

## Research review

# There's no place like home? An exploration of the mechanisms behind plant litter–decomposer affinity in terrestrial ecosystems

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## Summary

Litter decomposition in terrestrial ecosystems is an important first step for carbon and nutrient cycling, as senescent plant material is degraded and consequently incorporated, along with microbial products, into soil organic matter. The identification of litter affinity effects, whereby decomposition is accelerated in its home environment (home-field advantage, HFA), highlights the importance of plant–soil interactions that have consequences for biogeochemical cycling. While not universal, these affinity effects have been identified in a range of ecosystems, particularly in forests without disturbance. The optimization of the local decomposer community to degrade a particular combination of litter traits is the most oft-cited explanation for HFA effects, but the ways in which this specialized community can develop are only beginning to be understood. We explore ways in which HFA, or more broadly litter affinity effects, could arise in terrestrial ecosystems. Plant–herbivore interactions, microbial symbiosis, legacies from phyllosphere communities and attractors of specific soil fauna could contribute to spatially defined affinity effects for litter decomposition. Pyrosequencing soil communities and functional linkages of soil fauna provide great promise in advancing our mechanistic understanding of these interactions, and could lead to a greater appreciation of the role of litter–decomposer affinity in the maintenance of soil functional diversity.

## Introduction

For terrestrial ecosystem ecology, decomposition of above-ground senescent plant material (litter) is among the most studied processes, and from the most remote lands of Antarctica to tropical forests, organic degradation and nutrient mineralization of plant litter have been evaluated in a range of climates and for many plant species. The decomposition of leaf litter has been seen as the starting point for carbon (C) and nutrient cycling in the soil, and as a result of extensive studies, several large-scale patterns have emerged: the importance of climate tends to dominate at regional scales with positive relationships between litter decomposition and both temperature and precipitation (Gholz *et al.*, 2000; Powers *et al.*, 2009); at smaller spatial scales or without climatic variation, litter chemistry, including nutrient and lignin content, and soil organisms play a decisive role in determining litter turnover and nutrient release (Cornwell *et al.*, 2008; Wall *et al.*, 2008).

In spite of more than three decades of litterbag experiments designed to examine climate, litter quality and decomposer organism effects on decomposition, there is still substantial debate as to the relative importance of biotic interactions on C and nitrogen (N) release from above-ground litter. Several competing theories have focused on the importance of biotic effects of litter quality and chemical changes during decomposition. One hypothesis postulates a chemical convergence of litter quality and resources where, over time, all litter becomes invariable in its chemical composition (Wickings *et al.*, 2012; Wallenstein *et al.*, 2013) and thus of uniform value for decomposers. A second line of thinking is that the initial litter quality alone, both chemical and morphological, determines the trajectory of decomposition and the decomposer community adjusts its functionality in response to these initial conditions (Manzoni *et al.*, 2010). However, in spite of the stated importance of the decomposer community and its demonstrated regional variation (Fierer *et al.*, 2012), a general integrated

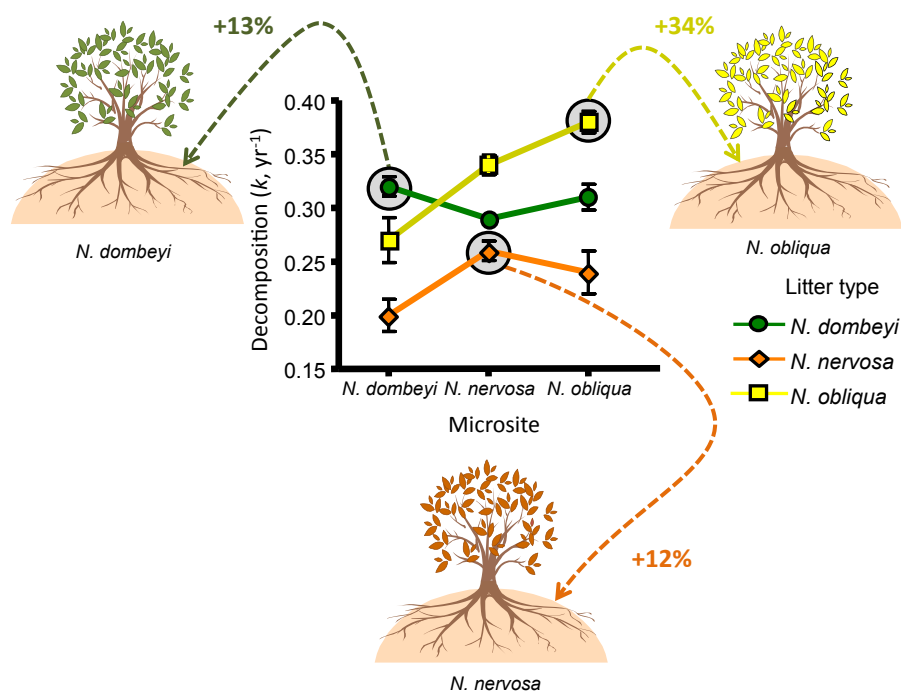
theory regarding the mechanistic interactions of plants and their decomposer community is still a matter of debate (Makkonen *et al.*, 2012; Wickings *et al.*, 2012).

One interaction between soil organisms and plant species that is particularly relevant for leaf litter decomposition in terrestrial ecosystems has been identified as home-field advantage (HFA). HFA is the observation that litter derived from the plants growing above or near the plant (home) decomposes more quickly than when placed far from its plant of origin (away) (Fig. 1). Analogous to a sports team playing in its home stadium, HFA implies that, over time, a decomposer community can become specialized to degrade specific litter types, with a quantitative demonstrated advantage for decomposition in its home environment. Plants respond to available resources through competitive and other interactions and persist or are eliminated, which can determine functional aspects of the plant community. This could also apply to the decomposer species, where the totality of the soil resources and particular characteristics of litter quality, in the absence of disturbance, should dictate the persistence of decomposer organisms that are best able to take advantage of the specific suite of available resources. However, a mechanistic understanding of this phenomenon, as well as its ecological relevance across terrestrial ecosystems, has been elusive, given the complex nature of plant–soil interactions and the

multiple controls in space and time that could affect litter affinity relationships.

The idea that microorganisms are ubiquitous and that microbial community composition responds rapidly to environmental variation including changes in litter input has been substantially challenged in the last decade (Strickland *et al.*, 2009; Wallenstein *et al.*, 2010). There is a growing awareness that microorganisms do not simply passively respond to variation in resource availability, but can actively modulate their metabolic activities as a function of available energy and substrate. The recent demonstrations, for example, that microbial enzyme activity may be coordinated through quorum sensing affecting soil N mineralization (DeAngelis *et al.*, 2008) and litter decomposition (Strickland *et al.*, 2013) clearly shows how underappreciated is the importance of microbial communication and interactions as a control on biogeochemical cycling. It seems clear that our changing view of what determines microbial community structure and function may be key to our understanding of litter affinity effects for decomposition.

The objective of this review is to explore the potential mechanisms that can affect plant litter affinity relationships, with a particular focus on what conditions and interactions can generate a specialized decomposer community that leads to HFA for litter decomposition. We will explore alternative possibilities beyond standard indices of litter quality and chemistry by which a



**Fig. 1** Litter decomposes faster at home. The home-field advantage (HFA) in litter decomposition implies that litter from a particular plant species decomposes faster beneath that particular species (home) than beneath a different species (away from home). HFA implies that there is an affinity between plant litter and soil biota affecting litter decomposition. HFA is substantially different from stimulatory effects of high litter quality and/or high microsite fertility. High-quality litter may decompose faster in a fertile microsite simply as a result of higher resource availability for decomposers independent of its origin (e.g. priming effect). But when a lower quality litter decomposes faster in its own low-fertility microsite than in unspecific microsites, true plant–decomposer affinity occurs. HFA is demonstrated here in the case of all three southern beech species (*Nothofagus* spp.), where litter is decomposed in its home environment (*in situ*) and in reciprocal transplants beneath nonhome species (*ex situ*). Green circles, *Nothofagus dombeyi*; orange diamonds, *Nothofagus nervosa*; yellow squares, *Nothofagus obliqua*; grey circles in the graph indicate HFA and the litter affinity effect for each species. Average HFA (%) indicated on each arrow is calculated as  $(k_{in\ situ} - k_{ex\ situ})/k_{ex\ situ} \times 100$ . (Figure modified from Vivanco & Austin 2008.)

specialized decomposer community could arise and have quantitative impacts on litter decomposition and nutrient turnover in terrestrial ecosystems.

### There's no place like home?

Home-field advantage effects for litter decomposition have been demonstrated in old-growth Patagonian forests (Vivanco & Austin, 2008; Fig. 1) and high-elevation forests in Europe (Ayres *et al.*, 2009a) and observed generally across temperate forest ecosystems (Ayres *et al.*, 2009b). While not universal, the magnitude of HFA effects can be substantial, with observed stimulatory effects of up to 35% (Vivanco & Austin, 2008; Ayres *et al.*, 2009b). Particularly in long-lived ecosystems in the absence of human or natural disturbance, such as mature forest ecosystems, over 75% of reciprocal transplant studies demonstrated HFA for leaf litter decomposition (Ayres *et al.*, 2009b). Additional evidence suggests that litter chemistry may change more rapidly during the course of decomposition when litter is decomposed in its home environment (Wallenstein *et al.*, 2013), and that leaf litter affinity effects are most often pronounced for recalcitrant litter types (Milcu & Manning, 2011; Wallenstein *et al.*, 2013). More recently, the definition of this observed affinity between leaf litter and the decomposers that degrade this litter has been expanded to include affinities among *types* of litter, rather than species-specific home litter, called the substrate–matrix interaction (SMI; Freschet *et al.*, 2012). SMI predicts that with increasing difference between the quality of the litter placed in a microsite and the litter present in that microsite, there will be less affinity for litter decomposition. This affinity effect has been further expanded to a temporal axis, called the phenology–substrate match (PSM) hypothesis (Pearse *et al.*, 2014). The PSM postulates that observed litter affinity effects of the decomposer and its litter can occur seasonally, resulting in an affinity for the decomposer community to decompose litter during the season with maximum litterfall for that particular species.

The identification of these affinity effects, and particularly HFA, in leaf litter decomposition has sparked substantial controversy regarding its generality and the magnitude of impact on litter decomposition (Giebelmann *et al.*, 2011; St John *et al.*, 2011; Freschet *et al.*, 2012; Makkonen *et al.*, 2012; Perez *et al.*, 2013). Several studies do not support the idea of increased decomposition of litter in its home environment (Giebelmann *et al.*, 2011; St John *et al.*, 2011; Makkonen *et al.*, 2012), while others offer limited support for the SMI hypothesis rather than species-specific HFA effects (Freschet *et al.*, 2012; Perez *et al.*, 2013). There are challenges in accurately assessing HFA as a result of the fact that complete reciprocal transplants are not often done, and the use of litterbags with restrictive mesh sizes may underestimate the effects of larger soil fauna (Milcu & Manning, 2011). Perhaps more importantly, recent analyses suggest that the innate ability, or functional breadth, of the microbial community may overestimate or obscure HFA effects using standard measures of comparison (Keiser *et al.*, 2014). The capacity of the decomposer community to respond to a range of litter qualities may be defined by its local adaptation to low-quality litter, for example, thus leading to complementary or antagonistic effects of HFA and

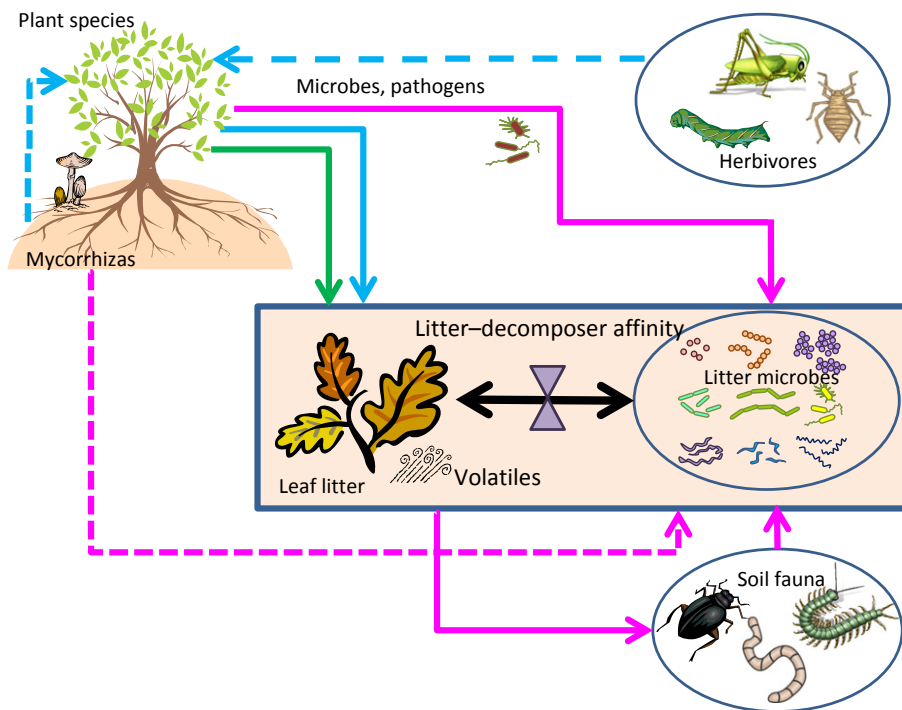
functional breadth when rates of litter decomposition are evaluated (Keiser *et al.*, 2014).

These contrasting results may indicate some important contextual limitations for the possibility of detecting HFA effects, including longevity of species, disturbance and environmental contrasts among sites of origin. For example, comparison among strongly contrasting environmental conditions are not likely to demonstrate HFA effects as a result of variation in climate, soil nutrient availability and pH, which function as macro-controls on rates of C and nutrient turnover (Gholz *et al.*, 2000; Powers *et al.*, 2009). In addition, there are several situations where litter affinity effects may indeed be undetectable or nonexistent: where abiotic controls dominate C turnover such as aridland ecosystems (Austin, 2011); in areas of recent disturbance or early successional stages (Giebelmann *et al.*, 2011); in nonequilibrium conditions resulting from human impact such as N deposition (Vivanco & Austin, 2011); and, in particular, in areas of high plant diversity or rapid turnover where the litter input 'signal' may not clearly define a microsite for decomposer specialization (Giebelmann *et al.*, 2011). Nevertheless, there is increasing evidence that biotic interactions of litter and its specific decomposer community can generate litter-decomposer affinity, which warrants further exploration to define the mechanisms that contribute to the emergence of these litter-decomposer affinity effects in terrestrial ecosystems.

In the following sections, we will discuss conditions and mechanisms that could lead to the existence of HFA, or, more broadly, litter affinity effects focusing primarily on the possible ways in which a specialized decomposer community could develop (Fig. 2). In addition to direct effects of litter chemistry on the microbial decomposer community, we will explore a number of other biotic interactions, including plant–insect interactions in plants and soil, microbial symbiosis, and legacies from phyllosphere communities that could explain the spatially defined affinity effects for litter decomposition.

### Subterranean collaboration: what role do the plants play?

The most cited explanation for litter affinity effects is the specialization of the microbial community in sites where HFA is observed. This means that in microsites with a constant and chronic input of a similar litter quality, the microbial community, over time, may become 'optimized' to degrade this particular kind of litter (Vivanco & Austin, 2008; Ayres *et al.*, 2009b; Freschet *et al.*, 2012). What is still open to question are the actual mechanisms behind this optimization, as standard indices of lignin, C : N ratios, or nutrient content alone are not sufficient to explain most HFA effects (Vivanco & Austin, 2008; Strickland *et al.*, 2009). This is illustrated by the fact that recalcitrant litter will decompose more quickly in a less favorable home environment and not simply as a function of its litter quality or site fertility (Fig. 1). The origin of the optimized soil community should stem from the differential metabolic capacity of the decomposers and competition in the soil or litter environment (Wickings *et al.*, 2012); additionally, the functional breadth of the decomposer community could be determined over time by its interaction with particular litter types



**Fig. 2** Interactive effects of plant and soil biota that could modulate affinity effects for litter decomposition. Plant species determine leaf litter characteristics through their green leaf traits, which can be greatly modified by plant interactions with above- and below-ground organisms. Interactions among phyllosphere microbes and pathogens, herbivorous arthropods, soil fauna (including detritivores) and rhizosphere biota can all directly or indirectly affect the specificity of the decomposer community. Solid lines indicate direct effects and dashed lines indicate indirect effects on leaf traits (green), leaf chemistry (blue) or microbial community composition (pink).

(Keiser *et al.*, 2014). It is important to note here that the emergence of these relationships should be considered in a long-term context, as this type of specialization invariably comes with a cost (Keiser *et al.*, 2011), and therefore should demonstrate a selective advantage for the populations of decomposer organisms.

There are several recent lines of evidence that clearly demonstrate the importance of substrate–microbial interactions, based principally in the recognition that the microbial community is not functionally redundant (Strickland *et al.*, 2009) and differs in its metabolic capacity (Wickings *et al.*, 2012; Keiser *et al.*, 2014). Strong evidence of these interactions comes from recent work examining metabolic outcomes of litter decomposition, which demonstrate unique microbial products based on the interaction of the microbial community and the litter substrate that is being degraded (Wallenstein *et al.*, 2010; Wickings *et al.*, 2012). Moreover, successional changes of fungal and bacterial communities in decomposing litter, associated with changes in litter quality over the course of decomposition, have been documented (Voříšková & Baldrian, 2013). The demonstration that similar initial litter chemistry diverged when decomposed in different decomposer communities (Wickings *et al.*, 2012) supports the idea of a strong interactive effect of plant litter and microbial community composition, although this is not always observed, particularly in later stages of litter decomposition (Wallenstein *et al.*, 2013). These studies are a very important step forward for our understanding of litter–microbe interactions, as they demonstrate a clear link between microbial community composition and function.

Plants may have a range of other effects on the decomposer community beyond that of substrate quality that stem from rhizosphere effects and symbiotic interactions with other organisms (Van der Wal *et al.*, 2013). Plant species can strongly influence the composition and activity of rhizosphere biota, directly through

leaching or release of exudates (Pfeiffer *et al.*, 2013) or indirectly by affecting competitive interactions among soil organisms (Cesarz *et al.*, 2013a). Differences in root morphology, as well as in the amount and type of rhizodeposition among plant species, contribute greatly to this species-specific effect (Berg & Smalla, 2009; Cesarz *et al.*, 2013a). Additionally, associations with arbuscular mycorrhizas can modify the rhizosphere biota and have both a positive and negative impact on organic matter decomposition (Hättenschwiler *et al.*, 2011; Nottingham *et al.*, 2013). There is evidence that there is a large degree of specificity of these symbiotic relationships in ecological groups (Öpik *et al.*, 2009). The net effect of rhizosphere microbiota has important consequences for growth, nutrition and health of plants (Berendsen *et al.*, 2012) that could ultimately affect the chemical composition of their litter (Fig. 2). These cascading effects of specialized mycorrhizal associations and specific rhizosphere biota could generate conditions for a specificity of a microbial community with a particular plant species and its associated microsite. It is unclear, at the present time, however, if these community-specific differences may actually translate to litter affinity effects for decomposition, but it is an area that warrants further exploration in order to establish these mechanistic links (Van der Wal *et al.*, 2013).

### Green leaf hitchhikers: do microbes come along for the ride?

A necessary criterion for the development of local adaptation in soil bacteria is successful dispersal to a given location (Belotte *et al.*, 2003), although this factor may be less appreciated than the selective pressure on the local community perceived through differences in litter quality. Nevertheless, the ways in which decomposer microbes differentially disperse to microsites may be of

substantial import for determining a specialized decomposer community. While effects of litter quality have been explored extensively for litter decomposition, an alternative perspective is that another legacy of green leaves, the resident phyllosphere community, could make an important contribution to affinity effects for litter decomposition. Interactions between above-ground plant tissues and their associated phyllosphere microbes have been seldom connected with below-ground processes such as decomposition. Microbial communities, present on green leaves, may persist through the process of retranslocation and abscission of senescent leaf litter, providing an effective means of dispersal and a large advantage for saprotrophic microbes for initial colonization of the decomposing litter (Fig. 2). Empirical evidence for this suggested mechanism was recently demonstrated with pyrosequencing of the fungal community over the trajectory of decomposition, which demonstrated that the fungal community present on green leaves was the most abundant taxa in litter through the early stages of decomposition (Voříšková & Baldrian, 2013). Additional evidence from a study of beech litter decomposition demonstrated that the green leaf fungal community and the highly decomposed leaf litter fungal community were indistinguishable (Peršoh *et al.*, 2013). This recent evidence supports the idea that phyllosphere microbes may exert effects on the decomposition of the senescent tissue that harbors them as green leaves.

Pathogens that infect green leaf tissue have been shown to be highly host-specific (Barrett *et al.*, 2009), and could also have consequences for decomposition of senescent plant litter. On the one hand, pathogens can produce changes in leaf chemistry, impacting litter quality and subsequent decomposition (Guidi *et al.*, 2007). Additionally, specific pathogens could generate leaf damage that could facilitate access for decomposers once this material has senesced. Perhaps most importantly, many of these pathogenic microbes have the ability to survive saprophytically in soil or on plant debris, which suggests that a part of the decomposer community could be derived directly from the pathogen community on green leaves (Olson *et al.*, 2012). As such, the sum of the interactions among above-ground microbes, host plants and the soil microbial community could contribute to litter affinity effects and the acceleration of litter decomposition. Although current information is scarce, the suggestion of the importance of green leaf legacies is an alternative twist on litter affinity effects, highlighting the relative importance of dispersal and initial colonization in affecting local adaptation of soil microbial populations, rather than specificity for degradation of specific compounds in litter.

### Litter perfume in the air: what determines the specificity of invertebrate decomposers?

While the importance of soil invertebrates directly participating in litter decomposition has been demonstrated across biomes (Wall *et al.*, 2008), it is not clear in what way soil invertebrates and herbivorous insects might affect specificity of decomposer organisms that could lead to conditions of HFA or litter affinity for decomposition (Fig. 2). Although many soil organisms are omnivorous, increasing evidence has demonstrated that soil faunal

groups do show preferences for food resources and a strong degree of specificity with above-ground components in terrestrial ecosystems (Wardle *et al.*, 2004). These complex above- and below-ground interactions can be reciprocal, as below-ground herbivores (Bezemer & van Dam, 2005) as well as detritivores (González Megías & Müller, 2010) can induce plant metabolites that modify the quality and attractiveness of plants to their herbivores and parasitoids. Moreover, indirect effects of specificity of the soil invertebrate community could arise, given that soil organisms that are not decomposers could modulate the structure of the soil food web (Biere & Tack, 2013; Cesarz *et al.*, 2013b). For example, predators such as spiders or carabid beetles might also play a key role in engineering these interactions by regulating herbivore as well as detritivore populations (Miyashita & Takada, 2007) and their stoichiometry (Hawlena *et al.*, 2012), with impacts on rates of leaf litter decomposition (Lawrence & Wise, 2004).

There is evidence that plant species can generate conditions for a specific soil faunal community in forest ecosystems (Negrete-Yankelevich *et al.*, 2008; Cesarz *et al.*, 2013b) and specialization of invertebrate decomposer communities in grassland–forest transitions (St John *et al.*, 2011). Additionally, three-way interactions among plants, microbes and soil arthropods could be quite important in determining these specialized communities that are spatially defined by the plants' sphere of influence through litter inputs or root exudates (Biere & Tack, 2013). The importance of higher trophic groups affecting litter affinity effects is supported by results showing that a range of soil fauna size classes contributed to the strength of HFA effects (Milcu & Manning, 2011). Finally, given the specificity of most herbivorous arthropods (Dicke & Baldwin, 2010), herbivory can modulate plant–soil microbe interactions through the production of nutrient-rich frass (Meehan *et al.*, 2014) or altering properties of their host plants as plant tissue quality or the stimulation of root exudates (Hamilton *et al.*, 2008), all of which could in turn affect the microbial community (Biere & Tack, 2013).

The last two decades have resulted in an explosion of new understanding regarding the role of plant volatile compounds in modulating plant communication and their interactions. The effects of communication through volatile compounds have largely focused on plant–plant or plant–herbivore interactions (i.e. Dicke & Baldwin, 2010; Karban *et al.*, 2014; Zhu *et al.*, 2014). It is well known that plants emit volatiles that act as attractants or repellants of herbivores, and that induced volatiles can contribute to increased efficiency of foraging insects as a result of the identification of a specific food source (Dicke & Baldwin, 2010). An intriguing idea to consider, given our understanding of the importance of these volatile cues, is the role of plant litter volatiles as a signal for specific groups of invertebrates. The unique nature of these volatile compounds associated with particular types of leaf litter could attract or ward off certain soil invertebrates, and contribute to the development of a specialized decomposer community with consequent litter affinity effects. These effects would thus be inherently direct, with olfactory cues potentially attracting decomposer invertebrates that are specialized in decomposing substrates with a specific volatile signature. But is there any evidence to support this connection?

Extending the idea of herbivore-induced volatile cues to leaf litter and soil invertebrates, it is clear that leaf litter emits small oxidized volatile organic compounds (VOCs; Gray *et al.*, 2010; Gray & Fierer, 2012; He *et al.*, 2013), particularly in conifers (Ludley *et al.*, 2009; Faiola *et al.*, 2014) and members of the Myrtaceae family such as *Eucalyptus* spp. (Gray *et al.*, 2010). The source of these VOCs originates from microbial emissions and, to a lesser degree, abiotic emissions (Gray *et al.*, 2010), but have a specific signature that is, in some cases, in a similar concentration to their green leaf counterparts. These compounds, in sufficient concentration, should have the capacity to both attract and repel soil organisms to a specific location. Secondly, there is evidence that soil invertebrates may choose their location or food source in response to volatile cues. Detritivore groups such as millipedes (Sombke *et al.*, 2012), earthworms (Zirbes *et al.*, 2011), and coleopterans, oribatid mites and nematodes can use olfactory cues to recognize their food resources. Dung beetles demonstrate a preference for different types of substrate based on their volatile emissions (Dormont *et al.*, 2010) and a detritivore species was observed to be attracted by herbivore-induced plant volatiles (Braasch *et al.*, 2012). Taken together, this evidence, along with the demonstrated importance of induced volatile cues for plant–insect interactions, suggests that volatile compounds from leaf litter could be sufficient to directly affect the specificity of the invertebrate decomposer community, with possible indirect effects on soil food webs. This area seems ripe for exploration of its possible mechanistic links to litter affinity effects for decomposition.

## Conclusions and future directions

There are a multitude of ways in which plants and other organisms interact, many with quantitative effects on ecosystems energy flow and nutrient turnover. This review has demonstrated a number of potential interactions that could affect litter–decomposer affinity and thus have consequences for litter decomposition, while also highlighting a number of open questions that could be explored further. A central message, however, is that standard indices of leaf litter quality, such as lignin concentration or stoichiometric nutrient ratios, which have been the focus of much research in understanding patterns of litter decomposition, are not sufficient to explain the mechanistic underpinning of litter affinity effects in terrestrial ecosystems. We must broaden the scope of understanding to include the possible ways in which biotic interactions modulate this important ecosystem process. As such, the importance of plant–decomposer affinities may be a currently underappreciated element of the controls on litter decomposition in terrestrial ecosystems, particularly in undisturbed natural ecosystems where there has been sufficient time for these relationships to emerge. It seems imperative to move beyond the traditional approach of the litter chemistry control on rates of decomposition and incorporate the newly identified ways in which organisms interact and communicate, such as quorum sensing, shifting functional roles from phyllosphere to decomposers or reading the environment in ways we had not considered, such as detection of leaf litter volatile cues.

One of the continuing unknowns in soil microbial ecology is the link between identity and function – that is, how changes in community composition and diversity in the soil translate to functional significance. The taxonomic identification of soil communities through pyrosequencing and their link to functionality through metagenomic analysis (Fierer *et al.*, 2012) demonstrate the enormous potential that this technology has to elucidate the mechanistic basis for these litter affinity relationships and effectively establish the specificity and functional role of decomposer organisms (Keiser *et al.*, 2014). In addition, our meagre understanding of the role of larger soil organisms in determining these relationships highlights the need for identifying functional roles of soil invertebrates. The wealth of information that can be gained from understanding soil faunal feeding preferences, cues for spatial distribution and direct and indirect effects on soil fauna–microbe interactions will greatly enhance our understanding of the mechanistic controls on litter–microbe affinity and litter decomposition. The recent demonstration that soil biota are highly diverse and may far exceed the diversity of above-ground plant communities (Taylor *et al.*, 2014) suggests that our understanding of the functional significance of this microbial diversity is in its primordial stages. As we are provided with more quantitative information, it is clear that increasing our capacity to identify the functional breadth and importance of soil organisms will provide a more precise mechanistic understanding of litter affinity effects in terrestrial ecosystems.

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