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Climate history shapes contemporary leaf litter decomposition

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Abstract Litter decomposition is mediated by multiple variables, of which climate is expected to be a dominant factor at global scales. However, like other organisms, traits of decomposers and their communities are shaped not just by the contemporary climate but also their climate history. Whether or not this affects decomposition rates is underexplored. Here we source decomposer communities from three forest sites contrasting in climate (tropical, temperate, boreal), and, using experimental microcosms, quantify decomposition of a common litter under a factorial combination of four temperature (15, 20, 25, and 30 °C) and five moisture regimes (35, 55, 70, 85, and 100 % water holding capacity). We find that the climate history of the decomposer community is an important determinant of litter decomposition, explaining the same amount of variance in decomposition as both temperature and moisture. Further, climate history also shapes the effect of contemporary climate (i.e. experimental) on decomposition, both in terms of the magnitude of decomposition under optimal conditions and the range of abiotic conditions at which high decomposition rates are maintained. For example, at optimal conditions (i.e. 25 °C/70 % WHC) the tropical site has a greater decomposition rate than the other two sites. However, the temperate and boreal sites have greater 'niche breadth', where decomposition rates are more sustained (i.e. decrease less) as temperature and moisture deviate further from the optimum. Our data suggest that climate history shapes the functional response of the soil decomposer community, as it does for animals and plants. Yet how this shaping affects decomposition rates across regional and global climate gradients, and how such relationships are applied to temporal predictions, remain unanswered questions.

Keywords Carbon mineralization · Climate · Forests · Litter decomposition · Niche breadth · Niche optima

Introduction

Leaf litter decomposition, an important ecosystem process, is controlled by a suite of hierarchically-organized, interacting factors (Adair et al. 2008;

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Lavelle et al. 1993; Wall et al. 2008). Of these factors the contemporary climate has often been considered a dominant controlling variable over litter decomposition at broad spatial scales, whereas at finer spatial scales, factors like leaf litter quality and the decomposer community begin to play a more important role (Carrillo et al. 2012; Lavelle et al. 1993). While there is a growing realization that litter quality is as, or more important, than contemporary climate at broad spatial scales (Cornwell et al. 2008; Currie et al. 2010), the relative contribution that decomposer communities make to litter decomposition across this same scale has been less well studied compared to either climate or litter quality. A primary reason for this imbalance appears to be the expectation that decomposer community composition only influences decomposition rates at local scales and that the community only responds to contemporary conditions and not the historical legacy of these conditions (Bradford and Fierer 2012; Bradford et al. 2014).

Yet, there is growing evidence that suggests decomposer communities do play an important role in leaf litter decomposition and that in many instances this role may fundamentally alter decomposition dynamics (Ayres et al. 2009a; Hattenschwiler and Gasser 2005; Schimel and Schaeffer 2012). For instance, Garcia-Palacios et al. (2013) showed in a meta-analysis that soil faunal communities enhanced overall leaf litter decomposition and that such effects were mediated directly by the contemporary climate. Additionally the role of soil fauna appears dependent on the constraints of climate, whereby fauna affect decomposition to a greater extent under contemporary climatic conditions that do not constrain biological activity (Wall et al. 2008). Whereas we are beginning to understand the functional role of soil decomposer fauna in light of how they are shaped by climate, our understanding of the role of decomposer communities still seems primarily related to how their function is shaped by litter quality, both from a contemporary and historical perspective (Keiser et al. 2013; Strickland et al. 2009a, b).

Of great recent interest has been the role that the history of leaf litter inputs, both quality and identity, play in shaping the functional response of decomposer communities to contemporary leaf litter inputs (Ayres et al. 2009b; Gholz et al. 2000; Keiser et al. 2014). Research in this area has often been placed in the context of "home-field advantage" (HFA), whereby HFA is due to community-level adaptation to the litter species with which that community co-occurs (i.e. shares a common history), leading to decomposition rates that are higher than expected based on litter quality and climate alone (Ayres et al. 2009b; Keiser et al. 2014). The HFA effect seems to be most pronounced when litter quality is more chemically recalcitrant (Ayres et al. 2009b). Ultimately, the historical exposure to varying levels of resource quality shapes the manner in which communities degrade litter of varying quality (Strickland et al. 2009b). We now appreciate that litter quality and the historical legacy of litter inputs shape the function of decomposer communities and that the interaction between these two factors influences litter decomposition rates (Keiser et al. 2014). However, the importance of the interaction between contemporary climate and how climate history might shape decomposer community function during litter decomposition is less well understood.

It is well known that the contemporary climate is a major mediator of decomposer activity, such that relatively warm and moist environments are optimal for litter decomposition (Swift et al. 1979). However this static view of the decomposer community response to climate has recently become more nuanced. There is growing evidence, for example, that decomposer communities may adapt and/or acclimate to long-term changes in climatic regimes (i.e. climate history shapes the community's functional response). For example, soil decomposer communities and isolates of dominant heterotrophic microbes acclimate to both experimental warming, as well as seasonal variation in temperatures (Bradford 2013; Bradford and Crowther 2013; Bradford et al. 2008). Additionally, microbial communities show compositional shifts due to niche partitioning in response to changing moisture regimes (Evans et al. 2014), and fungal and bacterial isolates vary markedly in their tolerance of moisture stress and the range of moisture limitation over which they remain active (Lennon et al. 2012). Furthermore, these compositional changes are not short-lived (i.e. composition does not simply track moisture) but exhibit a historical legacy with regards to moisture regimes (Evans and Wallenstein 2012, 2014). Such phenomena suggest that microbial communities—and potentially their function—will be shaped in part by the historical climate to which they were exposed. That is, contemporary climate together with the decomposer community's climate history could shape current leaf litter decomposition dynamics, although this possibility appears largely untested.

While the role of climate history has been largely unexplored with regards to decomposer communities, its role with regards to shaping the structure and ecosystem function of plant communities is well established and as such provides vital insight into its potential role as a driver of decomposer function. For instance, angiosperms dominate in temperate and tropical environments and gymnosperms in boreal zones (Bond 1989). An explanation for this distribution is that under optimal conditions (i.e. relatively warm annual temperature and high nutrient availability) angiosperms exhibit greater growth rates than gymnosperms but under suboptimal conditions (i.e. colder and/or drier) gymnosperms exhibit greater growth rates than angiosperms (Bond 1989; Sprugel 1989). Pronounced morphological, anatomical and physiological differences between angiosperms and gymnosperms then shape ecosystem function beyond climate alone. However, even where there are not deep-rooted differences in plant life forms, climate history shapes the contemporary function of plant communities. Lauenroth and Sala (1992), for example, found that plant production in grasslands differed in their response to the same precipitation events depending on their climate history. That is, across a precipitation gradient, communities from more arid sites exhibited greater production under drier conditions compared to communities from less arid sites. Conversely, under wetter conditions the arid-adapted communities exhibited lower rates of production. If such results extrapolate to decomposer communities, then it suggests that those communities adapted to suboptimal climate conditions (i.e. drier and/or colder) may have lower overall process rates at optimal climate conditions compared to communities sourced from more optimal climes. Such a phenomenon would likely be a result of trade-offs between stress tolerance and competition (sensu Grime 1977), meaning that although stress-adapted communities have their function suppressed at optimal climate regimes, they are likely to maintain higher function at suboptimal conditions.

Here we test the possibility that decomposer communities differentially interact with contemporary climate to influence litter decomposition rates and that this interaction may be ascribed to the climate history associated with that community. We sourced decomposer communities from one of three habitats representing different climatic regimes (i.e. tropical rainforest, temperate deciduous forest, and boreal forest). We then used a controlled microcosm approach to test whether these communities exhibited different responses to 20 simulated climate regimes (i.e. 4 temperature × 5 moisture regimes). We hypothesize that if communities are shaped by climate legacies then an interaction between contemporary climate and the source of the decomposer community (i.e. climate history) should be apparent. We further expand this hypothesis by predicting that this interaction would manifest itself through greater than expected rates of decomposition under experimental climatic conditions most similar to the decomposer community's source climate. That is, the climate history of the community akin to that observed for litter quality, would generate a climate-based HFA.

Materials and methods

Experimental microcosm assembly

To investigate the potential for an interaction between contemporary and historical climate to shape the functioning of decomposer communities, we employed methods similar to those used by Strickland et al. (2009a, b). Soil for use as a decomposer inoculum was sourced from three climatically-distinct sites: Luquillo LTER (18.30N, 65.80W), Coweeta LTER (35.00N, 83.50W), and Bonanza Creek LTER (64.86N, 147.85W), hereafter referred to as tropical, temperate and boreal forest, respectively. Together these sites gave us a marked range of temperature and moisture regimes (Supplementary Material) and represent the decomposer communities' climate histories.

Soil (0.25-m^2 quadrat; 10-cm depth) was collected beneath the dominant forest cover at each location in the Fall of 2009. Soil was then placed on ice and shipped to Yale University. Soils were passed through a 4-mm sieve, homogenized, and stored at 5 °C until used to inoculate sterile leaf litter (next paragraph). We also determined several attributes for these inocula (Table 1), including soil texture determined using the hydrometer method as per Gee and Or (2002); pH determined using a bench-top pH meter (1:1; soil: H_2O

by volume); soil percentage C and N determined using an NA1500 CHN Analyzer (Carlo Erba Strumentazione, Milan, Italy); and soil microbial biomass determined via substrate induced respiration (SIR), following Strickland et al. (2010). Briefly SIR, a measure of active microbial biomass, was determined using soil slurries (4 g dry mass equivalent soil) incubated at 20 °C for 5 h with excess substrate (i.e. autolyzed yeast). After incubation, respiration was determined on an infrared gas analyzer (IRGA; Model LI-7000, Li-Cor Biosciences, Lincoln, Nebraska, USA).

We used grass litter (*Poa* spp.), collected from Yale Myers Forest (41.91N, 72.16W), as a common leaf litter substrate. We chose this litter for the following reasons: (1) its litter chemistry is relatively simple, meaning that the potentially confounding influence of litter quality would be minimized in this experiment (see Strickland et al. 2009a); (2) this litter is novel to each of the sites that soil was sourced from, meaning that no single community was adapted to this litter allowing us to avoid the phenomenon of HFA (Strickland et al. 2009a). Litter was collected as standing dead material, Wiley milled (2 mm), and then autoclaved (121 °C, 15 psi, 20 min) twice in succession and again 24 h later. Autoclaving may affect litter quality (e.g. through volatilization of N) but the purpose in our experiment was to explore relative effects of the interaction between microbial community climate history and contemporary climate, meaning we simply required a common sterile substrate for the assessment. Additionally, litter percentage C and N was determined using an NA1500 CHN Analyzer (Carlo Erba Strumentazione, Milan, Italy) and was 42.5 and 0.65 %, respectively.

Microcosms were constructed by inoculating 1 g (dry weight equivalent) of sterilized litter with 0.5 g (dry weight equivalent) of soil in a 50-mL sterile centrifuge tube. This microcosm design has been employed in various studies (e.g. Cleveland et al. 2014; Keiser et al. 2013, 2011; Strickland et al. 2009a, b) and essentially treats a large volume of litter as the "environment" which is inoculated with a small volume of soil, providing a source of decomposers to colonize the litter environment. Additionally, litter C and N represented ~93 and ~78 % of the C and N across the microcosms, meaning that while the soil inoculum was approximately one third of the total mass it represented a minor percentage of C and N. As such, the approach is intended to enable quantification of the inherent potential of the decomposer inoculum to mineralize litter under controlled experimental conditions.

Experimental treatments and measures

We applied one of four temperature treatments and one of five moisture treatments to each microcosm, giving us a total of 20 temperature by moisture regimes ($n = 3$ for each, in total giving 4 temperatures × 5 moistures × 3 sites × 3 replicates = 180 experimental microcosms). We used four temperatures: 15, 20, 25 and 30 °C selected to approximate the growing season mean monthly temperatures from where each soil was sourced (boreal: 13.7 °C, temperate: 18.7 °C, and tropical: 24.4 °C).

To vary moisture availability, we first calculated 100 % water holding capacity (WHC) of the grass litter-soil mix. We accomplished this by saturating the litter-soil mix completely with water, allowing it to drain for 2 h. Wet litter-soil mass was determined immediately after 2 h and then the litter-soil mix was dried at 105 °C for 24 h. One hundred percent WHC was then calculated by subtracting the dry litter-soil mix mass from wet mass, divided by wet litter-soil mass. Optimum WHC for soil microbial activity is expected to be ~50–70 % WHC and declines at higher and lower values of WHC (Ilstedt et al. 2000;

Table 1 Characteristics of the three soils sourced from distinct climates and used to inoculate the common litter

Inoculum source	Sand (%)	Silt (%)	Clay (%)	Textural class	pH	Carbon (%)	Nitrogen (%)	SIR microbial biomass (μg CO_2 g dry wt soil^{-1} h^{-1})
Tropical forest	24.0	31.8	44.2	Clay loam	4.97	6.10	0.45	1.89
Temperate forest	63.8	26.4	9.8	Sandy loam	4.63	7.61	0.37	2.13
Boreal forest	23.8	68.4	7.8	Silt loam	5.80	5.16	0.31	4.73

Moyano et al. 2013). Our treatments (i.e. 35, 55, 70, 85, 100 % WHC) then likely encompass the optimal and both sub-optimal extremes for litter mineralization. Moisture was checked weekly and, when necessary, brought back to the imposed experimental condition through addition of deionized water.

Carbon mineralization of the leaf litter was determined 14 times across 90 days using the static incubation procedure described in Fierer et al. (2003). Briefly, the microcosms (50 mL centrifuge tubes) were capped with gastight lids fitted with septa. Once capped, tube headspace was flushed with CO_2-free air and incubated at the appropriate temperature treatment for 24 h. After the 24-h incubation period, an infrared gas analyzer (IRGA; LI-7000; Li-Cor) was used to measure CO_2 produced and hence track C-mineralization rates for each tube.

Data analysis

Cumulative C-mineralization was calculated by integrating the values under the curve for the entire time course of the incubation. Results were analyzed using analysis of variance (ANOVA), and when appropriate, interactions were further investigated using post hoc analyses. Cumulative litter C-mineralization was the dependent variable and decomposer community climate history, temperature, and moisture were the independent variables. All independent variables were permitted to interact. Values were log transformed when necessary to meet assumptions of normality. To determine if there was evidence for local adaptation of microbial communities to climate, we calculated z-scores. These allowed us to evaluate under which temperature by moisture regimes litter mineralization associated with a particular community was greater than the mean for that regime (Fierer et al. 2012). All analyses were conducted using R (R Core Team). Statistical significance was considered $P < 0.05$ and marginal statistical significance was considered $P < 0.10$ (Hurlbert and Lombardi 2009).

Results

Across the three decomposer climate histories, cumulative litter mineralization peaked around 70 % WHC and tended to increase with temperature, although the highest temperature regime (i.e. 30 °C) was typically associated with a drop in mineralization rates from the optimum at 25 °C (Fig. 1). Mineralization rates were influenced by climate history, moisture regime, and temperature regime (Table 2; Fig. 1), and these three factors were involved in a significant interaction (Table 2) suggesting that the influence of any one factor was dependent on the values of the other two. So, for example, the relative effects of experimental climate (i.e. moisture availability and temperature) on litter mineralization rates appeared dependent on a given decomposer community's climate history. Indeed, post hoc analyses for each community's climate history generally suggested that they responded uniquely to the climate manipulations. That is, there were moisture by temperature interactions for the communities sourced from temperate ($F_{1,56} = 7.81$; $P < 0.01$) and boreal forests ($F_{1,56} = 3.55$; $P = 0.07$), respectively, but not for the tropical forest ($F_{1,56} = 0.22$; $P = 0.64$).

For the community with a temperate climate history the moisture by temperature interaction appeared due to greater cumulative mineralization under warm-dry conditions (25–30 °C; 35 % WHC) as opposed to cold-dry conditions (15–20 °C; 35 % WHC), an increase in cumulative mineralization under 25 °C up to 70 % WHC and a convergence in mineralization rates at 85 and 100 % WHC (Fig. 1). The community with a boreal climate history had greater cumulative mineralization under cold-dry conditions (15–20 °C; 35 % WHC) compared to warm-dry conditions (25–30 °C; 35 % WHC) but this pattern was reversed under more moist conditions (Fig. 1). The community with a tropical climate history exhibited no interaction between temperature and moisture but tended to have greater mineralization under intermediate WHC and increased mineralization up to 25 °C, usually followed by a slight decrease at 30 °C (Fig. 1).

All three climate histories had roughly similar optimal contemporary climates. That is litter mineralization rates tended to be greatest between 20 and 25 °C at 70 % WHC (Fig. 1). However, while optimal conditions for mineralization rates were similar across climate histories, the change from this optimum across the experimental climate regimes was very different. For the tropical climate history, litter mineralization tended to decline rapidly from the optimum and this was particularly true across changing moisture regimes. For the temperate climate history, the change from the optimum tended to be more gradual compared to the community sourced from a tropical

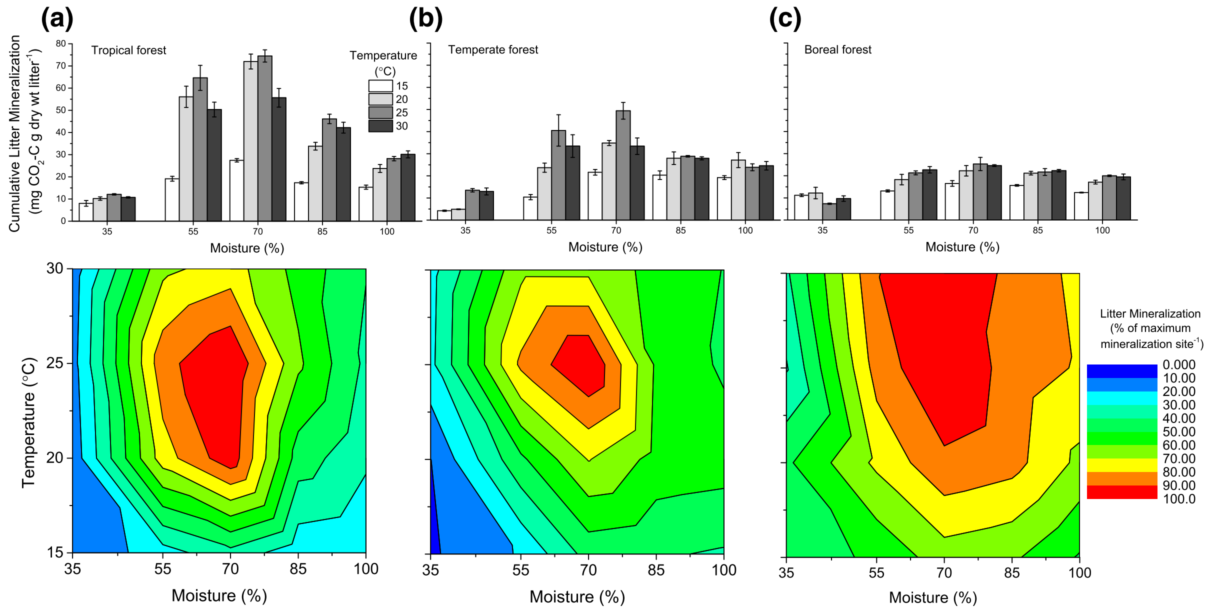

Fig. 1 Cumulative mineralization of a common grass litter across 90 days under one of four temperature regimes (15, 20, 25, or 30 °C) and one of five moisture regimes (35, 55, 70, 85, and 100 % water holding capacity) for three decomposer communities sourced from climates representative of either **a** tropical, **b** temperate, or **c** boreal forests. The *top half* of each *panel* shows the mean ± 1 SE of cumulative litter mineralization across the temperature and moisture regimes, while the *bottom half* illustrates the percentage change (from the maximum mean for each community) in mineralization across both regimes

Table 2 Analysis of variance results for the effects of the decomposer communities' climate history and experimental/contemporary temperature and moisture regimes on cumulative litter mineralization rates

Source of variation	d.f.	SS	%SS	F value	*P* value
Community climate history (CCH)	2	8.3	12.0	18.6	**<0.001**
Temperature	1	7.7	11.3	34.9	**<0.001**
Moisture	1	11.6	16.9	52.3	**<0.001**
CCH × temperature	2	0.9	1.3	2.0	0.13
CCH × moisture	2	0.9	1.3	2.0	0.14
Temperature × moisture	1	0.1	0.1	0.3	0.60
CCH × temperature × moisture	2	1.9	2.8	4.3	**<0.05**
Residuals	168	37.3	54.3		

All data were log transformed to meet assumptions of normality

Significant *P* values are denoted in bold

Also shown are the percentage sums of squares explained (%SS)

climate. This was particularly apparent across higher moisture regimes at lower temperatures and lower moisture regimes at higher temperatures (Fig. 1). Finally, the boreal climate history tended to be the least responsive to climatic conditions, with relatively little change from its optimal mineralization rate across the entire spectrum of experimental climate regimes (Fig. 1).

We also compared cumulative mineralization between the communities' climate histories at the same experimental climate regime. To do this we examined z-scores between treatments at each

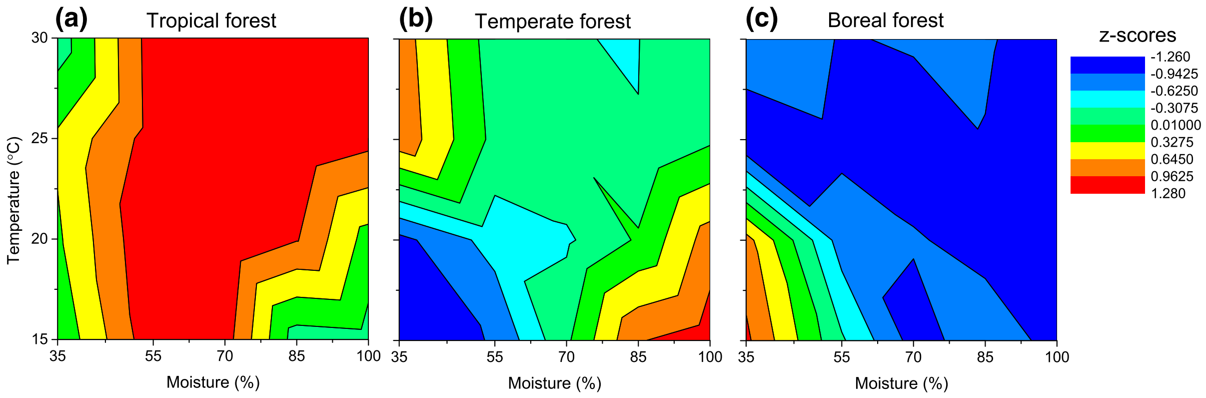

Fig. 2 Standardized scores (i.e. z-scores) of cumulative litter mineralization for decomposer inocula sourced from climates representative of either **a** tropical, **b** temperate, or **c** boreal forests across the experimental/contemporary temperature and moisture regimes. *Red* indicates z-scores that were higher than the mean under a given experimental/contemporary temperature × moisture regime across all three climate histories (e.g. litter mineralization for the boreal forest was greater than the mean for all three communities at 15 °C and 35 %WHC). (Color figure online)

moisture and temperature regime (Fig. 2). This examination indicated that the community with a boreal climate history tended to have greater mean cumulative mineralization than either of the communities with a temperate or tropical climate history under cool-dry conditions. Under hot and dry—and cool and wet—conditions, mineralization rates were greatest for the community with a temperate climate history; and the community with a tropical history had the highest mineralization rates only when it was both moist (>50 % WHC) and warm (>20 °C).

Discussion

We tested whether the climate history of a decomposer community interacted with contemporary climatic conditions to influence litter decomposition rates. Our findings suggest that climate history does shape the contemporary functioning of decomposer communities, and in a manner consistent with trade-offs between functional rates and stress tolerance observed in plant communities (Bond 1989; Grime 1977; Lauenroth and Sala 1992; Sprugel 1989). For example, the community sourced from the boreal forest exhibited greater litter mineralization, compared to the other two communities, under the coldest, driest experimental climate regimes. The climate history of the boreal forest site (Bonanza Creek) can be represented by a mean annual temperature of −0.98 °C and annual precipitation of 319.1 mm, making it the coldest and driest of the three sites (Supplementary Material). The community sourced from the temperate forest (Coweeta), on the other hand, exhibited greater litter mineralization, compared to the other two communities, under both cool-wet and warm-dry experimental conditions. Such climate regimes occur at this temperate site in the non-growing and growing season, respectively (Supplementary Material). The community sourced from the tropical (Luquillo) site exhibited greater litter mineralization under wetter conditions and tended to have greater rates of mineralization, compared to the other two communities, at the warmest and wettest experimental climate regimes. That is, under conditions most similar to the tropical climate that this community was sourced from (Supplementary Material). Together these results highlight that the expected adaptation of decomposer communities to a specific climate regime (Barcenas-Moreno et al. 2009; Lennon et al. 2012; Manzoni et al. 2012; Rinnan et al. 2009) influences their function—at least in terms of litter decomposition—under contemporary climatic conditions and is indicative of HFA with regards to climate.

That decomposer communities are adapted to their climate regime is not unexpected. It has been demonstrated that decomposer communities acclimate and/or adapt to temperature and moisture regimes via multiple mechanisms including changes in enzyme properties and community composition, with consequences for their functioning (Bradford 2013). Further, the functioning of plant communities also seems influenced by their historical climate. For instance, Lauenroth and Sala (1992) noted that under drier conditions plant communities shifted toward drought-tolerant species with overall lower productivity and that under prolonged exposure to moister conditions communities were shifted toward mesic-adapted species with higher productivity. It is likely that decomposer communities exhibit similar characteristics (Lennon et al. 2012). Future research that explicitly examines community composition and the active component of the community would be needed to verify the hypothesis that climate shapes community function. However, results from simulations of aquatic microbial community responses to changing temperature show the potential for climate to shape function (Hall et al. 2008).

Temperature regime, moisture regime, and community climate history explained ~11, ~17, and ~12 % of the variation in cumulative litter mineralization during this 90 day experiment, respectively. These results suggest that community climate history explained about the same order of magnitude variation in litter decomposition as each of the manipulated climate variables (i.e. temperature and moisture). Further, the significant interaction between temperature, moisture and the community climate history suggests that contemporary climate effects on decomposition do not simply occur through a direct influence on microbial activity, but rather are modified by the resident decomposer community's climate history. Such phenomena may then play a role in shaping relationships between climate and decomposition rates observed in regional and global decomposition experiments (Berg et al. 1993; Bradford et al. 2014; Meentemeyer 1978; Parton et al. 2007). In fact, it is worth noting that cumulative mineralization was lowest for the community sourced from boreal forest, intermediate for temperate forest, and greatest for the tropical forest community. This pattern is the same as the one we would attribute to latitudinal/elevational variation in climate and its effect on decomposer activity (Bradford et al. 2014). Future studies should determine if this patterning holds when multiple sites across multiple biomes are compared. If it does hold, then our data suggest that a more favorable climate does not simply increases the activity of decomposers. Rather, climate induces a history-based shift in the ability of microbial communities to decompose litter, influencing both the magnitude of decomposition rates and the breadth of climate conditions across which they are sustained.

Our observations of climate history-induced differences in decomposition rate and breadth are akin to those for niche breadth and climate optima for growth between angiosperms and gymnosperms (Bond 1989). That is, both groups have similar optimum temperature for growth but gymnosperms grow more slowly at this optimum while maintaining higher growth rates over a broader range of temperature and moisture conditions. Similarly, the three soil communities we investigated, had a similar climate optimum for litter mineralization, regardless of climate history. One possibility, is that decomposer growth and enzyme activity is thermodynamically most favorable at a single climate optimum (Schipper et al. 2014). At suboptimal conditions, decomposer organisms and enzymes more active under these less thermodynamically favorable conditions are selected for but due to this trade-off can never obtain the same level of activity as organisms at optimal conditions (Schipper et al. 2014). This may explain, what appears to be a trade-off between the mineralization rate at this optimum and niche breadth. For instance, the community sourced from the tropical forest had the greatest litter mineralization rate at the optimum (compared to the other two communities) but also had much narrower niche breadth (i.e. much lower rates as climate conditions moved away from the optimum). On the other hand, the community with a boreal climate history had a lower litter mineralization rate at the optimum but had a greater niche breadth with regards to temperature and moisture, where rates were maintained at values closer to those observed under optimal conditions. More research must be conducted to confirm or refute this pattern, but our observations do raise the intriguing possibility that climate shapes the functioning of these decomposer communities as it does for plant communities. As such, a community's climate history might play a part in regulating rates of leaf litter decomposition and the functional response of the decomposer community to climate change.

Here we have demonstrated the potential for an interaction between historical and contemporary climate to shape litter decomposition, arising because climate history shapes the functioning of decomposer communities. Similar experimental studies have revealed the potential for historical and contemporary litter quality to drive decomposition dynamics (Keiser et al. 2011; Strickland et al. 2009a, b). Functional consequences of adaptation to historic climate regimes therefore appear analogous to the phenomenon of HFA, coined to suggest that communities are adapted to decompose the dominant litter with which they co-occur (Ayres et al. 2009a, b; Gholz et al. 2000; Keiser et al. 2014). Future research into decomposition must therefore move beyond the traditional view of a hierarchy of climate, litter quality and decomposer communities as factors controlling litter decomposition. Instead, research should emphasize the interactions between the historic and contemporary environment as key elements shaping controls on this vital ecosystem process.

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