



Climate masks decomposer influence in a cross-site litter decomposition study



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ABSTRACT

Leaf litter is a significant input of carbon and nutrients to forested systems. Rates of foliar decomposition, and cycling of carbon and nutrients, appear consistently explained by climate and litter quality. Although the soil decomposer community actually mineralizes litter, its independent role is often undetected in cross-site studies. At three sites along an elevational gradient in eastern U.S. temperate forest, we used a reciprocal litter transplant design to explore whether climate masks the functional influence of the decomposer community on litter decomposition dynamics in the short- and longer-term. Climate, measured as the climate decomposition index, best predicted mass loss in the longer term, over 23 and 31 months (the maximum incubation period). However, decomposer community function also predicted mass loss dynamics across the same time period. Therefore, climate effects on mass loss correlated positively with differences in the functional ability of the three soil decomposer communities. Our findings suggest that climate ‘masks’ the independent influence of the soil decomposer community over litter mass loss dynamics, because direct positive effects of more favorable climate on decomposition rates appear correlated with greater functional potential of the decomposer communities. These results fit within existing theory and experimental evidence that soil microorganisms both adapt to their climate regime, and are directly, through biotic activity, and indirectly, via community structure or function, affected by climate. These non-linear effects of climate may then amplify decomposer function in warm environments and suppress function in cool environments. Hence, our results suggest that decomposition relationships observed across spatial gradients may fail to adequately represent how decomposition will respond to changing climate across time.

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1. Introduction

Leaf litter inputs are a major source of carbon (C) and nutrients to forested systems (Moorhead and Sinsabaugh, 2006; Jacob et al., 2009). The rate at which foliar litter is decomposed and nutrients returned to the system, is thought to be primarily controlled by climate at broad scales and litter quality at both broad and local scales (Meentemeyer, 1978; Couteaux et al., 1995; Wall et al., 2008). The decomposer community is thought to influence litter dynamics only locally (Aerts, 2006), and hence its role may minimally explain decomposition across broader spatial scales (but see Wall et al.,

2008). Indeed, across biomes climate and litter quality appear to best describe decomposition rates (Harmon et al., 2009; Currie et al., 2010; but see Bradford et al., 2016), especially in the shorter-term (one year decomposition). Yet such broad-scale studies have also revealed a possible role for the decomposer community independent of climate and litter quality (Gholz et al., 2000), highlighting the potential for this controlling factor to also influence broader-scale decomposition patterns.

There is now growing evidence that decomposer community composition influences litter decomposition rates over and above climate and litter quality controls (Schimel and Schaeffer, 2012; Bradford et al., 2016). Typically invoked is the role of litter quality in shaping the function of the decomposer community. Across short- (Hunt et al., 1988; Wallenstein et al., 2010) and long-term (Ayres et al., 2009) decomposition dynamics, field studies controlling for microclimatic variation among sites have demonstrated home-field advantage (HFA), whereby a litter species decomposes

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fastest with its “home” decomposer community (but see Veen et al., 2015). Such local adaptation to the resident litter types has also been demonstrated in laboratory microcosm studies (Ayres et al., 2009; Cleveland et al., 2014), where for example, Strickland et al. (2009a) found that the decomposer community explained between 22% and 86% of the variation in mass loss across three litter types.

Field and lab studies continue to provide evidence that litter quality shapes soil decomposer community functional abilities (Schimel and Schaeffer, 2012; Strickland et al., 2015) and consequently the rate of litter decomposition. Yet whether or how climate shapes soil decomposer community functional ability appears virtually unknown. Climate might shape ability because a community can become adapted to a climate regime (Strickland et al., 2015) thus affecting its function outside of that climatic window. For example, warm and moist conditions typically select for fast-growing, competitive organisms, which yield higher rates of ecosystem processes than would be achieved by a stress-adapted community (e.g. low temperature and/or moisture) placed under similarly favorable abiotic conditions (de Vries et al., 2012; Crowther and Bradford, 2013). Such selection by climate for community structures that differ in their response to contemporary climate seems well established for plant communities, where for example, net primary productivity is much higher for similar rainfall in communities from more mesic as opposed to drier ends of regional gradients (Lauenroth and Sala, 1992). Climate may also influence soil decomposer community function through substrate-specific enzyme production whereby cold- or warm-adapted enzyme production is dependent upon microbial habitat (Wallenstein et al., 2011). Therefore, shifts in climate may induce differential enzyme production and thus, altered decomposition rates of various chemical structures (Schimel and Schaeffer, 2012). Given that moisture availability and temperature influences decomposer (Aerts, 2006; Evans and Wallenstein, 2014) and enzyme (Steinweg et al., 2012; Averill et al., 2016) activity, and that microbial taxa differ in the magnitude of their responses to this variation (Crowther and Bradford, 2013), climate might interact with substrate-specific enzyme production and other functional traits to determine decomposition rates. Therefore, indirect effects of climate, through the shaping of decomposer community composition and function, could heighten decomposition responses to contemporary climate at a warm site and dampen responses at a cool site.

We designed a reciprocal, litter transplant study at three sites along an elevational gradient with varying climate and dominant, overstory tree species. Litter quality and favorable climate for decomposition declined moving upslope. We applied two regression models (Keiser et al., 2014) on both our field data and a previous microcosm study (Keiser et al., 2013) to elucidate the influence of climate, decomposer community function, and litter quality on litter decomposition (see section 2.7). The microcosm study replicated our experimental design under controlled, laboratory conditions (temperature × moisture), providing us an opportunity to quantify differences in decomposer community function independent of climate using a new regression approach, and then compare the output across studies. We hypothesized that if climate and functional ability are correlated, then the direct influence of climate on decomposition will be enhanced or diminished indirectly by differences in the functional ability of the decomposer communities (Hyp. 1a). Conversely, if the independent influence of the decomposer community is not correlated (i.e. mismatched) with climate, then climate will explain much less of the variation in decomposition rates (Hyp. 1b).

2. Methods

2.1. Site and species selection

The experiment took place at the Coweeta Long Term Experimental Research (LTER) site located in southwestern North Carolina and within the southwestern section of Blue Ridge Parkway National Park, North Carolina (Supporting Information: Appendix A, Table A1). At Coweeta, two sites were selected from a long-term terrestrial gradient study: the cove hardwood site (Low) (35°04'N, 83°43'W) and the northern hardwood site (Mid) (35°03'N, 83°43'W). The third site was located on National Park Service lands adjacent to the Blue Ridge Parkway (High) (35°17'N, 82°54'W), and provided a high-elevation spruce-fir stand.

The dominant, overstory tree species was selected at each site: *Liriodendron tulipifera* L. at the Low site, *Betula alleghaniensis* Britton at the Mid site and *Picea rubens* Sarg. at the High site; the latter species being representative of tree species found at higher elevations and latitudes. The three study species represent a range in leaf litter chemical quality, from chemically labile (*L. tulipifera*) to recalcitrant (*P. rubens*). Initial litter quality, including %C, %N, and C:N values, is presented in Table 1 of Keiser et al. (2013). Briefly, the acid unhydrolyzable fraction (AUF):N values (mean ± SE, $n = 4$) are 9.07 (±0.048), 11.9 (±0.044), and 26.0 (±0.18) for *L. tulipifera*, *B. alleghaniensis*, and *P. rubens*, respectively. Henceforth, litter quality refers to the AUF:N ratio.

2.2. 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). Litterbags were 22 cm² and composed of two different mesh sizes: 52 μm (bottom) and 2 mm (top). This design prevents loss of *P. rubens* through the bottom of the bag (Harmon et al., 1999; Adair et al., 2008). Each bag contained 5 g (±0.1) air-dried leaf litter.

Four sets of each litterbag type (individual species) were placed at each sampling site in a randomized block design for each of six collection dates spanning 31 months ($n = 216$ bags total). The first three collection events occurred across the first year (4, 7 and 11 months) to account for the initial fast phase of decomposition (Couteaux et al., 1995; Adair et al., 2008). The final three collections

Table 1

ANOVA approximation (Type III SS) from a linear mixed effects model for the effects of litter quality (AUF:N), climate (CDI) and time on % AFDM Lost. The r^2 values are presented for the full model, and also the univariate relationships which include the model's random effect (Block).

Variables	df	F	P	r^2
Intercept	1197	3.94	0.0485	na
Litter quality	1197	3.94	0.0486	0.05
Climate	1197	11.73	0.0007	0.38
Time	1197	1.68	0.197	0.22
Litter quality × Climate	1197	0.61	0.4359	0.58
Litter quality × Time	1197	5.7	0.0179	0.36
Climate × Time	1197	0.24	0.625	0.40
Litter quality × Climate × Time	1197	0.68	0.4097	0.53

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