Soil Biology & Biochemistry 107 (2017) 180–187

Contents lists available at ScienceDirect

Soil Biology & Biochemistry

journal homepage: www.elsevier.com/locate/soilbio

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

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ARTICLE INFO

Article history:
Received 6 September 2016
Received in revised form
20 December 2016
Accepted 21 December 2016

Keywords:
Decomposition
Functional ability
Gradient
Litter
Space-for-time
Soil decomposer community

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.

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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http://dx.doi.org/10.1016/j.soilbio.2016.12.022

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 cm^2 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
				0.53
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

occurred at 16, 23, and 31 months. The duration between collections gradually increased as we expected the rate of change in C and N to slow (Couteaux et al., 1995). Three additional litter bags (travel bags) were prepared for each species ($n = 9$), and were exposed to the same treatment during site establishment, but were recovered immediately to allow for a transport correction.

At each site, four blocks were established. Each block contained multiple rows with each row randomly assigned to a single litter type. The six litterbags per litter type were pinned to the forest floor in a single row among that year's senesced leaves. One bag of the initial six for each species per block was randomly selected for collection at each of the six sampling times. Soil cores were also collected from all blocks during each collection event (10 cm depth, 8 cm dia.). Soils were transported to the lab on ice. Additional soils were collected at site establishment for bulk density analysis.

2.3. *Litter analysis*

At each sampling time, litterbags were returned to the lab where they were air-dried for a week. For added consistency, all bags were then dried at 60 °C for 24 h. Foreign material (including fine roots) was removed from bags using forceps before weighing. The remaining material was weighed and then milled using a Spex CertiPrep 8000-D Mixer Mill (Spex, Metuchen, New Jersey, USA). Ash-free dry mass (AFDM) was measured through incineration at 500 °C for 8 h. Carbon and N concentrations were determined for milled samples using a NA 1500 CHN analyzer (Carlo Erba Strumentazione, Milan, Italy). Initial leaf litter cellulose, hemicellulose, and AUF fractions were determined using an Ankom A200 Fiber Analyzer (Ankom, Macedon, New York, USA).

2.4. *Soil analysis*

Soils were homogenized by block then sieved to 2 mm before analysis. Soil pH was determined in a water solution, 1:1 by volume (Allen, 1989). Labile carbon was estimated using a 30-day incubation at 20 °C using methods described in Bradford et al. (2008). This method provides an estimate of microbially-available C resources. Active microbial biomass was estimated through substrate-induced respiration (SIR) (Anderson and Domsch, 1978; Bradford et al., 2008). Chloroform fumigation extraction (CFE) was used to measure active and inactive microbial biomass C as well as K_2SO_4-extractable NH_4^+ and NO_3^- concentrations. We followed CFE methods described by Fierer and Schimel (2003). Samples were run on an Astoria 2 Flow Analyzer (Astoria-Pacific, Clackamas, OR, USA) and Shimadzu TOC-V (Shimadzu, Maryland, USA). Total C and N contents were analyzed on a Thermo DeltaPlus Advantage (Thermo Fisher Scientific, Waltham, MA, USA). Air-dried soil was analyzed for texture using the hydrometer method (Gee and Bauder, 1979). Bulk density of dried soil was calculated on a mass basis (Kramer et al., 2012) and used to determine areal-based mass estimates of soil C and N.

2.5. *Climate decomposition index*

The Climate Decomposition Index (CDI) incorporates air temperature, precipitation, and potential evapotranspiration to predict the impact of climate on litter decomposition, with higher values correlating with faster decomposition rates (Currie et al., 2010). The CDI metric (eqn. (1)) is calculated as a function of air temperature (T_i), precipitation (PPT_i), plus potential evapotranspiration (PET_i) for month i whereby F_T (T_i) and F_W (PPT_i, PET_i) are the effects of temperature and water stress on decomposition in month i (Adair et al., 2008).

$$\mathrm{CDI}_i = F_T(T_i) \times F_W(\mathrm{PPT}_i,\ \mathrm{PET}_i) \tag{1}$$

Three local climate stations at similar elevation to the study sites were used for sources of air temperature and precipitation data (see Appendix A, Fig. A1). The proxy sites were located at: Coweeta (35.18N, 83.39W; 685.5 m) for Low; Highlands Biological Station (35.057N, 83.198W; 1174 m) for Mid; and Mount LeConte (35.65N, 83.44W; 1979 m) for High. Values for CDI were calculated monthly across the study years of 2008–2011. The CDI values for each collection point used in the linear mixed-effects (LME) models described below were averaged across months in the field. The CDI values were consistent with the presumption that favorable climate for decomposition declined moving upslope (Appendix A, Table A2).

2.6. *%Carbon versus %AFDM*

Litter decomposition dynamics are often based on either %C or %AFDM values. Having both variables for all litterbags, we ran a linear regression of %C against %AFDM remaining (Appendix A, Fig. A2). The relationship ($r = 0.96$) demonstrates that the two metrics can be used interchangeably.

2.7. *Statistical analyses*

2.7.1. *Conventional approach: testing the effects of litter quality and climate*

Statistical analysis was conducted in R (R Core Team, 2012). Using the R package nlme (Pinheiro et al., 2015), we used a LME model (method = "ML", type III SS) where litter quality (initial AUF:N), climate (CDI), and time (days of field incubation – continuous) were treated as fixed effects and allowed to interact. The response variable was %AFDM loss (representing mass loss dynamics). Plotting the residuals and running a Shapiro-Wilk test ($p = 0.4$) confirmed the data is normally distributed. Block was included as a random effect to account for spatial auto-correlation associated with multiple litterbag collections over time (Pinheiro and Bates, 2000). The corAR1 function was used to account for temporal autocorrelation of our litter bag collections, with time (days) defining the correlation structure. We used 18 unique CDI values (month × site) for analysis, reflecting climate conditions for a site across the time of incubation in the field. Given the significance of time, we ran post-hoc LME models per month sampled. The first set of models tested the effects of litter quality and climate, plus their interaction (all discrete variables), with block again included as a random effect. Because Site and CDI could not be included in the same model due to collinearity but Site encompasses a range of potentially influential variables, including climate, edaphic characteristics or the soil microbial community, a second set of post-hoc LME models tested the effects of litter type and Site, plus their interaction (all discrete variables), with block as a random effect. Using the R package multcomp (Hothorn et al., 2008), we used 'glht' with 'Tukey' to run pairwise comparisons on significant Litter × Site interactions. We then used model selection with Akaike Information Criterion (AIC) to identify which overall model (site × litter quality × time versus CDI × litter quality × time) was the better fit for predicting mass loss. We again applied LME models (method = "ML", type III SS), with block included as a random effect, and temporal autocorrelation accounted for using the corAR1 function.

We also wanted to test whether soil characteristics or climate best described mass loss by running model selection with AIC. This separate analysis examining the effects of soil characteristics and climate on %AFDM lost ensured that site-specific soil characteristics were explicitly accounted for as controlling variables over mass loss. This test included 12 soil variables (Appendix A, Table A3) ranging from pH and labile C to active microbial biomass (SIR) and microbial biomass C and N (CFE), plus CDI. All variables were tested for collinearity using a variance inflation factor (VIF) test. Those variables with a VIF <10 were included in model selection. Based on the DART results (section 3.2), we reran the model selection for only the two latter collection points (23 and 31 months).

A final set of LME models (method = "ML") were run on mass remaining (% AFDM remaining) data sorted by Site to test the effects of litter type and time (days in the field), plus their interaction. Block was again treated as a random effect with the corAR1 function accounting for temporal autocorrelation ("days"). Specifically, these models were to test an observed "late-phase" stabilization of mass across all litterbags (Appendix A, Fig. A3), and we ran two LME models to investigate the effect of time on each phase.

The fraction of initial N data appears to form two diverging trends when graphed across % AFDM remaining (Appendix A, Fig. A4). We ran a quantile regression (Cade and Noon, 2003) to capture an upper limit in net N immobilization.

2.7.2. DART: testing whether climate correlates with decomposer functional ability

We applied the regression test proposed by Keiser et al. (2014), named herein as the 'Decomposer Ability Regression Test' (DART), to our field data. This least squares regression (eqn. (2)) defines decomposition (Y_i) for observation i as the ability of litter species l (β_l), the ability of soil community s (γ_s), plus a home combination, or HFA (η_h). "Litter$_l$, Soil$_s$ and Home$_h$ are dummy variables that equal 1 or 0 depending on the presence or absence of the litter species, soil community or home combination, respectively. The parameters to be estimated are β_l, γ_s and η_h" (Keiser et al., 2014). The intercept (α) represents the average decomposition across all i in a data set, after controlling for litter, soil and home combinations, while the error term is defined by ε. Two terms are restricted to prevent perfect collinearity: $\sum_{l=1}^{N}\beta_l = 0$, and $\sum_{f=1}^{M}\gamma_s = 0$.

$$Y_i = \alpha + \sum_{l=1}^{N}\beta_l Litter_{l_i} + \sum_{s=1}^{M}\gamma_s Soil_{s_i} + \sum_{h=1}^{K}\eta_h Home_{h_i} + \varepsilon_i \qquad (2)$$

The parameter β produces a litter quality index (QI), or a ranking of the chemical quality of litters within a study, and the parameter γ specifically models the inherent functional capacity (the Ability metric) of the soil decomposer community (γ_s). The final parameter, η, estimates the strength/advantage of a decomposer community decomposing its home litter type (HFA). Each parameter (QI, Ability, and HFA) produces unitless estimates by which the soil communities or litter types can be compared. The estimates should not be compared across parameters, and do not indicate importance over another parameter or decomposition. In this study, we focus on the Ability metric (γ_s), which provides two, potential biological indicators within a single parameter estimate. The first indicator estimates each decomposer community's overall capacity to decompose all litter types within the context of a specific study. For example, Keiser et al. (2014) use a dataset to demonstrate that the lowest ability estimate corresponds with the decomposer community which decomposed all litter species the least, while the highest ability estimate corresponds to the decomposer community which decomposed the greatest amount of all litter species. The second indicator demonstrates the functional differences among decomposer communities.

Analyses were run using SAS 9.3 (SAS Institute, Cary, NC) on both the mass loss (% AFDM) and N gain/loss (fraction of initial N) data at the six collection points. For the mass loss (%AFDM) data, we also ran a single DART model including all data points to examine the overall effects of QI, Ability, and HFA on decomposition. We ran a final DART model with previously published data (Keiser et al., 2013), which replicates the experimental design in a laboratory microcosm study where climate was controlled (hence removing any possibility that climate differences might obscure functional community differences). Again, because climate (CDI) and Site cannot be included in the same model due to collinearity, we compared DART output from the field (with climate effects) and microcosm (without climate effects) data to further test our hypotheses. Briefly, the microcosm study reciprocally combined three litter species with the three "home" soil communities in a 50 mL centrifuge tube kept at 20 °C and 65% water holding capacity. An inoculum approach was used whereby a small mass (0.5 g) of 2-mm sieved soil was thoroughly mixed with litter in each microcosm. Respiration rates (as an index of decomposition) were then measured across 300 days (corrected by soils-only contribution), following an overall study approach specifically designed to test for functional differences among soil decomposer communities (Strickland et al., 2009a, 2009b; Keiser et al., 2011).

3. Results

3.1. Conventional approach: testing the effects of litter quality and climate

We first examined the effects of litter quality, climate (CDI), and time on patterns in litter mass loss to see if the results confirmed previous cross-site studies. That is, we first had to verify that climate and litter quality appeared as predominant controls over decomposition, before asking whether microbial community functional differences likely played a role (and hence potentially correlated with) these two other controls. The overall model explained 53% of the variation in mass loss. There was a significant litter quality × time ($P = 0.0179$) interaction on mass loss (Table 1). This interaction was explored both within and across collection points to see how the explanatory variables changed as the litter decomposed. Initial litter quality explained most of the variation in mass remaining (upwards of 76%) across the first year (Table 2), and was significant ($P \le 0.05$) at three of the six collection points. The most chemically labile litter, *L. tulipifera*, lost the most mass within a site across the first three collections, whereas the most chemically recalcitrant, *P. rubens*, lost the least. As would become the trend across the final three collections, *P. rubens* lost equivalent mass to *L. tulipifera* at the High site (its 'home' site) at 7 months (the 2nd collection) (Fig. 1). For the final two collections, cumulative mass loss for all three litters combined was greatest at the Low site and least at the High site. At the end of the second year of decomposition (23 months), climate was significant and explained 29% of the variation in mass lost. Climate remained statistically significant (albeit marginally) through 31 months (Table 2), explaining 16% of the variation in mass lost. At collection months 4, 16 (marginally), and 23, there was a significant litter quality × climate interaction, which reflects the relative difference in mass loss among species across sites within a sampling point (Table 2). We compared these patterns to LME models with Litter type and Site for each collection month (Appendix A, Table A4). Whereas "site" often represents the decomposer community in microcosm studies (e.g. Strickland et al., 2009a), a range of variables, including climate, may drive "site" differences in the field. Significant Litter × Site interactions generally overlapped, but Litter was significant across more months and consistently explained a greater proportion of the variance. We then compared the two full models (i.e. site versus climate) using model selection with AIC. The CDI × litter quality × time model had the lowest ΔAIC and explained a greater proportion of the variance

Table 2
ANOVA approximation (Type III SS) from a linear mixed effects model for the effects of litter quality (AUF:N) and climate (CDI) on % AFDM Lost at each sampling point (Collection Month). The r^2 values are given for the full model (by month) and the univariate factors, which still includes the random effect (Block).

Collection Month		AUF:N				CDI				AUF:N × CDI		
	r^2	df	*F*	*P*	r^2	*df*	*F*	*P*	r^2	*df*	*F*	*P*
4	0.81	1,22	37.18	*<0.0001*	0.76	1,10	7.04	*0.0242*	0.01	1,22	5.53	*0.028*
7	0.42	1,22	0.11	0.741	0.34	1,10	0.2	0.6624	0.05	1,22	1.85	0.1879
11	0.65	1,22	4.93	*0.0371*	0.65	1,10	0.17	0.6922	0.00	1,22	0.24	0.6287
16	0.28	1,22	1.2	0.286	0.19	1,10	1.61	0.2326	0.01	1,22	3.42	*0.0778*
23	0.45	1,22	7.28	*0.0131*	0.19	1,10	19.91	*0.0012*	0.29	1,22	8.45	*0.0082*
31	0.27	1,22	1.72	0.2025	0.24	1,10	4.27	*0.0657*	0.16	1,22	0.92	0.3482

as designated by a greater r^2 value (0.67 compared to 0.43 for the Site model).

3.2. *DART: testing whether climate correlates with decomposer functional ability*

We next asked whether the climate effect in the conventional models might, at least in part, be driven by differing functional abilities of the decomposer community. First we used the DART model (Keiser et al., 2014) with data from Keiser et al. (2013), which replicated our field study design in the lab with controlled and common climate conditions. The DART model was applied to the cumulative C mineralization data (measured as total CO_2 efflux across 300 days). The analysis revealed differences in decomposer community functional ability among the sites (Table 3). Specifically, the functional Ability metric estimated that the High site decomposer community had the lowest functional Ability and the Low site the highest (Table 3). That is, the most favorable site climate for decomposition (in the field study) co-occurred with the decomposer community best equipped to decompose litter most rapidly.

Similar patterns in the Ability estimates were observed for our field litterbag data (Table 4) whereby the High site had the lowest functional Ability and the Low site the highest. In this model, Ability significantly influences decomposition dynamics, with the High soil decomposer community significant and the Low community marginally significant. Separated by sampling date, Ability was significant at four of the six collections, with all three site Abilities significant at 23 months (Fig. 1), matching the time when climate (and site) became significant in the conventional models (Table 2; Appendix A, Table A4). The Ability estimates at 23 months decreased moving upslope, matching the same patterns detected under the common-climate laboratory conditions and also the conventional analyses for the litterbags with field climate or site. Site climate and decomposer community functional Ability therefore appear perfectly overlapping.

4. Discussion

We tested whether differences in the functional ability among decomposer communities, arrayed along an elevational gradient, were positively correlated with favorable climate for decomposition (Hyp. 1a) or independent (Hyp. 1b). Climate is commonly identified as a predominant control of decomposition rates (Meentemeyer, 1978; Currie et al., 2010) and it is expected that communities developing under favorable climate are those that grow and hence perform biogeochemical processes most rapidly (Crowther and Bradford, 2013; Strickland et al., 2015). Climate effects detected across space might then be composed of the direct influence of temperature and moisture on biotic activity, reaction rates and substrate availability, and an indirect effect mediated via the structuring (Averill et al., 2016) of the decomposer community. Our collective analyses support Hyp. 1a: climate positively correlates with – and hence could be considered to mask across climate gradients – the functional ability of decomposer communities (Appendix A, Fig. A5).

To assess whether the outcome of our analyses might apply broadly to cross-site studies, we first tested whether the decomposition patterns we observed were consistent with previous gradient studies (Meentemeyer, 1978; Couteaux et al., 1995; Currie et al., 2010). Our analyses, both conventional and DART, confirmed that litter quality is the dominant driver through the initial, fast phase of decomposition (Adair et al., 2008), with initial AUF:N alone (Currie et al., 2010; Jacob et al., 2010) driving the first pulse (four months) of decomposition dynamics (Appendix B). Initial decomposition dynamics are largely controlled by the release of soluble organics and break-down of labile compounds, and thus linked to the initial AUF:N of the litter (Harmon et al., 2009). At the end of the second year and as field decomposition progressed into a second phase, climate became more important (Adair et al., 2008; Harmon et al., 2009). When CDI explains the greatest variance in mass lost at 23 months (conventional analyses), the Ability estimates reflect the range in favorable climate among our three field sites. For example, greatest mass loss for all three species occurred at the Low site, where climate is most favorable. Importantly, our results (Table 2) mirror other cross-site studies where the relationship between climate indices and later-phase decomposition dynamics is weaker ($r^2 < 0.30$) than controlling variables, namely litter chemical quality, of the initial decomposition phase ($r^2 > 0.60$) (Harmon et al., 2009; Currie et al., 2010). This suggests that site environmental factors (Cornwell et al., 2008; Harmon et al., 2009), such as decomposer functional ability, could be an influential, yet hidden, driver of later decomposition dynamics. While edaphic characteristics hold the potential to be influential site factors, our analyses suggest they are not critical drivers of variation in mass loss (Appendix B), especially when the Ability metric is statistically significant. The laboratory microcosm study further supports this in that the experimental design used minimal soil (an inoculum approach) to isolate the community effect independent of other factors including soil abiotic variables. Therefore, when significant, and as expected from DART, the Ability estimates appear to reflect climate and each decomposer community's overall functional capacity to decompose all three litter types or the total mass loss across litter species. The overlap between favorable climate and high Ability supports the idea that temperature, much like soil moisture (Averill et al., 2016), influences (Aerts, 2006) litter decomposition both directly and indirectly by structuring the function of decomposer communities.

Our combined analyses further suggest that Ability estimates reflect functional differences among decomposer communities. The High community from the least-favorable climate had both the lowest overall mass loss rates and Ability estimate. Therefore, a low overall Ability may indicate a stress-adapted community with lower relative function; or suppressed decomposition across all litters. These results would suggest that climate is a structuring

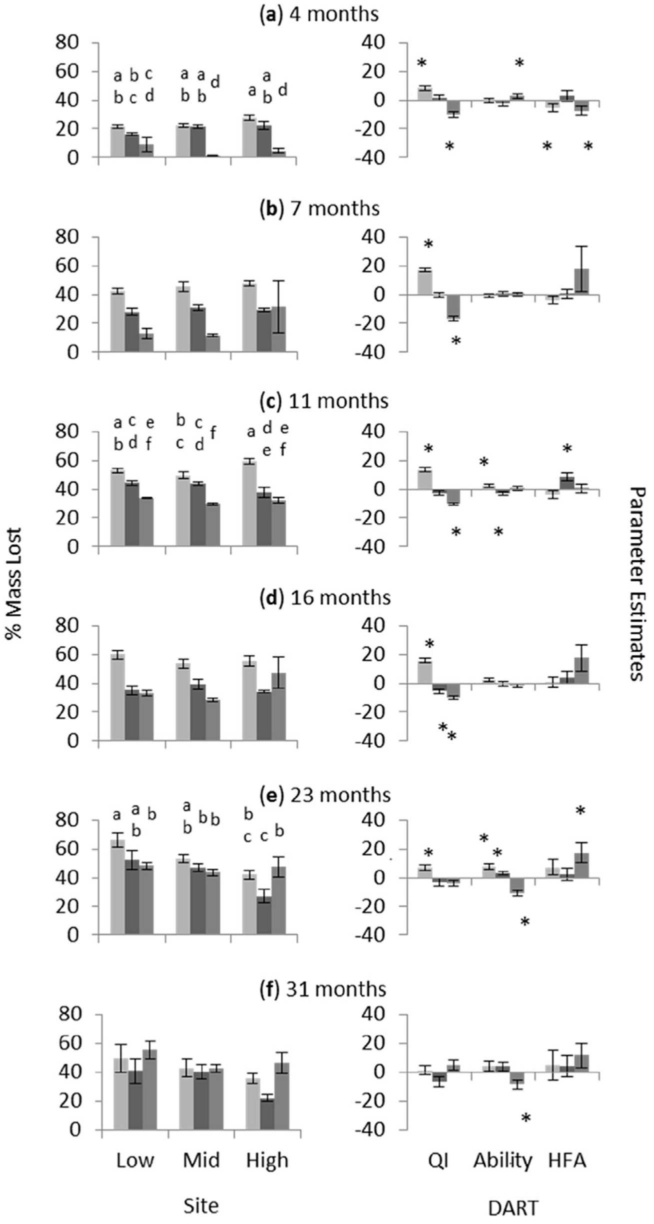

Fig. 1. Six rounds of litter mass loss data and DART output. At each sampling month (a – f) the left panel shows % AFDM Lost for the three litter species across the three sites (Low, Mid, High), and the right panel shows the DART output: QI (litter quality index, or a ranking of the chemical quality of litters within a study), Ability (the functional capacity of the decomposer community), and HFA (home-field advantage, or the strength/advantage of a decomposer community decomposing its home litter type). The light bars represent *L. tulipifera* (for mass loss and QI) and the Low site (Ability and HFA), the dark bars represent *B. alleghaniensis* (for mass loss and QI) and the Mid site (Ability and HFA), and the medium bars represent *P. rubens* (for mass loss and QI) and the High site (Ability and HFA). The bars are mean (±SE). In the left panel, letters designate significant differences among Litter × Site treatments at the $P \leq 0.05$ level for those sampling months with significant Litter × Site interactions (see Appendix A, Table A4). In the right panel, "*" signifies statistical significance at $P \leq 0.05$.

Table 3
Output from DART (Keiser et al., 2014) on the complementary microcosm data (Keiser et al., 2013). Quality index (QI) is given for the three foliar litters. Ability is given for the three soil communities. Home-field advantage (HFA) is given for the three litter × soil combinations designated by soil community origin.

Variable	Estimate	SE	*P*
Intercept	97.26	1.39	<0.0001
QI: *L. tulipifera*	26.32	2.45	*<0.0001*
QI: *B. alleghaniensis*	−1.04	2.12	0.6270
QI: *P. rubens*	−25.28	2.21	*<0.0001*
Ability: LOW	6.05	1.62	*0.0005*
Ability: MID	1.39	2.61	0.5967
Ability: HIGH	−7.44	2.44	*0.0038*
HFA: LOW	0.06	9.17	0.9946
HFA: MID	14.80	4.54	*0.0021*
HFA: HIGH	13.09	4.74	*0.0083*

Table 4
Output from DART (Keiser et al., 2014) on the full litterbag data set encompassing the six collection points. Quality index (QI) is given for the three foliar litters. Ability is given for the three soil communities. Home-field advantage (HFA) is given for the three litter × soil combinations designated by soil community origin.

Variable	Estimate	SE	P
Intercept	35.96	0.88	*<0.0001*
QI: *L. tulipifera*	10.44	1.6	*<0.0001*
QI: *B. alleghaniensis*	−2.81	1.68	0.0957
QI: *P. rubens*	−7.62	1.97	*0.0001*
Ability: LOW	2.51	1.41	0.0755
Ability: MID	0.33	1.43	0.815
Ability: HIGH	−2.84	1.17	*0.0157*
HFA: LOW	−0.18	4.27	0.9669
HFA: MID	3.64	3.38	0.282
HFA: HIGH	9.4	5.36	0.0809

agent for microbial community function. At the same time, the Ability estimates also confirm the DART results from the lab-based, microcosm data (Table 3) where the contemporary influence of climate is removed, and the authors (Keiser et al., 2013) concluded that the data support the Functional Breadth Hypothesis (van der Heijden et al., 2008; Keiser et al., 2011). This Hypothesis states that decomposer communities with a history of receiving chemically-labile litter inputs have much lower decomposition rates of more chemically-recalcitrant litters. In nutrient-poor ecosystems, there is high decomposer functional diversity as a result of the broad range of compounds found in chemically-complex litters, and consequently, these communities do not perceive differences between more recalcitrant and labile litters. As such, decomposer communities 'perceive' litter quality differences more or less acutely depending on the quality of the litters they typically receive (Strickland et al., 2009b; Milcu and Manning, 2011). Keiser et al. (2013) determined in the lab-based study that the High soil decomposer community perceived the smallest difference between litter types, and as such, had the widest functional breadth. In other words, the High community from the most nutrient limited environment had the functional breadth (van der Heijden et al., 2008; Keiser et al., 2011) to decompose the three litter types at a more similar rate than the Low or Mid communities. Applying DART to the same microcosm data, we find that High community has the lowest Ability estimate, which suggests that a low Ability may be indicative of the narrow difference in decomposition rates between litter types and thus, a wide functional breadth. These data suggest that there appears to be a trade-off between a decomposer community's capacity to decompose all litter types and its functional breadth, which also reflects a recent microcosm study applying the DART regression to a lab-based reciprocal transplant litter decomposition experiment (see Fanin et al., 2016). This trade-off is consistent with the idea that soil decomposer communities from labile litter environments are dominated by fast-growing copiotrophs (*r*-strategists) while recalcitrant litter environments are dominated by slow-growing oligotrophs (*K*-strategists) (Fierer et al., 2007).

Our study suggests that the later phase of litter decomposition is driven by both the functional ability of the decomposer community and climate, with each mapping on top of the other. Cross-site studies may then be able to unambiguously identify the initial control exerted by litter quality, yet the influence of climate in such studies may be non-independent of the microbial community. That is, the climate effect is likely composed of direct effects on microbial metabolism (Schimel and Schaeffer, 2012) and indirect effects, mediated by how climate shapes microbial community composition and hence functional ability (de Vries et al., 2012). Our results suggest that decomposer community effects on mass loss may need to be considered in addition to direct effects of climate and litter quality to make reliable projections of decomposition, where temporal patterns are extrapolated from spatial variation in climate (Fukami and Wardle, 2005). However, these spatial relationships may be a poor predictor of temporal dynamics when a mismatch arises between changing climate and decomposer functional ability. Such a situation seems to exist for plant productivity. For example, Lauenroth and Sala (1992) showed that local vegetation structure interacted with climate, meaning that temporal responses of plant productivity to precipitation variation were much smaller than spatial variation in productivity observed across a marked precipitation gradient. Our data suggest the same may be true for the process of decomposition, with climate interacting with decomposer community structure to shape decomposition rates.

Substantive debate still remains regarding the role that decomposer communities play in explaining variation in litter decomposition dynamics across space (Harmon et al., 2009; Hattenschwiler et al., 2011; García-Palacios et al., 2016). Given the potential for rapid adaptation (Allison and Martiny, 2008) and high dispersal (Nemergut et al., 2013; Talbot et al., 2014; Bahram et al., 2016), our study leaves unresolved the possibility that the functional ability of decomposer communities will closely track changing climate (making space-for-time substitutions robust). Although we demonstrate the correlation between climate and functional potential, our experimental design cannot disentangle the relative effects of each on decomposition rates. To date, these effects have only been resolved in lab studies, but whether they map to the field is unknown. Our data do show, however, that the climate effect on field decomposition dynamics appears to be a product of both direct and indirect processes. Future work combining functional and genomic analyses may help us disentangle these relative effects in the field. Perhaps most important, however, is that we have established the possibility of an indirect climate effect shaping decomposer community function in the field.

Our work shows that variation in field decomposition rates across space, often solely attributed to climate, may be in part associational and not causal. Instead, we reveal the potential for differences in decomposer community functional ability to modify direct climate effects on litter decomposition rates. Moving forward, we must experimentally separate climate from soil decomposer functional abilities to better capture their interaction, quantify the importance of climate versus functional ability, and increase our mechanistic understanding of how litter decomposition will respond to changing climate.

Acknowledgements

This research was funded by the National Science Foundation via the Coweeta LTER to MAB, and the U.S. Environmental Protection Agency through a STAR Fellowship to ADK. EPA has not formally reviewed this publication, and the views expressed herein may not reflect the views of the EPA. We thank the National Park Service for granting a research permit, and David Keiser for field assistance. We also thank Miami Aqua-culture, Inc. for a discounted rate on 52-μm screen plus free freight. The authors have no conflicts of interest to declare.

Appendix A. Supplementary tables and figures

Appendix B. Additional results

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.soilbio.2016.12.022.

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