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REGULAR ARTICLE

Microbial communities may modify how litter quality affects potential decomposition rates as tree species migrate

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Abstract
Background and aims Climate change alters regional plant species distributions, creating new combinations of litter species and soil communities. Biogeographic patterns in microbial communities relate to dissimilarity in microbial community function, meaning novel litters to communities may decompose differently than predicted from their chemical composition. Therefore, the effect of a litter species in the biogeochemical cycle of its current environment may not predict patterns after migration. Under a tree migration sequence we test whether litter quality alone drives litter decomposition, or whether soil communities modify quality effects.
Methods Litter and soils were sampled across an elevation gradient of different overstory species where lower elevation species are predicted to migrate upslope. We use a common garden, laboratory microcosm design (soil community x litter environment) with single and mixed-species litters.
Results We find significant litter quality and microbial community effects ($P<0.001$), explaining 47 % of the variation in decomposition for mixed-litters.
Conclusion Soil community effects are driven by the functional breadth, or historical exposure, of the microbial communities, resulting in lower decomposition of litters inoculated with upslope communities. The litter x soil community interaction suggests that litter decomposition rates in forests of changing tree species composition will be a product of both litter quality and the recipient soil community.

Keywords Litter decomposition · Carbon mineralization · Microbial community function · Functional breadth · Environmental gradient

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Introduction

Leaf litter has been recognized as an essential component of nutrient cycling and availability (Perala and Alban 1982) with foliar inputs accounting for the majority of aboveground litter in forested systems (Jacob et al. 2009; Kamei et al. 2009; Kang et al. 2009). Litter decomposition patterns are traditionally thought to be controlled by three main drivers: climate > litter quality > the decomposer community (Aerts 1997; Meentemeyer 1978). At a global scale, climate appears to drive patterns of decomposition (Gholz et al. 2000; Parton et al. 2007; Adair et al. 2008; Cusack et al. 2009), but regionally, litter quality is the strongest predictor (Aerts 1997; Cornwell et al. 2008). Both physical and chemical litter properties can drive variation seen

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among decomposition rates due to varying surface leaf area, defense compounds (e.g. waxes), or chemical composition (e.g. lignin concentration) (Cornelissen et al. 2003; Cornwell et al. 2008; Hoorens et al. 2010). Soil communities can modify all drivers, even at global scales (Wall et al. 2008), but it is locally that the soil community, interacting with litter quality, is thought to most strongly influence decay rates (Cornelissen et al. 2003; Kang et al. 2009). It has been demonstrated that the resource history of the soil microbial community appears to influence contemporary function, in terms of litter decomposition (Strickland et al. 2009a). This phenomenon is explained by the theory of functional breadth whereby microbial communities exposed to recalcitrant litter will have a wide functional breadth to deal with a range of compounds (van der Heijden et al. 2008; Keiser et al. 2011), and vice-versa. Therefore, the decomposer community, due to its range in functional breadth (van der Heijden et al. 2008), may hold a larger role in litter decomposition than initially expected.

The view that soil communities are functionally redundant (de Wit and Bouvier 2006; Wertz et al. 2006) has slowly eroded as dissimilarity in function is demonstrated across different communities. For example, litter is often decomposed faster with its local soil community (Strickland et al. 2009a; Ayres et al. 2009; Wallenstein et al. 2010). Despite the expectation of rapid adaptation in soil microbial communities, such functional differences between communities appear to be maintained over time in a common environment (Keiser et al. 2011). Furthermore, biogeographic patterns have been observed across microbial communities (Martiny et al. 2006; Ramette and Tiedje 2007), but it is unknown as to whether migration will alter existing variation among communities. New individuals can arrive at a site, but are not guaranteed to establish. If functional differences between soil communities persist within regional gradients, range shifts among tree species may result in unanticipated changes in decomposition, and, in turn, carbon and nitrogen cycling.

Under climate change predictions, tree species are expected to move upward in elevation and poleward (Wolters et al. 2000; McKenney et al. 2007; Lee et al. 2005). This may present novel litter inputs to resident soil microbial communities. Given that soil microbial communities can sustain historical differences in function, novel litter inputs to upslope communities may decompose at rates different than would be expected based on litter identity or climate alone. In this study, we examined whether litter identity has the potential to drive decomposition patterns under relevant scenarios of tree species migration, independent of the soil community. We used materials from three field sites in the southern Appalachian Mountains, in western North Carolina across an elevation gradient (782–1,364 m asl) and a transition in dominant overstory tree species. Soil communities and freshly-fallen, senesced leaf material were collected from each of the sites and combined in a full-factorial, and litter-mixing design. Using experimental microcosms, to control for climate differences which commonly occur along elevation gradients (Laganiere et al. 2010; Carpenter 1996), we tested two competing hypotheses: (H1) If "litter quality" is the sole driver, then more recalcitrant litters will decompose more slowly with any soil microbial community, regardless of its origin (Chapin et al. 1996). (H2) If the soil microbial community modifies litter decomposition, then patterns will emerge representing "functional breadth" (van der Heijden et al. 2008) whereby low-nutrient ecosystems have high microbial functional diversity in response to the diversity of compounds found in chemically-complex litters. The opposite is true for nutrient-rich ecosystems (van der Heijden et al. 2008; Keiser et al. 2011). Therefore, the soil microbial community from the higher elevation, nutrient-poor site will decompose litter of differing chemical recalcitrance at similar rates. The microbial community from the lower-elevation, comparably nutrient-rich site will decompose more recalcitrant litters (e.g. higher C:N ratio) at slower rates. Previous work demonstrates the potential for microbial community function to influence litter decomposition patterns (Strickland et al. 2009a; Schimel and Schaeffer 2012), but few analytical studies provide direct evidence for historical processes influencing function (Hanson et al. 2012). We examine whether these patterns exist within a single ecotype, a forested, elevation gradient, where we might expect functional differences between soil microbial communities to disappear under a single plant functional group.

Methodology

Species and site selection

Three tree species were selected whose ranges are predicted to shift both upslope and poleward under both conservative (PCM Low) and extreme (Hadley High)

global climate change scenarios: *Betula alleghaniensis* (yellow birch), *Liriodendron tulipifera* (tulip poplar), and *Picea rubens* (red spruce) (Prasad et al. 2007-ongoing). *Betula alleghaniensis* belongs to the list of 25 North American trees with the largest projected shift northward under full dispersal scenarios (McKenney et al. 2007). Due to its occupation of high elevation habitat, *P. rubens* is expected to be extirpated from the United States (Iverson and Prasad 2001). As *B. alleghaniensis* decreases in abundance by migrating into current *P. rubens* territory, *L. tulipfera* could migrate into the habitat *B. alleghaniensis* leaves behind (Iverson and Prasad 2001; Prasad et al. 2007-ongoing). All three study species represent a range in leaf litter chemical quality, from chemically labile (*L. tulipifera*) to recalcitrant (*P. rubens*; Table 1). While C:N ratio tends to indicate early patterns in litter decomposition, lignin:N drives longer-term dynamics (Jacob et al. 2010). We examine both across the duration of our study (Table 1, Online Resource 1).

Soil and leaf litter were collected from the Coweeta Hydrologic Laboratory located in southwestern, North Carolina (35°00′N, 83°30′W) and a site within the Blue Ridge Parkway National Park, North Carolina. At Coweeta, two plots were selected from a long-term terrestrial gradient study established as part of the NSF-funded Coweeta LTER research program: the cove hardwood site (CH) (795 m asl) and the northern hardwood site (NH) (1,347 m asl). At CH, *L. tulipifera* is dominant, and at NH, *B. alleghaniensis* is dominant. The third site (1,634 m asl) is located on National Park Service lands adjacent to the Blue Ridge Parkway (BR), North Carolina (35°17′N, 82°54′W). BR is dominated by *P. rubens*, and is representative of tree species found at higher elevations and latitudes. For simplicity, the three locations are referred to as Low (CH), Mid (NH) and High (BR).

Table 1 Initial litter properties. Values shown are mean (± SE)

Parameter	Litter type		
	L. tulipifera (LITU)	*B. alleghaniensis (BEAL)*	*P. rubens (PIRU)*
% C	48.2±0.06	48.9±0.03	51.7±0.06
% N	0.83±0.003	0.99±0.004	0.86±0.004
C:N	58.3±0.26	49.3±0.18	60.1±0.28
Non-fibrous (%)	72.0±0.13	65.6±0.15	41.5±0.40
Hemi-cellulose (%)	9.9±0.06	12.2±0.15	12.2±0.19
Cellulose (%)	11.5±0.11	11.9±0.11	23.8±0.10
Lignin (%)	6.6±0.06	10.3±0.03	22.4±0.33

Experimental design

Leaf litter of each species was collected during autumnal senescence (October 2008) from the site at which each species is dominant. While *P. rubens* does not exclusively drop in the autumn, newly senesced needles were present for collection. Leaves were collected from the forest floor by hand, and transported to the laboratory for additional sorting and drying. Those leaves which appeared to be free from fungal colonization and herbivory were retained and air-dried to a consistent mass (minimum of 96 h). Laboratory microcosms were prepared following the approaches described in Strickland et al. (2009a, b) and Keiser et al. (2011). First, litter was milled (Wiley mill, 2 mm) to create a consistent size class across species. The litter was then sterilized by autoclaving (121 °C, 20 min) twice in succession, and again 24 h later. Finally, the litter was oven-dried at 65 °C. A composite soil sample was collected from the surface 7.5 cm (mineral soils) after carefully removing the litter layer (Strickland et al. 2009a; Keiser et al. 2011). Typical of the southeastern U.S., there is not a developed Oa (H) horizon at the surface. Soils were returned to the lab on ice, homogenized, and sieved to 2 mm. Litter and soils were then combined in 50 mL plastic, centrifuge tubes. We used 0.5 g of soil inoculum mixed with 1.0 g of litter following protocols in Strickland et al. (2009a) and Keiser et al. (2011). Water-holding capacities of the microcosms were adjusted to and maintained at 65 %, which is within the favorable range for microbial activity (Langenheder and Prosser 2008).

Monoculture litter x soil combinations composed a 3 × 3 factorial design. Since we were interested in upslope migration, our litter mixtures represented a transition in dominance from one species to another to simulate a gradual, upslope migration as opposed to a 50–50 mix that is often used in litter mixture studies. For example, *P. rubens* and *B. alleghaniensis* were established in three mixtures (80 %–20 %, 50 %–50 %, 20 %–80 %) and combined with soils from their respective "home" sites (High and Mid, respectively). In total, there were 6 litter mixtures (Table 2). Six replicates were established for each combination (total experimental units=126). Litter – soil mixtures were dried at 65 °C

Table 2 A summary of the litter types (single and mixed-species) combined with each soil inoculum. Each litter type is represented by species code: LITU = *L. tulipifera*, BEAL = *B. alleghaniensis*, and PIRU = *P. rubens*. Low, mid and high refers to elevation and sampling location of the respective soil inocula. For each combination there were 6 replicates (n=126)

Litter	Soil Inoculum		
	Low	Mid	High
100 % LITU	x	x	x
100 % BEAL	x	x	x
100 % PIRU	x	x	x
80 % BEAL, 20 % LITU	x	x	
50 % BEAL, 50 % LITU	x	x	
20 % BEAL, 80 % LITU	x	x	
80 % PIRU, 20 % BEAL		x	x
50 % PIRU, 50 % BEAL		x	x
20 % PIRU, 80 % BEALs		x	x

for 72 h at the end of 300 days to calculate total litter mass loss.

Carbon mineralization rates

Carbon mineralization rates were measured 18 times across the 300-day experiment, following Strickland et al. (2009a). Briefly, for each measurement, centrifuge tubes were fitted with gas-tight lids modified with septa for gas analysis. They were flushed with CO_2-free air and incubated for 24 h. Headspace CO_2 concentrations were measured using infra-red gas analysis (IRGA) (Li-COR model LI-7000, Lincoln, NE, USA). Soils-only tubes were also established for each soil type (n=9) to determine soil-derived CO_2 efflux. These values were subtracted from the litter microcosm fluxes to estimate litter mineralization rates. Cumulative litter-carbon mineralized for each replicate was determined by integrating rate values across the 300 days.

Initial litter chemistry

A subsample of each original litter species was ball-milled for chemical analysis using a Spex CertiPrep 8000-D Mixer Mill (Spex, Metuchen, New Jersey, USA). Carbon and nitrogen concentrations were determined using a NA 1500 CHN analyzer (Carlo Erba Strumentazione, Milan, Italy). Leaf litter cellulose, hemicellulose, and lignin concentrations were determined using an Ankom A200 Fiber Analyzer (Ankom, Macedon, New York, USA).

Statistical analyses

To test between our competing hypotheses related to whether litter quality effects are modified by the soil community, the data were separated by litter monocultures versus mixtures. ANOVA was used to test the interactive effects of microbial community (Low, Mid, High) and litter identity (single litters, 3 types) on cumulative carbon mineralization. Tukey's HSD, post-hoc analysis was used to help disentangle differences among the soil x litter combinations. Percent sum of squares was used to describe the variation explained by each main effect. A second ANOVA was run to test the interactive effects of microbial community (Low, Mid, High) and litter identity (6 mixtures, see Table 2) on cumulative carbon mineralization. All analyses were performed using the statistical package R (Team 2009).

To test for the presence of additive effects and examine whether the soil community modified litter quality effects in the mixed-litter microcosms, we calculated the observed – expected values. This was calculated as % difference $= [(\text{observed} - \text{expected})/\text{expected}] * 100$.

A mixture of soil communities was used in the calculation to account for the site from which each litter species is dominant. The expected value was derived from a combination of each litter's "home" soil inoculum x single litter microcosm, in the correct percentage. For example, 80 % *B. alleghaniensis*+20 %*L. tulipifera* was 80 % of the cumulative value from *B. alleghaniensis* on the Mid inoculum+20 % of the cumulative value from *L. tulipifera* on the Low inoculum. The observed value was strictly the cumulative value for the mixed-litter microcosm on the upslope inoculum, or the site to which the lower elevation species is expected to travel. For example, the observed cumulative value for 80 % *B. alleghaniensis*+20 %*L. tulipifera* was taken from that mixture on the Mid inoculum.

In order to quantitatively assess the presence of functional breadth in the single-species microcosms, the percentage difference between litters was averaged within each soil community. In this calculation, only observed values were used (e.g. $[L.\ tulipifera_{\text{Low}} - P.\ rubens_{\text{Low}}]/P.\ rubens_{\text{Low}}$).

Results

We addressed two competing hypotheses examining whether the soil microbial community modifies litter quality effects on decomposition. Litter quality (H1) examined through litter identity ($P<0.001$, $F_{2,45}=87.66$) explained 70 % of the variation in cumulative carbon mineralized for the single species microcosms. Within a single soil community (Fig. 1a), the variation in cumulative carbon mineralized reflected the chemical quality of the litter (Table 1). For example, *L. tulipifera*, *B. alleghaniensis*, and *P. rubens* on the Low soil community were significantly different from each other ($P<0.05$), and showed decreasing CO_2 production with decreasing chemical quality. *L. tulipifera* was the most chemically labile and had the highest cumulative carbon mineralization while *P. rubens* was the lowest and most chemically recalcitrant. The variation in carbon mineralization according to litter quality was reflected across all three soil communities.

The variable rates of carbon mineralization across soil communities supported a significant litter x soil community interaction ($P=0.01$, $F_{4,45}=3.66$). The differences in magnitude among litter types across soil communities provided evidence for the functional breadth hypothesis (H2). The hypothesis states that soil

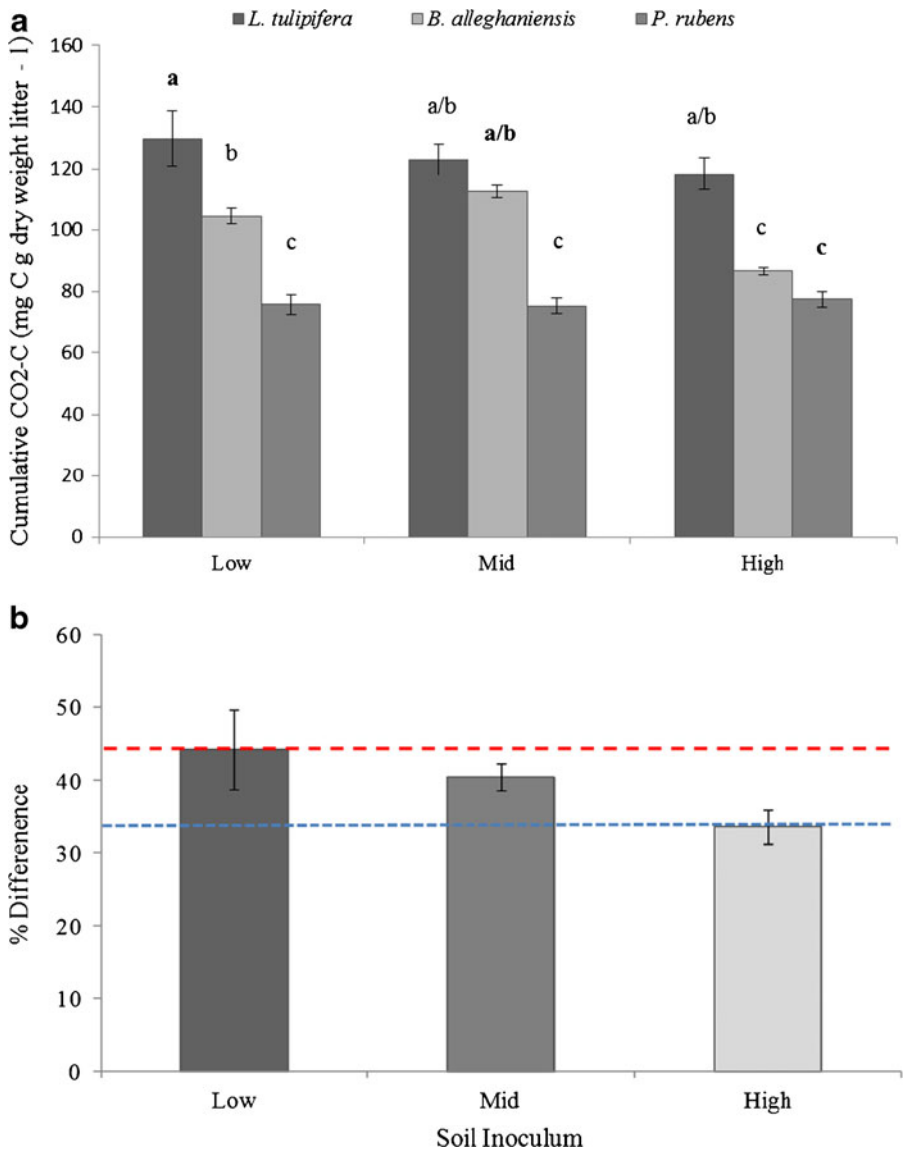

Fig. 1 **a** Cumulative carbon mineralization after 300 days (mean ± SE) for the single-litter microcosms grouped by soil community inoculum. The *color* of the bar indicates litter species. *Letters* represent significant differences between treatments ($P<0.05$), with *bold* indicating the home litter×soil community inoculum treatment combination. Low, mid and high refers to elevation and sampling location of the respective soil inocula. **b** The average percentage difference between all three litter types on a single soil community inoculum. The *dashed lines* represent the percentage difference for the litters on the Low (*red*) and High (*blue*) soil community inocula

communities from recalcitrant environments will have a wider functional breadth to deal with the wide-range in chemical compounds present, while communities from a more labile environment will have a more narrow functional breadth (van der Heijden et al. 2008; Keiser et al. 2011). If there is complete functional breadth, we would have expected the overall percentage difference among litters on a single soil community to be zero. Moving from a more labile environment with a lower expected functional breadth (Low) to a more recalcitrant environment with a higher expected functional breadth (High), the percentage difference among the three litters dropped 11 % (Fig. 1b). There was a strong statistical soil community effect across the single litter microcosms ($P<0.001$, $F_{2,45}=8.09$). Generally, *P. rubens* maintained consistent cumulative values across the three communities. However, the relative differences in carbon mineralization between litters, especially *B. alleghaniensis* and *L. tulipifera* with respect to each other and *P. rubens*, changed depending on soil community (Fig. 1a). For example, *B. alleghaniensis* was 25 %, 9 %, and 36 % less than the more labile *L. tulipifera* on the Low, Mid, and High soil communities, respectively. We present cumulative carbon mineralization because it makes interpretation of the results more clear; however, the patterns are the same with the time course data (Online Resource 1).

We can further explore the role of the soil microbial community in litter decomposition with the mixed-species microcosms, where both litter ($P<0.001$, $F_{2,60}=35.73$) and soil community ($P<0.001$, $F_{2,60}=115.72$) explained 36 and 47 % of the variation, respectively. In each species pairing (Fig. 2a, b), the higher-quality litter is expected to move into the more recalcitrant litter's current habitat. Both litter combinations showed increasing negative, non-additivity with an increasing proportion of the more labile litter (*L. tulipifera*, Fig. 2a and *B. alleghaniensis*, Fig. 2b). This reflected the single-litter results (Fig. 1a) where the more labile litter decomposed faster on its "home" inoculum (*L. tulipifera* on Low and *B. alleghaniensis* on Mid) compared to the upslope site (Mid and High, respectively). Therefore, as the more labile litter increased in proportion within the mixture on the upslope inoculum, the negative, non-additivity increased (Fig. 2a, b). For the *B. alleghaniensis* - *L. tulipifera* mixture (Fig. 2a), the effect was non-significant, which may have reflected the non-significant pair-wise comparison

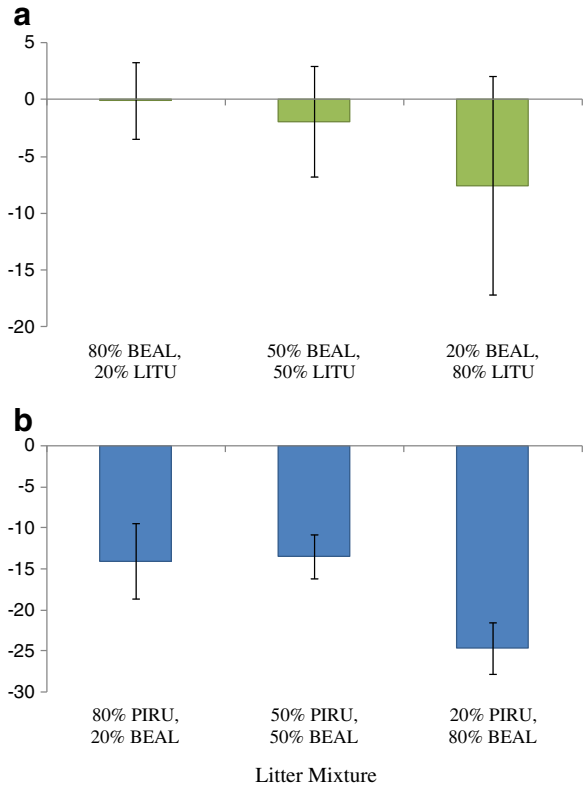

Fig. 2 The percentage difference between the two litter species in each of three proportions (80 %–20 %, 50 %–50 %, 20 %–80 %). The *bar* represents the percentage [observed-expected]/expected value (± CI). **a** A transition from a *B. alleghaniensis* (BEAL) dominated system to one dominated by *L. tulipifera* (LITU). **b** A second, two-species mixture with a transition from a *P. rubens* (PIRU) dominated system to one dominated by B. *alleghaniensis* (BEAL)

($P<0.05$) between *B. alleghaniensis* on the Mid soil inoculum and *L. tulipifera* on the Low soil inoculum. The non-additivity observed among all litter mixtures support the significant litter x microbial community interaction ($P<0.001$, $F_{4,60}=5.93$).

Percent mass remaining was run as a separate linear model. Percent mass remaining was significant ($P<0.001$, $F_{1,124}=375.2$) and explained 75 % (adj. R^2) of the variation in cumulative carbon mineralized.

Discussion

We set out to test whether soil microbial communities impact litter decomposition patterns along a path of predicted tree species migration in the southern

Appalachian Mountains. The functional breadth (H2) of the soil microbial community appears to modify litter quality (H1) effects, which emphasizes the complex interaction between litter chemistry and microbial community function. There is substantial evidence that litter quality, defined as chemical recalcitrance, affects the rate at which organic matter breaks-down due to the inconsistencies among, and strong chemical bonds within, lignin compounds (Rouifed et al. 2010; Hoorens et al. 2010). There are also decomposition studies, especially when examining patterns within a region, where litter quality is not the sole determinant but is instead influenced by microbial community function (Butenschoen et al. 2011; Strickland et al. 2009a). While litter quality produces an over-arching effect on our single-litter mineralization data, the 11 % reduction in relative differences between litter types (shifting from Low to High soil communities) indicates that the soil microbial community modifies decomposition dynamics.

Our results demonstrate that the functional breadth (see van der Heijden et al. 2008), or the historical functional capacity, of a microbial community influences its contemporary functional capacity. Whereby if the microbial community is derived from a location where the dominant overstory species is chemically recalcitrant, then that "home" litter type and any litter more chemically labile will be mineralized at levels that are statistically similar (e.g. *B. alleghaniensis* and *L. tulipifera*, respectively, on Mid-elevation soils, Fig. 1). However, when a litter type more chemically recalcitrant than the "home" litter is introduced, mineralization is lower and significantly different for that new species (e.g. *P. rubens* on the Mid-elevation soil). This reinforces the idea of functional breadth in that a soil microbial community exposed to more chemically recalcitrant materials will have a wider functional breadth to deal with a wide range of compounds, and therefore not differentiate between litter types. The opposite is true for those soil communities derived from environments consisting of more labile organic matter (van der Heijden et al. 2008; Keiser et al. 2011). In the case of *L. tulipifera*, there was a 9 % reduction in decomposition from Low to High, albeit not statistically significant. Within our relevant elevation gradient, the effects are not as dramatic among all litter species as seen in more abstract cases (e.g. Strickland et al. 2009a).

To further explore functional breadth quantitatively, we calculated the relative difference between all litters, as a percentage, on a single soil community. Complete functional breadth would have a percentage difference of zero. This would indicate that the soil community does not functionally perceive differences among litter types, and consequently, different litter species would decompose at the same rate. As perceived differences between litter species increases, the percentage difference would also increase. Shifting upslope from a community with a lower expected functional breadth (Low), with an overstory dominated by the more chemically labile *L. tulipifera*, to one of higher expected functional breadth (High), currently a more recalcitrant spruce-fir stand, the percentage difference among litters drops 11 %. This reduction indicates a decrease in perceived differences among litter types by the High soil community, and subsequently, reduced litter decomposition across the same time period.

The non-linear pattern we observed within litter monocultures for carbon mineralization reflects expected outcomes under functional breadth, but also "home-field advantage". Strickland et al. (2009a) found evidence for "home-field advantage" in conjunction with functional breadth across a large geographic gradient and a range of plant types. The phenomenon of home-field advantage (HFA) suggests that litter from its native environment degrades faster on its native/home soil than it would on soil from a geographically distinct site (Gholz et al. 2000). In this study, HFA may explain the mineralization peak for *B. alleghaniensis* occurring on the Mid soil community. Additionally, the presence of HFA, stronger with increasing chemical recalcitrance of the litter (Milcu and Manning 2011), further emphasizes functional breadth; whereby the functional memory of soil microbial communities influences contemporary functional capacity on foreign litter environments in relation to its "home" litter.

We may expect a litter x soil interaction on monocultures to cause non-additive effects for litter mixtures. Non-additive effects, both positive and negative, have been attributed to varying chemical properties of mixed litters (Bardgett and Shine 1999; Gartner and Cardon 2004; Smith and Bradford 2003; Jacob et al. 2009), as well as the microbial community, through such processes as nutrient transfer (Schimel and Hattenschwiler 2007; Gartner and Cardon 2004; Gessner et al. 2010; Hoorens et al. 2003). Our litter mixtures produce consistent non-additive effects. For both mixture types, the non-additivity became more negative as the percentage

of downslope litter increased within the mixture. According to functional breadth, the upslope soil community, sourced from a more chemically recalcitrant litter environment, should mineralize the "home" litter and any litter more labile at a similar rate. As the downslope species became increasingly dominant in mixture, negative, non-additivity increased. An increase in negativity reflects two factors: (1) a decrease in mineralization of the more labile litter on the upslope soil community, and (2) the upslope soil community mineralizing the more labile, downslope litter at a rate equal to its "home" litter species. Negative, non-additivity illustrates that a slow shift in the relative abundance of two species at an upslope site may result in decreased carbon mineralization. Overall, the results from this study strongly advocate for a decomposition model which incorporates the functional breadth of microbial communities.

The phenomenon of functional breadth has been observed across soil inocula sourced from a large geographic gradient (Strickland et al. 2009a) and contrasting litter types (Keiser et al. 2011). However, we might have expected the effect of the soil microbial community to fall-out within a local, forest gradient where the microbial community deals mainly with a single litter source: trees. We demonstrate here that the diversity of chemical lability among tree litter still produces a soil community effect and a strong litter x soil community interaction. Chapman and Newman (2010) quantified the idea linking microbial community diversity with litter decomposition, and observed microbial diversity increased with increasing litter chemical diversity. However, changes to microbial community composition were irrespective of observed decomposition patterns (Chapman and Newman 2010; Keiser et al. 2011) indicating the importance of the functional breadth of the individuals present. Greater functional diversity, not community diversity (Loreau 2001), may directly correlate to carbon mineralization rates, and, in turn, unanticipated decomposition patterns across the landscape.

Species are predicted to migrate in order to maintain their climate envelopes, but climatic changes are also predicted to outpace tree migration and establishment (McLachlan et al. 2005). This means that the climate conditions into which trees are migrating will likely be changing more rapidly than tree species composition. For example, trees are expected to migrate <100 m yr^{-1} (McLachlan et al. 2005), with recent projections in the New England states of rates as low as 0.5 to 1.7 m yr^{-1} upslope (Tang et al. 2012). This means that trees might migrate only 25 m upslope in 50 years. However, climate projections suggest a warming of 0.5° per decade (IPCC 2007), or 2.5° within the same timeframe. This temporal mismatch might influence how microbial communities perceive the litter quality of the migrating species. For example, 18 years of experimental soil warming (but not durations <10 years) resulted in microbial communities more efficient at using recalcitrant carbon compounds (Frey et al. 2012). This suggests that microbial adaptation to higher temperatures at the decadal scale might influence how they decompose more recalcitrant litters (Frey et al. 2012), altering the functional legacies of microbial communities. It seems unlikely, however, that this will entirely negate the influence of functional breath because both lab assays (Keiser et al. 2011) and long-term field data (Gholz et al. 2000) demonstrate that soil microbial communities retain functional legacies over time. Further research is required to determine whether this means tree migration under warmer temperatures will outpace microbial adaptation to new litter assemblages.

In this study we examined carbon mineralization to better understand the role of soil microbial community function on litter decomposition in the face of impending tree species migration. Through the use of laboratory microcosms, we were able to explore an ecological process while controlling for climatic differences along an elevation gradient (Laganiere et al. 2010). While litter mass remaining and carbon mineralization were highly correlated, it is unknown whether the non-linear decomposition patterns discovered here will be realized in the field. Additional field-based studies are necessary to infer the larger application of these findings. Litter decomposition is a major contributor to organic matter turnover and the total annual carbon flux (Butenschoen et al. 2011). Because of the large contribution of leaf litter decomposition into annual carbon fluxes, as shown here, any shift in the composition of these inputs could scale to dramatic changes in global carbon budgets (Butenschoen et al. 2011; Cornwell et al. 2008). As tree species migrate, microbial communities may have the capacity to adapt to new litter inputs. However, it has been demonstrated that soil microbial communities hold onto functional legacies over time (Keiser et al. 2011). Therefore, if tree species migration and new forest composition is realized, then litter may decompose at a slower rate upslope, both in monoculture and in mixture, than would be expected based on current expectations. There is little experimental work

linking historical process to microbial community function (Hanson et al. 2012; Keiser et al. 2011), but we have demonstrated here, under an applied setting, that functional breadth of the soil microbial community modifies litter quality effects on decomposition.

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