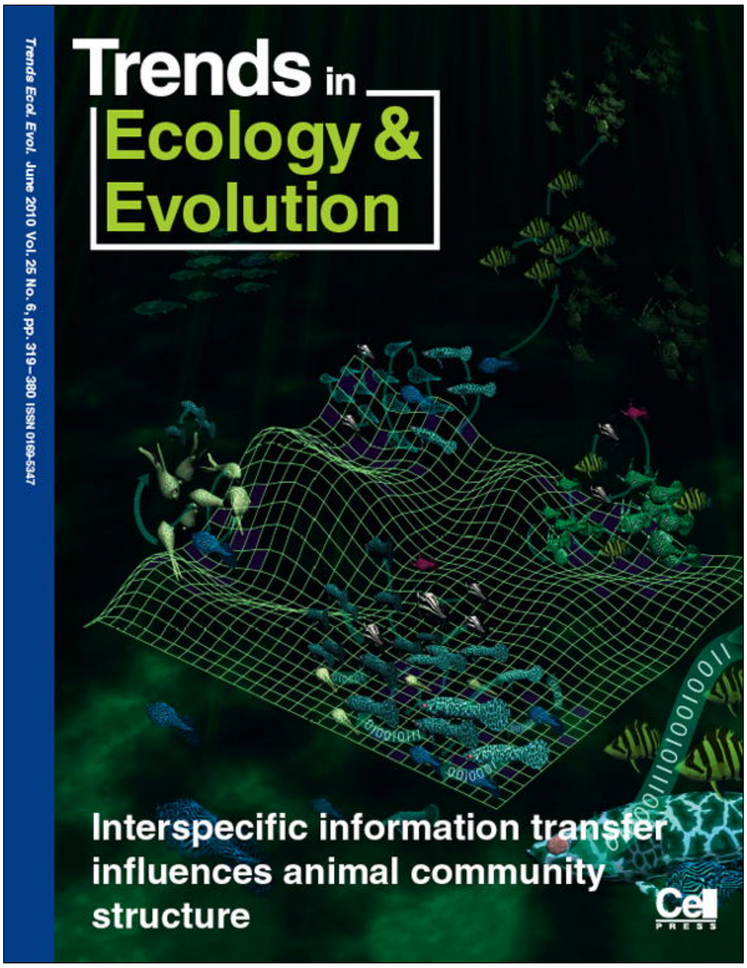
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Review

Diversity meets decomposition

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Over 100 gigatons of terrestrial plant biomass are produced globally each year. Ninety percent of this biomass escapes herbivory and enters the dead organic matter pool, thus supporting complex detritus-based food webs that determine the critical balance between carbon mineralization and sequestration. How will changes in biodiversity affect this vital component of ecosystem functioning? Based on our analysis of concepts and experiments of leaf decomposition in forest floors and streams, we suggest that changes in species diversity within and across trophic levels can significantly alter decomposition. This happens through various mechanisms that are broadly similar in forest floors and streams. Differences in diversity effects between these systems relate to divergent habitat conditions and evolutionary trajectories of aquatic and terrestrial decomposers.

Why assess diversity effects on decomposition?

With up to 90% of global terrestrial plant production entering the dead organic matter pool [1], decomposition and the sequestration of organic carbon in soils and sediments stand out as central components of ecosystem functioning. In forests, most of the plant litter from aboveground plant production is supplied in the form of leaves, which decompose much faster than the woody litter components produced both above- and below-ground. Changes in biodiversity (Box 1) can alter the decomposition process [2,3], indicating that understanding the significance of biodiversity, as well as the mechanistic basis behind synergistic or antagonistic diversity effects (see glossary) on decomposition, is essential to assess the consequences of biodiversity change for carbon and nutrient cycles [4,5].

Glossary

Compensatory feeding: enhanced consumption rate and accelerated gut passage of detritivores feeding on poor-quality food to ensure resource assimilation is sufficient to meet metabolic needs.

Complementarity: a generic term used in the biodiversity-ecosystem functioning literature that encompasses all mechanisms leading to diversity effects on ecosystem process rates that cannot be attributed to any single species. The term was originally conceived to capture positive diversity effects, especially resource partitioning and facilitation.

Decomposition: all biological processes contributing to organic matter mass loss and transformation, and not including physical losses caused by abrasion, fragmentation or leaching.

Degradation: the enzymatic transformation of organic carbon compounds that result is smaller molecules.

Density-dependent diversity effect: a type of complementarity effect, which can arise when the densities of individuals within species decline as diversity increases. Lowered intraspecific densities can lead to increased process rates, for instance by reducing intraspecific competition, by reducing accumulation of specific toxic waste products, or by reducing parasite and pathogen loads. Alternatively, process rates can be reduced if the activities of species are stimulated in aggregations with conspecifics.

Diversity effect: the contribution of a community to a process rate that cannot be explained by summing the weighted individual contributions of the constituent species. Diversity effects can be due to complementarity or selection effects.

Ecosystem functioning: sum of all ecosystem-level processes.

Facilitation: in a biodiversity-ecosystem functioning context, facilitation occurs when some species of a community affect others in ways that enhance the contribution of the affected species to an ecosystem process. Facilitation is one of several complementarity mechanisms leading to diversity effects.

Functional effect trait: phenotypic feature of an organism that has implications for ecosystem processes such as decomposition (e.g. feeding preference, consumption rate, mouth part morphology, enzymatic capabilities, litter quality parameters such as C:N ratio).

Horizontal diversity: any aspect of diversity (e.g. species richness, evenness, functional trait diversity, genetic diversity) within a trophic level.

Overyielding: the phenomenon that the process rate caused by a diverse community exceed the average rate achieved by the individual constituent species. Overyielding indicates a positive diversity effect as defined here, caused by positive selection or complementarity effects.

Resource complementarity: the availability of two or more resource types that provide complementary components of species needs (e.g. provision to decomposers of P at high concentration in one type of litter and N at high concentration in another type of litter).

Resource partitioning: the use of different food types or other resources by different microbial decomposer or detritivore species. Resource partitioning is one of several complementarity mechanisms leading to diversity effects.

Selection effect: the greater probability of diverse communities including species that at the same time dominate communities and have a strong positive or negative effect on a given process. The selection effect is a generalization of the so-called sampling effect, which refers to positive effects only.

Transgressive overyielding: the phenomenon whereby process rates caused by a diverse community exceeds the rate caused by the most effective constituent species in isolation. Transgressive overyielding cannot occur without one or more of the mechanisms of complementarity operating.

Vertical diversity: attributes of food webs that describe complexity across trophic levels (e.g. food-chain length, degree of omnivory, odd vs even number of trophic levels).

A growing number of studies in both terrestrial and aquatic systems have tested whether rates of ecosystem processes decrease when species are lost from decomposer systems [6]. The focus of these studies varies from changing the diversity of leaf litter [7–10], and altering diversity within microbial [11,12] and detritivore communities [13,14], to, in rare cases, modifying biodiversity at several trophic levels of the food web simultaneously [15,16] (Figure 1). Despite similarities across many terrestrial

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Box 1. A glimpse of biodiversity change relevant to litter decomposition in forest floors and streams

Several lines of evidence point to currently rapid rates of biodiversity loss and change caused by a broad array of anthropogenic impacts on ecosystems worldwide [77]. Comparisons of contemporary extinction rates with the appearance and disappearance of bird and mammal species in the fossil record has resulted in an estimated recent acceleration of species extinction rates 100–1000 times above background rates [78]. Similar quantitative estimates for microbes and arthropods are not possible. This notwithstanding, there is ample evidence that human activities profoundly affect forests and forest streams with consequences on tree, microbial decomposer and detritivore diversity (Table I).

Table I. Drivers of biodiversity change at leaf litter, microbial and detritivore levels in forests [79,80,81,82] and streams [83,84,85]. The listed disturbances have been associated with species loss in at least some regions of the world. The list is not exhaustive.

Disturbance	Remarks
Silviculture	Forest management typically reduces tree species numbers, which limits diversity of litter inputs to forest floors and streams, with knock-on effects on detritivore and microbial decomposer diversity
Pests and diseases	Pest and disease outbreaks, facilitated by anthropogenic exchange of biological materials worldwide, can remove plant species from the litter pool (e.g. Dutch elm disease, chestnut blight disease, alder root rot, gypsy moth outbreaks) and eliminate key detritivores (e.g. crayfish plague in Europe)
Invasive species	Exotic trees can change the composition and reduce the diversity of litter inputs (e.g. *Fallopia japonica* in Europe, *Salix fragilis* in Australia and New Zealand, *Eucalyptus globulus* in Mediterranean regions, *Rhododendron ponticum* in western Europe, *Morella faya* in Hawaii). Exotic invertebrates can reduce native detritivore diversity directly (e.g. invasive flatworms, *Arthurdendyus triangulate*, prey on native earthworms in the U.K.) or indirectly (e.g. exotic earthworms invade forests in North and South America where they can reduce the diversity of other detritivores by altering soil structure).
Habitat simplification	Simplification of stream channels and flow regimes reduces litter retention and habitat heterogeneity, with effects on local invertebrate diversity, including of detritivores Breaking-up of forest soils in managed forests (scarification) affects soil moisture, structure and heterogeneity, with effects on microbial decomposers and detritivores
Acidification	Acidification alters fungal and detritivore community composition and reduces their diversity in forests and forest streams, affecting particularly acid-sensitive, often large-sized detritivores (e.g. amphipods in streams and isopods on forest floors)
Pesticide and metal pollution	Pesticides, which usually affect both target and non-target organisms, and heavy metal contamination (e.g. by mining activities) reduce the diversity of microbial decomposers and detritivores in forest soils and streams
Nutrient and organic pollution	Nitrogen enrichment can reduce fungal decomposer diversity in forests, although effects on soil arthropods are variable Cultural stream eutrophication shifts and simplifies microbial and detritivore communities, especially when associated with anoxia
Climate change	Changes in the means, extremes, and variability of climate factors such as temperature and precipitation induce range shifts and local extinction of forest trees, probably accompanied by shifts of microbial decomposer and detritivore communities

and aquatic decomposer systems, research on the significance of biodiversity for ecosystem processes has developed largely independently in these two types of systems, reflecting the historical lack of intellectual exchange between terrestrial and aquatic ecologists [17].

Here we synthesize ideas and experimental evidence on how leaf litter decomposition in terrestrial and aquatic ecosystems is shaped by the diversity of resources (i.e. leaf litter), microbial decomposers and invertebrate consumers at different trophic levels (Figure 1 and Figure 2). Focusing on temperate forest floors and streams, we assess whether general relationships exist between biodiversity and decomposition in these two closely connected environments, which share many basic features, but differ in environmental conditions and decomposer community composition and diversity (Box 2). First, we examine, in three separate sections, the significance of diversity at the plant litter, microbial and detritivore levels for decomposition in forest floors and streams. Next, we consider the role of interactions across multiple trophic levels and variation in food-web complexity. Finally, we synthesize some general insights from our comparative analysis and highlight challenges for future investigations. The experimental evidence and deductive arguments we provide will allow better integration of concepts and should encourage data exploitation across historically separated sub-disciplines, thus fostering understanding of biodiversity effects on ecosystem functioning independent of specific ecosystem features.

Leaf litter diversity and decomposition

Leaf litter varies tremendously in chemical composition [18]. Some types of litter are rich in nutrients or carbon that can easily be utilized (labile carbon), whereas others are nutrient-poor or contain high concentrations of organic compounds such as lignin that are resistant to degradation (recalcitrant carbon). Secondary compounds in some litter types can even be detrimental to microbial decomposers and detritivorous consumers. The resulting chemical and associated physical diversity of litter is highly relevant for both microbial decomposers and detritivores. Both tend to prefer resources rich in labile compounds and nutrients [5,19,20] to maximize their net energy intake and overcome imbalances in carbon:nitrogen:phophorus (C:N:P) ratios of leaf litter and their own body tissues [21,22]. Changes in the species composition and diversity of leaf litter supplied to forest floors and streams thus entail profound changes in the patterns and rates of leaf litter utilization and decomposition by both microbial decomposers and detritivores.

In addition, there is scope for microbes and detritivores to derive different resources from different types of litter

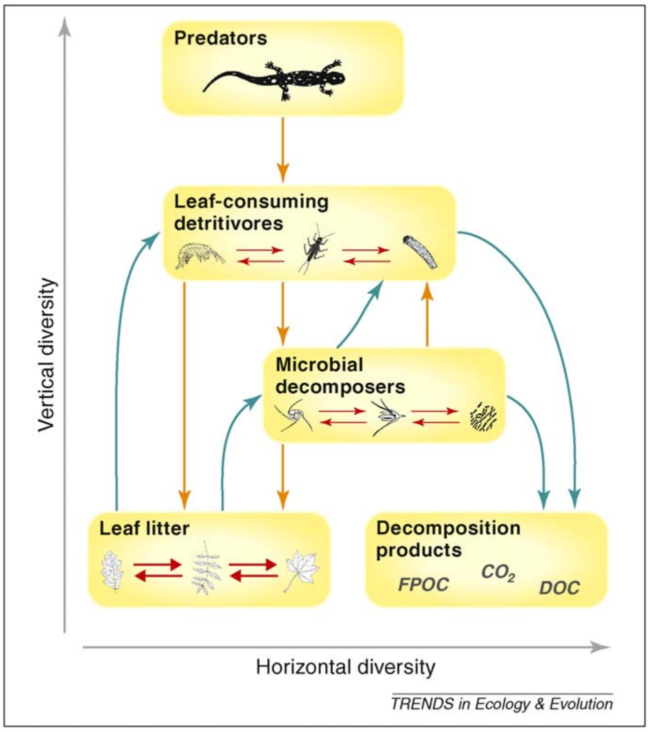

Figure 1. Conceptual diagram depicting relationships between types and levels of diversity important for litter decomposition in forest floors and streams. Horizontal diversity refers to measures of diversity within trophic levels, and vertical diversity refers to complexity across trophic levels within food webs (see glossary). Red horizontal arrows indicate biotic interactions within trophic levels, which can result in effects of horizontal diversity on leaf decomposition. The interactions shown for dead leaf litter are mediated by microbes or detritivores, whereas those within microbial or detritivore communities are direct interactions among living organisms. Orange vertical arrows indicate biotic interactions between trophic levels in food webs, which can give rise to effects of vertical diversity on decomposition. Curved turquoise arrows indicate the major pathways of litter carbon flow during decomposition, resulting in mineral and organic decomposition products such as CO_2, dissolved organic carbon (DOC) and fine-particulate organic carbon (FPOC) [94].

Figure 2. Key microbial decomposers and detritivores in forest floors and streams: **(a)** an unidentified fungus (Basidiomycota) fruiting in the litter layer of an Amazonian rainforest (photo: S. Hättenschwiler); **(b)** densely sporulating stream microfungi (aquatic hyphomycetes) on a decomposing alder (*Alnus glutinosa*) leaf; most obvious are sturdy tetraradiate spores with conical branches of *Lemonniera terrestris*, but larger, more delicate tetraradiate spores of *Tetrachaetum elegans* are also abundant in the upper left part (photo: M.O. Gessner and E. Chauvet; hyphae and spores stained with trypan blue); **(c)** millipedes (*Cylindrojulus caeruleocinctus*, Diplopoda) in a mixed-species litter layer of a Mediterranean woodland (photo: S. Hättenschwiler); **(d)** nymph of *Pteronarcys* sp. (Plecoptera), an efficient litter-feeding detritivore that can be abundant in North American streams (photo: R.W. Merritt, with permission).

(complementary resource use) when chemically divergent leaf species are present in their habitat [2,3]. For example, N and P concentrations vary distinctly among leaf species. This provides opportunities for detritivores and microbes to optimize nutrient acquisition when colonizing litter mixtures, thereby potentially altering overall decomposition rates compared with those of the individual constituent litter species. Further, litter that is potentially attractive, for example because of high N concentration, can contain secondary compounds (e.g. tannins or alkaloids) that suppress microbial resource assimilation and deter animals from feeding [23]. In view of the resulting trade-offs, it is perhaps not surprising that litter-mixing experiments in forest floors [2,3] and streams [7,9,24,25] report the full range of positive, negative and no effects of plant litter diversity on decomposition [6]. Consequently, decomposition rates of litter mixtures are not easily predicted from rates known for the constituent species [26].

One of the mechanisms behind litter mixture effects on decomposition involves active microbial nutrient transfer from one litter type to another [27,28]. Fungi growing in nutrient-poor litter can tap limiting nutrients, such as N, by extending their hyphae to alternative nutrient-rich litter species, and redistributing the assimilated nutrients within their hyphal network. The same mechanism could apply to essential rare compounds such as certain fatty acids, amino acids or vitamins. In addition to this active microbial transfer of selected leaf constituents, there can be passive transfers via leaching and subsequent transport by water flow of both soluble nutrients and carbon compounds. Such passive transfers can involve negative effects on decomposition if inhibitory compounds leached from some leaf species curb microbial activity in others. The strengths of these positive and negative effects undoubtedly vary among litter constituents, depending on their mobility; for example, P is much more easily leached from litter than is N [29]. Transfer of nutrients and carbon compounds by either passive or active means could increase or decrease microbial exploitation of the litter species with low concentrations of the transferred leaf constituents, leading to either accelerated or decelerated decomposition [3].

Active transfer of litter constituents can arise in both forest floors and streams. However, a more patchy litter distribution, as well as disruption of litter accumulations by stream flow, creates stronger physical barriers to simultaneous fungal colonization of different litter species in streams. Thus, diversity effects through active nutrient or carbon transfer are likely to be more intense on forest floors. Passive transfer of litter constituents, likewise, should be more prevalent in terrestrial environments where water films remain undisturbed between leaf surfaces. In streams, the leached compounds are easily diluted before microbes can assimilate them. Positive or negative litter mixture effects are therefore less likely.

Detritivores should also benefit from complementary acquisition of resources from distinct litter types in mixtures. If the simultaneous use of different litter types stimulates total consumption, decomposition is accelerated. Over longer time-scales this might boost detritivore populations and further accelerate decomposition. Although scarce, some experimental evidence supports the idea that detritivores mediate litter diversity effects on decomposition in both forest floors and streams. When fed mixed-species litter, terrestrial detritivores accelerated decomposition of recalcitrant leaf species [15], indicating a positive diversity effect on the decomposition of poor-quality litter. In contrast, stream detritivores confronted with diverse litter fed preferentially on high-quality leaves, resulting in slower than predicted decomposition of the recalcitrant species in the litter mixture [30].

If confirmed in future studies, the above differences in the responses of terrestrial and aquatic detritivores to litter diversity might be tied (1) to variation in life histories between consumers in forest floors and streams, and (2) to the physical template offered by the contrasting environmental conditions on land and in flowing water (Box 2). In particular, litter resources in streams are more short-lived than in forest floors, because periodically high water flow fragments leaves and flushes them downstream. The resulting ephemeral resource availability, facilitated by unlimited water availability and continuous nutrient supply from upstream, should favour fast exploitation strategies and hence rapid decomposition. Accordingly, opportunistic resource exploitation behaviour should evolve. Swift utilization of high-quality litter should be favoured, coupled with fast growth and reproduction to ensure rapid completion of life cycles, as shown for example by leaf-colonizing stream fungi [20,31]. In contrast, terrestrial invertebrate consumers of leaf litter are predominantly adults that often complete their life cycle over many years. Since litter on forest floors is also physically more stable than in streams, selection pressure towards rapid resource capture is dampened. This extends the absolute time scale of possible species interactions. Consequently, litter diversity effects mediated by both microbes and detritivores are expected to be greater in forest floors than streams.

Microbial decomposer diversity

Diversity at the microbial decomposer level (Figure 2a,b) can also affect decomposition rate, producing effects even when only a single litter type is present. The type of mechanisms behind such decomposer-mediated diversity effects are similar to those invoked in explaining plant diversity effects on primary production [32]. First, there is a large potential for facilitative interactions among microbial decomposers. For example, fungi facilitate the penetration of bacteria into leaf tissue where both can degrade specific structural polymers into smaller molecules that are subsequently assimilated [33], potentially increasing litter decomposition rate. Second, resource partitioning can occur, for example when different species possess complementary enzymes to degrade a range of plant polymers. Even when species have similar enzymatic complements, activity patterns can vary among species and with environmental conditions [20,34]. The presence of many species in microbial communities should therefore improve the communities' efficiency to degrade a wide range of litter constituents and thus enhance litter decomposition rate. In experiments involving two to five species of soil or stream fungi, facilitation or resource partitioning has indeed been observed [35,36]. However, this outcome is not universal, and in those cases where facilitation or resource partitioning occurred, average decomposition rate saturated at low fungal species richness [36,37,38].

Comparison of species traits in fungal communities indicates that the scope for microbially mediated diversity effects on leaf decomposition is greater in forest floors than streams. Terrestrial litter fungi display a wide range of adaptations to degrading specific chemical compounds, indicating that resource partitioning is common [39,40,41]. This is reflected in well-defined successional patterns. The classical view is that so-called sugar fungi with limited capacity to degrade structural polymers dominate the initial decomposition stage. Fungi degrading cellulose and other hydrolysable plant polymers assume importance during a second stage, and lignin-degraders, especially among the basidiomycetes, dominate the final stage [39]. Stream fungi also show successional patterns in decomposing leaves, but these are less clearly defined and do not involve species replacement [31]. Furthermore, qualitative differences in enzymatic capacities are rare among species, basidiomycetes are uncommon in aquatic ecosystems, and although most stream fungi colonizing leaves are capable of hydrolyzing a wide range of plant polymers, effective degradation of lignin has not been well documented [20]. Thus, functional redundancy of litter fungi is likely to limit the scope for complementarity effects on leaf decomposition especially in streams and significantly less so in forest floors.

In addition to facilitative interactions leading to positive diversity effects on decomposition, there can be antagonistic interactions among litter fungi. These also appear more common in forest floors. Many terrestrial fungi release inhibitory substances [42], some very potent, to ward off competitors and predators. Intense competition among these fungi manifests in clear demarcation zones when two growing colonies meet [43]. This is in contrast to leaf-colonizing stream fungi, where toxin production is rare [44] and hyphae of different species readily intermingle when colonies meet [31]. This discrepancy in competitive capabilities and behaviour could reflect differences in the habitat templates that shape decomposer communities in forest floors and streams (Box 2). Dilution by stream flow reduces the benefit of producing antibiotics. Furthermore, the short-term availability of resources in streams fosters life-history traits such as fast resource exploitation, growth and reproduction while discouraging investment in defence. Given the costs involved in antagonistic species interactions, fungal growth at a given resource level is likely to be reduced when competing species co-occur in diverse communities. Such competition could counteract positive diversity effects that result from facilitative species interactions. Thus, in spite of a greater potential for microbial species interactions in forest floors, the simultaneous occurrence of both synergistic and antagonistic relations indicates that net diversity effects on decompo-

Box 2. Features of forest floors and streams and of their decomposer communities

The terrestrial and aquatic elements of forest ecosystems are linked by both chemical and biological transfers. In addition, forest floors and streams share many features of importance to decomposition dynamics [86]. Both are shaded under tree canopies and receive large inputs of organic matter during leaf fall. Consequently, food webs in both systems largely rely on the same litter resource derived from forest trees [86,87]. However, there are also important differences in the environmental conditions experienced by litter-associated communities (Table I).

Broadly speaking, decomposer communities in forest floors and streams are taxonomically and functionally similar. Fungi are the key microbial decomposers whose activities are modified and complemented by litter-consuming detritivores (Figure 2). However, differences exist at finer scales of taxonomic resolution. Some estimates for soil fungi are very high [88]. Pyrosequencing has revealed an average of approximately 1000 distinct fungi (operational taxonomic units) in just 4 g of forest soil [89]. The fraction colonizing the litter layer is unknown, but even a small percentage would correspond to a large number of species. Little more than 300 species of typical leaf-colonizing stream fungi (aquatic hyphomycetes, Figure 2b) have been described worldwide, of which about 40–60 species commonly coexist in temperate streams [90]. Molecular analyses have yielded higher estimates of stream fungi associated with leaf litter than traditional identification methods relying on morphological features [91]. This included fungi other than aquatic hyphomycetes. However, the total number of species involved in leaf decomposition still appears to be lower than in forest floors. Another important distinction is that litter on forest floors is colonized by efficient lignin-degraders, particularly among the basidiomycetes [41], which rarely occur in streams [20,90,91].

Invertebrate abundance and diversity also tends to be higher in soils [62,92] and life-history patterns differ in that many detritivores in forests grow slowly, have low reproduction rates and spend their entire lives in the same environment. Many stream detritivores, by contrast, are insect larvae with flying adult stages. They can consume ten times more litter than terrestrial detritivores [92], and show higher tissue turnover, faster growth and shorter generation times [93].

Table I. Environmental contrasts relevant to decomposer communities and decomposition in forest floors and streams

Feature	Forest floors	Forest streams
Moisture availability	Typically a key factor limiting biological processes, including leaf litter decomposition	Not limiting for biological processes, except during extreme drought
Temperature variability	Often strong temporal fluctuations at diel, seasonal and other scales	Moderate temperature fluctuations
Nutrient limitation	Weathering and leaching results in increasing nutrient limitation	Nutrient limitation mitigated by constant supply through flowing water, although concentrations can still be limiting
Extraneous carbon supply	Supply of labile carbon through roots can facilitate degradation of refractory litter constituents (priming effect)	Dissolved organic carbon supplied with flowing water is mostly refractory
Spatial heterogeneity	Horizontally rather homogeneous litter carpet, but litter layering results in strong vertical gradients in moisture, temperature, pH, etc.	Litter accumulates in discrete patches that are only connected and sometimes redistributed by water flow
Disturbance	Storms, landslides or flooding are mostly rare stochastic events not regularly affecting decomposer systems; freezing, drought and fire can be common	Frequent but often temporally unpredictable bed-moving floods; other disturbances such as debris flows, fire or droughts are rare

sition are not necessarily more likely in forest floors than streams.

Detritivore diversity

Species richness of litter-associated fauna (Figure 2c,d) is considerably higher in forest floors than streams, and thus, the potential for detritivore diversity effects on decomposition is also greater. This statement rests on the premise that taxonomic diversity translates into functional diversity, but this assumption is very plausible at least at the relatively low diversity levels used in biodiversity-ecosystem functioning experiments. Body size, for example, is an important functional trait [45] that varies widely among litter-associated detritivores in terrestrial ecosystems (from microfauna to mesofauna to macrofauna) and facilitates differential modes of resource use [4,5].

Empirical evidence for the role of terrestrial detritivore diversity in litter decomposition is scarce, partly because few pertinent studies have been conducted. One study that used eight detritivore species from different taxonomic groups found no influence of species richness on litter decomposition [13]; this result corroborates conclusions from an earlier report on collembolans [46]. However, trait dissimilarity within the detritivore communities of the former study was positively correlated with decomposition rate, indicating that facilitative interactions promoting decomposition are greatest when the species in a community diverge in their functional effect traits [13]. This conclusion is also supported by an independent experiment that found synergistic effects on decomposition when high-quality litter was offered to a detritivore community composed of an isopod and an earthworm species [47]. The synergistic effect in this study disappeared when the detritivores were offered recalcitrant litter [47], suggesting that complementarity effects on decomposition mediated by terrestrial detritivores vary with resource quality. Overall, results from these few studies indicate that experiments involving both the complete size range of litter fauna and different litter qualities are needed to assess the full potential for detritivores to induce complementarity effects.

Effects of detritivore diversity and decomposition have been studied more extensively in streams. Greater species richness has been associated with faster decomposition [48], although neutral outcomes and negative effects have also been observed [14,49]. In some cases, average decomposition rates caused by mixed communities exceeded those achieved by the most effective detritivore species alone [14,48]. This pattern is known as transgressive overyielding and clearly indicates diversity effects due to biological mechanisms such as resource partitioning or facilitation. In contrast to forest floors, microfauna (e.g.

nematodes, protozoa [50]) are thought to be unimportant for litter decomposition in streams [51]. Conversely, large litter-consumers in streams can play an important role in the decomposition process [52]. Such macroconsumers include crayfish and, in tropical and some subtropical regions, some species of freshwater shrimps and crabs as well as detritivorous fishes. It would be instructive to include these macroconsumers in experiments that assess detritivore species richness effects on decomposition and to test explicitly for effects of body-size variability.

Detection of negative detritivore richness effects in streams has been associated with negative (antagonistic) species interactions [14,49]. The studied species are typically very active, occur at rather high densities, and often show aggressive behaviour [53]. Antagonistic interactions could therefore outweigh any positive diversity effects (through complementary resource use, facilitation or selection effects) on decomposition. The net outcome between positive and negative effects of species interactions is likely to depend on environmental context [14,54]. Accordingly, spatiotemporal variability in environmental conditions and detritivore community structure needs to be explicitly incorporated into experimental designs to understand when and why diversity affects leaf decomposition [14]. This involves assessment of variation in the distribution of species and species traits caused by phenological shifts (e.g. altered periods of insect hatching, diapause and emergence), which could have repercussions for diversity effects on decomposition rates.

The role of food-web complexity

Diversity effects on litter decomposition have mostly been tested separately at the litter, microbial and detritivore levels. In a food-web context, this represents a focus on horizontal (within-trophic level) diversity, which needs to be complemented by research on the significance of vertical (across-trophic level) diversity (Figure 1), and the combination of both [45,55,56]. Changes in vertical diversity could enhance or reduce diversity effects on decomposition. For example, apart from affecting overall detritivore abundance, predators could alter patterns of competitive dominance among detritivore species, either by selective preying, or by causing a particular species to feed less in order to minimize conspicuousness [57]. Such predator effects would reduce litter decomposition if the affected species are efficient consumers, instrumental in facilitative interactions [58], or complementary to the remaining species in their feeding mode or food choice. Alternatively, the presence of predators could enhance decomposition if the affected species are inefficient consumers or compete with more efficient species [55].

Such top-down effects of predators could also have cascading consequences at the microbial level, but this is complicated by the fact that detritivores effectively feed on two trophic levels (Figure 1), consuming both leaf tissue and microbes [59,60]. Importantly, detritivore feeding is selective, with some fungal species preferred to others and preferences also varying across detritivore species [59,60]. Therefore, predator suppression of detritivores might slow invertebrate-mediated leaf decomposition and, by allowing more extensive fungal growth, simultaneously enhance microbial decomposition. In addition, it could affect decomposition indirectly by changing competitive interactions in litter-associated microbial communities. This would alter microbial diversity by shifting dominance within the communities.

At the basal trophic level, diversity effects on decomposition have been attributed to a bottom-up effect of resource heterogeneity (i.e. litter diversity) on microbial activity [3], for example by facilitating nutrient transfer from one leaf species to another (see above). Such effects can extend to detritivores. One possible mechanism is that colonization of leaf litter by palatable fungal species can render even relatively refractory leaf species attractive to detritivores and stimulate consumption, as indicated by experiments in both terrestrial and aquatic systems [15,16,58,61]. Alternatively, enhanced leaf palatability across a litter mixture could promote overall decomposition by mitigating negative density-dependent effects (see glossary for this type of diversity effect) on detritivore consumption [14,49] that can result from aggregation of detritivores on the most attractive litter types.

Differences in environmental characteristics between terrestrial and aquatic habitats, and their resident species (Box 2), could regulate how vertical diversity influences litter decomposition [55,62]. Cascading top-down effects on decomposition have been observed in streams [61,63], in part reflecting behaviourally mediated reductions in feeding of detritivores in the presence of predators. Results from similar experiments in terrestrial habitats are less consistent, with positive [64], negative [65] and neutral [66] effects of predators on decomposition observed.

Overall, the available data indicate that cascading effects of predator and detritivore diversity on microbes and leaf decomposition might be more common in forest streams than forest floors. In contrast, the potential for bottom-up influences of litter and microbial diversity should be stronger in terrestrial systems if the greater physical stability and habitat complexity of the forest litter layer favours nutrient transfer and other mechanisms such as resource partitioning. A recent meta-analysis of 28 studies found a positive top-down effect of detritivore or microbial diversity on detritus decomposition (i.e. not just litter decomposition) but detected no consistent bottom-up effect of detritus diversity, in part reflecting variation in positive and negative influences of detritus diversity among studies [6]. However, no differences emerged in either top-down or bottom-up effects across the wide variety of aquatic and terrestrial systems included in the meta-analysis [6].

Do general patterns emerge and where to go from here?

A general theme emerging from our cross-systems perspective is that while the basic mechanisms underlying diversity effects on leaf decomposition are the same in forest floors and streams, their relative importance and scope appear to vary. We propose that this is related, on the one hand, to the many similarities of litter-based food webs in forest floors and streams and, on the other hand, to notable differences in habitat templates (Box 2). Divergence in habitat conditions creates contrasting selection pressures that shape the evolutionary trajectories of microbes and detritivores in forest floors and streams in different ways. This has repercussions for the type and strength of species interactions (within and across tree, microbial and invertebrate communities) that can translate into diversity effects on litter decomposition (Figure 1). Although a conclusive answer is premature, we propose that this situation leads to a greater tendency for leaf decomposition in forest floors to respond to variation in diversity at the basal trophic level (i.e. leaf litter), whereas in streams decomposition tends to respond more strongly to diversity variation at higher trophic levels (i.e. detritivores).

Great strides in understanding biodiversity effects on litter decomposition could be made when a new generation of experiments unravels mechanisms behind such effects [32] and incorporates greater realism in their design [67]. These calls have several facets. First, actual patterns of species loss in real ecosystems under environmental change (Box 1) should receive greater attention. For example, the response of leaf decomposition to the loss of detritivore species simulated in an experiment strongly depended on the sequence in which species were lost, not primarily on the number of species present [68]. This was due to varying sensitivities to stream acidification and organic pollution (the two stressors considered) among the detritivore species used, coupled with pronounced differences in feeding capacities. Devising experiments based on similarly realistic extinction scenarios should yield much insight into the relevance of changing biodiversity for the dynamics of leaf litter decomposition.

Second, greater realism of experiments would be achieved by moving from simple laboratory tests to field settings [49]. Although logistically challenging, such field experiments are feasible, even when biodiversity manipulations are combined with manipulations of environmental conditions [49,69]. The value of such experiments would be further enhanced if trophic complexity were incorporated [45,56,67] and time scales were chosen in experiments that allow for temporal resource partitioning and cross-generational effects to play out.

Third, diversity effects can only arise when species differ in their functional characteristics relevant to the studied process. Species richness and other measures of taxonomic diversity (e.g. intraspecific diversity [70,71] and evenness [72,73]) can be useful proxies of functional diversity in a community. However, direct functional characterization of communities such as functional effect trait distributions (see [45,67] and, for a conceptual framework, [74]), including dissimilarity patterns [13,26,75] are likely to be more compelling predictors of biodiversity effects on leaf decomposition. To date, the value of functional biodiversity measures on decomposition have been insufficiently explored, although they are likely to be more powerful than taxonomic measures in detecting [14] and understanding the mechanistic basis of diversity effects on the decomposition process [26].

Last, the question arises to what extent patterns that have been detected at one time in one place are representative. Meta-analyses are an elegant quantitative means to summarize information collected in disparate studies, and this approach to synthesis has provided important insights into effects of biodiversity and ecosystem processes in general [76] as well as on detritus decomposition systems [6]. A more direct approach is to build variation in environmental conditions [8,24] and evolutionary contingencies directly into experimental designs [8,24]. Such experiments designed to evaluate the significance of environmental and evolutionary context could be particularly rewarding when conducted in forest soils and streams using identical methodology across a broad range of biomes.

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