

BIODIVERSITY AND LITTER DECOMPOSITION IN TERRESTRIAL ECOSYSTEMS

Stephan Hättenschwiler,¹ Alexei V. Tiunov,² and
Stefan Scheu³

¹*Center of Functional Ecology and Evolution, CEFE-CNRS, 34293 Montpellier, France;
email: stephan.hattenschwiler@cefe.cnrs.fr*

²*Institute of Ecology and Evolution, Laboratory of Soil Zoology, 119071 Moscow, Russia;
email: a_tiunov@mail.ru*

³*Institute of Zoology, University of Technology Darmstadt, 64287 Darmstadt, Germany;
email: scheu@bio.tu-darmstadt.de*

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■ **Abstract** We explore empirical and theoretical evidence for the functional significance of plant-litter diversity and the extraordinary high diversity of decomposer organisms in the process of litter decomposition and the consequences for biogeochemical cycles. Potential mechanisms for the frequently observed litter-diversity effects on mass loss and nitrogen dynamics include fungi-driven nutrient transfer among litter species, inhibition or stimulation of microorganisms by specific litter compounds, and positive feedback of soil fauna due to greater habitat and food diversity. Theory predicts positive effects of microbial diversity that result from functional niche complementarity, but the few existing experiments provide conflicting results. Microbial succession with shifting enzymatic capabilities enhances decomposition, whereas antagonistic interactions among fungi that compete for similar resources slow litter decay. Soil-fauna diversity manipulations indicate that the number of trophic levels, species identity, and the presence of keystone species have a strong impact on decomposition, whereas the importance of diversity within functional groups is not clear at present. In conclusion, litter species and decomposer diversity can significantly influence carbon and nutrient turnover rates; however, no general or predictable pattern has emerged. Proposed mechanisms for diversity effects need confirmation and a link to functional traits for a comprehensive understanding of how biodiversity interacts with decomposition processes and the consequences of ongoing biodiversity loss for ecosystem functioning.

INTRODUCTION

The current fast rate of biodiversity loss warrants concern for several reasons (Wilson 1992, Chapin et al. 2000). One major consequence of decreasing diversity is associated changes in ecosystem functioning because ecosystem processes

likely depend on the presence of a specific number of functional groups, species, and genotypes of organisms (Ehrlich & Ehrlich 1981). The biodiversity crisis documented a quite unanticipated ignorance among biologists and ecologists on some basic questions: How important is biodiversity for ecosystem processes? How much biodiversity is needed to maintain ecosystem functioning? Past research typically measured aboveground plant biomass production as one variable of ecosystem functioning and its dependence on plant-species richness. Experiments have shown that, in grassland ecosystems, primary productivity is positively related to plant-species diversity (see reviews by Schläpfer & Schmid 1999, Loreau et al. 2001, Roy 2001). Much less is known about how biodiversity affects other key ecosystem processes, such as decomposition and nutrient cycling.

In terrestrial ecosystems, the above- and belowground plant-litter input constitutes the main resource of energy and matter for an extraordinarily diverse community of soil organisms connected by highly complex interactions. In terms of biomass and species numbers, the largest number of soil organisms are involved in organic matter turnover, particularly the large groups of bacteria and fungi. Recycling of carbon and nutrients during decomposition is a fundamentally important ecosystem process (Swift et al. 1979, Cadish & Giller 1997) that has major control over the carbon cycle, nutrient availability, and, consequently, plant growth and community structure (Wardle 2002, Bardgett 2005). Plant-species composition, in turn, significantly affects ecosystem nutrient cycling through plant-nutrient uptake and use, rhizosphere interactions, production of litter of specific quality, and microenvironmental changes (Hobbie 1992, Eviner & Chapin 2003). Distinguishing these different controls is essential for a mechanistic understanding of biodiversity effects on ecosystem functioning.

The role of litter diversity for the composition and activity of soil communities and processes during decomposition has rarely been studied. This circumstance is surprising because litter quality as the overriding determinant for decomposition within a given climate (Coûteaux et al. 1995, Cadish & Giller 1997) varies tremendously among species (Perez-Harguindeguy et al. 2000, Hättenschwiler 2005). Similarly, the ecosystem consequences of the diversity of soil organisms are little understood, except for some keystone species or ecosystem engineers such as earthworms, termites, and ants (Jones et al. 1994, Anderson 1995). Despite the reasonable expectation that the diversity and composition of functional groups or feeding groups are important for ecosystem processes (Setälä 2002, Heemsbergen et al. 2004), the existence and the significance of the great species diversity within functional groups is puzzling (Scheu & Setälä 2002).

A strong need exists for increased efforts to investigate interactions among litter diversity, the diversity of soil organisms, and the processes that occur during mineralization and soil organic-matter formation. In this review, we summarize current knowledge on the functional significance of litter diversity and the decomposer system that depends on the litter for decomposition processes and feedbacks to plants. We also specify what we think are the most promising areas for future research.

DOES DECOMPOSITION CHANGE WITH ALTERED LITTER DIVERSITY?

The physicochemical environment, litter quality, and the composition of the decomposer community are the three main factors controlling litter decomposition (Berg et al. 1993, Coûteaux et al. 1995, Cadish & Giller 1997). Under given environmental conditions, the remaining two factors—litter quality and decomposers—are directly related to biological diversity. Litter-decay rates differ widely among species that decompose under identical environmental conditions (Cornelissen 1996, Wardle et al. 1997). These differences in decomposition are attributed to variation in litter traits, such as leaf toughness, nitrogen, lignin, and polyphenol concentrations, and the carbon/nitrogen and lignin/nitrogen ratios and their consequences for microbial activity and substrate utilization (Berg et al. 1993, Cadish & Giller 1997, Perez-Harguindeguy et al. 2000). On the basis of the close correlation between litter quality and decomposition, litter traits can be used as predictors for decay rates across species (Aber et al. 1990) and also serve as key variables in biogeochemical models (Parton et al. 1994, Nicolardot et al. 2001). These correlations, however, are commonly determined from decomposition of single-species litters in mesh bags, from which larger soil animals are excluded. In reality, a specific litter type rarely occurs in isolation, and the important question arises as to whether data on single-species decomposition can be combined to accurately scale up to community-level decomposition and to predict ecosystem processes. Theoretically, this combination is possible only for purely additive effects (i.e., the decomposition rate of a litter mixture is calculated as the sum of the proportions of individual litter species), but it does not work if synergistic or antagonistic effects occur among litter species.

The Influence of Litter-Species Richness on Litter-Mass Loss

In sharp contrast to the large body of literature on single litter-species decomposition, data on litter mixtures and the monocultures of each species included in the test are still rare. No more than approximately 30 studies exist (Gartner & Cardon 2004), even though species-mixture effects were first investigated more than 60 years ago (Gustafson 1943). These studies show a wide range of litter-mixing effects that can be grouped according to three distinct patterns. Roughly half of all litter mixes studied showed accelerated litter-decay rates compared with what would have been predicted from monocultures of the respective species included in the mix (Gartner & Cardon 2004). These synergistic responses ranged between 1% and 65% (mean of 17%) of increased total litter-mass loss in mixes compared with the arithmetic mean of component species. In ~30% of all cases, no significant differences occurred in observed and predicted mass losses in litter mixes (i.e., additive effects), and in the remaining 20% of mixes, antagonistic effects with a slower than predicted litter decomposition were observed. Antagonistic responses ranged between 1.5% and 22%; the mean decrease was 9% (Gartner & Cardon 2004).

Apparently, synergistic interactions among litter species are twice as frequent as antagonistic interactions, and nonadditive litter-mixing effects are overall predominant, whereas purely additive responses are more the exception than the rule.

However, such a broad comparison among studies should be interpreted with great caution, and at present, one should refrain from generalizations for at least three reasons. First, although the reports on litter-species interactions cover a wide range of different ecosystems, from the high arctic to the tropical rainforest, a strong bias exists toward temperate forest studies (roughly 60% of all studies available today). Important and highly species-diverse ecosystems, such as tropical forests, are critically underrepresented (only one study by Montagnini et al. 1993), and grassland studies are similarly rare (two studies: Bardgett & Shine 1999 and Hector et al. 2000). Second, distillation of a mean mixing effect from the different studies is difficult because it reflects a momentary state in a dynamic process that has been interrupted at different stages. The high temporal resolution of CO₂ efflux measurements by McTiernan et al. (1997) showed, for example, that an initial lower CO₂ release from a *Quercus petraea*/*Betula pendula* leaf-litter mix was followed by a phase of higher CO₂ release, and no net difference occurred compared with the single-species treatments over the entire incubation period. Given the large differences in the duration of experiments (between 56 and 1780 days) and in experimental protocols (leaf litter exposed under artificial laboratory conditions, litterbags, or field microcosms), an average relative-mixing effect appears ecologically rather meaningless. Third, most experiments done to date have included only two or three species and compared monocultures with just one mixing treatment. This narrow range strongly limits a thorough assessment of diversity effects and a more general description of litter-mass loss as a function of litter diversity.

The available data indicate that litter-species interactions are quite common and lead to distinct decomposition trajectories that differ from those expected from monocultures of litter. However, idiosyncratic responses to increasing species richness seem to predominate (Wardle et al. 1997), which leads to the following question: Why do some mixtures decompose faster than others? The question is addressed below in the discussion of potential mechanisms involved in litter-mixing effects.

Responses of Individual Species within Litter Mixtures

In most of the past experiments, mass loss was measured in litter mixtures as a whole and compared with the predicted or expected value on the basis of single-species decomposition. This approach may mask species-specific responses to mixing litter that might well be important for decomposition processes. Individual species might behave distinctly, as was observed in most of the few studies that separated decomposition among species within mixtures (Briones & Ineson 1996, Salamanca et al. 1998, Conn & Dighton 2000, Prescott et al. 2000, Wardle et al. 2003, Hättenschwiler & Gasser 2005). Depending on the size of the effect and the

variation, such species-specific responses may not be detected at the level of the whole litter mix. Observations of five different two-species mixtures by Prescott et al. (2000) indicate that contrasting mixture effects on mass loss of component species are particularly important during the initial phase of decomposition (up to 1 year) but may disappear in later stages (after 2 years). In the litter mixtures of temperate forest trees studied by Hättenschwiler & Gasser (2005), decomposition of the three most-recalcitrant litter species, *Fagus sylvatica*, *Quercus petraea*, and *Acer campestre*, increased significantly along the diversity gradient from one to six species mixtures. In contrast, no overall diversity effect occurred on the decomposition of the more rapidly decomposing species, *Carpinus betulus*, *Prunus avium*, and *Tilia platyphyllos*. The entire litter mixture collectively, or, alternatively, the presence of one or a few specific species, influences the decay rate of certain litter types and, thus, the temporal dynamics of the litter layer composition and possibly nutrient dynamics. Changes in the litter-layer composition caused by distinct diversity effects among species may alter microhabitat structure and food availability for litter-feeding animals, which, in turn, have direct or indirect consequences for the further course of decomposition. Species-specific responses to litter mixtures may actually be more common than anticipated but remained largely undetected because species were not separately analyzed.

Litter-Mixing Effects on Nitrogen Dynamics

In addition to, or independent of, mass loss, litter diversity may also influence nitrogen (N) mineralization or immobilization in decomposing litter. Gartner & Cardon (2004) concluded that in the majority of all mixtures tested (76%), non-additive nutrient dynamics have been observed that range from 100% decreased to 25% increased net N mineralization in mixtures compared with the predicted values from monocultures. In most experiments that report a change in N dynamics caused by mixing litter species, the change did not correlate with the responses in mass loss. Briones & Ineson (1996), who differentiated between species, observed an increased N release and mass loss from *Eucalyptus globulus* when mixed with *Betula pendula*. However, *B. pendula* mass loss did not change, and N release actually decreased, which largely neutralized the enhanced N loss from *E. globulus* leaf litter. Two other studies that reported a significantly higher N release from mixtures did not detect a concomitant change in CO₂ release (McTiernan et al. 1997, for the *Picea abies/Alnus glutinosa* mix) or in mass loss (Blair et al. 1990). A higher nitrogen flux from a more diverse litter than from single-species litter most likely results in higher plant N availability (Finzi & Canham 1998) that possibly increases plant growth or alters the competitive balance among species. In contrast, decreased N loss from mixtures may indicate a diminished plant N availability caused by increased N immobilization or decreased N mineralization. This condition, however, does not necessarily imply negative consequences for ecosystem properties. For example, negative litter-mixture effects on N release can help to prevent N losses from the system after disturbances. Also, mixtures

may not actually decrease N availability over longer time periods but may change the timing of N release not assessed in most experiments, which typically have a relative short duration. A different pattern of N availability over time could better match plant requirements or could favor some plant species over others.

Similar to the diversity effects on litter-mass loss, the mixing of different litter species has nonadditive, largely idiosyncratic effects on N release. The currently available data suggest little or no correlation between diversity effects on mass loss and on N release. Variable effects on nutrients other than N have been reported as well (Staaf 1980, Briones & Ineson 1996), but the studies are too few for unequivocal conclusions.

MECHANISMS AND CONSEQUENCES OF LITTER-MIXTURE EFFECTS

The investigation of litter-diversity effects on decomposition is still mostly in the exploratory stage of experimental tests designed to determine if and how litter-mass loss and nutrient mineralization is changed in mixtures of different litter types. Only a few attempts have been made to identify the underlying mechanisms and to explain observed diversity effects. The data currently at hand, however, provide some insights into potential processes that are likely involved and may help to direct future research. With some overlaps, these processes may be grouped into four complexes of mechanisms: (a) synergistic effects caused by nutrient transfer among litter types, (b) stimulating or inhibiting influences of specific litter compounds, (c) synergistic effects that result from improved microclimatic conditions or habitat diversity in a structurally more diverse litter layer, and (d) synergistic or antagonistic effects that result from interactions across trophic levels.

Nutrient Transfer

Differences in chemical composition and physical properties among different litter types and their interactions is the most obvious and promising starting point from which to build and test hypotheses. Theoretical considerations and experimental evidence suggest that a nutrient-rich litter type with a low carbon/nitrogen (C/N) ratio, and, thus, a relatively fast decomposition rate, enhances the decomposition of other, poor-quality litters (Seastedt 1984, Chapman et al. 1988, Wardle et al. 1997). The rationale behind such synergistic interaction is a preferential exploitation of the high-quality litter by decomposer organisms that eventually leads to a high nutrient availability and allows nutrient transfer to the low-quality litter. Transferred nutrients, in turn, lead to a more rapid decomposition of the low-quality litter and, consequently, of the entire litter mixture. Much of the past research was motivated by this hypothesis and, because of practical considerations in forestry, aimed at answering the question of whether the addition of an easily decomposable broadleaf tree litter accelerates decomposition of a poor-quality conifer needle litter.

N transfer from the N-rich to the N-poor litter, as well as increased microbial activity accompanied by increased mass loss in the more slowly decomposing litter type, was reported by Salamanca et al. (1998) and Briones & Ineson (1996) in one of the species pairs tested. The results of this latter study additionally suggest a net transfer of other nutrients such as potassium (K), calcium (Ca), and magnesium (Mg) between litter types. Nutrient transfer by fungal hyphae or leaching alleviates nutrient limitation to poor-quality litter decomposition and, therefore, is an intuitively compelling mechanism for synergistic effects among litter species. This process is, however, rarely convincingly demonstrated. Even if apparent nutrient transfer from one to the other litter type occurs, decomposition does not necessarily change (Staaf 1980). Nutrient-rich and easily decomposing leaf litter from *Cornus florida* did not accelerate decomposition of *Pinus taeda* needle litter after 1 year of exposure in the field (Thomas 1968). In line with this finding, no synergistic effects occurred in mixtures of *Pinus ponderosa* and *Quercus gambelii*, which differed significantly in litter quality (Klemmedson 1992). In a recent test of the nutrient-transfer hypothesis that included numerous two-species mixtures, Hoorens et al. (2003) found considerable nonadditive litter-mixing effects on decomposition that, however, were not related to differences in litter chemistry. They analyzed the differences in C, N, phosphorus (P), and phenol concentrations between litter species and their relationship to differences between observed and predicted decomposition rates and found no significant correlations. These data suggest that interactions between litter species occur equally likely in chemically similar and dissimilar species (Hoorens et al. 2003) and, thus, provide evidence against the nutrient-transfer hypothesis. However, nutrient dynamics have not been measured, and whether a net transfer from one litter species to the other actually occurred and how it might be related to differences in mass loss rates is not known.

Nutrient transfer among litter species appear to be involved occasionally as a driving mechanism for litter-mixing effects, but currently available data is contradictory and suggest rather a limited importance in the determination of litter-species interactions.

Effects of Specific Compounds

Besides the variation in nutrient concentrations, litter species differ in their composition of other compounds that might inhibit or stimulate decomposition. Inhibition of microbial growth or activity by a species-specific compound can diminish, compensate, or reverse other, simultaneously operating, stimulating effects such as nutrient transfer among litter types. Polyphenols are commonly viewed as a group of secondary plant metabolites that typically inhibit decomposition. The perception of polyphenols as inhibitors, however, is far too simple, and the variety of phenolic compounds can have many different functions within the litter layer and the underlying soil (Hättenschwiler & Vitousek 2000). Even intraspecific variation in litter polyphenol concentrations can strongly influence soil processes and ecosystem functioning (Schweitzer et al. 2004). Polyphenols as regulatory

compounds are critical for a better understanding of decomposition processes in general and of litter-diversity effects in particular.

The studies by Schimel and colleagues in the Alaskan taiga (e.g., Schimel et al. 1998) provide some of the most comprehensive examinations of the diversity of polyphenol effects on soil processes. Secondary succession in these forests starts with *Salix/Alnus* communities and continues to an *Alnus/Populus*, a *Populus*, and finally a *Picea alba*-dominated community. *Populus balsamifera* was found to play a key role during succession by the production of polyphenols that interfere with soil processes (Figure 1). *P. balsamifera* leaf litter releases phenolic acids that are a microbial growth substrate; this substrate leads to increased microbial N immobilization. *P. balsamifera*-specific condensed tannins, on the other hand, inhibit microbial activity that results in reduced decomposition and N mineralization rates. Even more importantly, these condensed tannins in *P. balsamifera* leaf litter suppress *Frankia* symbionts and, consequently, reduce N₂ fixation by the early successional *Alnus*. *Alnus*-specific condensed tannins have no negative influence on N₂ fixation. Taken together, the diverse effects of *Populus*-specific phenolic compounds may ultimately enhance successional dynamics and change the nitrogen availability in these ecosystems (Figure 1).

In the boreal forest ecosystem of northern Europe, observational and experimental studies have shown that the release of the species-specific phenolic

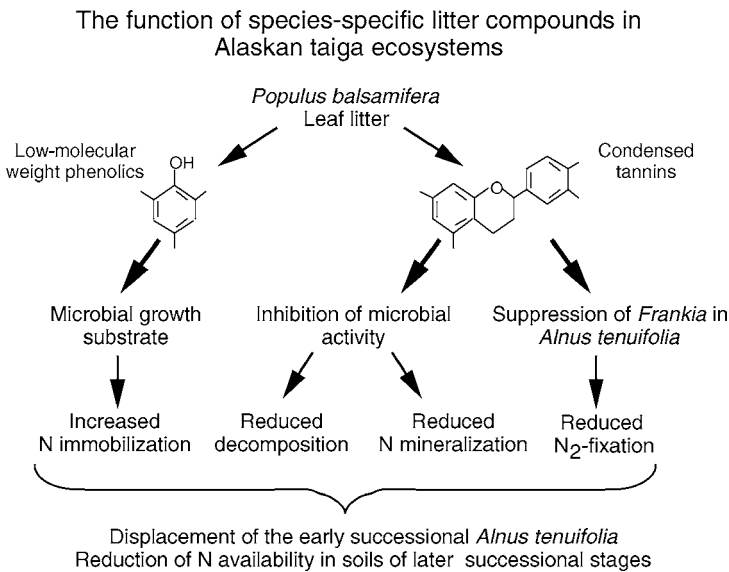


Figure 1 Schematic overview of the effects of different phenolic compounds from *Populus balsamifera* leaf litter on various soil processes and its consequences for the nitrogen cycle and successional dynamics in Alaskan taiga ecosystems. Based on research by Schimel and colleagues (e.g., Schimel et al. 1998).

compound Batatasin-III from leaf litter of the dwarf shrub *Empetrum hermaphroditum* negatively affects tree-seedling growth (Nilsson 1994). In field and laboratory experiments, the influences of allelopathy and belowground resource competition on *Pinus sylvestris* seedlings were separated (Nilsson 1994). Both allelopathy and competition independently decreased seed emergence and growth of seedlings compared with controls, and the combination of both factors led to a stronger inhibition. The negative effect of Batatasin-III on pine-seedling growth was explained by inhibition of the infection by the ectomycorrhizal fungus *Paxillus involutus* and an impaired N uptake by pine possibly caused by decreased mineralization rates. This finding documents that *E. hermaphroditum* alters soil processes by the synthesis of a specific phenolic compound in a way that its dominance is maintained in late successional stages of boreal forest ecosystems.

Even though the examples of polyphenol effects outlined above have not been studied explicitly in the context of litter-diversity effects, they suggest a strong impact of species-specific phenolic compounds on decomposition processes. A thorough analysis of the functional significance of polyphenols during decomposition of litter mixtures is lacking so far, but presumably, such an analysis will contribute to a mechanistic understanding of litter-diversity effects.

Improved Microenvironmental Conditions

A higher diverse litter layer can reasonably be assumed to be structurally richer than a monospecific litter layer. Different leaf sizes, leaf shapes, leaf-surface structures, and leaf colors all contribute to a distinct geometric organization, water-holding capacity, and radiative-energy balance in a species-rich litter layer. Such differences influence microclimatic conditions and microhabitat structure for soil animals and, therefore, have indirect consequences for decomposition.

Wardle et al. (2003) used litterbags of two adjacent compartments to study the influence of 10 different boreal forest litter species on each other's decomposition. One of the most interesting findings was the promotion of litter-mass loss and N loss of associated litter species by the presence of feather mosses (*Pleurozium schreberi* and *Hylocomium splendens*). Although feather mosses themselves are slowly decomposing, their high water-holding capacity apparently stimulated decomposition of adjacent litter species, which shows clear evidence for improved microclimatic conditions for decomposition by the presence of certain species or a particular functional group of litter species.

In a litterbag decomposition experiment that involved litter of three different broadleaf deciduous tree species, Hansen & Coleman (1998) found significantly greater microhabitat diversity and associated species richness of oribatid mites in mixed litter than in the three monocultures but found no difference in mite abundance. A similar result was obtained by Kaneko & Salamanca (1999), who observed a higher species richness of oribatid mites and a higher abundance of microarthropods in litter mixtures compared with single-species litterbags. However, the two studies are in contrast with respect to litter-mass loss. Whereas the greater

faunal abundance and diversity correlated with increased mass loss in the experiment by Kaneko & Salamanca (1999), the study by Hansen & Coleman (1998) found no effect on litter-decay rate. These results might be seen as evidence for a greater importance of faunal abundance over faunal diversity for process rates.

A significantly greater initial N loss followed by a lower N immobilization was observed in three-species mixtures compared with monocultures in another litterbag study, findings that were explained by reduced fungal biomass in litter mixtures (Blair et al. 1990) (Figure 2). Moreover, fewer fungal hyphae correlated with more nematodes, apparently including fungal feeders, that might have benefited from a more diverse or microclimatically more suitable habitat in litter mixtures. Although these studies cannot fully distinguish nontrophic microenvironmental factors from trophic factors, they present convincing evidence that microenvironment-driven positive litter-species interactions contribute to a mechanistic understanding of synergistic litter-diversity effects on decomposition and nutrient dynamics.

Interactions Across Trophic Levels

Generally, the influence of soil fauna on decomposition is more difficult to quantify than that of microorganisms because it is largely an indirect effect. By regulating bacterial and fungal populations, protozoa and nematodes that make up the microfauna can alter litter decay and nutrient turnover. The mesofauna, of which springtails (*Collembola*) and mites (*Acari*) as the two main groups, have a similar function, but the saprophages among them additionally consume and process a

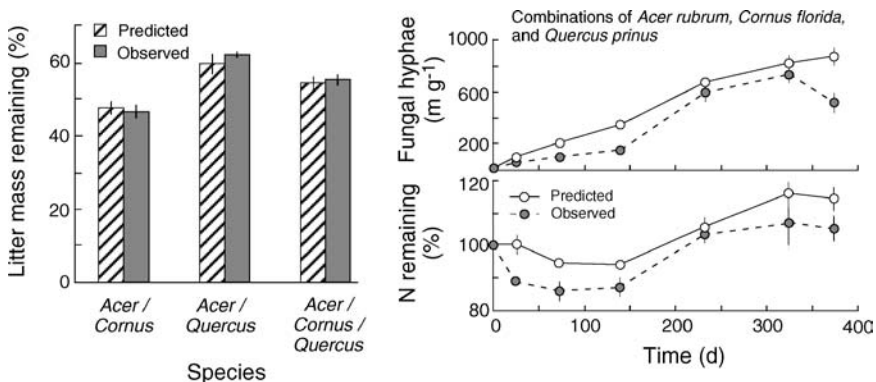


Figure 2 Comparisons of remaining litter mass after 378 days of exposure (*left*), remaining nitrogen (*bottom right*), and length of fungal hyphae (*top right*) of litter mixtures with predicted values calculated from measurements of component species. Litter mass and nitrogen are shown as percent of initial amounts, and length of hyphae is indicated in meters per gram of soil. Data points represent mean values of $n = 3$ litter bags. Reproduced with permission from Blair et al. (1990).

considerable amount of litter. Litter displacement and fragmentation and the conversion to large quantities of feces by macrofauna such as millipedes, isopods, and earthworms stimulate microbial activity and facilitate decomposition. The composition and richness of the litter layer can affect soil fauna in essentially two ways: (a) by shaping the microenvironment and, thus, habitat richness and patchiness, as discussed in the previous paragraph and (b) by providing a range of different food resources, which is the topic of the paragraph to follow.

Litter-feeding macrofauna have a tremendous impact on decomposition because they process large amounts of litter (Càrcamo et al. 2000, David & Gillon 2002) and because of their feedback on performance, activity, and community composition of microbial decomposers and smaller litter and soil fauna (Seastedt 1984, Scheu 1987, Anderson 1988, Brown 1995, Maraun et al. 1999). The saprophagous macrofauna preferentially feed on certain litter types (Zimmer & Topp 2000, Càrcamo et al. 2000, Hättenschwiler & Bretscher 2001) and are quite sensitive to changes in quality, even within a single-litter species (Hassall et al. 1987, Hättenschwiler et al. 1999). For example, isopods changed their feeding rates in particular litter species, depending on whether they did or did not have a choice among three different species (Figure 3). Consumption rates differed much less among litter species provided in monocultures than when the same species were provided in mixtures. Compared with monocultures, consumption rates of mixtures declined by factors of 1.8 for *Acer pseudoplatanus*, 3.6 for *Fagus sylvatica*, and of 4.4 for *Quercus robur* (Figure 3). On the basis of the assumption of a stimulating effect of litter

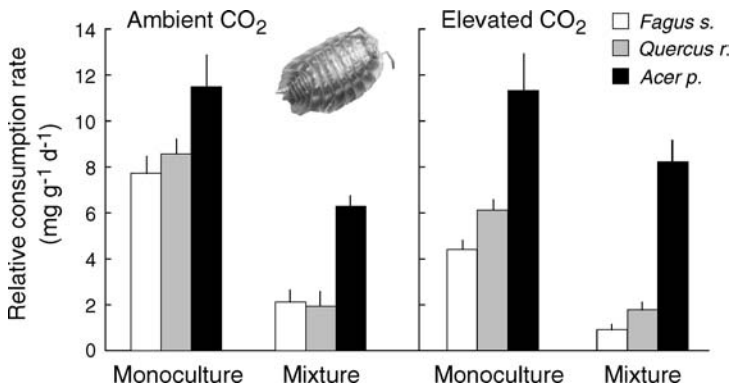


Figure 3 Relative consumption rates (in milligrams of leaf litter per grams of animal body mass per day) of the isopod *Oniscus asellus* feeding on any one of three litter species (*Fagus sylvatica*, *Quercus robur*, or *Acer pseudoplatanus*) or a mixture of all three litter species ($n = 5$ microcosms). Litter has been produced at either current ambient CO₂ (left) or elevated CO₂ (right) concentrations under otherwise identical growth conditions in the field. Total litter consumption in mixtures is the sum of the three individual columns. Data modified from Hättenschwiler & Bretscher (2001).

processing by isopods on further decay, this result suggests a faster decomposition of some preferred litter species (in this case *Acer*) compared with others when they occur together in mixtures but not when they occur in monocultures. Interestingly, when litter of the same species was produced in a CO₂-enriched atmosphere, shifts in the relative consumption of different litter species became more pronounced in both the monocultures and the mixtures (Figure 3). Litter-quality changes induced by rising atmospheric CO₂ concentration or other environmental changes, thus, can affect food selection and overall litter consumption by macrofauna. This behavior likely has consequences for decomposition and nutrient mineralization.

The influence of litter-feeding macrofauna on the decomposition of particular litter species can depend on litter-species diversity, as indicated by highly significant interactions between litter-species number and macrofauna presence in a recent field study (Hättenschwiler & Gasser 2005). For example, recalcitrant *Quercus petraea* leaf litter decomposed substantially faster with increasing litter diversity in the presence of the millipedes *Glomeris marginata*/*G. conspersa* (Figure 4). However, when *Glomeris* was absent, the number of associated litter species no longer influenced *Q. petraea* decomposition. Although another important litter-feeding animal, the anecic earthworm *Aporrectodea longa*, had no effect on *Q. petraea* decomposition, regardless of litter diversity, earthworm presence slowed the mass loss of the rapidly decomposing species *Prunus avium* with increasing litter-species number (Figure 4). In contrast, a significant positive relationship was seen between *P. avium* decomposition and litter-species diversity in absence of earthworms. These results clearly show that macrofauna presence can be an important driver of litter-species diversity effects.

Feedback effects between the composition and richness of litter and soil fauna appear to be important mechanisms for the understanding of how decomposition is influenced by litter diversity. Detection and quantification of such mechanisms is intellectually and methodologically challenging. In particular, litter-diversity effects on macrofauna feeding behavior and performance and the consequences for decomposition remained largely unexplored, because the litterbag method most often used in field experiments excludes larger animals.

THE ROLE OF DECOMPOSER COMMUNITY DIVERSITY

Diversity of Soil Microorganisms

Soil carbon and energy flow is mainly driven by microbial activity. The diversity of soil microorganisms is assumed to be extraordinarily high but is largely unidentified (Prosser 2002). The number of bacterial species is on the order of hundreds to thousands in 1 g of soil; total species number is estimated at 2 to 3 million (Torsvik et al. 1994, Dejonghe et al. 2001). Species diversity of soil fungi is probably only slightly less than that of bacteria (Bridge & Spooner 2001, Hawksworth 2001). One likely reason for the enormous diversity of soil microorganisms is their high fecundity combined with very short generation times and rapid growth. These

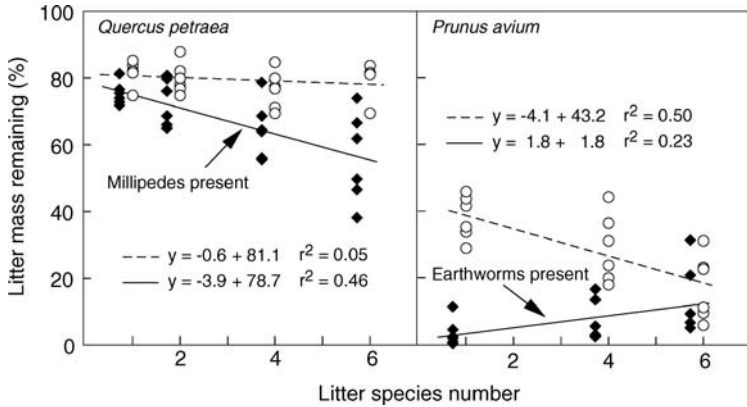


Figure 4 Remaining litter mass (percentage of initial) of a slowly decomposing species (*Quercus petraea*) (left) and a rapidly decomposing species (*Prunus avium*) (right) as a function of total litter-species number after 204 days of litter decay in the field. Data for *Q. petraea* are separated in microcosms in the presence of millipedes (black diamonds, solid line) and in absence of millipedes (open circles, dashed line). Data for *P. avium* are separated in microcosms in the presence of earthworms (black diamonds, solid line) and in absence of earthworms (open circles, dashed line). The respective regression equation along with r^2 values are indicated in the graphs. Slopes of the two regressions within litter species were significantly different. Data modified from Hättenschwiler & Gasser (2005).

factors promote a fast speciation in response to relatively small environmental changes.

Soil microbial diversity has been hypothesized to correlate positively with process rates within soils. In one of the few models that linked microbial diversity and decomposition processes, Loreau (2001) suggested that microbial diversity has a positive effect on nutrient-cycling efficiency and ecosystem processes through either greater intensity of microbial exploitation of organic matter or functional niche complementarity. Ekschmitt et al. (2001) drew similar conclusions, but few studies have been conducted to specifically address the effects of microbial diversity on process rates.

Experimental reduction in microbial diversity often did not affect gross soil processes or even increased the rate of decomposition of plant residues. After manipulation of the diversity of decomposer biota by use of chloroform fumigation, Griffiths et al. (2000) reported no consistent relationship between microbial diversity and process rates. Although nitrification, denitrification, and methane oxidation decreased along with decreasing biodiversity, plant-residue decomposition tended to be faster in pauperized soil. Similarly, decomposition of straw in fumigated and reinoculated soil consistently exceeded that in nonfumigated soil, despite reduced functional diversity of soil microorganisms (Degens 1998). In contrast, other studies found slower decomposition in response to decreased bacterial

functional diversity caused by depleted uranium application (Meyer et al. 1998) or chloroform fumigation (Horwath et al. 1996). The studies that used a “synthetic” approach to create artificial microbial communities in initially sterilized substrates also gave controversial results. Salenius (1981) diluted soil suspensions to produce a gradient of microbial diversity in sterile soil microcosms. Metabolic capabilities of microbial communities were significantly reduced in less-diverse systems. In a similar experiment, no consistent effects of microbial diversity on different soil processes were found (Griffiths et al. 2001). Experiments so far provide conflicting results on the relationship between microbial diversity and rates of soil processes. However, real diversity effects could not always be separated from those introduced by disturbances. For example, chloroform fumigation selected for certain species, and diversity changed along with composition of the soil community (Griffiths et al. 2000).

Soil processes carried out by few microbial species, such as those that involve specific nutrient transformations, have been suggested to be more likely affected by shifts in diversity (Wardle 2002). Indeed, a positive correlation between overall functional or taxonomic diversity of soil bacteria and denitrification rates was found in both laboratory and field studies (Martin et al. 1999, Griffiths et al. 2000). However, even within specific functional groups of soil bacteria (e.g., denitrifying or nitrogen-fixing bacteria) a high genetic diversity (and, thus, functional redundancy) may exist in soil and litter (Priemé et al. 2002, Widmer et al. 1999).

Does Diversity of Saprotrophic Fungi Matter?

Litter decomposition in temperate and boreal forests is mainly driven by fungal activity. Local genetic diversity of soil fungi is large, but a large portion of this diversity is present as resting stages such as conidia, spores, and inactive mycelium. The functional significance of fungal diversity can be important at small spatial scales of specific microsites within the litter layer, where only a few actively foraging hyphal tips interact with each other. The experiment by Setälä & McLean (2004) showed a clear positive effect of fungal diversity on decomposition at relatively low diversity but no influence beyond an actual diversity of 5 to 10 fungal taxa. Similarly, the decomposition of soil organic matter, and especially of pure cellulose, increased strongly with increasing number of soil fungi from monocultures to five-species mixtures (A.V. Tiunov & S. Scheu 2005a). In another experimental test, Robinson et al. (1993) reported significantly greater CO₂ release from plant litter in pairwise combinations of four fungal species compared with single-fungal-species treatments. Also, in support of positive diversity effects, Dobranic & Zak (1999) found that litter decomposition was faster at sites with high fungal diversity determined by the BIOLOG approach.

In contrast, Cox et al. (2001) documented faster pine-litter decomposition in the presence of a single fungal species compared with the same litter colonized by a diverse fungal community. In other experiments, litter decomposition by two-species or three-species mixtures of fungi did not exceed corresponding values in

the best-performing monoculture (Janzen et al. 1995, Hedlund & Sjögren Öhrn 2000). Evidently, competitive interactions among fungi in a diverse community can result in reduced decomposition rates, whereas in other cases, fungal species appear to interact synergistically.

Abiotic conditions within the litter layer and litter chemical composition vary greatly. In relation to this variability, litter-decomposing fungi differ in temperature and moisture optima, and they have distinct enzymatic capabilities (Domsch et al. 1980). Niche differentiation among fungi, therefore, seems to provide a likely explanation for positive effects of fungal-species richness on litter decomposition. Common saprotrophic fungi, such as *Trichoderma*, *Mucor*, and *Rhizoctonia*, exploit spatially heterogeneous substrates by distinct strategies (Ritz 1995). The impact of fungal-species richness on litter decomposition may, therefore, be more important in heterogeneous than in homogeneous substrates, which points to the possibility of litter-diversity multiplied by fungal-diversity interactions, similar to those expected between litter diversity and litter-feeding animals discussed above. However, the only experimental test of this hypothesis to date showed larger effects of fungal diversity on decomposition of cellulose than of heterogeneous forest soil (A.V. Tiunov & S. Scheu 2005a), which suggests that facilitation rather than niche differentiation are important for interactions in species-rich fungal communities.

Interactions Between Saprotrophic and Mycorrhizal Fungi

The interaction between two main functional groups of fungi, the saprotrophic litter decomposers and the biotrophic mycorrhizal fungi, may be of greater importance for carbon and nutrient turnover than interactions within saprotrophs. Although some tree species possess arbuscular mycorrhiza, ectomycorrhizal (EM) fungi generally predominate in temperate forest ecosystems. Saprotrophic fungi (ST) gain energy from decomposing litter, whereas EM fungi receive carbon, in the form of sugars and other low-molecular-weight compounds, from their host plants. EM fungi show a considerable variation in mycelium morphology, growth pattern, enzymatic capability, and foraging strategy (Olsson et al. 2002, Lilleskov et al. 2002), but they share a wide and active set of enzymes that enables them to forage complex organic materials. Strong evidence suggests that at least some species of EM fungi gain a substantial proportion of their carbon directly from soil organic matter (Chapela et al. 2001). Competition between ST and EM fungi for nutrient and energy in the litter layer, thus, seems inevitable and may affect litter decomposition.

EM and ST basidiomycetes share many functional and structural features, including the ability for bidirectional translocation of nutrients along vegetative mycelium or particular mycelial cords and rhizomorphs (Leake et al. 2002). EM and ST fungi compete for nutrients (including organic nitrogen compounds) in forest soil, and antagonistic interactions are presumably common between these organisms (Baar & Stanton 2000, Lindahl et al. 2002). ST fungi, especially basidiomycetes, are generally more effective in breaking down dead organic matter and

are almost exclusively responsible for decomposition of lignocellulose (Tanesaka et al. 1993, Colpaert & vanLaere 1996). However, because of the wide C/N ratio in most litter types, the activity of litter-decomposing fungi in temperate forests is often restricted by N availability (Ekblad & Nordgren 2002). To compensate for this deficiency, fungi translocate N from mineral soil (relatively rich in available N) to decomposing litter (Schimel & Firestone 1989, Frey et al. 2000). The activity of saprotrophs may, therefore, be strongly limited by nutrient (mainly N) sequestration by EM fungi foraging in litter or in mineral soil. Indeed, litter decomposition may be reduced in the presence of EM tree roots (Gadgil & Gadgil 1975; A.V. Tiunov, unpublished data). However, other experiments did not confirm this finding (Staaf 1988), and the interactions between ST and EM fungi remain poorly understood [cf. reviews by Leake et al. (2002) and Cairney & Meharg (2002)]. The mechanisms for either synergistic or antagonistic fungal-species interactions have been rarely addressed in a comprehensive way, which makes generalizations about the significance of fungal diversity for process rates very difficult.

The Importance of Soil-Animal Diversity

As with the microbial community, little is known about the role of animal-decomposer diversity in decomposition processes. The direct contribution of decomposer invertebrates to energy flow and carbon mineralization is low (about 10%) (Reichle et al. 1975, Schaefer 1991), whereas the direct effect on nutrient mineralization is somewhat higher (~30%) (Verhoef & Brussaard 1990, De Ruiter et al. 1993). However, the indirect effect of soil invertebrates on litter decomposition through litter fragmentation and modifications of the structure and activity of the microbial community considerably exceeds the direct effect via their own metabolism (Coleman et al. 1983, Anderson 1987, Wolters 1991). A data compilation that included 24 studies indicated that in virtually all cases, soil animals of the entire decomposer spectrum, from protists to macroarthropods, stimulated decomposition and nutrient mineralization through their effects on microorganisms (Mikola et al. 2002).

In natural ecosystems, and less so in agricultural ecosystems, the soil represents the habitat for a tremendous diversity of organisms. Moreover, soil itself is largely built through the action of animals, particularly primary and secondary decomposers (Anderson 1995, Lavelle et al. 1997, Waid 1999). Effects of soil organisms on soil processes are intimately linked to their size. Small organisms such as bacteria, fungi, and protozoa are the key drivers of energy and nutrient transformations, whereas larger decomposer organisms such as earthworms, millipedes, and isopods are the dominant habitat transformers (Lavelle et al. 1997, Anderson 2000, Scheu & Setälä 2002). These relationships suggest that at least among key-stone soil-animal species, modification of the activity and structure of the microbial community, niche complementarity, and, therefore, diversity has a significant impact on decomposition and nutrient cycling. For example, evidence suggests that the diversity of earthworm species is important for microbial community

composition and activity. However, in most ecosystems, earthworm diversity is comparatively low. In central Europe, for example, typically 3 to 10 species coexist. Ample evidence indicates that the different ecological groups of earthworms differentially affect the activity of soil microorganisms and decomposition processes (Shaw & Pawluk 1986, Brown et al. 2000). Experimental manipulations suggest that the loss of both functional groups and species diversity within functional groups of earthworms alters the ability of soil microorganisms to process organic substrates (Scheu et al. 2002). The functional significance of species diversity within other functional groups of soil organisms is poorly studied, and the relationship between soil-animal species diversity and soil processes remains controversial (Andr n et al. 1995, Mikola et al. 2002, Wardle 2002).

A serious difficulty for understanding the diversity–ecosystem functioning relationship in decomposer invertebrates is that knowledge on the driving forces for the evolution of soil-animal diversity is poor. The packing of animal species in soil is exceptionally dense. In forest soil, hundreds of species and thousands of individuals are concentrated in the litter layer and the uppermost mineral-soil layer the size of a footprint. Both the diversity within and the diversity between trophic groups are high. Food relationships between soil-animal species are not well studied, but some evidence shows that most taxa are food generalists rather than specialists (Anderson 1977, Petersen 2002, Maraun et al. 2003). The dominance of food generalists suggests high redundancy among soil animals, which supports evidence of a weak relationship between soil-animal diversity and ecosystem processes observed in various experiments (Bardgett & Shine 1999, Laakso & Set l  1999, Ekschmitt et al. 2001, Cragg & Bardgett 2001). In line with these findings, the trophic structure of the decomposer community assessed with stable isotopes also indicates a high redundancy in soil-animal communities (Ponsard & Arditi 2000, Scheu & Falca 2000).

Some evidence supports the functional significance of animal diversity for soil processes (Scheu et al. 2002, Heemsbergen et al. 2004). However, studies that have explicitly addressed this question are still too few and are limited to narrow diversity gradients and low species numbers (Mikola et al. 2002). To date, the number of trophic levels and feeding guilds of soil animals (Mikola & Set l  1998, Laakso & Set l  1999, Set l  2002) and the presence of certain keystone taxa (Huhta et al. 1998, Set l  2002, Wardle 2002) appear to be more important for decomposition processes than is species diversity per se. Accordingly, Heemsbergen et al. (2004) have recently shown that functional dissimilarity rather than the number of macrofauna species drives community compositional effects on leaf litter-mass loss and soil respiration.

SOIL-DIVERSITY FEEDBACKS TO PLANTS

Changes in diversity and community structure of soil organisms likely feed back to plants and the aboveground world. On the other hand, belowground processes themselves depend on plant-community composition and diversity (Wardle 2002).

In the long-term Gisburn Forest experiment, four tree species have been planted as monocultures and all possible two-species mixtures (Chapman et al. 1988). The investigators reported significant increases in soil-fauna abundance, litter respiration, and nutrient mineralization in mixtures of *Picea abies* and *Pinus sylvestris* compared with their monocultures; a positive feedback was seen on *Picea abies* growth (Figure 5). In contrast, mixing *Picea abies* with *Alnus glutinosa* did not significantly change fauna abundance, but decreased litter respiration and mineralization compared with the predicted values of monocultures; marginally significant negative effects on *Alnus* growth and positive effects on *Picea* growth were observed. In another experiment, Nilsson et al. (1999) documented that competitive interactions among plant species change when plants are grown in humus formed from monotypic versus mixed litters, although these effects were small and tended to be idiosyncratic. In a meta-analysis of 35 studies that investigated the effects of plant litter on vegetation characteristics, Xiong & Nilsson (1999) found that plant-species richness is strongly affected by litter, which supports the notion that litter has important afterlife effects (Facelli & Pickett 1991). Despite the unequivocal

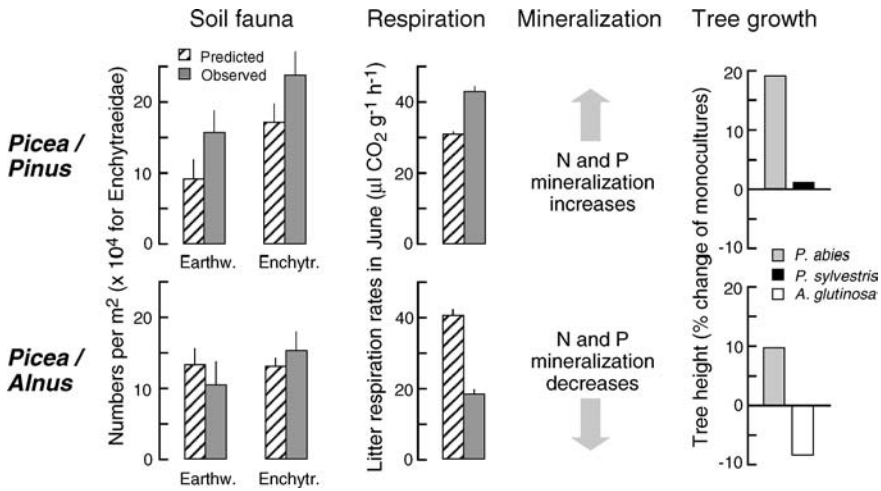


Figure 5 The consequences of mixed tree-species stands on soil-fauna abundance (numbers of individuals of earthworms and Enchytraeidae), litter-respiration rates, nitrogen (N) and phosphorus (P) mineralization rates, and their feedbacks on tree growth compared with the monocultures of the respective tree species ($n = 3$). Data for the two different tree-species mixtures *Picea abies*/*Pinus sylvestris* (top) and *Picea abies*/*Alnus glutinosa* (bottom) are shown. Soil fauna and respiration data are given as absolute numbers of actually measured values in comparison with predicted values based on measurements of monocultures. N and P mineralization are indicated as qualitative changes compared with monocultures, and tree-height growth is shown as relative changes compared with trees grown in monocultures. Data modified after Chapman et al. (1988) from the long-term Gisburn Forest experiment.

feedback of litter to plant communities, the relationship is little understood. As shown by Xiong & Nilsson (1999), litter affects plant resource competition and controls plant-community composition via the suppression of seedling establishment, particularly in early successional stages.

Soil organisms process litter that enters the detrital system not only from above ground but also from below ground. Translocation of carbon resources to below the ground in the form of roots and root exudates fuels the belowground food web and has significant implications for decomposition processes. Microorganisms are the primary recipients of this resource translocation, but they form an integral part of the soil-food web and influence the activity of litter-transforming macrofauna. Interactions between soil invertebrates and plants, mediated by soil microorganisms, are particularly numerous and important (Scheu 2001) and include, for example, grazing on mycorrhizal fungi (Klironomos & Kendrick 1995, Setälä 1995) and on plant pathogens (Curl et al. 1988, Pussard et al. 1994). Rhizosphere interactions intimately link the below- and aboveground communities. Despite their great importance, information on how these interactions affect plant growth, vegetation structure, and the aboveground food web is surprisingly limited (Van der Putten et al. 2001, Scheu & Setälä 2002, Wardle & Van der Putten 2002).

Among soil invertebrates, fungivores (Collembola, Oribatida, Nematodes) are highly abundant and usually dominate soil communities in terms of species numbers. Fungivores feed on both mycorrhizal and saprotrophic fungi, which has consequences for how these two groups of fungi interact (Tiunov & Scheu 2005b) and for nutrient transfers between plant litter, mineral soil, and plant roots (see above). Selective grazing affects fungal biomass and activity, interrupts bidirectional nutrient transfer between decomposing litter and plant roots, regulates fungal succession in decaying litter (Parkinson et al. 1979, Lussenhop 1992), and can strongly reduce mycorrhizal mycelium (Setälä 1995). However, the consequences of these grazing activities for litter decomposition are poorly studied (Sulkava & Huhta 1998). Laboratory experiments suggest that some fungivores (Collembola, Nematoda) prefer ectomycorrhizal over saprotrophic fungi (Shaw 1985, Ruess et al. 2000), but this pattern varies according to specific features of animal and fungal species. In particular, collembolans avoid toxic species of mycorrhizal basidiomycetes (Shaw 1992, Hiol et al. 1994). Furthermore, many fungivorous invertebrates function as ecosystem engineers by modifying the physical status of plant litter, and they may also feed on plant roots. Each of these trophic interactions influences plant performance, but the significance of diversity of fungivorous species is not known.

So far, we have stressed that changes in the structure of the belowground system feed back to plant community structure and the aboveground food web via modifications in plant growth, which may be viewed as bottom-up control of the plant-herbivore system. In addition, soil organisms may affect the plant-herbivore system by modifying top-down forces. Many herbivore species live within the soil at certain life stages and are integrated into the belowground food web and, thus, are subjected to belowground predation. Furthermore, some predators in their juvenile phase, such as spiders, carabid beetles, and staphylinid beetles, feed on

decomposer animals. However, as adults, these predators leave the soil and forage on herbivores in the plant canopy and, thereby, foster top-down control of herbivores in their own habitat. Both processes significantly contribute to top-down control on plant herbivores and, for example, may prevent pest outbreaks. The generalist feeding habit of soil predators is an important prerequisite for this interconnection of the belowground and aboveground food web. Generalist feeding, including polyphagy, omnivory, and intraguild predation, appears to be a characteristic feature of soil predators (Scheu & Setälä 2002). This feeding habit allows switching between prey from the decomposer food web and from the aboveground system (Settle et al. 1996, Symondson et al. 2000, Halaj & Wise 2002).

In forest and agricultural ecosystems, plant-species diversity and composition may determine the susceptibility to insect outbreaks (Andow 1991, Watt 1992). Predators may reach considerably higher population densities in more diverse plant communities compared with monocultures, which increases the internal control mechanisms of prey populations. Plant-litter diversity is an important component of the positive effect of high plant-species diversity on community composition of soil predators. In agricultural systems, a clear positive correlation between the amount and composition of plant residues and the density and diversity of decomposer and predator organisms has been observed (Riechert & Bishop 1990, Mäder et al. 2002). These relationships are of key importance for successful pest management, and, therefore, a thorough understanding of trophic interactions and controls in food webs is necessary. Such understanding will only be possible if the belowground system and its key driving factors, such as the amount and diversity of litter materials, are considered in detail.

CONCLUSIONS

The literature reviewed here provides clear evidence that the diversity of litter species and decomposer organisms can significantly influence litter decomposition and nutrient mineralization and have important feedback effects to plant growth, community composition, and ecosystem functioning. However, no general relationship between species diversity and process rate has emerged so far. Responses to increasing species richness are predominantly idiosyncratic, and results are contrasting at a given level of diversity. Past research convincingly demonstrated that species identity and community composition play a critical role, but the importance of diversity per se is difficult to judge, because studies with representative gradients of species numbers, particularly for soil organisms, are rare. The characterization of functional traits that explain specific effects of a given species within the community is considered a high research priority. This effort will provide the mechanistic basis for a generalization of species-diversity effects and could promote understanding and interpretation of the conflicting results summarized here. Rather than studies to accumulate experimental evidence for diversity effects, a comprehensive approach to test hypothesized mechanisms such as nutrient transfer

among litter species, or niche complementarity among soil animals, is needed to assess the functional significance of biodiversity for decomposition. Missing data have created a major gap in knowledge on interactions between substrate diversity and decomposer diversity. Although a few studies exist on how litter diversity influences microbial-community composition or soil-fauna abundance and diversity, the level of litter diversity and that of consumer diversity have not been experimentally manipulated in the same experiment. We believe that such feedback effects will elucidate the mechanisms involved in the observed processes.

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