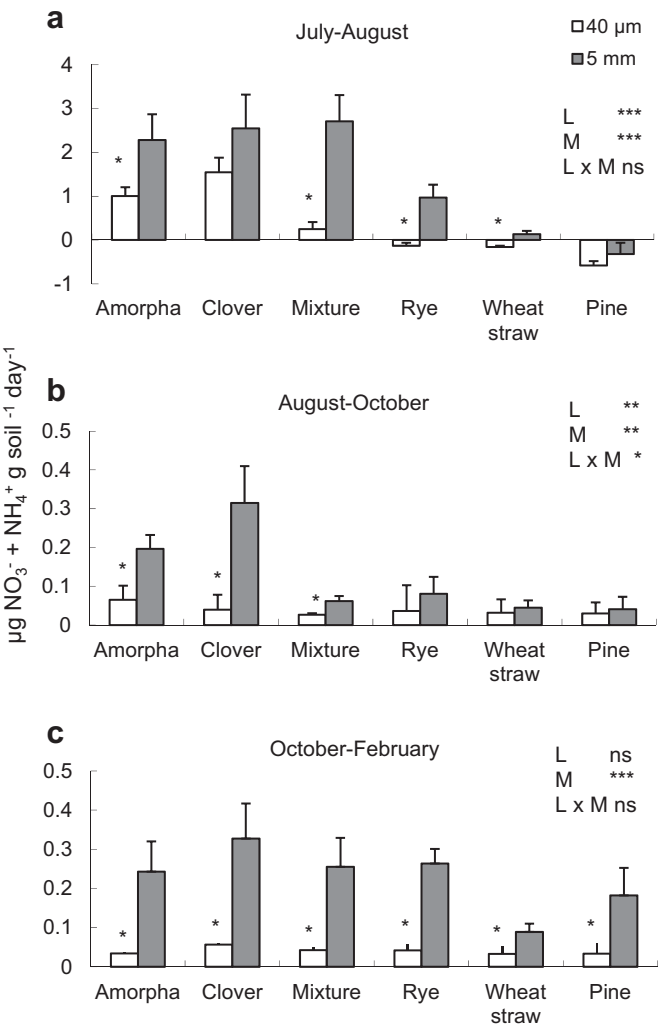

Fig. 3. Mean daily nitrogen mineralization rates ($\mu g\ NO_3^- + NH_4^+\ g\ soil^{-1}\ day^{-1}$), across three periods (Fig. 3a–c) over six months of decomposition, in mineral soils with different surface litters applied. Asterisks associated with a pair of bars indicate a significant ($P < 0.05$) mesh effect for that litter and sampling period. Note that *y*-axes have different scales. See Fig. 1 legend for further details on design and statistical results.

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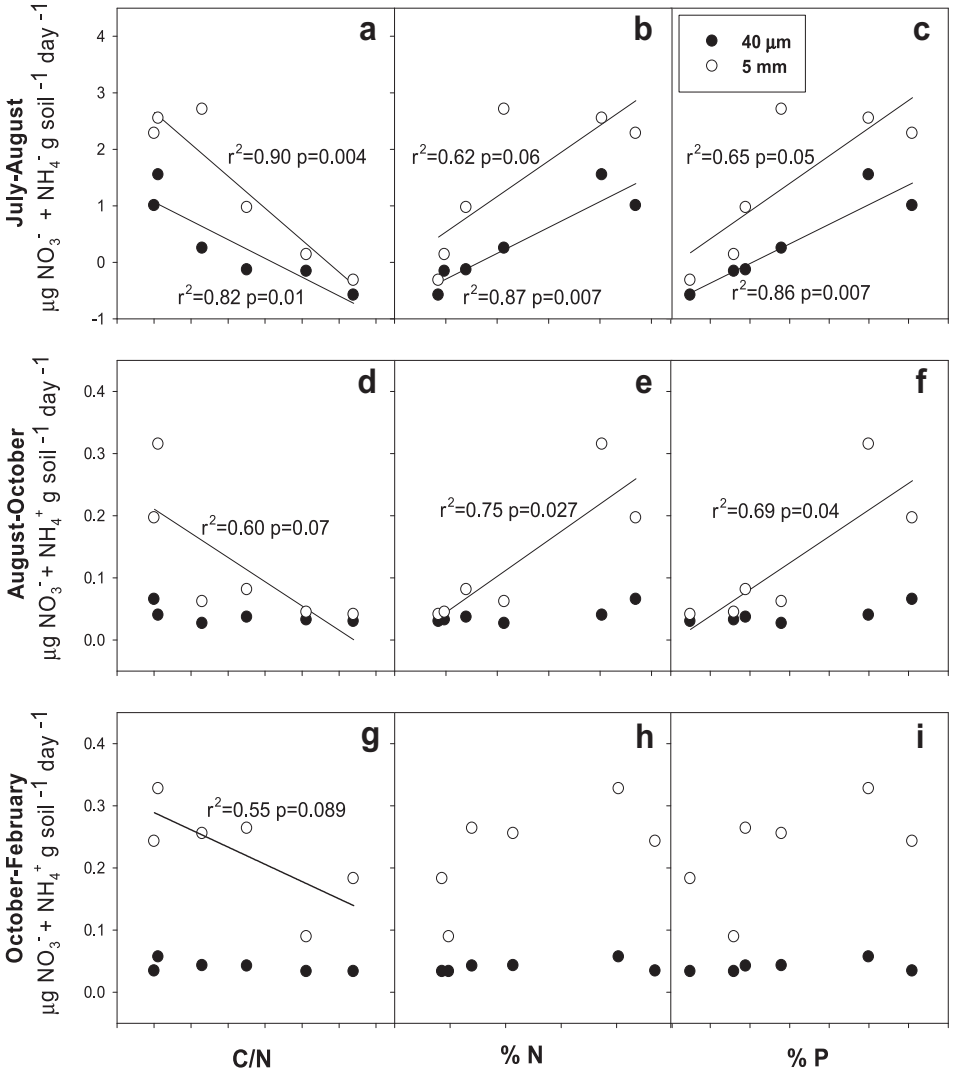

Fig. 4. Relationships between N mineralization/immobilization rates with litter quality parameters in the 40-µm and 5-mm mesh treatments during the three time periods studied (Fig. 4a–c). Linear regressions were performed on mean N mineralization/immobilization of the four replicates for each time period, mesh size and litter type ($n = 6$ for each mesh size). See Table 2 for ANCOVA results.

20:2ω6,9c; 20:3ω6,9,12c and 20:4ω6,9,12,15c were used as indicators of protozoan abundance (Cavigelli et al., 1995; Mauclaire et al., 2003).

Nematodes were extracted from approximately 6 g of fresh soil with the Baermann funnel method for 72 h and preserved in 5% formaldehyde. Total nematode counts to the level of trophic group were performed for each sample. Tylenchidae were included in the fungivorous trophic group. Microarthropods were extracted from approximately 25 g of fresh soil for 5 days on modified Tullgren-type extractors. Mites were identified to suborder (Oribatei, Mesostigmata and Prostigmata). The Collembola detected in samples were assigned to the following families: Isotomidae, Entomobryidae, Onychiuridae, Tomoceridae, Sminthuridae. No differences in the responses of the groups of mites or collembolans were observed so numbers were pooled for further analyses. At the October sampling date, we conducted microarthropod extractions of soils from intact plots, from which soil was not excavated, homogenized or frozen. The purpose was to determine the natural abundance of mites and collembolans and how they compared to soils that had been manipulated. Estimated abundances were similar or lower than in mesocosms soils, indicating that the experimental manipulation, re-colonization time (6 weeks) and duration of the exposure to litter allowed for the development of communities of comparable size to the indigenous one.

2.5. Statistical analyses

Litter mass loss, N release, N mineralization/immobilization in soil and biota data were analyzed by repeated measures two-factor ANOVA with mesh size and litter type as factors and time as the repeated measure and subsequently by time period with two-factor ANOVA; *t*-test was used to assess mesh effects for each litter type. Faunal densities were log $(n + 1)$ transformed prior to analysis. Linear regression was used to assess relationships of litter quality parameters with N mineralization/immobilization. ANCOVA was used to test for effects of interactions between initial litter quality parameters values and mesh size on N mineralization/immobilization at each sampling period. To evaluate the causes of observed effects with ANCOVA, we regressed individual quality parameters against measured rates for each mesh size. As there was only one initial value for each quality parameter in each one of the litter types, ANCOVAs and linear regressions were performed on

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mean N mineralization/immobilization rates of the four replicates in each time period, mesh size and litter type ($n = 12$), thus avoiding pseudoreplication of the continuous variable (quality parameter). Models were checked for assumptions of normality and homoscedasticity, and analyses were performed in the statistical software JMP 8.

3. Results

3.1. Process measurements

Mass loss was more rapid across the first sampling period and for litter chemical compositions with higher initial concentrations of N and P (Fig. 1, Table 1). By the end of the incubation, clover had lost about 80% of its mass, *Amorpha* 60%, wheat straw and rye ~45%, and pine 30% (Fig. 1c). Mass loss of the legume species (clover and *Amorpha*) decreased with lignin and hemicellulose content, and thus was slower for *Amorpha* (Fig. 1, Table 1). No significant effect was observed due to mesh size of the boxes, or its interaction with litter type or time on the remaining percentage of ashed-free dry mass (Fig. 1a–c). Using the remaining masses and N concentrations in litter, the amount of N mobilized from or immobilized within the litter over the course of the whole incubation was calculated (initial N content minus final N content per gram of litter; Fig. 2). N mobilization was not affected by the interaction between mesh size and litter type.

Mean daily net N mineralization/immobilization rates in the mineral soil (measured with resin bags and soil N concentrations) were greater for the July–August period than for the August–October and October–February periods, which exhibited similar rates (Fig. 3a–c). In general, net N mineralization occurred and net immobilization was only observed under rye, pine and wheat straw between July and August in the 40-μm mesh boxes. What was evident was the changing influence of mesh size and litter type across the three periods, in addition to their combined influence. Specifically, in the July–August period (Fig. 3a) there were significant main effects of both mesh size and litter type, but no significant interaction. The mesh effect is explained by the greater net mineralization (or lower net immobilization) in boxes that permitted larger fauna access (i.e. 5-cm mesh). During the second period (August–October; Fig. 3b), mesh and litter type interacted to determine net N mineralization rates. Specifically, while mean values of net N mineralization were consistently greater in the boxes lined with the 5-cm mesh, mesh effects were only significant for *Amorpha*, clover and the litter mixture. In the third period (Fig. 3c) net N mineralization was, again, significantly greater in the 5-cm than 40-μm boxes but in contrast to the first and second periods, litter type had no apparent influence on net N mineralization.

The strongest relationships among N mineralization/immobilization rates and litter quality parameters were observed in the July–August period (Fig. 4a–c), when N mineralization was negatively related to C/N and positively related to %N and %P. No significant relationships between mineralization rates and cellulose, hemicellulose and lignin content or lignin-to-N ratios were found (plots not shown). ANCOVAs (Table 2) indicated that in the August–October period the effect of litter initial C/N, %N and %P on rates was dependent on the mesh size treatment (significant interactions of the three litter parameters and mesh size; Table 2). This effect was due to significant to marginally significant relationships in the 5-mm mesh treatment vs. no relationships in the 40-μm mesh (Fig. 4d–f). The same was the case for the relationship with C/N in the final period (Fig. 4g) (marginally significant interactions of C/N with mesh size, Table 2).

3.2. Biotic measurements

Mesh size and litter type significantly influenced total microbial PLFAs at both sampling dates (Fig. 5a and b). The main effect of mesh size at each sampling point was due to higher mean values of total microbial PLFA in soils contained within 5-cm mesh boxes. There were clear differences in total microbial PLFA of soils under different litter types but it was not clear that these differences were related to the initial chemical compositions of these litters. The marginally significant statistical interaction between mesh size and litter type in August likely arose because the relative effect of mesh size appeared more pronounced for rye than other litter types.

Litter type had significant effects on the relative abundance of fungi and bacterial PLFA markers (Fig. 5c–h) except in February for the Gram-positive bacteria. There was no apparent relationship between marker abundance and litter composition. Significant effects due to mesh size were only observed in August, when greater abundance of the fungal (Fig. 5c) and Gram-negative bacterial markers (Fig. 5g) were observed in soils in 5-mm mesh boxes, while the Gram-positive bacteria (Fig. 5e) were more abundant in the 40-μm mesh soils in two types of litter only.

PLFA 20:4ω6, an indicator of protozoan abundance, showed consistent and statistically significant effects of mesh size in August, when abundance was greater in the 5-cm mesh boxes, independent of litter type (Fig. 6a). Litter type also had a pronounced effect in August but not in a manner that readily equated to the "quality" of litter, as defined by their initial chemical compositions.

Only total and bacterial-feeding nematode trophic groups responded in a consistent manner to any of the treatments, and so we only report data for them. Notably, fungal-feeders were rare, representing only about 2% of individuals across plots and boxes. There were significant effects of litter type on the densities of bacterivorous nematodes and on total nematode abundance (Fig. 7a–d).

Table 2
F and *p* values from ANCOVA to test for effects of interactions between initial litter quality parameter values and mesh size on N mineralization/immobilization at each sampling period. ANCOVAs were performed on mean N mineralization/immobilization values for each time period, mesh size and litter type ($n = 12$). Degrees of freedom for mesh size, quality parameter and mesh size × quality parameter = 1. Significant effects are indicated with p values in bold.

Period	Parameter	Mesh size		Quality parameter		Mesh size × parameter	
		F	*p*	*F*	*p*	*F*	*p*
July–August	C/N	18.54	**0.003**	52.47	**<0.0001**	3.57	0.100
	% N	7.44	**0.026**	17.25	**0.003**	0.43	0.529
	% P	7.98	**0.023**	18.79	**0.003**	0.55	0.482
August–October	C/N	6.94	**0.030**	7.02	**0.029**	4.73	**0.061**
	% N	11.01	**0.011**	14.38	**0.005**	8.97	**0.017**
	% P	9.16	**0.017**	11.22	**0.010**	6.84	**0.031**
October–February	C/N	54.59	**<0.0001**	5.70	**0.044**	4.01	**0.080**
	% N	40.53	**0.0002**	2.95	0.124	2.19	0.177
	% P	36.89	**0.0003**	2.28	0.170	1.68	0.230

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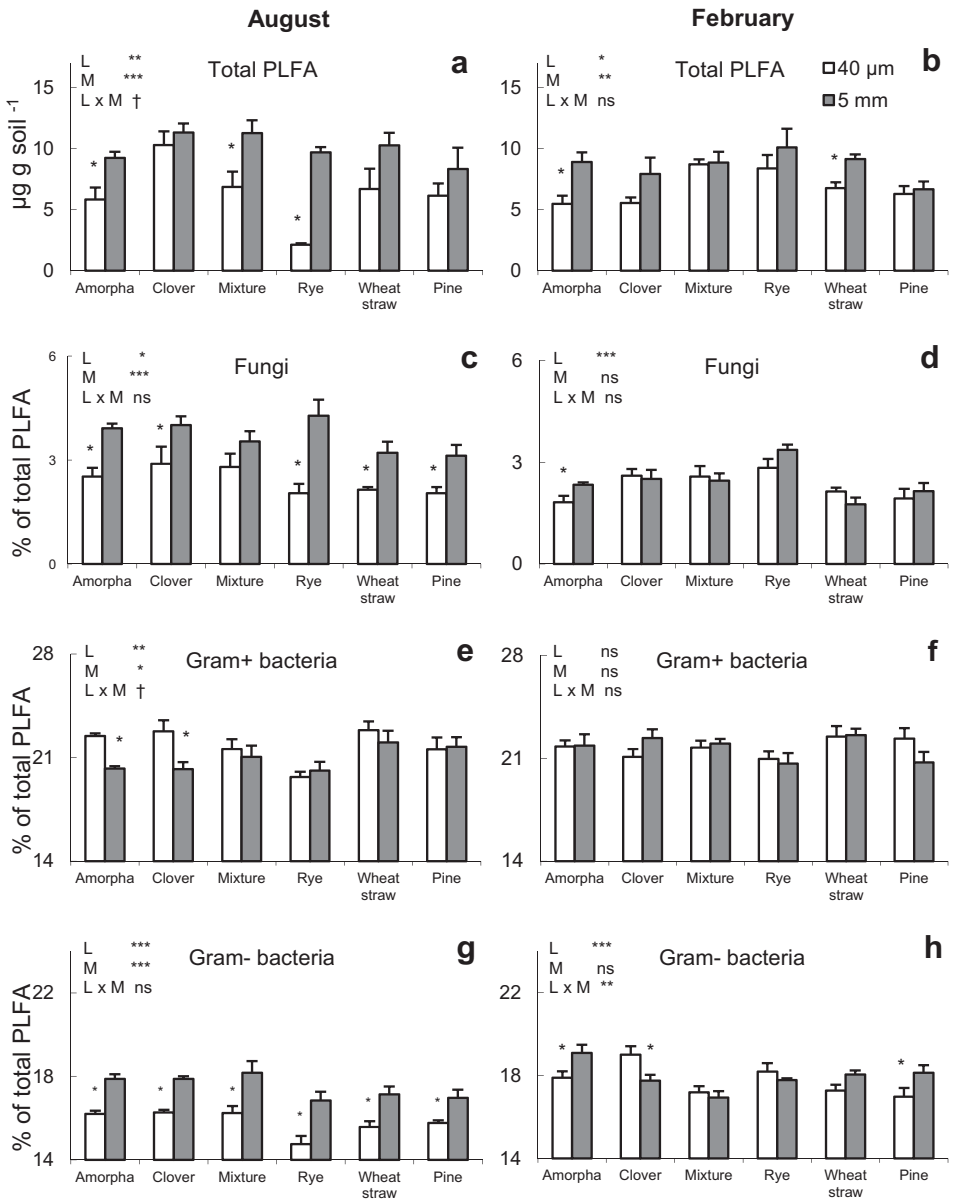

Fig. 5. Total PLFA (as µg PLFA g soil^{-1}) and relative abundances of microbial groups (as % of total PLFA) in mineral soil (0–5 cm depth) after 21 days (August; Fig. 5a,c,e and g) and after six months of decomposition (February; Fig. 5b,d,f and h) of surface-applied litters. See Fig. 1 legend for further details on design and statistical results.

These effects did not appear to be related to litter chemical composition. Mesh size effects were due to greater densities of nematodes in the 5-mm mesh treatment soils (Fig. 7a–d).

The abundances of soil microarthropods were low (up to 0.4 individuals per gram of soil). No differences in the responses of mite suborders were observed so numbers were pooled for further analysis. Increasing the mesh size had both positive and negative effects on mite abundance depending on litter type but these effects did not appear to be related to litter composition (interaction of litter by mesh size $P = 0.007$) (data not shown). No apparent effects of mesh size, litter type or the interaction of both on Collembola densities were detected (data not shown).

4. Discussion

We hypothesized that the structure of the soil community would alter the control by litter chemical composition on N dynamics. Specifically we expected that in the presence of larger-bodied fauna the effects of litter chemical composition on net N mineralization in mineral soil would be magnified. The amount of N collected in resins together with the net increase in inorganic N in soil (a measure of N availability resulting from N mineralization/immobilization) was greater in the soils where larger fauna were present, which supports earlier findings on the positive effect of fauna body size on N mineralization (Alphei et al., 1996; Couteaux et al., 1991; Vedder et al., 1996). The extent of this effect, however, was dependent on litter type and time. The significant interaction of litter type and mesh size found for the August–October period arose because N mineralization was greater in the presence of an unrestricted faunal community but only under clover, *Amorpha* and the mixture. This indicates that the role of fauna on N dynamics was more important for the faster decomposing litters. This is consistent with the observations of mass disappearance by Schadler and Brandl (2005), but has not been previously observed for N mineralization. N

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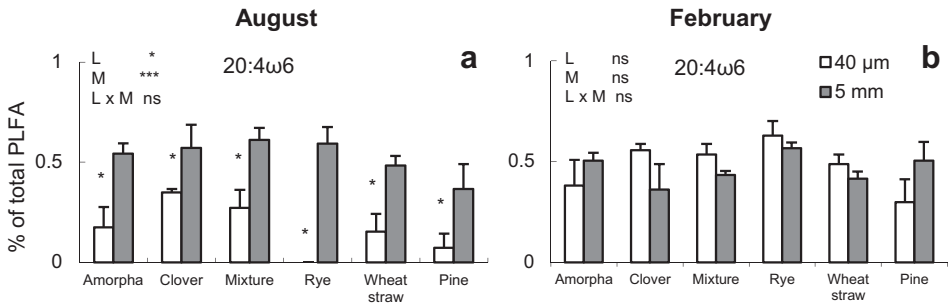

Fig. 6. Relative abundance of protozoan marker 20:4ω6 (as % of total PLFA) in mineral soil (0–5 cm depth) after 21 days (August; Fig. 6a) and after six months of decomposition (February, Fig. 6b) of surface-applied litters. See Fig. 1 legend for further details on design and statistical results. Asterisks associated with a pair of bars indicate a significant ($P < 0.05$) mesh effect for that litter. Note that *y*-axes have different scales.

mineralization/immobilization was negatively related to litter C/N and positively related to %N and %P. ANCOVA and linear regressions demonstrated that in the August–October period, these relationships were stronger in the presence of an unrestricted faunal community. Thus, our study showed that the larger fauna were able to enhance the control over N dynamics in the mineral soil by litter chemical composition. Further work is required to test the specific mechanisms by which fauna could have this effect. We speculate that this could occur because of greater availability to soil microbes of litter-derived substrates due to the activity of fauna. By increasing exposure of litter materials to the microbes, the effect of the differences in chemical composition on decomposition could be enhanced. The presence of larger fauna in the 5-mm mesh could have increased the mixing and distribution of litter-derived materials in the mineral soil, thus increasing substrate availability. These materials could include labile C substrates and nutrients or inhibitory substances, thereby enhancing the overall response to litter chemistry. In addition, some members of the fauna can seek high quality litter (Kadamannaya and Sridhar, 2009; Satchell and Lowe, 1967) which could also make the overall response to litter quality more pronounced.

In contrast to the August–October period, interactive effects between litter type/quality parameters and mesh size were absent during the initial period suggesting that the mediation by the soil community of the effect of litter composition on N mineralization is time dependent. Smith and Bradford (2003) found greater complexity of fauna was associated with a more pronounced relationship between litter C/N and litter mass loss after 30 days of decomposition but this effect was reversed after 60 days. In the case of net N mineralization in the mineral soil, however, we would expect the opposite pattern: that the enhancing effects of fauna on the effect of litter chemistry would tend to be stronger as decomposition progresses. This is because with time more fragmentation, active mobilization, mixing and redistribution of litter materials by fauna will have taken place, allowing the realization of differences among litters in the mineral soil. The absence of any interactive effect in the initial period supports our expectation. For the third period, the relationships were still stronger in the 5-mm mesh size than in the 40-µm mesh (Fig. 4) but the interactive effect of mesh size and soil fauna was only marginally significant. We suggest this is due to the fact that the third period took place in the winter when overall fauna activity was likely reduced (Gongalsky et al., 2008). Due to the fast decomposition pace at this site, our six month study allowed us to demonstrate that during early and intermediate stages of decomposition the role of the fauna in regulating the effect of litter composition on N dynamics is time dependent. The

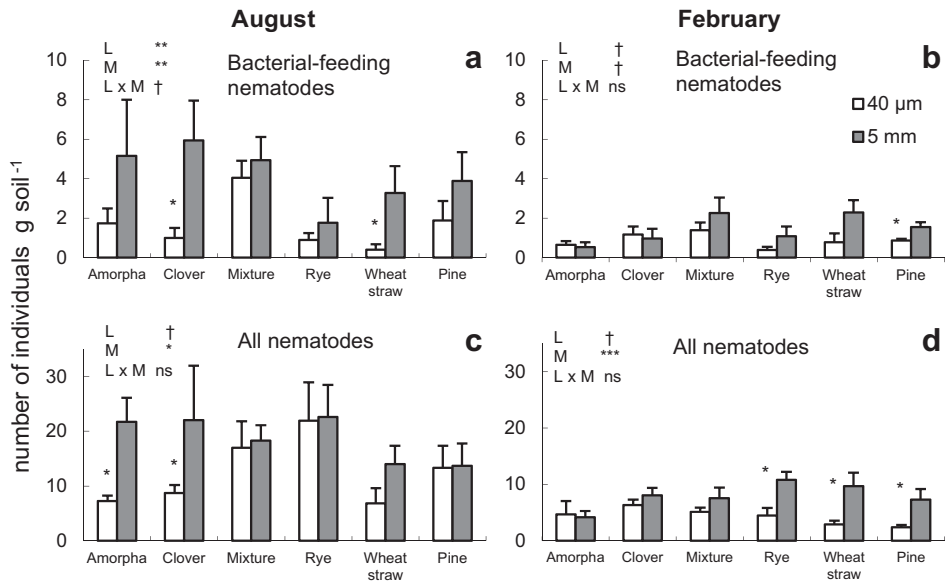

Fig. 7. Bacterial-feeding and total nematode densities in mineral soil (0–5 cm depth) after 21 days (August, Fig. 7a and c) and after six months of decomposition (February; Fig. 7b and d) of surface-applied litters. See Fig. 1 legend for further details on design and statistical results. ANOVA and *t*-tests were performed on log $(n + 1)$ transformed data. Asterisks associated with a pair of bars indicate a significant ($P < 0.05$) mesh effect for that litter and sampling period. Note that *y*-axes have different scales.

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role of fauna in mediating the effect of litter quality on soil N dynamics in advanced stages of decomposition remains undetermined.

Fauna can modify the structure of the micro-food web via trophic interactions, impacts on the physical and chemical habitat, and by modifying resource availability (Wardle, 2002). We anticipated that the microbes and the microfauna would be affected by the presence of larger fauna and that their response would be consistent with the response of N dynamics. We found a trend of greater abundances of the detritivores (fungi and Gram-negative bacteria) as well as the microbivores (Protozoa, bacterial-feeding nematodes) in the 5-mm mesh treatment, particularly in August. This trend was consistent with greater N availability during the July–August period, which was when the majority of the N released was available in the mineral soil (Fig. 2). A greater availability of N and decomposition substrates for detritivores in the presence of larger fauna could support larger microbial biomass in the mineral layer (Frouz et al., 2006). Thus, litter type did affect the microbes and microfauna but, in contrast to N dynamics, the presence of larger fauna did not seem to strongly affect the relationship between microbes or microfauna and litter composition. This suggests that while the fauna were able to affect the size of the micro-food web (the detritivores and their direct consumers), potentially by increasing resources, they did not impact the effect of litter composition on the abundance of the members of the micro-food web.

We looked at how litter chemical composition and the soil community interact to regulate N dynamics in the soil underlying the litter layer, the main destination of litter-derived materials and the main source of nutrients for other ecosystem compartments. Ours is the first field study that addresses interactive effects of the soil community and substrate quality on N dynamics and in the mineral soil. Using litters that spanned a wide range in quality parameters, our work showed that the structure of the soil community can alter the effect of surface-litter chemical composition on N mineralization in the mineral soil. In particular, we found that the presence of members of the meso and macrofauna can magnify the control of N mineralization by litter quality and that this effect is time dependent. By controlling the strength of the impact of litter quality on N dynamics, the larger fauna can alter N availability and temporal dynamics which, in turn, can have important implications for ecosystem productivity and long-term dynamics. Our findings contribute to evidence demonstrating that the soil fauna can shape plant litter effects on ecosystem function (Hättenschwiler and Gasser, 2005). In the context of agroecosystems, this research suggests that the effectiveness of plant litter amendments intended to manage soil fertility is dependent on the integrity of the soil faunal community.

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