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A traits-based test of the home-field advantage in mixed-species tree litter decomposition

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• **Background and Aims** Litter often decomposes faster in its environment of origin (at 'home') than in a foreign environment ('away'), which has become known as the home-field advantage (HFA). However, many studies have highlighted the conditional nature of the HFA, suggesting that current understanding of this phenomenon is not yet sufficient to generalize across systems.
• **Methods** The HFA hypothesis was tested for mono-specific and mixed-species litter using a tree-based experiment that manipulated the functional identity and diversity of the host tree community. Litter types of varying quality were transplanted between several host tree communities and decomposition rates were measured using litterbags. Since the decomposer community should respond to traits of the litter input and not their taxonomic identity, a traits-based index of litter–tree similarity was developed.
• **Key Results** Mono-specific litter exhibited HFA, but when the same litter was decomposed in mixture, this trend was not observed. Mixed-species litter decomposed on average no faster or slower than monoculture litter and exhibited both positive and negative species interactions. These non-additive interactions of decomposition rates in mixture were influenced by the degree of similarity between litter and tree traits. Both synergistic and antagonistic interactions decreased in magnitude with increasing litter–tree similarity such that mixture rates were predictable from monocultures.
• **Conclusions** The HFA occurred more strongly for mono-specific litter than for the litter types mixed together because interactions between species may have masked this effect. However, when expressed as a function of trait similarity between litters and tree communities, the HFA was not detected.

Key words: Home-field advantage, HFA, tree litter decomposition, mixed-species litter, biodiversity, plant functional traits.

INTRODUCTION

In terrestrial ecosystems, the vast majority of plant net primary production escapes herbivory and returns to the soil as litter (Cebrian, 1999). The decomposition of this litter is a key ecosystem process critical to both carbon and nutrient cycling, determining both the flux of CO_2 from the soil to the atmosphere and soil nutrient availability. Besides climate, which is important over large spatial scales, the decomposition of leaf litter at more local scales is controlled by three main factors: the physico-chemical environment of the soil, the quality of the litter and the properties of the decomposer community (Coûteaux et al., 1995; Cadisch, 1997; Cornwell et al., 2008). The host plant community can play a major role in the decomposition process by influencing all of these factors (Scherer-Lorenzen et al., 2007; Vivanco and Austin, 2008; Aubert et al., 2010; Scherber et al., 2010; Barantal et al., 2011; Eisenhauer et al., 2012). Interactions between above-ground and below-ground components that are generated through litter inputs, plant nutrient uptake and root activity could significantly affect the biotic and abiotic properties of the decomposition microenvironment.

Feedbacks between the litter and the soil could create a situation where the soil decomposer community is specialized to the litter it receives. Leaf litter has large variation in chemical and physical traits between species. Because this litter is an important source of nutrients and energy for soil biota, and because the ability to extract such resources from different types of litter differs between soil organisms, there is likely competition between soil biota for these nutrients. This competition could generate selective pressure for decomposers to become efficient at breaking down (and taking up nutrients from) the litter produced by the plants above them (Ayres et al., 2009). If there are evolutionary trade-offs in evolving specific enzymatic capacities or other traits relevant to this specialization, then decomposers may become specifically adapted to the litter they receive over the long term.

In ecological time, the relevant temporal scale for the present experiment, species filtering (sorting) of soil biota would lead to specialized decomposer communities. The dynamics of such filtering of microbial communities can be very fast – measured in weeks or months (Nemergut *et al.*, 2013). This would result in what has become known as the 'home-field advantage' (HFA), where litter decomposes faster in its own host plant environment (at 'home') than elsewhere ('away') (Gholz *et al.*, 2000). HFA appears to be widespread in forest ecosystems (Ayres *et al.*, 2009; Wang *et al.*, 2013), as reciprocal transplant experiments of monoculture litter between plant communities often find accelerated decomposition of litter in its home environment (Hunt *et al.*, 1988; Gholz *et al.*, 2000; Vivanco and Austin, 2008; Milcu and Manning, 2011; Osanai *et al.*, 2012; Kagata and Ohgushi, 2013). Meta-analyses of such experiments in forests of several continents report that HFA can lead to faster decomposition rates (between 4 and 8 %) of litter at home than away (Ayres *et al.*, 2009; Wang *et al.*, 2013). However, studies are not universal in their support for this hypothesis and some studies have failed to detect an HFA (Chapman and Koch, 2007; Gießelmann *et al.*, 2011; St John *et al.*, 2011). Freschet *et al.* (2012*a*) noted that, of the studies reporting a positive HFA effect, most transplanted mono-specific litter, often with dramatic differences in quality, usually between two strongly contrasting decomposition environments. Conversely, studies using more chemically similar litter species and those from more diverse communities often failed to detect HFA.

Natural forests are composed of more than one tree species, and so litter usually decomposes in mixture. However, only three experiments to our knowledge have tested the HFA hypothesis using mixed species litter and these report conflicting results (Barantal *et al.*, 2011; Gießelmann *et al.*, 2011; St John *et al.*, 2011). When litter decomposes in mixture, litter species often interact such that the mixture decomposition rate is faster or slower than would be predicted from monocultures (Gartner and Cardon, 2004). It is not yet known whether these litter interactions could prevent or increase an HFA. Barantal *et al.* (2011) hypothesized that HFA could increase the magnitude of synergistic interactions between litter species due to the possibility of a specialized decomposer community exhibiting increased efficiency of complementary resource use of a recurrent heterogeneous resource input from the canopy. Their experiment, a transplant of mixed-species and component monoculture litter between two systems, showed that interactions (positive and negative) of litter mixing are stronger in the natural home environment than in a common garden away environment. On the other hand, Tardif and Shipley (2013) and Tardif *et al.* (2014) reported an 'idiosyncratic' mixing of interactions between species in litters such that, as the number of species increases, positive and negative interactions tend to cancel out. If this phenomenon is common, there is no reason to expect a home environment to display any particular tendency with respect to the rate of decomposition. Gessner *et al.* (2010) review some of the more common mechanisms of litter interactions that are affected by the number of species in the litter mixture.

Although the description of home versus away has been overwhelmingly taxonomic (which *species* compose the vegetation), decomposers would likely be specialized to different chemical or morphological traits of the litter produced by the host plants rather than to the species themselves. Therefore, a trait-based approach to the HFA hypothesis could prove useful. Freschet *et al.* (2012*a*) highlighted that the HFA hypothesis falls apart in mixed-species systems as it is unlikely for a decomposer community to be simultaneously specialized to multiple litter types of various qualities. For instance, a decomposer community cannot be dominated by both fungi, which are efficient at degrading low-quality litter types, and bacteria, which are efficient at degrading high-quality litter types (Wardle *et al.*, 2004). According to Grime's mass ratio hypothesis (Grime, 1998; Garnier *et al.*, 2004), the extent to which a species affects ecosystem functioning should be proportional to its contribution to total community biomass. If this were the case, the decomposer community would instead respond to the average values of the plant community's litter traits. More specifically, the average value of a trait should be calculated as a community-weighted mean (Garnier *et al.*, 2004), which is the average trait value of all the species in the community, weighted by their relative abundances. Therefore, for multispecies systems, decomposition rates of a specific litter type should not depend on whether or not the decomposing litter species is present in the host community, but rather on the similarity between the average value of litter quality between the decomposing litter and the long-term litter input.

In this study we tested the HFA hypothesis for both monospecific litter types and for mixed-species litter. We also tested, in an exploratory manner, the effect of HFA on the non-additive interactions of litter mixing. To quantify home and away, we used two methods: a taxonomic approach based on the presence/absence of the litter species in the host plant community (home versus away); and a multivariate measure of trait dissimilarity between the community-weighted means of traits of the litter and the host plant community. We hypothesized that (1) HFA is stronger for monoculture litter than for mixtures, and that (2) trait similarity better captures this HFA than taxonomic similarity.

Ideally, one would test such hypotheses by randomly assigning, and then experimentally manipulating, different levels of trait dissimilarity in natural forests and then transplanting litters between them. Since this is impossible in practice, one can either choose established forests that differ in trait similarity (and in many other variables that cannot be controlled) or else experimentally manipulate the degree of trait dissimilarity in young, densely planted common garden tree mixtures where as many environmental conditions as possible are controlled and mostly homogeneous prior to establishment. These two methods have complementary strengths and weaknesses. In this study we use the second option, which better separates cause–effect relationships while acknowledging the limitations when extrapolating from experimental field mesocosms to older natural forests.

METHODS

Experimental site

The experiment, part of the International Diversity Experiment Network with Trees (IDENT; Tobner *et al.*, 2013) linked to TreeDivNet, was located at McGill University (Sainte-Anne-de-Bellevue, Quebec, Canada, 45·5° N, 73·9° W). The experiment was established in spring 2009 on a former

agricultural field that had been intensively managed for several decades. The annual temperature was 6·1 °C with a mean annual precipitation of 967 mm. The soil was a Humic Gleysol (Typic Endoaquent) with a pH_{water} of 6·3 in the 0- to 20-cm sandy loam layer (containing, on average, 78 % sand, 6 % silt and 16 % clay). One-year-old angiosperm and 2-year-old gymnosperm seedlings from a species pool of 12 North American temperate tree species were used to create 37 different tree communities, each replicated in four blocks. Each tree community (4 × 4 m) consisted of 64 individual trees. This density of individuals was higher than that of adult trees in a mature forest but was similar to, or even lower than, that of regenerating forests and was chosen in order to accelerate interactions and quickly form a full canopy. 'Communities' were separated by 1·25-m corridors to reduce interactions between communities and allow movement of personnel and equipment without disturbing the plots. These corridors were trenched with a 30-cm incision during the summer in 2011 and 2012 to prevent roots from neighbouring communities from interacting. Species combinations were chosen in order to create two independent gradients of taxonomic richness and functional diversity. To detect potential effects of functional diversity while holding taxonomic richness constant, communities were established with large and comparable gradients of functional diversity within each level of taxonomic richness; see Tobner *et al*. (2013) for more detail. At the beginning of the present experiment (spring 2012), individuals (averaged by species) varied in height from 1·32 m (*Picea glauca*) to 4·14 m (*Betula papyrifera*). Each block consisted of 12 monoculture communities, 14 two-species mixtures, ten four-species mixtures and one 12-species mixture. Component species of each mixed-species community were planted in equal frequency. Individual tree location within a community and community location within a block were randomized with restrictions to prevent the clumping of species and to maintain the same diversity in both the outside perimeter row (i.e. a buffer) and the inside 6 × 6 tree grid. Communities were regularly weeded manually to keep them free of any herbaceous competition. Information on soil nutrient and humidity levels as well as fungal and bacterial biomasses in the soil across the different tree communities is given in Rivest *et al*. (2015).

Experimental design

We performed a litterbag experiment in which we decomposed litter from four different tree species in monoculture and mixture in a variety of host tree communities.

Litter

The four mono-specific litter types used in our experiment were *Acer saccharum*, *Acer rubrum*, *Quercus rubra* and *Betula papyrifera*. Newly senesced leaf litters from these four species were collected in mid-October 2011 from natural monoculture stands in the Morgan Arboretum of McGill University, adjacent to the experimental site. We constructed five types of litter bag: each litter type in monoculture, and one mixed-species bag containing equal parts of dry mass of the four species, giving a total of 2·0 g on an equivalent dry-mass basis. These mixtures were placed in fibreglass mesh (2 mm) litterbags (15 × 15 cm). This mesh size allowed macro- and meso-fauna, including earthworms and mites, to enter, and all these were observed inside litterbags upon collection. Petioles were removed from the leaves prior to weighing and not included in the bags. We placed these five different litterbag types in ten different tree communities replicated in four blocks in mid-April 2012. In each tree community, in each block and for each litter type, we placed four identical litterbags (to be destructively harvested at four different dates) directly on the soil surface. In total there were 4 blocks × 10 communities/block × 5 litter types/community × 4 litterbags/litter type = 800 litterbags. Litterbags were destructively harvested 28, 59, 124 and 184 d after incubation. The remaining litter was carefully cleaned by hand to remove all soil particles and then dried to a constant weight. Percentage dry mass remaining was calculated for each individual litterbag after harvest. Decomposition rates, k (g g^{-1} d^{-1}), were estimated for each litter type in each tree community in each block. This was done by fitting the least-squares regression slope of ln[% dry mass remaining(t)] on time, thus assuming a negative exponential decay of dry mass. This resulted in 4 × 10 × 5 = 200 independent estimates of k.

Host tree communities The ten host tree communities used in our experiment all comprised different four-species combinations of tree species from a pool of 12 native conifer and deciduous species (Table 1). This species pool included the four species used as litter types. Each tree community was replicated in four blocks. Since a maximum of only two different tree communities were used to test the HFA hypothesis in previous publications, we considered the ten diverse communities used here to be a robust test of the hypothesis.

Trait measurements

For each species in monoculture, we measured five leaf traits. Water-saturated leaf dry matter content (LDMC) and

TABLE 1. *Composition of tree species in each of ten host communities*

Host community	Component species			
1	*Abies balsamea*	*Picea glauca*	*Pinus resinosa*	*Picea rubens*
2	*Acer rubrum*	*Betula alleghaniensis*	*Betula papyrifera*	*Quercus rubra*
3	*Pinus resinosa*	*Pinus strobus*	*Picea rubens*	*Picea glauca*
4	*Betula alleghaniensis*	*Pinus resinosa*	*Picea rubens*	*Pinus strobus*
5	*Abies balsamea*	*Betula papyrifera*	*Larix laricina*	*Picea glauca*
6	*Abies balsamea*	*Acer saccharum*	*Picea rubens*	*Picea glauca*
7	*Larix laricina*	*Pinus strobus*	*Quercus rubra*	*Thuja occidentalis*
8	*Acer rubrum*	*Quercus rubra*	*Pinus strobus*	*Thuja occidentalis*
9	*Betula papyrifera*	*Pinus strobus*	*Acer saccharum*	*Picea glauca*
10	*Acer saccharum*	*Betula alleghaniensis*	*Picea glauca*	*Thuja occidentalis*

specific leaf area (SLA) of living leaves were measured using a standardized protocol (Garnier *et al.*, 2001). Average values were calculated for each species from 36 measurements: three leaves from three individuals from four blocks. Leaf size of living leaves was recorded ordinally as follows: 1, needle or scale; 2, small leaf (<10 cm); 3, large leaf. Total leaf carbon (C_M) and nitrogen (N_M) contents, on a dry mass basis, were measured for recently senesced litter by high-temperature combustion (960 °C) followed by thermo-conductometric detection using a Vario Macro Elementar multi-element analyser (Elementar Analysensysteme, Hanau, Germany). The traits SLA, LDMC, C_M and N_M were chosen because these have been shown to predict litter decomposition (Garnier *et al.*, 2004; Kazakou *et al.*, 2006). Average values for each species were calculated from three replicate measurements of ground and mixed plant material collected from numerous individuals in all blocks.

Measuring similarity

In order to test the HFA hypothesis, we measured the similarity between the litter and the host tree community in two ways.

(1) *Taxonomic similarity.* In accordance with the initial formulation of the HFA hypothesis (Hunt *et al.*, 1988; Gholz *et al.*, 2000), we first calculated an index of similarity based on whether or not the litter species were present in the host tree community. We calculated a value of similarity between 0 and 1 as the proportion of species in the litter type that were also present in the host tree community, where 0 indicated no species in common between the litter and the host tree community and 1 indicated that all species in the litter were also in the host tree community. For monoculture litter, the value of taxonomic similarity would then be binary (0 or 1); the litter species was either included in the host community (at home) or not (away.) For the litter mixture, we calculated the proportion of shared species using Sørensen's index of similarity (eqn 1) where the proportion of species shared with the host community could be 0, 0·25, 0·5, 0·75 or 1. In eqn (1), S_T is the total number of species in the host tree community and S_{LT} is the number of species in both the litter mixture and the tree community. We refer to this measure as 'taxonomic similarity'.

$$Similarity = \frac{2S_{LT}}{(S_L + S_T)} \qquad (1)$$

(2) *Trait similarity.* Secondly, we calculated a measure of similarity between the litter and the host community that was based on a set of functional traits rather than on taxonomic presence. Grime's mass-ratio hypothesis predicts that species effects on ecosystem properties should be proportional to their abundance in the community. The effect of litter input on the decomposer community should then be related to the average litter quality, or the 'community-weighted means' of litter traits. We therefore calculated the difference between the community-weighted mean values for several litter quality traits of the litter and those of the host tree community.

We calculated the community-weighted means for the above-mentioned five litter quality traits (LDMC, SLA, N_M, litter C_M and leaf size) all of which have been shown to influence litter decomposition rates (Aerts, 1997; Cornwell *et al.*, 2008; Fortunel *et al.*, 2009; Freschet *et al.*, 2012*b*; Makkonen *et al.*, 2012). Since mixed-species litterbags contained equal parts of dry mass of each species, community-weighted means were simply the average trait value of the four species. Although the four tree species were planted in equal abundance in each community, the effect of the tree community on the soil community should be related to the quantity of litter input from each tree species, and not simply the number of individuals. Therefore, as a proxy of litter input that takes into consideration both the density and the size of individuals, we measured stem volume (height and diameter at 5 cm) for each individual tree during summer 2011. Community-weighted means of the host tree community were then calculated as the product of the species' trait value and its relative volume, summed across all species in the community. This assumes that the amount of leaf litter produced by an individual is proportional to its stem volume.

To quantify the difference between the community-weighted means of the litter and the host tree community for several traits simultaneously, we measured the Euclidian distance (D_{TL}, eqn 2) between the community-weighted mean trait values of the species comprising the litter (L) and the tree community (T). So that our two measures (taxonomic and trait-based) would be consistent, we multiplied the value by –1, so a large negative value indicates a large distance (i.e. greater dissimilarity) between litter and tree trait values and a small negative value indicates a small distance (i.e. greater similarity); $\bar{t}_{Tj}, \bar{t}_{Lj}$ are the community-weighted values of trait j measured for the tree community and litter, respectively.

$$D_{TL} = -1\sum_{j=1}^{5}(\bar{t}_{Tj} - \bar{t}_{Lj})^2 \qquad (2)$$

Statistical analysis

The overall decomposition rate of mixed-species litter is often faster or slower than would be predicted from the decomposition rates of each component species in monoculture. To quantify the net interactive effect of litter mixing for the litter mixture in each host tree community in each block, we compared each observed decomposition rate of the litter mixture (k_{obs}) to the predicted rate (k_{pred}). These predicted rates were calculated for each community in each block as the community-weighted decomposition rate of the four litter species decomposing in monoculture, i.e.

$$\widehat{k}_j = \sum_i k_i p_{ij} \qquad (3)$$

where k_i is the monoculture decomposition rate of species i and p_{ij} is its relative abundance in litter mixture j. These predicted values therefore assume no net interactions between species with respect to the mixture rate and serve as a null hypothesis when testing for a diversity effect. The 'mixing effect' was then calculated as
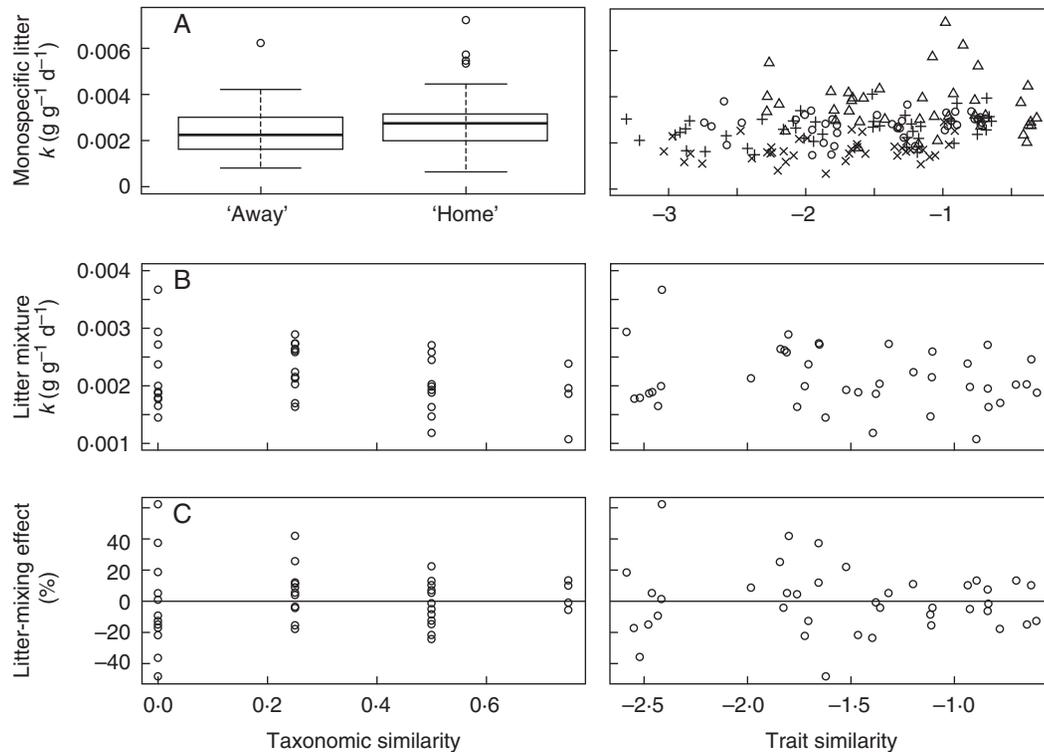
$$\frac{k_{obs} - k_{pred}}{k_{pred}} \qquad (4)$$

Fig. 1. Home-field advantage of litter decomposition. (A) Decomposition rates, k (in g g^{-1} d^{-1}), of the four mono-specific litter types as a function of litter–tree similarity. Point symbol indicates litter type: $\bigcirc$ = *Acer saccharum*, $\triangle$ = *Acer rubrum*, + = *Betula papyrifera*, $\times$ = *Quercus rubra*. (B) Overall decomposition rates, k (in g g^{-1} d^{-1}), of the four species decomposing in mixture as a function of litter–tree similarity. (C) Litter-mixing effect (% change in decomposition from monoculture predictions) as a function of litter–tree similarity. Taxonomic similarity measures the number of species in the litter mixture present in the host tree community. Trait similarity measures the similarity in chemical and physical trait values between the decomposing litter and the long-term litter input of the host tree community.

Therefore, a positive value (x) is interpreted as species interactions increasing the overall mixture decomposition rate by proportion x, and a negative value ($-y$) is interpreted as species interactions decreasing the overall mixture decomposition rate by proportion y. To test for HFA using taxonomic and trait similarity, we used linear models with k values as response variables and with similarity (continuous), litter type (factor) and block (factor) as fixed factors. The significance ($\alpha = 0.05$) of these terms, including interactions, was tested using ANOVA. Analysis was done using the R statistical program (R Development Core Team, 2008). From here, we refer to the k value simply as the 'decomposition rate'.

RESULTS

By the end of the litterbag experiment, remaining mean litter dry mass was 56 % for *A. saccharum*, 46 % for *A. rubrum*, 59 % for *B. papyrifera*, 70 % for *Q. rubra* and 56 % for the four-species litter mixture. The negative exponential decay model from which the decomposition rates (k values) were calculated provided a good fit to the data in every case. An ANOVA of decomposition rates, with litter type and host community as the fixed factors, showed that decomposition rates differed between litter types ($F_{4,185} = 38.3$, $P < 2 \times 10^{-16}$) and between host tree communities ($F_{9,185} = 2.7$, $P = 0.004$), indicating that the identity of both the litter and the host tree community independently affected decomposition.

Mono-specific litter exhibited an HFA, decomposing 10 % faster at home than away, as determined from an ANOVA of decomposition rates contrasting home (i.e. a taxonomic similarity of 1) with away (i.e. a taxonomic similarity of 0), ($F_{1,150} = 4.0$, $P = 0.05$). However, we did not detect an HFA for mono-specific litters when using trait similarity, since a regression of decomposition rates of mono-specific litter types on the degree of litter–tree trait similarity revealed no significant relationship (slope = 1.4×10^{-4}, $t_{150} = 1.4$, $P = 0.11$). Similarly, we found no HFA for the litter mixture. Regressions of decomposition rates of the litter mixture on either the degree of taxonomic (slope = -4.8×10^{-4}, $t_{34} = 1.6$, $P = 0.20$) or trait similarity (slope = -1.7×10^{-4}, $t_{34} = 1.3$, $P = 0.19$) with native litter revealed no significant relationships. Decomposition rates of litter mixtures often deviated from the predicted community-weighted values, ranging from +18 % (mean synergistic mixing effect) to –15% (mean antagonistic mixing effect). However, these deviations had no overall tendency to be synergistic or antagonistic (Fig. 1C), as the overall mixing effect did not differ significantly from 0 using a one-sample two-tailed *t*-test ($t_{39} = 0.15$, $P = 0.88$). A regression of the mixing effect on either taxonomic (slope = 0.04, $t_{34} = 0.28$, $P = 0.78$) or trait similarity (slope = -0.03, $t_{34} = 0.56$, $P = 0.58$) was not significant. Although the litter mixing effect was not correlated with litter–tree similarity, its variance visibly decreased with increasing litter–tree similarity (Fig. 1C). The absolute magnitude of litter mixing effects decreased with both increasing taxonomic

similarity (slope $= -0.21$, $t_{34} = 2.6$, $P = 0.01$) and increasing trait similarity (slope $= -0.07$, $t_{34} = 2.1$, $P = 0.04$).

DISCUSSION

Our first hypothesis was that an HFA would be manifested more strongly for mono-specific litter than for the litter types mixed together because interactions between species could mask this effect. Mono-specific litter did exhibit a large (but only marginally significant) HFA (Fig. 1A). However, when the litter types were mixed together, there was no evidence for HFA; if fact, the litter mixture exhibited the opposite tendency (Fig. 1B). We detected deviations from the predicted community-weighted decomposition rates but these were idiosyncratic (equally positive and negative) (Fig. 1C). The presence of interactions involving particular combinations of species but without any overall deviation from additivity is consistent with the results of Tardif and Shipley (2013), and Tardif *et al*. (2014) and with the simulation results of Hui and Jackson (2009). We therefore cautiously accept our first hypothesis, concluding that litter interactions can hide the presence of HFA. Our results are consistent with meta-analyses that reported an overall idiosyncratic effect of litter taxonomic richness on terrestrial litter decomposition rates (Gartner and Cardon, 2004; Srivastava *et al*., 2009; Cardinale *et al*., 2011). Studies in several systems have failed to detect an HFA for litter decomposition (Chapman and Koch, 2007; Gießelmann *et al*., 2011; St John *et al*., 2011), calling into question the universality, but not the existence, of HFA. Our results further highlight the context-dependent nature of the HFA of litter decomposition. There are several potential explanations for a lack of HFA. First, most reports of an HFA come from studies that transplanted strongly contrasting litter types between their respective systems, e.g. grasslands versus forests or deciduous versus coniferous. It is possible that the sorting of specialized decomposers occurs only at these larger habitat scales. Second, it has been suggested that HFA should be more pronounced for more recalcitrant litter types that are rich in lignin and other compounds, which are resistant to degradation and require specific decomposers for their breakdown (Milcu and Manning, 2011; Osanai *et al*., 2012; Wallenstein *et al*., 2013). The importance of recalcitrant carbon compounds for overall decomposition rates increases in later stages of decomposition after the easily digestible labile compounds have been lost from the litter (Melillo *et al*., 1989; Coûteaux *et al*., 1995). Therefore, it is possible that the rapid breakdown of labile compounds greatly exceeded that of recalcitrant compounds in overall contribution to decomposition rates during our 6-month experiment, thus hiding an HFA that would have become more pronounced in later stages of decomposition. Another possible explanation of our lack of HFA is that 4 years (the duration of our experimental site) is not sufficient time for effective environmental filtering of soil biota and for the presence of the host tree community to exhibit its full effect on the soil system. We did, however, find a strong and significant effect of host community identity on overall decomposition rates. Furthermore, soil microbial community structure and composition are known to change rapidly, within weeks or months, following changes in soil abiotic conditions or plant community composition (Nemergut *et al*., 2013), and our common garden

experiment was located on a previously farmed site with very homogeneous soil. In fact, Rivest *et al*. (2015) found strong and significant differences in many soil biochemical properties and in soil microbial resistance and resilience to drought among three monocultures and two mixtures of the same experimental tree plantation in the same year (2012, after 4 years). It is less clear whether the soil macrobiota can respond as quickly. Since these experimental communities were spatially adjacent (within <45 m within a single block and 100 m of each other for the most distant plots), it seems unlikely that dispersal limitation of the micro- and macrobiotic soil species would play an important role.

Our second hypothesis was that an HFA would be better captured by trait similarity than by taxonomic similarity. We found no support for this hypothesis. If the often observed HFA of litter decomposition is due to specialization of decomposer organisms, a mechanistic understanding will necessarily involve a characterization of plant traits. Freschet *et al*. (2012*a*) extended the HFA hypothesis for litter mixtures, where individual litter types in an away environment could have increased or decreased decomposition depending on their similarity in litter quality to the litter matrix (host community litter input). Quantifying similarity with chemical (lignin:nitrogen) and physical (LDMC) litter traits, they report an HFA, but only in situations of extreme trait dissimilarity. It is possible that our lack of HFA is because we did not include litter traits that explicitly quantify recalcitrant components of the litter. However, LDMC, which we did measure, is closely associated with leaf tissues (xylem, collenchyma, fibres) that increase recalcitrance. Since recalcitrant compounds such as lignin require specialized fungal taxa for their degradation (Baldrian and Snajdr, 2011), we would predict these compounds to be important for HFA. However, in order for their breakdown to contribute significantly to rates of litter mass loss, this would necessitate a much longer incubation time for litterbags. Conversely, HFA could be tested by measuring rates of loss of lignin and other recalcitrant compounds from the litter instead of rates of overall mass loss. If HFA is to be incorporated into decomposition models and more generally into ecological theory, a better understanding of its mechanisms is required. A future challenge is to identify the traits that drive HFA and their direct effects on decomposer activity.

The decomposition rates of the litter mixture often deviated from predictions based on community-weighted means of monoculture rates but did not exhibit any *systematic* accelerated or decelerated decomposition when in mixture. Barantal *et al*. (2011) decomposed several litter mixtures in two decomposition environments, a natural forest (containing no species included in the litter) and an adjacent plantation where litter decomposed under the same tree species that were present in the decomposing litter. They found that the magnitude of litter-mixing effects was greater and on average more positive in the plantation, and attributed this to the long-term input of litter from the home species, concluding that HFA can increase litter mixing effects. Here we report the opposite: that the magnitude of litter interactions decreases when litter is at home. In our experiment we used ten different decomposition environments that were created using a randomized experiment, thus experimentally controlling for initial differences while manipulating only the identity of the host tree community. Both positive and

negative litter interactions decreased in magnitude with increasing taxonomic similarity between the litter and the host tree community. This effect was further reflected when using our index of trait similarity, providing a possible mechanistic explanation. When a decomposer community received litter with chemical and physical trait values distant from those of the long-term litter input, there was increased potential for large non-additive interactions to increase or decrease decomposition rates. However, the direction of the interactions was not related to the degree of trait dissimilarity and so, on average, they cancelled out. Since our research group has now observed non-additive positive and negative interactions that cancel out on average in two other independent studies (Tardif and Shipley, 2013; Tardif *et al.*, 2014), this may be a common phenomenon. We do not know whether our results would remain the same if we allowed our litters to decompose over multiple years, in which more recalcitrant components dominate the remaining litter. Our results further show that the host tree community has an important indirect effect on decomposition above and beyond its effect on litter quality. This highlights the importance of *in situ* decomposition when investigating non-additive effects of litter mixing.

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