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SPECIAL FEATURE – STANDARD PAPER

WHETHER IN LIFE OR IN DEATH: FRESH PERSPECTIVES ON HOW PLANTS AFFECT BIOGEOCHEMICAL CYCLING

Decay rates of leaf litters from arbuscular mycorrhizal trees are more sensitive to soil effects than litters from ectomycorrhizal trees

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Summary

1. While it is well established that leaf litter decomposition is controlled by climate and substrate quality at broad spatial scales, conceptual frameworks that consider how local-scale factors affect litter decay in heterogeneous landscapes are generally lacking.

2. A critical challenge in disentangling the relative impacts of and interactions among local-scale factors is that these factors frequently covary due to feedbacks between plant and soil communities. For example, forest plots dominated by trees that associate with ectomycorrhizal (ECM) fungi often differ from those dominated by trees that associate with arbuscular mycorrhizal (AM) fungi in terms of their litter quality, microbial community structure and inorganic nutrient availability. Here, we evaluate the extent to which such factors alter leaf litter decomposition rates.

3. To characterize variations in decomposition rates, we compared decay rates of high-quality litter (maple; AM) and low-quality litter (oak; ECM) across forest plots representing a gradient in litter matrix quality and nitrogen (N) availability driven by the relative proportions of AM and ECM trees in each plot. In experiment two, we added litter from two AM and three ECM tree species to forest plots with either a high-quality litter matrix and high N availability (i.e. AM-dominated plots) or a low-quality litter matrix and low N availability (i.e. ECM-dominated plots). In both experiments, we found that AM litter decomposed more rapidly than ECM litter, and this effect was enhanced in AM-dominated plots.

4. Then, to separate the contributions of litter matrix effects from N availability effects, we added N fertilizer to a subset of plots from experiment two. Nitrogen addition increased decay rates of high-quality litter across all sites, but had no effect on low-quality litter, suggesting that low N availability, not litter matrix quality, constrains decomposition of high-quality litters. Hence, N availability appears to alter litter decomposition patterns independently of litter matrix properties.

5. *Synthesis.* Our results indicate that shifts in the relative abundance of ECM- and AM-associated trees in a plot or stand have the potential to affect litter decay rates through both changes in litter quality as well as through alterations of the local-scale soil environment.

Key-words: decomposer community, home-field advantage, litter decomposition, mycorrhizal associations, nitrogen, plant–soil (below-ground) interactions, reciprocal transplant experiment

Introduction

Leaf litter decomposition is the rate-limiting step for nutrient cycling and soil organic matter formation and stabilization (Swift, Heal & Anderson 1979; Herman, Moorhead & Berg 2008; Cotrufo *et al.* 2013), but significant gaps remain in our understanding of what controls litter decomposition at local scales. While it is well accepted that litter decomposition rates depend primarily on temperature and soil moisture at global scales (Berg *et al.* 1993; Aerts 1997), global analyses suggest

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that ~40% of the variation in litter decomposition rates is explained by local (i.e. non-climatic) factors, such as litter quality, nutrient availability and decomposer community specialization (Cornwell *et al.* 2008; Wall *et al.* 2008). While the importance of local-scale drivers on decomposition rates is increasingly being recognized (Bradford *et al.* 2014), few conceptual frameworks have been proposed to explain how local-scale factors interact to affect litter decay in heterogeneous ecosystems (Gholz *et al.* 2000; Knorr, Frey & Curtis 2005; Freschet, Aerts & Cornelissen 2012; Keiser *et al.* 2014). Such frameworks are likely to be critical for accurately predicting decomposition rates in the wake of global change.

A formidable challenge in disentangling the relative impacts of local factors is that multiple factors – biotic and abiotic – frequently covary due to feedbacks between plants and their associated soil microbes. For example, plants that produce high-quality litters [e.g. low carbon (C): nitrogen (N) or lignin:N] often promote bacteria-dominated microbial communities that decompose litter and accelerate N cycling, resulting in soils with high N availability (Van der Heijden, Bardgett & van Straalen 2008). In contrast, plants that produce low-quality litters (e.g. high C:N or lignin:N) generally select for fungal-dominated communities that decompose litter slowly and are adapted to soils with low N availability (Van der Heijden, Bardgett & van Straalen 2008). As such, plants may influence litter decomposition rates directly by generating low- or high-quality litter (Melillo, Aber & Muratore 1982) and indirectly by altering the soil environment (Norris *et al.* 2013; Austin *et al.* 2014), but the relative importance of these factors is currently unknown.

A recent conceptual model that relates variations among a suite of biogeochemical properties to the mycorrhizal associations of dominant trees (Phillips, Brzostek & Midgley 2013) offers an ideal system for evaluating the interactive effects of local-scale factors on litter decay. Previous studies have found that leaf litters generated by arbuscular mycorrhizal (AM)-associated trees decompose more rapidly in a common soil than those generated by ectomycorrhizal (ECM)-associated trees (Cornelissen *et al.* 2001). At the ecosystem level, forest plots dominated by AM-associated tree species have an 'inorganic N economy' with rapid rates of N cycling and low fungal: bacterial ratios (Phillips, Brzostek & Midgley 2013). In contrast, forest plots dominated by ECM-associated tree species have an 'organic N economy' with slow rates of N cycling and high fungal:bacterial ratios. However, the degree to which the decomposition of AM and ECM leaf litters are mediated by these unique soil environments remains untested.

Here, we conducted two experiments in mature hardwood forests to evaluate how litter quality interacts with two soil factors – litter matrix quality and N availability – to affect leaf litter decomposition. We focus on these soil factors because both the composition of the ecosystem litter layer (i.e. the litter matrix) and N availability alter decomposition rates, but the magnitude and direction of these effects are dependent on litter quality (Knorr, Frey & Curtis 2005; Freschet, Aerts & Cornelissen 2012). First, we measured the decomposition rates of leaf litters across a 'mycorrhizal gradient' in an ~80-year-old hardwood forest. The mycorrhizal gradient includes a range of forest plots, from ones dominated by trees associating with AM fungi to ones dominated by ECM-associated trees (Phillips, Brzostek & Midgley 2013). While these plots vary in the abundance of trees that associate with either AM or ECM fungi, this study focuses on the suite of traits generated by AM- or ECM- associated trees rather than the properties of AM or ECM fungi *per se*. Hence, we use the terms AM- or ECM-dominated to refer to the relative dominance of AM or ECM-associated trees at the stand level, not the relative abundances of AM or ECM fungi. We placed low-quality (oak; ECM) and high-quality (maple; AM) litterbags in all plots across the gradient and measured their decomposition rates. In the second experiment, we tested whether decomposition rates varied between AM and ECM leaf litters. This experiment took place in paired end-member plots (i.e. greater than 85% AM- or ECM-dominated) where we performed a reciprocal transplant of two AM litters and three ECM litters. To disentangle the impacts of varied N ability from litter matrix effects, we added N to one pair of each end-member plot to evaluate whether N availability drove the observed variations in decomposition rates.

Materials and methods

SITE DESCRIPTIONS

Experiment 1: mycorrhizal gradient

The first experiment was conducted in a mixed deciduous hardwood forest in southern Indiana, USA. This research was conducted at two sites: Griffy Woods (GW; 39.19, −86.50) and Lilly-Dickey Woods (LDW; 39.24, −86.22). Most trees at GW are ~80 years old while trees at LDW are ~150 years old. Both forests are the result of settler land abandonment and natural forest regeneration (Braun 1947). Elevation ranges from 175 to 280 m at GW and 100 to 315 m at LDW. The climate in this area is humid continental, with mean annual precipitation of 1200 mm and mean annual temperature of 11.6 °C. Soils are thin, unglaciated Inceptisols, derived from siltstone, shale and, to a lesser extent, limestone (United States Department of Agriculture Soil Survey).

We identified 10 plots at each site that spanned a gradient in the distribution of ECM and AM trees based on the basal area of trees within a 15 × 15 m plot and their known mycorrhizal associations (Brundrett, Murase & Kendrick 1990; Wang & Qiu 2006). Dominant tree species include sugar maple (*Acer saccharum* Marsh; AM), tulip poplar (*Liriodendron tulipifera* L.; AM), black cherry (*Prunus serotina* Ehrh.; AM), northern red oak (*Quercus rubra* L.; ECM), black oak (*Quercus velutina* Lam.; ECM), chestnut oak (*Quercus prinus* L.; ECM), pignut hickory (*Carya glabra* P. Mill.; ECM) and American beech (*Fagus grandifolia* Ehrh.; ECM). The litter decomposition experiment was performed in the centre of each plot to avoid edge effects.

We collected leaf litter by placing four litter traps (30 × 30 cm milk crates lined with 1 mm mesh) in each plot at the corners of an internal 8 × 8 m square. We collected the contents of the traps biweekly during the litter fall period (September–November) in 2010 and 2011. In the laboratory, litter was spread on aluminium foil for 4 days to allow for air-drying at room temperature (23 °C). Leaf litter was then sorted by species.

Litter decomposition was assessed using mesh litterbags filled with senesced litter collected in 2010 (Bocock & Gilbert 1957; Verhoef & Brussaard 1990). Dried oak (a mixture of *Q. prinus*, *Q. rubra* and *Q. velutina*) and maple (mixed *A. saccharum* and *A. rubrum* L.) leaf litters were separately homogenized by forest (GW or LDW), and 4 g subsamples were placed in 10 × 20 cm 1-mm-mesh nylon bags. In October 2011, we set out 10 low-quality (oak; ECM) and 10 high-quality (maple; AM) litterbags in the centre of each plot between the top soil horizon and the leaf litter. Litterbags were collected five times between deployment and April 2013. At least one litterbag of each species was collected from each plot at each collection. After collection, litter from each bag was oven-dried (60 °C for 48 h), cleaned of soil and weighed. When more than one bag was collected, the average weight of the litter was used for all subsequent analyses.

Experiment 2: AM and ECM leaf litter and nitrogen fertilization

We conducted the second experiment at a third forested site – Moore's Creek – an ~80-year-old forest in south-central Indiana, USA, that is ~15 km away from GW and ~55 km from LDW (Vitousek 1984). Elevation ranges at Moore's Creek from 165 to 230 m. Site history, climate and soils are similar to the sites described above (USDA soil survey).

We identified 7 AM- and 7 ECM-dominated stands and established two 20 × 20 m paired plots in each stand. In all plots, trees from the dominant mycorrhizal type (AM vs. ECM) represented more than 85% of the basal area of the plot ($n = 7$ replicates for each mycorrhizal group × treatment). AM plots contained a mixture of sassafras (*Sassafras albidum* Nutt.), *A. saccharum* and *L. tulipifera*. ECM plots contained *F. grandifolia*, *C. glabra*, white oak (*Quercus alba* L.), *Q. rubra*, and *Q. velutina*. All stands were located in similar landscape positions and contained more than one species from each mycorrhizal group. The litter decomposition experiment was again performed in the centre of each plot to avoid edge effects.

One plot of each pair was treated with NH_4SO_4 and $NaNO_3$ granular fertilizer starting in May 2011. Fertilizer was applied monthly from May–October, resulting in a total addition of 50 kg N ha^{-1} $year^{-1}$. Fertilizer was equally applied to the whole plot and N was derived equally from NH_4SO_4 and $NaNO_3$. Fertilization significantly increased soil inorganic N concentrations by ~25% (Midgley and Phillips, unpublished). This addition rate is equivalent to the deposition rate projected to occur across large areas of the Midwest and Northeast USA by 2050 (Millennium Ecosystem Assessment 2005) and currently is detected at locations close to urban areas, power plants and intensive agriculture (National Atmospheric Deposition Program 2013). Currently, Moore's Creek is exposed to low levels (~5 kg N ha^{-1}) of ambient N deposition (National Atmospheric Deposition Program 2013).

We collected leaf litter fall by placing four litter traps (40 cm diameter tomato cages, 1 mm mesh) in each plot at the corners of an internal 12 × 12 m square. We collected the contents of the traps biweekly during the litter fall period (September–November) in 2011. In the laboratory, litter was spread on aluminium foil for 4 days to allow for air-drying at room temperature (23 °C). Leaf litter was then sorted by species.

To quantify litter decomposition, we created single-species litterbags containing 1 g of air-dried leaves (10 × 10 cm, 1 mm mesh size nylon) from *A. saccharum* (AM), *L. tulipifera* (AM), *Q. rubra* (ECM), *Q. alba* (ECM) and *C. glabra* (ECM) leaf litter. In July 2012, ten litterbags of each type were deployed in every plot. Litterbags were retrieved every 3–4 months from October 2012 to November 2013. Two litterbags for each type or species were collected from each plot at each time point. After collection, litter from each bag was oven-dried (60 °C for 48 h), cleaned of soil and weighed. The average weight of the two collected bags was used for all subsequent analyses.

LITTER QUALITY

Dried litterbag samples were ground to a fine powder, after which 4 mg subsamples were weighed into tin capsules and analysed for total C and N (Elemental Combustion System 4010; Costech Analytical Technologies, Valencia, CA, USA). Initial litter samples ($n = 3$ for each litter type) were also dried, ground and analysed for C and N as described above. In addition, lignin content of initial samples was assayed using a sequential extraction following Moorhead & Reynolds (1993). We recognize that the recalcitrant residue classified as lignin by this method may include a variety of polymers; thus, we use 'lignin' as an operational term for litter material that resisted degradation by a strong acid.

SOIL NITROGEN AVAILABILITY

Soil inorganic N concentrations were assessed with four soil cores taken to a depth of 5 cm in each plot along the mycorrhizal gradient. Soil cores were collected in May and October 2011. Soils were sieved (2 mm) and homogenized, and inorganic N (NH_4^+ and NO_3^-) was extracted using 2 M KCl. Specifically, 4 ± 0.1 g of sieved soil was placed into a 15-mL centrifuge tube, extracted with 10 mL of 2 M KCl, shaken for 1 h, centrifuged at 1200*g* and filtered through Whatman no. 1 filter paper that was pre-leached with 2 M KCl. Extracts were frozen prior to analysis. NH_4^+–N was measured colorimetrically using the salicylate–nitroprusside method, and NO_3^-–N concentrations were measured using the cadmium reduction technique on a Lachat QuikChem 8000 Flow Injection Analyzer (Lachat Instruments, Loveland, CO, USA). A subsample of soil was weighed and dried at 105 °C for 24 h for gravimetric soil moisture analysis. Total inorganic N (NH_4^+–N + NO_3^-–N) was scaled to mg N g $soil^{-1}$ using extract volume, sample mass and moisture content.

CALCULATIONS

We calculated the percentage of litter mass remaining at each collection point. Samples of air-dried unincubated leaves (three samples per species) were oven-dried and weighed to develop conversion factors to express the initial weights of leaf samples in the litterbags as dry mass. Despite removing most of the soil from dried leaf litter, a portion could not be removed without potentially removing leaf litter as well, particularly in the more decomposed leaf litters. In order to correct for this error in litter mass, we assumed that any reduction in litter C content was a result of contamination with topsoil and corrected for contamination following Dukes & Field (2000) and Janzen, Entz & Ellert (2002). Specifically, the correction is based on the initial litter carbon content (C_l), the decomposed sample carbon content (C_d) and the soil carbon content (C_s). Any changes in litter C should be due to contaminations rather than direct alterations of litter C content. Thus, the fraction: $(C_l - C_s/C_d - C_s)$ represents the fraction of the litter mass that is soil rather than litter. Soil C concentration was assessed with four soil cores taken to a depth of 5 cm in each plot.

Soil cores were collected from GW and LDW in June, July and September 2010 and from Moore's Creek in May, July and September 2012. Soils were sieved (2 mm), homogenized and oven-dried at 60 °C for 48 h. Dried soil samples were ground to a fine powder, after which 25 mg subsamples were weighed into tin capsules and analysed for total C and N as described above.

The percentage of mass remaining (y) over time was fitted to the simple exponential decay model of $y = e^{-kt}$ (Olson 1963) where k is the decomposition rate (year^{-1}) and t is that decomposition time (year). To calculate decomposition rate, the percentage of litter mass remaining was transformed to the natural logarithmic scale. A linear model was fit to the data by regressing the natural logarithm of the proportion of mass remaining over time in years, where k is equal to the slope. The intercept was set to zero. Ninety per cent of the R^2 values were >0.80.

In Experiment 1, we determined the plot-level effect of litter quality on decomposition by subtracting the decomposition rate of maple litter (high-quality) in a given plot from the decomposition rate of oak litter (low-quality) from the same plot. As this metric considers the quality of the leaf litter only (i.e. all soil characteristics held constant), we refer to this as the 'Litter Quality Effect.

In Experiment 2, we calculated the Litter Quality Effect by subtracting the average decomposition rate of all ECM leaf litters from the decomposition rate of all AM leaf litters in each plot. However, in order to account for variability among the decomposition rates of litter species, we also calculated variance in the decomposition rates of the litters in each plot as an additional indicator of the effect of litter quality. Greater difference or variability in decomposition rates indicates a greater Litter Quality Effect on decomposition rates. We calculated the effect of N fertilization on decomposition rates and the Litter Quality Effect by taking the natural log of the response ratio (mean in fertilized plots/mean in unfertilized plots). The effect sizes were log-transformed to create a normal distribution of effect sizes (Nakagawa & Cuthill 2007). This metric is positive when the variable of interest increases in response to fertilization and negative when the variable decreases in response to fertilization.

STATISTICAL ANALYSES

To test for differences in initial litter chemistry and decomposition rates among litter types and sites in Experiment 1, we conducted a two-way ANOVA with litter type (oak, maple) and site (GW, LDW) as fixed effects and litter chemistry and decomposition rate as dependent variables (%C, %N, %lignin, C:N, lignin:N, k). To test for differences in initial litter chemistry and decomposition rates among litter species in Experiment 2, we conducted a one-way ANOVA with litter species as fixed effect (*A. saccharum*, *L. tulipifera*, *C. glabra*, *Q. alba* and *Q. rubra*) and litter chemistry and decomposition rate as dependent variables. Comparisons among means were analysed with Tukey HSD *post hoc* tests. We also tested for differences between litter from AM-associated trees and ECM-associated trees in Experiment 2 by conducting a *t*-test with litter mycorrhizal association as a fixed effect (AM, ECM) and litter chemistry and decomposition rate as dependent variables.

We evaluated the relationships between decomposition rates and litter quality, litter matrix quality and soil N concentrations using data collected in Experiment 1. To test for interactions between matrix quality and litter decomposition rates, we regressed the decomposition rate for each litter type (maple, oak) against the average per cent ECM leaf litter collected from in each plot in 2010 and 2011. Because ECM litter is of lower quality than AM litter (Table 2), we used the average per cent ECM litter in the litter matrix as an indicator of matrix quality. Similarly, to test for interactions between soil N availability and litter decomposition rates, we regressed the decomposition rate for each litter type against the average soil inorganic N concentration. Finally, to assess how litter quality interacted with these gradients of litter matrix quality and soil N availability, we regressed our Litter Quality Effect against the average per cent ECM leaf litter collected from in each plot in 2010 and 2011 and the average soil inorganic N concentration.

To evaluate variability in litter decomposition rates in unfertilized plots in Experiment 2, we conducted two-way ANOVAs with plot mycorrhizal association (AM, ECM) and litter species or litter mycorrhizal association as fixed effects and litter decomposition rate as a dependent variable. To evaluate the Litter Quality Effect in Experiment 2, we used mixed linear models with plot mycorrhizal association (AM, ECM), plot treatment (unfertilized, fertilized), and litter species or litter mycorrhizal association as fixed effects, plot pair as a random effect and the Litter Quality Effect as a dependent variable. To assess the effect of N fertilization on decomposition patterns, we conducted a two-way ANOVA with plot mycorrhizal association and litter species or litter mycorrhizal association as fixed effects and the effect sizes of decomposition rate and Litter Quality Effect indices as dependent variables. Comparisons among means were analysed with Dunn–Šidák *post hoc* tests.

Prior to analysis, normal probability plots were used to check data distributions for normality and residual plots were used to check for homogeneity of variances. Log-transformations were applied when necessary. Results were considered significant at $P < 0.05$. The statistical package SPSS ver. 21 (Armonk, NY, USA) was used for all analyses.

Results

EXPERIMENT 1: MYCORRHIZAL GRADIENT

Oak litter differed from maple litter in concentrations of C, N and lignin as well as in decomposition rates. Carbon and lignin concentrations were significantly higher in oak litter than in maple litter ($P < 0.001$). N concentrations were significantly lower in oak litter than in maple litter ($P < 0.001$). Initial C:N and lignin:N ratios were wider for oak litter than maple litter, and maple litter decomposed significantly more rapidly than oak litter ($P < 0.001$; Table 1).

Across the mycorrhizal gradient, the decomposition rate of maple litter varied significantly while the decomposition rate of oak litter did not. The decomposition rate of maple litter significantly decreased as the average per cent ECM leaf litter in the plots increased ($P = 0.023$, $R^2 = 0.41$; Fig. 1a) and as the soil inorganic N concentrations decreased ($P = 0.005$, $R^2 = 0.38$; Fig. 1c). In contrast, the decomposition rate of oak litter was not significantly correlated with either per cent ECM litter ($P = 0.155$; Fig. 1a) or soil inorganic N concentrations ($P = 0.683$; Fig. 1c) in plots. However, the effect of litter quality significantly decreased as the proportion of ECM leaf litter inputs to the plots increased ($P < 0.001$, $R^2 = 0.65$; Fig. 1b) and as soil inorganic N concentrations decreased ($P = 0.001$, $R^2 = 0.47$; Fig. 1d). Only one plot contained less than 30% ECM leaf litter layer; when this plot was removed from the analysis, the effect of litter quality still increased as

Table 1. Initial quality (mean ± 1 SE; n = 3) and average decomposition rates (k; mean ± 1 SE; n = 9–10) of oak and maple litters used in Experiment 1 [at Griffy Woods (GW) and Lilly-Dickey Woods (LDW)]

Forest	Litter	%C	%N	% Lignin	C:N	Lignin:N	k
GW	Maple	44.44^{a} ± 0.12	1.31^{a} ± 0.03	26.77^{a} ± 0.76	34.00^{a} ± 0.66	20.49^{a} ± 0.87	0.64^{a} ± 0.05
	Oak	46.84^{b} ± 0.04	0.91^{b} ± 0.02	32.20^{bc} ± 0.61	51.32^{b} ± 0.99	35.26^{b} ± 0.15	0.46^{b} ± 0.04
LDW	Maple	45.41^{c} ± 0.05	1.00^{b} ± 0.04	27.88^{ac} ± 1.42	45.58^{b} ± 2.01	28.01^{c} ± 1.96	0.70^{a} ± 0.04
	Oak	47.59^{d} ± 0.03	0.67^{c} ± 0.02	34.05^{b} ± 0.87	70.94^{c} ± 1.84	50.70^{d} ± 0.35	0.53^{b} ± 0.03

Different letters indicate significant differences among litters from *post hoc* comparisons ($P < 0.05$).

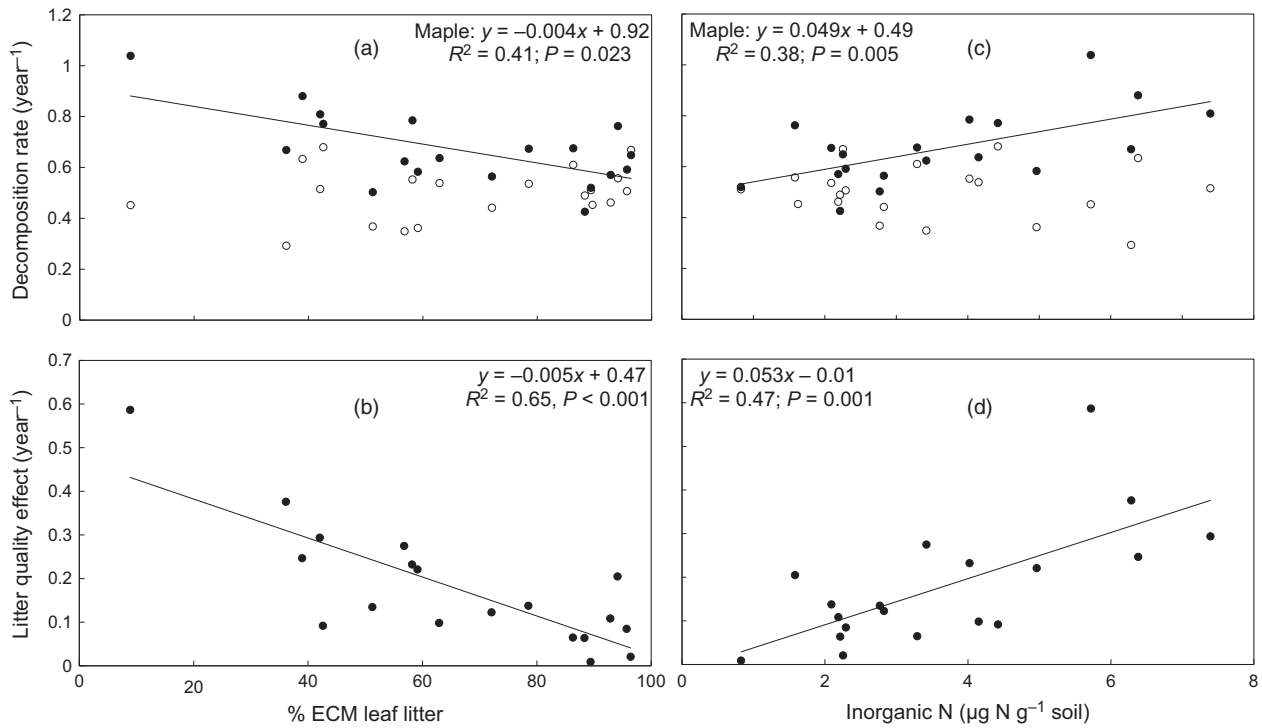

Fig. 1. Relationships between (a, c) the decomposition rates (k) of maple (solid circles; n = 19), oak (open circles; n = 20) and (b, d) the Litter Quality Effect (n = 19) and (a,b) the percentage of ECM leaf litter in the litter matrix and (c, d) soil inorganic N concentrations in plots across the mycorrhizal gradient. Litter Quality Effect was calculated as the k value of maple litter minus the k value of oak litter within each plot.

the proportion of ECM leaf litter inputs to the plots increased ($P < 0.001$, $R^2 = 0.49$).

EXPERIMENT 2A: AM AND ECM LEAF LITTER

Leaf litter used in Experiment 2 differed significantly in several chemical characteristics. There were significant effects of litter species on C concentration ($P < 0.001$), N concentration ($P = 0.003$) and lignin concentration ($P < 0.001$) as well as C:N and lignin:N ratios ($P < 0.001$ for both; Table 2). With respect to AM and ECM litters, N concentration was significantly greater in AM litter than in ECM litter ($P = 0.002$). In contrast, there were no significant differences between AM and ECM litters in C concentration ($P = 0.67$), and lignin concentration was only marginally higher in ECM litter compared to AM litter ($P = 0.055$). However, there were significant differences between AM and ECM litters with respect to C:N and lignin:N ratios; both C:N and lignin:N ratios were significantly greater in ECM litter than in AM litter ($P = 0.007$ and $P < 0.001$, respectively).

Decomposition rates also varied among leaf litters from different species ($P < 0.001$; Table 2). *Liriodendron tulipifera* decomposed the most rapidly while *Q. rubra* decomposed the slowest. Overall, AM litter decomposed more rapidly than ECM litter ($P < 0.001$). However, there was also a significant interaction between plot mycorrhizal association and litter mycorrhizal association ($P = 0.039$); AM litter decomposed more rapidly in AM plots than in ECM plots while the decomposition rate of ECM litter was not significantly different between AM and ECM plots (Fig. 2). However, the interaction between plot mycorrhizal association and litter species was not significant ($P = 0.107$; see Figure S1 in Supporting Information). The effect of litter quality on decomposition rates also varied between AM and ECM plots. The Litter Quality Effect was higher in AM plots compared to ECM plots (Fig. 3); the Litter Quality Effect was significantly dif-

Table 2. Initial quality (mean ± 1 SE; n = 6) and average decomposition rates (k; mean ± 1 SE; n = 14) of *Acer saccharum* (AM), *Liriodendron tulipifera* (AM), *Carya glabra* (ECM), *Quercus alba* (ECM) and *Quercus rubra* (ECM) litters used in Experiment 2 (at Moore's Creek)

Litter	%C	%N	% Lignin	C:N	Lignin:N	k
AM trees						
A. saccharum	$45.79^{a} \pm 0.32$	$0.94^{a} \pm 0.08$	$18.2^{a} \pm 0.94$	$50.04^{a} \pm 3.80$	$19.71^{a} \pm 1.23$	$0.64^{ab} \pm 0.04$
L. tulipifera	$47.59^{b} \pm 0.33$	$0.84^{ab} \pm 0.07$	$21.60^{ab} \pm 1.39$	$59.06^{ab} \pm 4.95$	$26.64^{ab} \pm 2.76$	$0.72^{a} \pm 0.08$
ECM trees						
C. glabra	$44.74^{c} \pm 0.09$	$0.80^{ab} \pm 0.02$	$26.73^{c} \pm 1.14$	$56.05^{ab} \pm 1.26$	$33.36^{bc} \pm 0.93$	$0.64^{ab} \pm 0.08$
Q. alba	$46.60^{a} \pm 0.11$	$0.69^{b} \pm 0.02$	$18.24^{a} \pm 0.64$	$67.40^{bc} \pm 1.67$	$26.44^{ab} \pm 1.37$	$0.60^{ab} \pm 0.03$
Q. rubra	$49.61^{d} \pm 0.17$	$0.65^{b} \pm 0.04$	$24.71^{bc} \pm 2.21$	$77.68^{c} \pm 4.82$	$37.95^{c} \pm 2.14$	$0.48^{b} \pm 0.03$
AM trees	46.69 ± 0.35	$0.89^{A} \pm 0.05$	19.92 ± 0.95	$54.55^{A} \pm 3.27$	$23.17^{A} \pm 1.78$	$0.67^{A} \pm 0.04$
ECM trees	46.98 ± 0.02	$0.72^{B} \pm 0.02$	23.24 ± 1.19	$67.04^{B} \pm 2.70$	$32.58^{B} \pm 1.43$	$0.57^{B} \pm 0.03$

Decomposition rates are from unfertilized plots. Different letters indicate significant differences among litters by species (lowercase letters) and by mycorrhizal association (uppercase letters) from *post hoc* comparisons ($P < 0.05$).

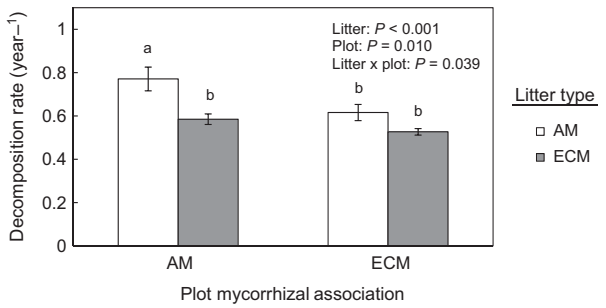

Fig. 2. Decomposition rates (k) of AM (n = 28) and ECM (n = 42) leaf litters in unfertilized AM and ECM plots at Moore's Creek. Bars are means for each litter type; one SE of the mean is presented. Different letters indicate significant differences from *post hoc* comparisons ($P < 0.05$). Open bars, AM litter; grey bars, ECM litter.

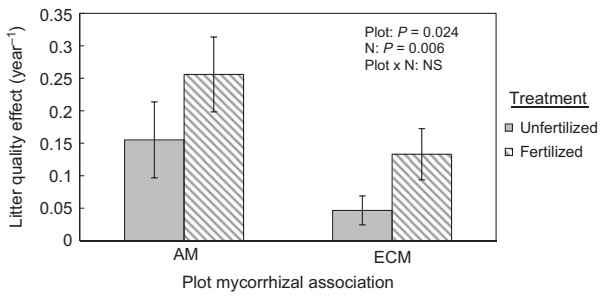

Fig. 3. The Litter Quality Effect (n = 7) in N-fertilized and unfertilized AM and ECM plots at Moore's Creek. Litter Quality Effect is calculated as the mean k value of AM litters minus the mean k values of ECM litters within each plot. Bars are means for each litter type; one SE of the mean is presented. Solid bars, unfertilized plots; hatched bars, fertilized plots.

ferent both when calculated as a range (P = 0.024) and as a variance (P = 0.012).

EXPERIMENT 2B: N FERTILIZATION

The Litter Quality Effect was altered by N addition (Fig. 3). The Litter Quality Effect significantly increased in response to N fertilization (P = 0.006), but the interaction between plot mycorrhizal association and N fertilization was not significant (P = 0.829). There was no significant change in variance in response to N fertilization (P = 0.561), and the interaction between plot mycorrhizal association and N fertilization was not significant (P = 0.871).

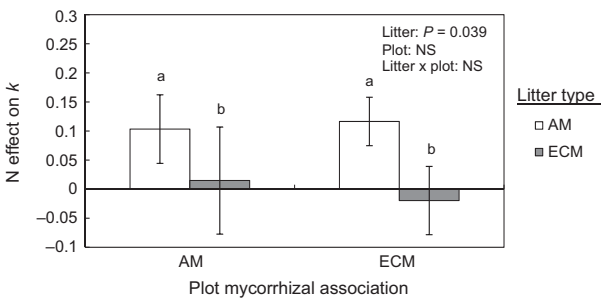

Fig. 4. Effect of N fertilization on decomposition rates (k) of AM (n = 56) and ECM (n = 84) leaf litters in AM and ECM plots at Moore's Creek. Bars are means for each litter type; one SE of the mean is presented. Different letters indicate significant main effect of litter type ($P < 0.05$). Open bars, AM plots; grey bars, ECM plots.

The effect of N fertilization on decomposition rates was significantly different between AM and ECM litters (P = 0.039), but not between AM and ECM plots (P = 0.632; Fig. 4). N fertilization increased the decomposition rate of AM litter while having no effect on ECM litter. In contrast, N fertilization effects on decomposition rates did not vary among leaf litter species (P = 0.230). There was also no interaction between plot mycorrhizal association and litter mycorrhizal association (P = 0.991).

Discussion

While climate and substrate quality control litter decomposition at broad spatial scales, a unified theory for understanding the factors that control local-scale variation in decay rates has been elusive. Numerous studies have shown that single litter types decay differently in adjacent plots that have identical climatic conditions (e.g. temperature and moisture) – indicating that local decomposer communities or differences in

nutrient availability play a critical role in controlling decay rates. Here, we found that AM litter was of higher quality than ECM litter, which resulted in more rapid decomposition of AM litter than ECM litter across all plots. However, the effect of varying litter quality on decomposition rates was enhanced in AM stands, but dampened in ECM stands. Overall, by altering the soil environment, AM trees enhance the decomposition of high-quality AM litter, while litter quality constrains the decomposition of ECM litter across sites.

The higher chemical quality of AM litter resulted in more rapid decomposition of AM litter than ECM litter across all plots (Tables 1 and 2), which complements previous studies (Cornelissen *et al.* 2001). ECM litter had wider C:N and lignin:N ratios than AM litter (Table 2), and these differences were driven by greater N concentrations of AM litter rather than differences in C or lignin concentrations between AM and ECM litters. This finding supports previous studies that have found litter decomposition rates to be positively correlated with litter N concentrations (Melillo, Aber & Muratore 1982; Aerts 1997; Hobbie 2005; Cornwell *et al.* 2008), presumably because at low N concentrations, N availability limits microbial C use and, thus, decomposition rates.

However, as the abundance of ECM litter in the litter matrix increased and soil N concentrations decreased, the Litter Quality Effect decreased (Fig. 1b,d). Similarly, varied litter quality resulted in more variable decomposition rates in AM stands than in ECM stands (Fig. 3). In addition, we found that only the decomposition of high-quality (AM, maple) leaf litter was affected by changes in the surrounding litter matrix and soil N availability, whereas low-quality (ECM, oak) litter decomposed at the same rate regardless of site soil properties (Figs 1a,c, and 2). In other words, oak and other ECM litter did not respond to natural variation in either litter matrix composition or soil N concentrations. One possibility for this lack of response is that the chemistry of ECM litter was above a lignin:N threshold that would make site factors (matrix quality, N availability) important (Prescott 2010). This threshold may also reflect the stoichiometric constraints that low-quality substrates place on microbial assimilation by reducing carbon-use efficiency (Keiblinger *et al.* 2010; Fanin *et al.* 2013). Regardless of the mechanism, neither litter matrix composition nor nutrient availability appears to have impacted the decomposition rates of low-quality litters. Instead, litter chemistry constrained decomposition of ECM litters across sites.

In contrast, AM litters responded strongly to changes in the local-scale soil environment. In particular, AM litter decomposed more rapidly in the soil environment generated by AM trees (i.e. a specialized decomposer community and high N availability) than in the soil environment generated by ECM trees. As N availability and litter matrix quality covary, a challenge lies in quantifying the extent to which litter matrix quality (a potential proxy for decomposer specialization) and/or nutrient availability drove variable decomposition rates of high-quality litter across sites. Two pieces of evidence suggest that N availability rather than litter matrix quality drove these patterns: (i) low-quality leaf litters did not respond to litter matrix quality, and (ii) high-quality litters responded uniformly to N fertilization, regardless of initial site properties.

At local scales, decomposer communities may be optimized to degrade site-specific leaf litter (as recently reviewed by Austin *et al.* 2014). Thus, litter in its native or 'home' environment will decompose more rapidly than in an 'away' environment (Hunt *et al.* 1988; Ayres, Dromph & Bardgett 2006). This prediction is commonly termed the 'home-field advantage' (HFA) hypothesis (Gholz *et al.* 2000). An extension of the HFA hypothesis, the substrate quality-matrix quality interactions (SMI) hypothesis, more broadly suggests that low-quality substrates will decompose more rapidly when incubated in a low-quality litter matrix than when incubated in a high-quality litter matrix and vice versa for high-quality litters due to resource history-driven decomposer community specialization (Freschet, Aerts & Cornelissen 2012). As litter matrix quality increased in AM-dominated plots, decomposition rates of high-quality litters increased (Figs 1a and 2), as predicted by the SMI hypothesis. However, oak and ECM litters did not respond to variation in matrix quality (Figs 1a and 2), limiting our support for the SMI hypothesis.

Alternatively, an emerging hypothesis, the functional breadth hypothesis, predicts that decomposer communities exposed to low-quality litter exhibit high functional capability or 'functional breadth' because low-quality litter matrices span the spectrum of chemical complexity. Conversely, decomposer communities exposed to high-quality litter matrices with lower chemical diversity will have a narrower functional breadth (Van der Heijden, Bardgett & van Straalen 2008; Keiser *et al.* 2011, 2014; Keiser, Knoepp & Bradford 2013). As such, microbial communities exposed to low-quality litter have a greater functional breadth than those exposed to high-quality litter (Keiser *et al.* 2014), leading to greater variation in litter decomposition rates in sites with high-quality litter matrixes than in low-quality litter matrices – a pattern we also observed (Figs 1b and 3). While the decomposition patterns we observed are more closely aligned with those predicted by the functional breadth hypothesis, they do not support the underlying mechanisms. In this hypothesis, the microbial ability to decompose high-quality substrates is thought to be ubiquitous whereas the ability to degrade low-quality substrates is limited to the environments where they are produced by plants (Osono 2007; Ayres *et al.* 2009; Freschet *et al.* 2011). In this study, we find the opposite pattern: variable Litter Quality Effects were the result of variations in the decomposition rates of high-quality litters across sites rather than those of low-quality litters.

The decomposition rate of maple litter increased across the N availability gradient (Fig. 1c) and responded uniformly to N fertilization (Fig. 4), suggesting that variation in N availability, constrained by litter quality, drove our observed decomposition patterns. While the decomposition rate of maple leaf litter increased as matrix litter quality increased (Fig. 1a), litter quality is highly correlated with inorganic N availability at these sites (Phillips, Brzostek & Midgley 2013). Additionally, in our second experiment, AM litter decomposition rates increased when N fertilizer was added,

regardless of plot type (Fig. 4) leading to a uniform increase in the Litter Quality Effect. This finding compliments other studies that have shown that litter decomposes faster in nutrient-rich sites than in nutrient-poor sites (Swift, Heal & Anderson 1979; Prescott 1996; Norris *et al.* 2013), and N fertilization increases decomposition rates of labile leaf litter (Hobbie & Vitousek 2000; Knorr, Frey & Curtis 2005). Increased N availability is hypothesized to increase rates of decay by alleviating N limitation of C-degrading enzymes (Sinsabaugh & Moorhead 1994; Carreiro *et al.* 2000; Allison, Hanson & Treseder 2007) or enhancing C-use efficiency (Manzoni *et al.* 2012). Several other studies have also found that labile litter is more responsive to changes in matrix quality than recalcitrant litters (Keiser, Knoepp & Bradford 2013; Perez *et al.* 2013; Wang, Zhong & He 2013), but ours is the first to clarify a mechanism driving this pattern. While Vivanco & Austin (2011) found that microbial specialization effects were disrupted by N addition, we suggest that in this study, microbial specialization effects were limited or non-existent before N addition. Instead, our results suggest that N availability controlled labile litter decomposition both across a gradient of N availability as well as in N-fertilized plots. Here, we show that N availability drives differences in the function of the microbial communities rather than decomposer specialization *per se.*

Our results do not support the hypothesis that the decomposition rates of low-quality litters would be dampened by N addition. The increase in high-quality litter decomposition that we observed is similar to that of Hobbie (2005), who found that after 1 year of decomposition N fertilization either increased decomposition or had no effect on leaf litter decomposition rates. Furthermore, in a follow-up study, Hobbie *et al.* (2012) found that while inorganic N increased decomposition rates, it did not alter microbial community composition. At the later stages of decomposition, however, N fertilization had negative or neutral effects on decomposition rates, regardless of initial litter chemistry (Hobbie 2008). This suggests that negative effects may become more prevalent over time, but were not detected during this 1.5-year study.

This study supports the emerging perspective that microbial community specialization effects are strongly context dependent (Freschet, Aerts & Cornelissen 2012; Veen *et al.* 2015). For instance, even when litters are inoculated with their 'home' microbes in laboratory microcosms where all other factors are controlled, support for the HFA is mixed (Ayres, Dromph & Bardgett 2006; Strickland *et al.* 2009). The reason for these variable results may lie in the spatial separation as well as the degree of contrast between the collected litters and soils; HFA is not apparent when samples are collected from forest stands separated by less than 500 m (Ayres, Dromph & Bardgett 2006), but emerges when samples are collected from distinct ecosystems within the continental United States (Strickland *et al.* (2009). Similar variability has been detected in microbial community development: site-specific microbial products are produced when litters and site properties are highly contrasting (Wallenstein *et al.* 2010), while microbial communities are litter-specific when sites are more similar (Aneja *et al.* 2006). These experiments, while useful for testing the broader relevance of HFA, thus do not consider whether fine-scale variation in decomposer communities influences litter decomposition dynamics. Thus, while the overall litter quality of the litter matrix decreased across the mycorrhizal gradient, microbial communities in AM-dominated sites appear to contain microbes capable of degrading lignin-rich, low-quality materials due to their proximity and relative similarity to ECM-dominated sites, decreasing specialization effects.

Our results have several implications for incorporating more detailed leaf litter decomposition dynamics into global climate models. We found that decomposition rates are less variable in forests where N is cycled slowly (ECM forests) and more variable in plots where N is cycled more rapidly (AM forests). As tree community compositions are expected to change as tree species migrate in response to climate change, our data suggest that modellers only need one litter decomposition rate to capture leaf litter decomposition dynamics in forests with low-quality litter matrices while a range of decomposition rates are needed to capture leaf litter decomposition dynamics in forests with high-quality litter matrices. When N deposition is included in models, leaf litter decomposition rates should span a much wider range of variation in ecosystems exposed to high N deposition rates, but be more narrowly constrained in low N deposition areas.

In addition to influencing decomposition rates though litter quality (Melillo, Aber & Muratore 1982), plants can alter soil properties that feedback to impact leaf litter decomposition rates (Vivanco & Austin 2008; Ward *et al.* 2015). Here, AM trees enhance the decomposition of their own leaf litter by increasing soil N availability while stands dominated by ECM trees have limited soil N, which dampens AM litter decomposition. In contrast, ECM litter decomposition rates are not altered by soil properties; low-quality ECM litter decomposes slowly across all sites. In temperate deciduous forests, the relative abundance of oak has declined and *A. saccharum* often replaces the oak trees. This may result in increased and more variable decomposition rates in these ecosystems if N cycling rates increase, or decomposition rates may be maintained if slow N cycling persists. Thus, our study supports the importance of litter quality for mediating decomposition rates, but also highlights the potential for plants to have indirect impacts on litter decomposition rates via their effects on soil properties.

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Data accessibility

Data deposited in the Dryad repository: http://datadryad.org/resource/doi:10.5061/dryad.6kp2n (Midgley, Brzostek & Phillips 2015).

References

Aerts, R. (1997) Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. *Oikos*, **79**, 439–449.

Allison, S.D., Hanson, C.A. & Treseder, K.K. (2007) Nitrogen fertilization reduces diversity and alters community structure of active fungi in boreal ecosystems. *Soil Biology and Biochemistry*, **39**, 1878–1887.

Aneja, M.K., Sharma, S., Fleischmann, F., Stich, S., Heller, W., Bahnweg, G., Munch, J.C. & Schloter, M. (2006) Microbial colonization of beech and spruce litter – influence of decomposition site and plant litter species on the diversity of microbial community. *Microbial Ecology*, **52**, 127–135.

Austin, A.T., Vivanco, L., González-Arzac, A. & Pérez, L.I. (2014) There's no place like home? An exploration of the mechanisms behind plant litter–decomposer affinity in terrestrial ecosystems. *New Phytologist*, **204**, 307–314.

Ayres, E., Dromph, K.M. & Bardgett, R.D. (2006) Do plant species encourage soil biota that specialise in the rapid decomposition of their litter? *Soil Biology and Biochemistry*, **38**, 183–186.

Ayres, E., Steltzer, H., Simmons, B.L., Simpson, R.T., Steinweg, J.M., Wallenstein, M.D., Mellor, N., Parton, W.J., Moore, J.C. & Wall, D.H. (2009) Home-field advantage accelerates leaf litter decomposition in forests. *Soil Biology and Biochemistry*, **41**, 606–610.

Berg, B., Berg, M.P., Bottner, P., Box, E., Breymeyer, A., de Anta, R.C. *et al.* (1993) Litter mass loss rates in pine forests of Europe and Eastern United States: some relationships with climate and litter quality. *Biogeochemistry*, **20**, 127–159.

Bocock, K.L. & Gilbert, O.J.W. (1957) The disappearance of leaf litter under different woodland conditions. *Plant and Soil*, **9**, 179–185.

Bradford, M.A., Warren, R.J., Baldrian, P., Crowther, T.W., Maynard, D.S., Oldfield, E.E., Wieder, W.R., Wood, S.A. & King, J.R. (2014) Climate fails to predict wood decomposition at regional scales. *Nature Climate Change*, **4**, 625–630.

Braun, E.L. (1947) Development of the deciduous forests of eastern North America. *Ecological Monographs*, **17**, 211–219.

Brundrett, M., Murase, G. & Kendrick, B. (1990) Comparative anatomy of roots and mycorrhizae of common Ontario trees. *Canadian Journal of Botany*, **68**, 551–578.

Carreiro, M.M., Sinsabaugh, R.L., Repert, D.A. & Parkhurst, D.F. (2000) Microbial enzyme shifts explain litter decay responses to simulated nitrogen deposition. *Ecology*, **81**, 2359–2365.

Cornelissen, J., Aerts, R., Cerabolini, B., Werger, M. & van der Heijden, M. (2001) Carbon cycling traits of plant species are linked with mycorrhizal strategy. *Oecologia*, **129**, 611–619.

Cornwell, W.K., Cornelissen, J.H.C., Amatangelo, K., Dorrepaal, E., Eviner, V.T., Godoy, O. *et al.* (2008) Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters*, **11**, 1065–1071.

Cotrufo, M.F., Wallenstein, M.D., Boot, C.M., Denef, K. & Paul, E. (2013) The Microbial Efficiency-Matrix Stabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: do labile plant inputs form stable soil organic matter? *Global Change Biology*, **19**, 988–995.

Dukes, J.S. & Field, C.B. (2000) Diverse mechanisms for CO_2 effects on grassland litter decomposition. *Global Change Biology*, **6**, 145–154.

Fanin, N., Fromin, N., Buatois, B. & Hättenschwiler, S. (2013) An experimental test of the hypothesis of non-homeostatic consumer stoichiometry in a plant litter-microbe system. *Ecology Letters*, **16**, 764–772.

Freschet, G.T., Aerts, R. & Cornelissen, J.H.C. (2012) Multiple mechanisms for trait effects on litter decomposition: moving beyond home-field advantage with a new hypothesis. *Journal of Ecology*, **100**, 619–630.

Freschet, G.T., Dias, A.T.C., Ackerly, D.D., Aerts, R., Van Bodegom, P.M., Cornwell, W.K. *et al.* (2011) Global to community scale differences in the prevalence of convergent over divergent leaf trait distributions in plant assemblages. *Global Ecology and Biogeography*, **20**, 755–765.

Gholz, H.L., Wedin, D.A., Smitherman, S.M., Harmon, M.E. & Parton, W.J. (2000) Long-term dynamics of pine and hardwood litter in contrasting environments: toward a global model of decomposition. *Global Change Biology*, **6**, 751–765.

Herman, J., Moorhead, D. & Berg, B. (2008) The relationship between rates of lignin and cellulose decay in aboveground forest litter. *Soil Biology and Biochemistry*, **40**, 2620–2626.

Hobbie, S.E. (2005) Contrasting effects of substrate and fertilizer nitrogen on the early stages of litter decomposition. *Ecosystems*, **8**, 644–656.

Hobbie, S.E. (2008) Nitrogen effects on decomposition: a five-year experiment in eight temperate sites. *Ecology*, **89**, 2633–2644.

Hobbie, S.E. & Vitousek, P.M. (2000) Nutrient limitation of decomposition in Hawaiian forests. *Ecology*, **81**, 1867–1877.

Hobbie, S.E., Eddy, W.C., Buyarski, C.R., Adair, E.C., Ogdahl, M.L. & Weisenhorn, P. (2012) Response of decomposing litter and its microbial community to multiple forms of nitrogen enrichment. *Ecological Monographs*, **82**, 389–405.

Hunt, H.W., Ingham, E.R., Coleman, D.C., Elliott, E.T. & Reid, C.P.P. (1988) Nitrogen limitation of production and decomposition in prairie, mountain meadow, and pine forest. *Ecology*, **69**, 1009–1016.

Janzen, H.H., Entz, T. & Ellert, B.H. (2002) Correcting mathematically for soil adhering to root samples. *Soil Biology and Biochemistry*, **34**, 1965–1968.

Keiblinger, K.M., Hall, E.K., Wanek, W., Szukics, U., Hämmerle, I., Ellersdorfer, G., Böck, S., Strauss, J., Sterflinger, K., Richter, A. & Zechmeister-Boltenstern, S. (2010) The effect of resource quantity and resource stoichiometry on microbial carbon-use-efficiency. *FEMS Microbiology Ecology*, **73**, 430–440.

Keiser, A.D., Knoepp, J.D. & Bradford, M.A. (2013) Microbial communities may modify how litter quality affects potential decomposition rates as tree species migrate. *Plant and Soil*, **372**, 167–176.

Keiser, A.D., Strickland, M.S., Fierer, N. & Bradford, M.A. (2011) The effect of resource history on the functioning of soil microbial communities is maintained across time. *Biogeosciences*, **8**, 1477–1486.

Keiser, A.D., Keiser, D.A., Strickland, M.S. & Bradford, M.A. (2014) Disentangling the mechanisms underlying functional differences among decomposer communities. *Journal of Ecology*, **102**, 603–609.

Knorr, M., Frey, S.D. & Curtis, P.S. (2005) Nitrogen additions and litter decomposition: a meta-analysis. *Ecology*, **86**, 3252–3257.

Manzoni, S., Taylor, P., Richter, A., Porporato, A. & Ågren, G.I. (2012) Environmental and stoichiometric controls on microbial carbon-use efficiency in soils. *New Phytologist*, **196**, 79–91.

Melillo, J.M., Aber, J.D. & Muratore, J.F. (1982) Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology*, **63**, 621–626.

Midgley, M.G., Brzostek, E. & Phillips, R.P. (2015) Data from: decay rates of high-quality AM leaf litters are more sensitive to soil properties than low-quality ECM litters. *Journal of Ecology*, http://datadryad.org/resource/doi:10.5061/dryad.6kp2n.

Millennium Ecosystem Assessment. (2005) *Ecosystems and Human Well-Being: Synthesis*. Island Press, Washington, DC, USA.

Moorhead, D.L. & Reynolds, J.F. (1993) Changing carbon-chemistry of buried creosote bush litter during decomposition in the northern Chihuahuan Desert. *American Midland Naturalist*, **130**, 83–89.

Nakagawa, S. & Cuthill, I.C. (2007) Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biological Reviews*, **82**, 591–605.

National Atmospheric Deposition Program. (2013) *2012 Annual summary – Illinois State Water Survey Miscellaneous Publication/NADP Data Report 2013–01*.

Norris, M.D., Avis, P.G., Reich, P.B. & Hobbie, S.E. (2013) Positive feedbacks between decomposition and soil nitrogen availability along fertility gradients. *Plant and Soil*, **367**, 347–361.

Olson, J.S. (1963) Energy storage and the balance of producers and decomposers in ecological systems. *Ecology*, **44**, 322–331.

Osono, T. (2007) Ecology of ligninolytic fungi associated with leaf litter decomposition. *Ecological Research*, **22**, 955–974.

Perez, G., Aubert, M., Decaens, T., Trap, J. & Chauvat, M. (2013) Home-field advantage: a matter of interaction between litter biochemistry and decomposer biota. *Soil Biology and Biochemistry*, **67**, 245–254.

Phillips, R.P., Brzostek, E. & Midgley, M.G. (2013) The mycorrhizal-associated nutrient economy: a new framework for predicting carbon-nutrient couplings in temperate forests. *New Phytologist*, **199**, 41–51.

Prescott, C.E. (1996) Influence of forest floor type on rates of litter decomposition in microcosms. *Soil Biology and Biochemistry*, **28**, 1319–1325.

Prescott, C.E. (2010) Litter decomposition: what controls it and how can we alter it to sequester more carbon in forest soils? *Biogeochemistry*, **101**, 133–149.

Sinsabaugh, R.L. & Moorhead, D.L. (1994) Resource allocation to extracellular enzyme production: a model for nitrogen and phosphorus control of litter decomposition. *Soil Biology & Biochemistry*, **26**, 1305–1311.
Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture. Web Soil Survey. URL http://websoilsurvey.nrcs.usda.gov/.
Strickland, M.S., Lauber, C., Fierer, N. & Bradford, M.A. (2009) Testing the functional significance of microbial community composition. *Ecology*, **90**, 441–451.
Swift, M.J., Heal, O.W. & Anderson, J.M. (1979) *Decomposition in Terrestrial Ecosystems*. University of California Press, Berkeley, CA, USA.
Van der Heijden, M.G.A., Bardgett, R.D. & van Straalen, N.M. (2008) The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. *Ecology Letters*, **11**, 296–310.
Veen, G.F.C., Freschet, G.T., Ordonez, A. & Wardle, D.A. (2015) Litter quality and environmental controls of home-field advantage effects on litter decomposition. *Oikos*, **124**, 187–195.
Verhoef, H.A. & Brussaard, L. (1990) Decomposition and nitrogen mineralization in natural and agroecosystems: the contribution of soil animals. *Biogeochemistry*, **11**, 175–211.
Vitousek, P.M. (1984) Anion fluxes in three Indiana forests. *Oecologia*, **61**, 105–108.
Vivanco, L. & Austin, A.T. (2008) Tree species identity alters forest litter decomposition through long-term plant and soil interactions in Patagonia, Argentina. *Journal of Ecology*, **96**, 727–736.
Vivanco, L. & Austin, A.T. (2011) Nitrogen addition stimulates forest litter decomposition and disrupts species interactions in Patagonia, Argentina. *Global Change Biology*, **17**, 1963–1974.
Wall, D.H., Bradford, M.A., St. John, M.G., Trofymow, J.A., Behan-Pelletier, V., Bignell, D.E. *et al.* (2008) Global decomposition experiment shows soil animal impacts on decomposition are climate-dependent. *Global Change Biology*, **14**, 2661–2677.
Wallenstein, M.D., Hess, A.M., Lewis, M.R., Steltzer, H. & Ayres, E. (2010) Decomposition of aspen leaf litter results in unique metabolomes when decomposed under different tree species. *Soil Biology and Biochemistry*, **42**, 484–490.
Wang, B. & Qiu, Y.-L. (2006) Phylogenetic distribution and evolution of mycorrhizas in land plants. *Mycorrhiza*, **16**, 299–363.
Wang, Q., Zhong, M. & He, T. (2013) Home-field advantage of litter decomposition and nitrogen release in forest ecosystems. *Biology and Fertility of Soils*, **49**, 427–434.
Ward, S.E., Orwin, K.H., Ostle, N.J., Briones, M.J.I., Thomson, B.C., Griffiths, R.I., Oakley, S., Quirk, H. & Bardgett, R.D. (2015) Vegetation exerts a greater control on litter decomposition than climate warming in peatlands. *Ecology*, **96**, 113–123.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Decomposition rates (k) of *Acer saccharum* (SM), *Liriodendron tulipifera* (TP), *Carya glabra* (PH), *Quercus alba* (WO) and *Quercus rubra* (RO) litters in AM and ECM plots at Moore's Creek (n = 7).