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Biodiversity at the plant–soil interface: microbial abundance and community structure respond to litter mixing

Samantha K. Chapman · Gregory S. Newman

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Abstract The interactive effects of diversity in plants and microbial communities at the litter interface are not well understood. Mixtures of plant litter from different species often decompose differently than when individual species decompose alone. Previously, we found that litter mixtures of multiple conifers decomposed more rapidly than expected, but litter mixtures that included conifer and aspen litter did not. Understanding the mechanisms underlying these diversity effects may help explain existing anomalous decay dynamics and provide a glimpse into the elusive linkage between plant diversity and the fungi and bacteria that carry out decomposition. We examined the microbial communities on litter from individual plant species decomposing both in mixture and alone. We assessed two main hypotheses to explain how the decomposer community could stimulate mixed-litter decomposition above predicted rates: either by being more abundant, or having a different or more diverse community structure than when microbes decompose a single species of litter. Fungal, bacterial and total phospholipid fatty acid microbial biomass increased by over 40% on both conifer and aspen litter types in mixture, and microbial community composition changed significantly when plant litter types were mixed. Microbial diversity also increased with increasing plant litter diversity. While our data provide support for both the increased

abundance hypothesis and the altered microbial community hypothesis, microbial changes do not translate to predictably altered litter decomposition and may only produce synergisms when mixed litters are functionally similar.

Keywords Bacteria · Fungi · Litter mixing · Litter decomposition · Microbial community

Introduction

Though the mechanisms by which plant diversity can affect plant productivity are well documented, links between plant diversity and litter decomposition remain elusive. Yet, in many forest ecosystems, litter decomposition is a rate-limiting step in ecosystem carbon and nutrient cycling, which may ultimately drive ecosystem productivity. Empirical evidence indicates that the diversity of plants can strongly influence the decomposition rate of the litter they produce (for review see Gartner and Cardon 2004). Moreover, the emergent properties of plant diversity could cascade through the detrital foodweb such that plant litter diversity may promote microbial diversity to influence decomposition, but this possibility has been insufficiently explored (Kominoski et al. 2009).

Mixed-litter decomposition can occur additively, as the average rate of the component litters (Blair et al. 1990; Rustad 1994; Ball et al. 2008). However, microbial communities often process mixtures of plant litter substrates (species and genotypes) at rates faster than expected from the average of the decomposition rates of the component litter types decomposing by themselves (Schweitzer et al. 2005; LeRoy and Marks 2006; Hättenschwiler and Gasser 2005; Madritch et al. 2006; Jonsson and Wardle 2008), a phenomenon termed a synergistic effect or synergism

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[as opposed to an antagonistic effect, which occurs less frequently (Wardle and Nicholson 1996; Bardgett and Shine 1999; Kominoski et al. 2007)]. Despite the relevance of synergistic effects of litter mixing to questions about biodiversity and ecosystem function and recent calls for more mechanistic studies (Gartner and Cardon 2004; Hättenschwiler et al. 2005), the mechanisms underlying synergistic decomposition remain elusive.

The hypotheses proposed to mechanistically explain synergisms in multi-species leaf litter decomposition include physical (Hansen and Coleman 1998; Gartner and Cardon 2004), chemical (Seastedt 1984; McTiernan et al. 1997; Wardle et al. 1997; Hoorens et al. 2003; Schimel and Hättenschwiler 2007; Meier and Bowman 2008), microbial (Blair et al. 1990; McArthur et al. 1994; Bardgett and Shine 1999) and macrofaunal mechanisms (Hansen and Coleman 1998; Kaneko and Salamanca 1999; Hättenschwiler and Gasser 2005; Hättenschwiler et al. 2005; Swan and Palmer 2006; Wardle et al. 2006), or some combination of the above. While there have been some studies of how microbes respond to litter mixing (Blair et al. 1990; Bardgett and Shine 1999; Kominoski et al. 2007, 2009; Keith et al. 2008), our understanding of how both microbial community composition and abundance can be altered by litter diversity, and potentially change litter decomposition, is limited (van der Heijden et al. 2008). We examined how microbial community and abundance respond to litter mixing and how these shifts correlate with observed litter synergisms.

In a previous study, we found that in situ decomposition rates of all possible 1:1 two-species mixtures of litter from three co-occurring conifer species were all significantly higher than expected from the average decomposition rates of the single-species litter types (Chapman and Koch 2007). Mixtures of conifers decomposed up to 50% faster than expected and single litter types within these mixtures decomposed up to 85% faster than expected. Unexpectedly, the decomposition rate of co-occurring aspen litter, which decomposes relatively rapidly, was not affected positively or negatively by the presence of conifer litter. Finally, the mixture of all four species did not decompose more rapidly than expected. The differential prevalence of synergisms in our previous study provides an excellent experimental framework for mechanistic explorations of litter synergistic effects.

In this study, we examine whether plant litter diversity drives variation in microbial community composition that may, in turn, elicit synergistic decomposition effects. The design of this experiment affords an opportunity to quantify the microbial responses to litter mixing because the morphologies of the co-occurring litter species are easily distinguishable. There are at least two ways that the microbial community could mediate synergistic effects on mixed-litter decomposition: increased decomposer abundance, and

an altered or more diverse microbial community composition. We hypothesize that a greater abundance of decomposers may colonize more diverse litter habitats. Second, we hypothesize that the microbial decomposer community structure will change in response to litter mixing. Finally, we hypothesize that microbial diversity will increase with increasing litter species richness (Hutchinson 1959; Siemann et al. 1998; Loreau 2001). Increases in microbial diversity could facilitate the aforementioned increases in microbial biomass. Because our previous findings suggest that synergistic decomposition occurs only with mixtures of functionally related species (conifers), we predict that microbial communities will be most distinct between conifer litter types in a mixture and conifer litter types in isolation and microbial decomposers will be most abundant on conifer litter in mixtures. We tested the “abundance” hypothesis by examining the total, fungal, and bacterial biomass on different plant litter types both in isolation and in mixture. We tested the “composition” hypothesis by investigating microbial decomposer community structure on individual species’ litter in isolation and in mixture after 10 months of field decomposition. Finally, we examined whether decomposer diversity is altered on litter mixtures as compared to litter decomposing alone.

Materials and methods

This study was performed in a mixed conifer forest on the San Francisco Peaks, 30 km north of Flagstaff, Arizona (35.19N, −111.66W). Six 25 × 25-m plots were randomly located within a 0.5-km² area at a constant elevation (2,950–3,050 m) and slope. We examined microbial responses to litter mixing in the context of an experiment investigating dominant tree litter decomposition in a Northern Arizona mixed conifer forest (Chapman and Koch 2007). All stands are co-dominated by four tree species: *Populus tremuloides* (Michx; quaking aspen), *Pseudotsuga menziesii* (Mirbel) Franco; (Douglas-fir), *Pinus flexilis* (James; limber pine), and *Pinus ponderosa* (P. and C. Lawson; ponderosa pine). The tree species we examined are referenced as follows: quaking aspen (A), Douglas-fir (D), limber pine (L), and ponderosa pine (P). These species range widely in their litter C:N and lignin:N ratios and their leaf morphology, therefore providing diverse substrates and habitat for microbial communities. Lignin:N ratio was 11.5 in aspen litter, 13.5 in Douglas-fir, 17.8 in limber pine and 25.9 in ponderosa pine.

Senescent litter was collected from all plots in randomly placed litter buckets in the fall 2002 and bulked by species. Any additional required litter was collected by shaking trees and plucking off freely abscising senescent needles. Litter bags were constructed 10 × 10 cm with the upper

side of white 0.8-mm polyester mesh (Nylon Net, Memphis, Tenn.) and the bottom of pool cover mesh (about 0.2 mm; no. 72191 polypropylene mesh; Synthetic Industries, Atlanta, Ga.), according to common standards (Parton et al. 2007). The larger upper mesh was used to allow terrestrial microarthropods access to the tree litter and the finer bottom mesh prevented the loss of small fragments. We excluded macrofauna from decomposing litter since microbial communities are thought to be the primary decomposers in coniferous forests (Wang et al. 2009). A total of 11 litter bag types including each individual species (A, D, L, P), each pair-wise combination (A + D, A + L, A + P, D + L, D + P, L + P) and all four species (A + D + L + P) were made by weighing 2 g of air-dried litter into each bag. The initial mass of individual species' litter placed in mixed-litter bags was equal to 2 g (air-dried) divided by the number of species. Litter decomposition bags were placed on the soil surface in each of the six plots at a randomly chosen common location within the larger 25 × 25-m plot. We replicated each "common litter bag garden" 3 times within a plot for three successive removal periods: 3, 10, and 27 months after placement in the field.

Microbial community composition

Litter was freeze-dried immediately upon removal from the field. We extracted litter from the second removal period (10 months) for microbial analyses. At the time of extraction, the average percentage of litter mass loss across all litter combinations was 25% (Chapman and Koch 2007).

To test the hypotheses described above, it is essential to examine the responses of microbial decomposers on individual kinds of litter within a mixture (i.e., Briones and Ineson 1996; Hättenschwiler and Gasser 2005) as well as within the whole mixture. Therefore, individual litter components (two components from two-species bags and four components from four-species bags) were sorted by species according to morphological differences from the six replicate mixtures. In order to obtain enough litter for extraction (1 g), we systematically bulked individual species litter from two litter bags of the same mixture from two different plots, generating three replicate samples for each treatment. Litter was ground using a ball mill grinder (model 2601; Cianflone Scientific Instruments, Pittsburgh, Pa.). Phospholipid fatty acids (PLFA) were extracted from the freeze-dried litter with a phosphate-buffered chloroform–methanol solvent [1 g litter: 6 ml buffer plus 15 ml methanol and 7.5 ml chloroform (Bligh and Dyer 1959; Schweitzer et al. 2008)]. After methylation of the polar lipids, signature fatty acids were separated and analyzed by gas chromatography and mass spectrometry [(White et al. 1979); 6890N GC/5973N MSD GC–mass spectrometer; Agilent Technologies, Palo Alto, Calif.]. Different PLFA are unique to different

taxonomic groups [e.g., gram-positive and gram-negative bacteria, and fungi (White et al. 1979; Zelles 1999; Leckie 2005)]. While PLFA provide a coarse measure of microbial community composition, recent evidence suggests PLFA analysis is more effective in detecting treatment differences than both functional analyses and molecular techniques (Ramsey et al. 2006). A total of 43 compounds were identified from the extractions. However, we limited our analyses to the 23 compounds between carbon chain lengths C14 and C19 to conservatively constrain our analyses to those known with relative certainty to be microbial (O'Leary and Wilkinson 1988; Wilkinson 1988; Frostegard and Baath 1996; Zelles 1999). Total PLFA concentration, calculated as the sum of all 23 compounds, was used as an index of total microbial biomass. Fungal PLFA concentration was calculated as the sum of C18:2n6t and C18:2n6c (Frostegard and Baath 1996). Bacterial PLFA concentration was calculated with the sum of the following compounds: i-15:0, a-15:0, C15:0, i-16:0, C16:1ω9, C16:1, cy17:0, C17:0, and cy19:0 (O'Leary and Wilkinson 1988; Wilkinson 1988; Frostegard and Baath 1996; Zelles 1999; similar to Bardgett and Walker 2004). Community composition analyses were performed using abundances of all 23 compounds. To assess how microbial diversity responds to plant species richness we combined the microbial communities (all PLFA biomarker concentrations) decomposing each litter within the litter bag to calculate a Shannon's diversity index for the whole litter bag. Though PLFA biomarkers do not represent microbial species, we use them as a proxy to indicate biochemical (lipid structure) diversity and thus provide a fingerprint of broad decomposer groups.

Statistical analyses

Multivariate analyses of microbial community composition were performed with non-metric multidimensional scaling (NMDS) and post hoc multi-response permutation (MRPP) procedures in PCORD 4 (MjM Software, Gleneden Beach, Ore.) to generate two-dimensional ordinations of community composition profiles. A standard linear regression was performed on the relationship between litter species richness and microbial community diversity indices. A paired *t*-test was used to examine microbial diversity in mixed-litter decomposition bags compared with single-litter decomposition bags. Our replication in this study occurred at the plot level ($n = 3$ due to bulking) and we used the mean of the litter types of interest (e.g., aspen decomposing alone, conifers decomposing in mixture) within the plots for biomass analyses. Total, fungal, and bacterial PLFA concentrations were compared between single and mixed-litter decomposition for aspen and conifer litter using paired *t*-tests. Litter decomposing alone was paired with litter decomposing in mixture by plot for community and biomass analyses. All

univariate statistics were performed using JMP IN 5.1 (SAS Institute, Cary, N.C.). Statistical significance was determined at $\alpha = 0.1$, though statistical significance at various levels are shown in Fig. 1.

Results

Microbial biomass

Mixing conifer litter with other litter significantly increased all microbial biomass parameters measured: total ($P = 0.03$; 54% increase; Fig. 1), fungal ($P = 0.07$; 43% increase; Fig. 1) and bacterial PLFA ($P = 0.002$; 71% increase; Fig. 1). Mixing aspen litter with other litter also increased total ($P = 0.07$; 52% increase), fungal ($P = 0.08$; 43% increase), and bacterial ($P = 0.008$; 122% increase; Fig. 1) biomass.

Microbial community composition

Using NMDS, we first examined the community structure of conifer litter in mixture versus decomposing alone and aspen litter in mixture versus decomposing alone. Mixing conifer litter resulted in insignificant impacts on microbial community colonization, driven by the presence of Douglas-fir which had a dramatically different community from the other two conifers ($P = 0.008$, data not shown). Therefore, in order to present a more detailed view of the microbial differences, we examined the individual species microbial community compositions. Each point on the ordination represents an entire profile of the microbial community

on a litter sample as defined by 23 PLFA biomarkers. Three of the four individual species ordinations showed significantly different communities on a litter decomposing in mixture vs. alone (aspen $P = 0.024$, limber pine $P = 0.025$, ponderosa $P = 0.032$; MRPP analysis; Fig. 2). We did not have enough power to test the significance of the Douglas-fir ordination because we lost one of the single species samples during extraction.

Microbial diversity and litter diversity

Microbial diversity increased as a result of increases in the number of litter species decomposing within a bag ($r^2 = 0.22$; $P < 0.01$; Fig. 3). Also, average diversity was higher for the microbial community in mixed-litter decomposition bags than for single-litter decomposition bags (t -test, $P = 0.002$; Fig. 3, inset).

Discussion

Most biodiversity–productivity studies have investigated how diversity of primary producers affects the functioning of producers or consumers. Here we investigated how varying diversity at the primary producer level may alter diversity and biomass at the decomposer level. This study provides evidence that litter mixing strongly affects microbial decomposer biomass and community composition (Figs. 1, 2). We found support for our hypotheses that litter mixing alters microbial communities for three of four species, suggesting niche differentiation due to an increased variety of substrates (Fig. 2; Chapman et al. 1988; Hooper and Vitousek 1998; Tilman et al. 1997). However, these microbial changes occurred irrespective of previously observed synergisms in litter decomposition (as reported in Chapman and Koch 2007). Similar to the findings of Kominoski et al. (2007), both fungal and bacterial biomass were altered significantly on litter in mixture compared to litter decomposing alone. Finally, within the whole litter bag, microbial diversity increased with increasing plant litter diversity, suggesting that diversity cascades from producers to decomposers (Fig. 3). In other words, diversity begets diversity.

Though we found support for the theoretical hypothesis predicting increases in microbial biomass with litter mixing, these results did not correlate with observed differences in synergisms driven by litter functional type. Microbial biomass parameters (total, fungi, and bacteria) all increased >40% for aspen and conifer litters in mixture, indicating substantial changes in decomposer abundance; yet aspen litter did not exhibit synergistic decomposition when in mixture (Chapman and Koch 2007). Across all litter types, increased microbial biomass correlated weakly with greater

Fig. 1 Total, fungal, and bacterial phospholipid fatty acid (PLFA) concentrations on conifer [Douglas-fir (*Pseudotsuga menziesii*), limber pine (*Pinus flexilis*), and ponderosa pine (*Pinus ponderosa*)] and aspen (*Populus tremuloides*) litter decomposing either singly or in mixed-litter combinations. Values shown are means $\pm$ 1 SE ($n = 3$). * $P < 0.1$, ** $P < 0.05$, *** $P < 0.01$ (statistically significant differences in paired t -tests between single and mixed-litter treatments)

Fig. 2 Non-metric multidimensional scaling ordination of the microbial communities on decomposing aspen (*P. tremuloides*), Douglas-fir (*P. menziesii*), ponderosa limber pine (*P. flexilis*), and ponderosa pine (*P. ponderosa*) litter based on PLFA profiles. Each symbol represents a “fingerprint” of the 23 microbial biomarkers found on the litter type decomposing either in mixed-litter bag (open symbols) or in a single-species litter bag (filled symbols). All mixtures within the three plots are shown but the multi-response permutation (MRPP)-derived *P*-values are based on the mean ($n = 3$) from each plot. Douglas-fir MRPP could not be run due to the loss of sample ($n = 2$ for Douglas-fir decomposing alone)

Fig. 3 Diversity, as measured by Shannon's diversity index (H), of the microbial decomposer community significantly increases as the number of plant litters in a mixture increases. Each point represents Shannon's H of the microbial biomarkers in a litter bag set (two litter-bags bulked for the PLFA analysis). Inset Average Shannon's H of the microbial community biomarkers for mixed-litter decomposition bags is significantly higher than average Shannon's H of single-litter bags (paired *t*-test)

average rates of decomposition ($r^2 = 0.31$; data not shown); yet, without measurements of microbial activity, we cannot explain the presence or absence of synergisms based on microbial dynamics.

Loreau (2001) predicted that increases in microbial diversity could lead to greater exploitation of organic matter through greater functional niche exploitation. Here, we

extend Loreau's predictions to propose that a diverse microbial community exploiting more niches on mixed litter may result in greater microbial biomass. Mixed-litter bags, regardless of plant litter identity, had higher microbial diversity and PLFA biomass than single-litter bags (Figs. 2, 3). The suppression of variation in microbial community diversity with increasing litter diversity is also evident in Fig. 3. Perhaps mixing litter types can cause a more consistent decomposition rate, driven by a distinct community and less affected by changes in microclimatic variables or external resources (Keith et al. 2008).

Microbial biomass and community composition both changed in response to litter mixing, even when synergisms in litter decomposition were not observed. Because these results indicate a difference between microbial community and decomposition responses to litter mixing, we propose the following idea to attempt to reconcile this disconnect. Litter synergisms may depend on the degree of functional difference among whole microbial communities on each particular litter. Where enzymatic capabilities partially overlap (yet still maintain different capacities) perhaps decomposition is stimulated due to breakdown of multiple substrates with reduced enzymatic effort, allowing for greater microbial efficiency. This mechanism would be analogous to those occurring in microbial consortia that are thought to be important in many substrate breakdown processes (Costerton et al. 1995). Though other studies have found otherwise (e.g., Wardle et al. 1997; Quedsted et al. 2002), our study suggests there may be more opportunity

for synergistic interactions between communities on two chemically similar plant litters (two conifers) than two, more chemically distinct litters (conifer and deciduous). That is to say, there is an optimal degree of functional difference among communities for microbial efficiency. To explore this pattern further, we examined microbial communities colonizing aspen litter vs. those on conifer litter regardless of litter mixture status. These two community types were significantly different ($P < 0.01$; ordination not shown), potentially indicating maintenance of distinct communities according to litter type even when litter types are mixed. Perhaps these distinct communities have high fidelity to certain substrate types (conifer vs. deciduous leaves) that are most efficiently processed by their respective enzymatic suites (Vivanco and Austin 2008). Thus, synergisms for aspen litter do not occur here due to a lack of a “partner community”. Testing any of these ideas requires measurement of microbial activity during decomposition of diverse litter types (Dehlin et al. 2006) and such research will advance our understanding of the functional implications for altered microbial communities.

This study is one of the few to examine biodiversity as it cascades across two trophic levels at the plant–soil interface during litter decomposition (Blair et al. 1990; Laitung and Chauvet 2005). We illustrate that though plant litter diversity can alter microbial community composition, these changes do not translate to predictably altered decomposition rates. Further, our findings demonstrate that the composition and the abundance hypotheses are not mutually exclusive (Gartner and Cardon 2004; Hättenschwiler et al. 2005). We propose that microbes require heightened attention in the context of biodiversity because they respond to altered plant diversity at a scale that we have not previously been able to detect, and may drive processes at scales we do not yet understand.

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References

- Ball BA, Hunter MD, Kominoski JS, Swan CM, Bradford MA (2008) Consequences of non-random species loss for decomposition dynamics: experimental evidence for additive and non-additive effects. *J Ecol* 96:303–313. doi:10.1111/j.1365-2745.2007.01346.x
- Bardgett RD, Shine A (1999) Linkages between plant litter diversity, soil microbial biomass and ecosystem function in temperate grasslands. *Soil Biol Biochem* 31:317–321
- Bardgett RD, Walker LR (2004) Impact of coloniser plant species on the development of decomposer microbial communities following deglaciation. *Soil Biol Biochem* 36:555–559. doi:10.1016/j.soilbio.2003.11.002
- Blair JM, Parmelee RW, Beare MH (1990) Decay-rates, nitrogen fluxes, and decomposer communities of single-species and mixed-species foliar litter. *Ecology* 71:1976–1985
- Bligh EG, Dyer WJ (1959) A rapid method of total lipid extraction and purification. *Can J Biochem Physiol* 37:911–917
- Briones MJ, Ineson P (1996) Decomposition of eucalyptus leaves in litter mixtures. *Soil Biol Biochem* 28:1381–1388
- Chapman SK, Koch GW (2007) What type of diversity yields synergy during mixed litter decomposition in a natural forest ecosystem? *Plant Soil* 299:153–162. doi:10.1007/s11104-007-9372-8ER
- Chapman K, Whittaker JB, Heal OW (1988) Metabolic and faunal activity in litters of tree mixtures compared with pure stands. *Agric Ecosyst Environ* 24:33–40
- Costerton JW, Lewandowski Z, Caldwell DE, Korber DR, Lappinscott HM (1995) Microbial biofilms. *Annu Rev Microbiol* 49:711–745
- Dehlin H, Nilsson MC, Wardle DA (2006) Aboveground and belowground responses to quality and heterogeneity of organic inputs to the boreal forest. *Oecologia* 150:108–118
- Frostegard A, Baath E (1996) The use of phospholipid fatty acid analysis to estimate bacterial and fungal biomass in soil. *Biol Fertil Soils* 22:59–65
- Gartner TB, Cardon ZG (2004) Decomposition dynamics in mixed-species leaf litter. *Oikos* 104:230–246
- Hansen RA, Coleman DC (1998) Litter complexity and composition are determinants of the diversity and species composition of oribatid mites (acari: Oribatida) in litterbags. *Appl Soil Ecol* 9:17–23
- Hättenschwiler S, Gasser P (2005) Soil animals alter plant litter diversity effects on decomposition. *Proc Natl Acad Sci USA* 102:1519–1524. doi:10.1073/pnas.0404977102
- Hättenschwiler S, Tiunov AV, Scheu S (2005) Biodiversity and litter decomposition in terrestrial ecosystems. *Annu Rev Ecol Evol Sys* 36:191–218. doi:10.1146/annurev.ecolsys.36.112904.51932
- Hooper DU, Vitousek PM (1998) Effects of plant composition and diversity on nutrient cycling. *Ecol Monogr* 68:121–149
- Hoorens B, Aerts R, Stroetenga M (2003) Litter quality and interactive effects in litter mixtures: more negative interactions under elevated CO₂? *J Ecol* 90:1009–1016
- Hutchinson GE (1959) Homage to Santa Rosalia or Why are there so many kinds of animals? *Am Nat* 93:145–159
- Jonsson M, Wardle DA (2008) Context dependency of litter-mixing effects on decomposition and nutrient release across a long-term chronosequence. *Oikos* 117:1674–1682
- Kaneko N, Salamanca EF (1999) Mixed leaf litter effects on decomposition rates and soil microarthropod communities in an oak-pine stand in Japan. *Ecol Res* 14:131–138
- Keith AM, van der Wal R, Brooker RW, Osler GHR, Chapman SJ, Burslem DFRP, Elston DA (2008) Increasing litter species richness reduces variability in a terrestrial decomposer system. *Ecology* 89:2657–2664
- Kominoski JS, Pringle CM, Ball BA, Bradford MA, Coleman DC, Hall DB, Hunter MD (2007) Nonadditive effects of litter species diversity on breakdown dynamics in a detritus-based stream. *Ecology* 88:1167–1176
- Kominoski JS, Hoellein TJ, Kelly JJ, Pringle CM (2009) Does mixing litter of different qualities alter stream microbial diversity and functioning on individual litter species? *Oikos* 118:457–463
- Laitung B, Chauvet E (2005) Vegetation diversity increases species richness of leaf-decaying fungal communities in woodland streams. *Arch Hydrobiol* 164:217–235

- Leckie SE (2005) Methods of microbial community profiling and their application to forest soils. For Ecol Manage 220:88–106. doi:[10.1016/j.foreco.2005.08.007](https://doi.org/10.1016/j.foreco.2005.08.007)
- LeRoy CJ, Marks JC (2006) Litter quality, stream characteristics and litter diversity influence decomposition rates and macroinvertebrates. Freshwater Biol 51:605–617
- Loreau M (2001) Microbial diversity, producer–decomposer interactions and ecosystem processes: a theoretical model. Proc R Soc Lond Biol 268:303–309
- Madritch M, Donaldson JR, Lindroth RL (2006) Genetic identity of populus tremuloides litter influences decomposition and nutrient release in a mixed forest stand. Ecosystems 9:528–537
- McArthur JV, Aho JM, Rader RB, Mills GL (1994) Interspecific leaf interactions during decomposition in aquatic and floodplain ecosystems. J N Am Benthol Soc 13:57–67
- McTiernan KB, Ineson P, Coward PA (1997) Respiration and nutrient release from tree leaf litter mixtures. Oikos 78:527–538
- Meier CL, Bowman WD (2008) Links between plant litter chemistry, species diversity and below-ground ecosystem function. Proc Natl Acad Sci USA 105:19780–19785
- O'Leary WM, Wilkinson WK (1988) Gram-positive bacteria. In: Ratledge C, Wilkinson SJ (eds) Microbial lipids. Academic Press, London, pp 117–207
- Parton W, Silver WL, Burke IC, Grassens L, Harmon ME, Currie WS, King JY, Adair EC, Brandt LA, Hart SC, Fasth B (2007) Global-scale similarities in nitrogen release patterns during long-term decomposition. Science 315:361–364. doi:[10.1126/science.1134853](https://doi.org/10.1126/science.1134853)
- Quested HM, Press MC, Callaghan CV, Cornelissen JHC (2002) The hemiparasitic angiosperm *Barsia alpina* has the potential to accelerate decomposition in subarctic communities. Oecologia 130:88–95
- Ramsey PW, Rillig MC, Feris KP, Holben WE, Gannon JE (2006) Choice of methods for soil microbial community analysis: PLFA maximizes power compared to CLPP and PCR-based approaches. Pedobiologia 50:275–280. doi:[10.1016/j.pedobi.2006.03.003](https://doi.org/10.1016/j.pedobi.2006.03.003)
- Rustad LE (1994) Element dynamics along a decay continuum in a red spruce ecosystem in Maine, USA. Ecology 75:867–879
- Schimel JP, Hättenschwiler S (2007) Nitrogen transfer between decomposing leaves of different N status. Soil Biol Biochem 39:1428–1436. doi:[10.1016/j.soilbio.2006.12.037](https://doi.org/10.1016/j.soilbio.2006.12.037)
- Schweitzer JA, Bailey JK, Hart SC, Whitham TG (2005) Nonadditive effects of mixing cottonwood genotypes on litter decomposition and nutrient dynamics. Ecology 86:2834–2840
- Schweitzer JA, Bailey JK, Fischer DG, LeRoy CJ, Lonsdorf EV, Whitham TG, Hart SC (2008) Plant–soil–microorganism interactions: heritable relationship between plant genotype and associated soil microorganisms. Ecology 89:773–781
- Seastedt TR (1984) The role of microarthropods in decomposition and mineralization processes. Annu Rev Entomol 29:25–46
- Siemann E, Tilman D, Harstaad J, Ritchie M (1998) Experimental tests of the dependence of arthropod diversity on plant diversity. Am Nat 152:738–750
- Swan CM, Palmer MA (2006) Composition of speciose leaf litter alters stream detritivore growth, feeding activity and leaf breakdown. Oecologia 147:469–478
- Tilman D, Lehman CL, Thomson KT (1997) Plant diversity and ecosystem productivity: theoretical considerations. Proc Natl Acad Sci USA 94:1857–1861
- van der Heijden MGA, Bardgett RD, van Straalen NM (2008) The unseen majority: Soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. Ecol Lett 11:296–310. doi:[10.1111/j.1461-0248.2007.01139.x](https://doi.org/10.1111/j.1461-0248.2007.01139.x) ER
- Vivanco L, Austin AT (2008) Tree species identity alters forest litter decomposition through long-term plant and soil interactions in Patagonia, Argentina. J Ecol 96:727–736
- Wang S, Ruan H, Wang B (2009) Effects of soil microarthropods on plant litter decomposition across an elevation gradient in the Wuyi Mountains. Soil Biol Biochem 41:891–897. doi:[10.1016/j.soilbio.2008.12.016](https://doi.org/10.1016/j.soilbio.2008.12.016)
- Wardle DA, Nicholson KS (1996) Synergistic effects of grassland plant species on soil microbial biomass and activity: Implications for ecosystem-level effects of enriched plant diversity. Funct Ecol 10:410–416
- Wardle DA, Bonner KI, Nicholson KS (1997) Biodiversity and plant litter: Experimental evidence which does not support the view that enhanced species richness improves ecosystem function. Oikos 79:247–258
- Wardle DA, Yeates GW, Barker GM, Bonner KI (2006) The influence of plant litter diversity on decomposer abundance and diversity. Soil Biol Biochem 38:1052–1062. doi:[10.1016/j.soilbio.2005.09.003](https://doi.org/10.1016/j.soilbio.2005.09.003)
- White DC, Davis WM, Nickels JS, King JD, Bobbie RJ (1979) Determination of the sedimentary microbial biomass by extractable lipid phosphate. Oecologia 40:51–62
- Wilkinson SJ (1988) Gram negative bacteria. In: Ratledge C, Wilkinson SJ (eds) Microbial lipids. Academic Press, London, pp 299–488
- Zelles L (1999) Fatty acid patterns of phospholipids and lipopolysaccharides in the characterisation of microbial communities in soil: a review. Biol Fertil Soils 29:111–129