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Decoupling direct and indirect effects of temperature on decomposition

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ABSTRACT

Functional changes to biotic communities arise in response to changes in the physical environment, often with profound implications for biogeochemical processes. Decomposition is regulated both by abiotic conditions (e.g. temperature and moisture) and by the biotic communities that mediate this process (e.g. bacteria and fungi). Given strong evolutionary trade-offs between tolerating stressful climatic conditions and competing under favorable conditions, past climate may indirectly affect decomposition rates by structuring the functional composition of microbial communities. In a controlled laboratory setting using samples from the Yale Myers Forest in northeast Connecticut USA, we tested how exposure to 15 °C, 20 °C, and 25 °C for three months shaped characteristics of wood-degrading fungal communities. We then measured how this indirect effect influenced contemporary decomposition rates during a second three-month incubation. As expected, contemporary effects of temperature had a strong influence on decomposition rates. Yet the effects of previous temperature exposure were also evident: fungal communities previously exposed to warmer conditions consistently decomposed wood faster than communities previously exposed to cooler conditions, regardless of the contemporary temperature regime. Across all contemporary temperatures, communities previously warmed to 20 °C and 25 °C degraded 1.08 and 1.12 times more wood, respectively, than communities previously warmed to 15 °C. The indirect effects of previous temperature were mediated by a larger fungal biomass in inocula sourced from warmer previous temperatures, as well as by shifts in functional rates independent of biomass. Overall, the relative influence of contemporary temperature was less than expected: the combined effect of the functional shift and fungal biomass – both a product of previous temperature – was nearly two-thirds that of contemporary temperature. Our findings demonstrate the dual role of climate in determining a fundamental ecosystem process, both directly via contemporary temperature and indirectly through the effects of previous temperature exposure on microbial activity.

1. Introduction

Atmospheric warming resulting from climate change is expected to cause significant changes in ecosystem processes, including the decomposition of organic matter (Bradford et al., 2016). Understanding the effects of warming on decomposition is complicated by the relationship between direct effects, which dictate the rate responses of enzyme-catalyzed microbial processes, and indirect effects, which alter the structure and composition of microbial communities (Allison et al., 2010; Bradford, 2013). The direct effects of warming are well established: microbial-mediated decomposition rates generally respond positively to temperature increases (Davidson and Janssens, 2006). Along with the quality of litter inputs, contemporary climate is generally viewed as the most important control on decomposition rates (Zhang et al., 2008). However, there is still considerable uncertainty as to how the changes in microbial community attributes brought on by anthropogenic climate change will in turn affect

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decomposition dynamics (Manning et al., 2006; Wieder et al., 2013).

Climate-driven changes in decomposition rates could have a profound effect on broader ecosystem function, including potentially significant changes to the size of the soil organic matter (SOM) stock and rates of nutrient cycling (Bradford, 2013). In this context, fungi capable of decomposing lignin and cellulose are of particular interest, since they are the dominant decomposing agents of wood (Boddy and Watkinson, 1995; Boddy, 2000) and therefore play an important role in soil-litter dynamics. In addition to contributing to soil enzyme activity and respiration (Crowther and Bradford, 2013), wood-decomposing fungi release significant stores of commonly limiting nutrients (e.g. nitrogen and phosphorus) into the soils of forested ecosystems (Boddy and Watkinson, 1995). Resolving uncertainty about how warming-induced changes in fungal communities might affect decomposition rates is therefore an important part of understanding the impacts of climate change on ecosystem function. Decomposition rates vary dramatically among fungal species (Hättenschwiler et al., 2005; Gessner et al., 2010; Crowther et al., 2011; A'Bear et al., 2013), which implies that community composition is important in governing wood decomposition rates. Typically, the effects of community composition has been considered only locally important (Bradford et al., 2014). Recent studies, however, have highlighted the prominent role of microbial community composition in governing decomposition rates (Reed and Martiny, 2007; Strickland et al., 2009; Schimel and Schaeffer, 2012; van der Wal et al., 2015) including across broad regional gradients in climate (Bradford et al., 2014; Talbot et al., 2014; Averill et al., 2016). In addition, multiple studies have demonstrated that the structure and composition of microbial communities respond to changing abiotic conditions, as the outcomes of competitive interactions are often temperature-dependent (Allison and Martiny, 2008; Crowther et al., 2012; Treseder et al., 2012). There is compelling evidence that historical temperature regimes select communities with different traits, and that these traits then determine community performance under common abiotic conditions (Strickland et al., 2015). Taken together, these fields of research underscore the importance of interactions between historical and contemporary temperature in determining both microbial community composition and decomposition rates, and suggest that direct responses alone are likely insufficient to fully explain microbial response to warming (Strickland et al., 2015; Averill et al., 2016).

Here, we explore the relative importance of direct and indirect effects of temperature on decomposition rates through experimental manipulation of historical and contemporary conditions (Mahecha et al., 2010; Wallenstein and Hall, 2011; Treseder et al., 2012; Strickland et al., 2015; Bradford et al., 2016). If warming drives functional changes in microbial community composition, the consequences for ecosystem processes are likely to be long-term and spatially dependent (Reich, 2010; Evans and Wallenstein, 2012). We used a two-phase laboratory experiment to examine wood decomposition rates by wood-rot fungal communities that were sourced from different forest stands and which were exposed to one of three historical temperatures. After controlling for differences in fungal biomass and substrate quality, we quantified the relative importance of direct and indirect effects of temperature on decomposition.

We tested two competing hypotheses: if contemporary temperature is the dominant factor governing variation in wood decomposition rates, then previous temperature exposure and any associated indirect effects will have a negligible impact (H1). Alternately, if prior temperature has a significant functional impact on microbial communities, then communities previously exposed to different temperatures will decompose wood at different rates, even when measured at a common contemporary temperature. Given expected trade-offs in performance under different temperatures (Barcenas-Moreno et al., 2009; Birgander et al., 2013; Bradford, 2013), communities previously exposed to warmer historical temperatures should decompose wood fastest at warmer temperatures, and communities previously exposed to cooler historical temperatures should decompose wood fastest at cooler temperatures (H2).

2. Materials and methods

2.1. Overview of experimental design

To decouple direct and indirect effects of temperature on decomposition rates, we first exposed fungal communities from three distinct forest stands to a range of initial temperatures (15°C, 20°C, and 25°C) for three months (i.e., the first incubation period, hereafter referred to as the "historical" temperature regime). Three months, although a limited period of time, corresponds roughly to the length of one season and is long enough to allow indirect temperatures to select for potentially distinct fungal communities (Fukami et al., 2010). In the second phase, the resulting communities were used as an inoculum to decompose blocks of wood along the same temperature gradient in a full factorial design, thereby assessing the direct effects of temperature (i.e., the "contemporary" temperature regime; see Fig. 1). We measured percent mass loss during the second incubation period, and compared decomposition rates between samples from different historical incubation groups.

2.2. Field collection

Wood-degrading fungal communities were collected from logs of northern red oak (*Quercus rubra* L.) from trees felled in three stands at the Yale-Myers Forest in northeastern Connecticut, USA (41.95–72.13). To achieve a broad range in inoculum fungal diversity, we selected stands that had been felled at different points in time, resulting in a range of maturity for the fungal communities. The stands had been harvested in 2005, 2008, and 2011, resulting in wood-degrading fungal communities that were established approximately 10, 5, and 2 years ago, respectively.

For the inocula, we identified red oak logs in stages II-IV of decay (see Waddell, 2002) with a diameter between 10 and 15 cm. We collected two 5-cm sections from 10 logs at each stand, with one sample taken from the end and one from the middle of each log, resulting in 20 wood samples per stand. Sections of the logs were brought to the lab, the bark was removed, and the wood was surface sterilized using 70% ethanol. The wood, still approximately at field moisture, was then milled in a Wiley mill, using a 2-mm mesh. Resulting sawdust from the 20 sections per stand was thoroughly homogenized, resulting in three sets of sawdust. Gravimetric moisture content of the sawdust was measured for each stand, as in Bradford et al. (2010), so that each sample would contain the same fresh weight equivalent of sawdust and so that each sample could be maintained at the field moisture level. Samples were stored for approximately 2 weeks in a sealed plastic bag at 4°C until incubation.

2.3. First incubation period: historical temperature

To establish samples for the first incubation period (i.e. exposure to "historical" temperature), twelve 15-cm diameter Petri dishes containing 7 g fresh weight equivalent of sawdust were established for each stand. This resulted in 36 total dishes, with four dishes from each stand placed at 15°C, 20°C, and 25°C (i.e. 12 plates total at

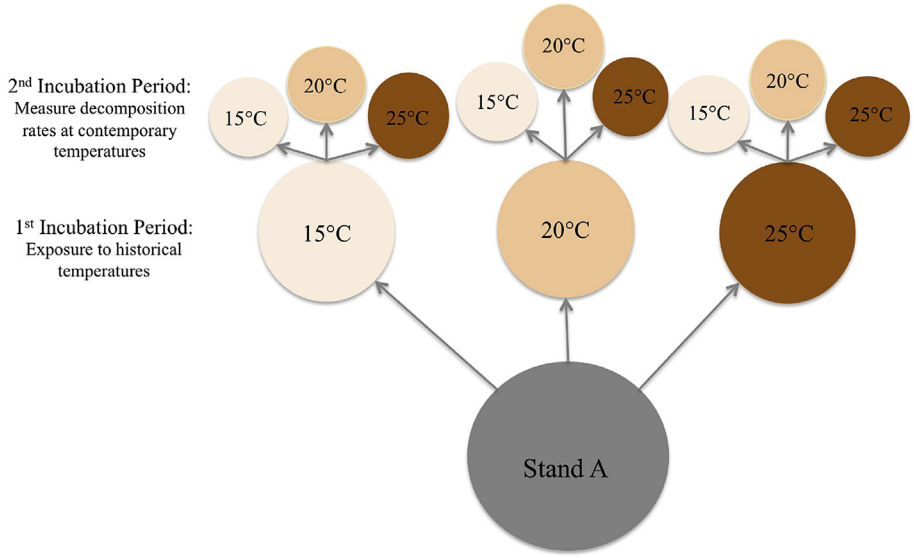

Fig. 1. Schematic of the experimental design. Samples from each of three forest stands (A, B, and C; only A is shown) were allowed to colonize discs at all three of the first incubation temperatures (i.e., exposure to "historical" temperature regime). For each disc resulting from the first incubation period, samples were then placed at all three of the second incubation temperatures (i.e., exposure to the "contemporary" temperature regime). All combinations of historical and contemporary temperatures were therefore represented for all three stands.

each temperature; 4 replicates per temperature per stand). The sawdust in each dish was maintained at the measured field-moisture value throughout the duration of the experiment via weekly addition of deionized water. Dishes were parafilm-sealed and incubated at their assigned temperature for two weeks to allow the community to physiologically acclimate prior to providing sterile discs to colonize.

A fresh, non-decomposed red-oak log, also collected from Yale Myers Forest, was cut into 36 discs. Each disc was ~1 cm thick and weighed between 90 and 100 g. To sterilize the discs prior to introducing them to the fungal communities, the bark was removed and the discs were surface sterilized with 70% ethanol. The discs were autoclaved three times for 60 min over three days at 121°C and 16 PSI pressure, and frozen overnight between autoclave sessions (Crowther et al., 2011; A'Bear et al., 2013). After the two-week acclimation period, a sterile disc of wood was placed on top of the sawdust in each dish. The dishes were incubated for three months and moisture adjusted weekly.

2.4. Second incubation period: contemporary temperature

After the original incubation period, dishes were placed at 20°C for two weeks to allow for physiological acclimation to a common temperature, while keeping the interval short enough to minimize community turnover (Bradford, 2013). The wood discs from each plate were then individually harvested and milled in a Wiley Mill, using a 2-mm mesh. To establish the decomposition assays, 2 g fresh weight equivalent mass from each set of sawdust was placed on a 9-cm diameter Petri dish. This process was repeated three times for each of the 36 discs, so that the community which had established in each disc during the first incubation period could then be assigned to each of the three temperatures for the second incubation period. This resulted in 108 total decomposition assays (36 discs x 3 contemporary temperatures; see Fig. 1).

To provide a substrate for decomposition, a fresh set of sterilized and frozen red oak blocks (2.5 by 2.5 by 2.5 cm cubes) were thawed and dried at 45°C to constant mass. The mass of each block was recorded, and then one block was placed on each dish. Deionized water (1 g) was added to each dish to compensate for moisture lost during handling and milling. The dishes were then incubated at 15°C, 20°C, and 25°C for three months, with weekly moisture adjustments. After three months, the blocks were harvested, dried to constant mass, and weighed.

2.5. Covariates: biomass & nitrogen

To effectively distinguish between direct and indirect effects of warming on decomposition rates, we recognized the need to control for microbial biomass and nitrogen availability, both of which determine decomposition rates. We expected that the inoculum derived from previously warmed communities would have different levels of fungal biomass and different carbon to nitrogen (C:N) ratios when compared to previously cooled communities. These differences in biomass and nitrogen availability could in turn influence the decomposition rates recorded in our second incubation period, which would confound the influence of historical temperature. Specifically, higher initial biomass would be expected to expedite decomposition rates, and wider C:N ratios (i.e. less nitrogen per unit carbon) to slow decomposition rates because nitrogen is required to form the enzymes that catalyze decomposition (Schimel and Weintraub, 2003). We therefore estimated biomass by measuring ergosterol in each of the 36 communities resulting from the first incubation period. Ergosterol was extracted from sawdust in methanol as described by Newell et al. (1988). To control for potential effects of altered nitrogen availability, we measured total carbon and nitrogen concentrations in each of the 36 inocula. Homogenized subsamples of sawdust from each wood disc were ball milled to a fine powder and carbon to nitrogen ratios were calculated using an ECS 4010 Elemental Analyzer (Costech Analytical Technologies Inc., Valencia, CA, USA).

2.6. Statistical analysis

We used linear mixed models to assess the effects of historical and contemporary temperature on decomposition rates. Temperature from the first incubation period, second incubation period,

their interaction, C:N ratio, and ergosterol estimates (μg ergosterol per g dry wood) were modeled as fixed effects, with stand as a random factor. Standardized coefficients were used to compare the relative importance of these factors as determinants of decomposition rates (see Bradford et al., 2014). A non-significant interaction ($p = 0.7$) between historical and contemporary temperature was removed because comparing the models with and without the interaction using maximum likelihood suggested no difference in their ability to explain the data. C:N ratio was removed for the same reason, giving an additive model that retained historical temperature, contemporary temperature and fungal colonization (i.e., ergosterol estimates). Variance inflation factors of <2.0 (square-root) indicated that collinearity was low among model variables. All analyses were performed in R (Version 3.0.2) using the 'lme4' package.

3. Results

There were pronounced effects of both historical and contemporary temperature on the rate of decomposition. As expected, mass loss was greater at higher contemporary temperatures (Fig. 2). There was also a significant indirect effect of historical temperature; within a given contemporary temperature, communities from higher historical temperatures decomposed more wood than communities previously incubated at lower historical temperatures (Fig. 2). Notably, there was no significant interaction ($p = 0.7$) between historical and contemporary temperature, nor did the retained covariate (fungal biomass) alter the magnitude of the temperature coefficients. This suggests that the effect of historical temperature was consistent across cool, intermediate and warm conditions.

Given the positive effect of inoculum fungal biomass on decomposition rates, we tested whether there were significant differences in ergosterol concentrations between initial incubation temperature groups using one-way ANOVA. There were no significant differences ($p = 0.72$) (Fig. 3a). In contrast, inocula from historically higher temperature regimes had, on average, higher C:N ratios (due to lower relative nitrogen content) than samples previously incubated at lower temperatures (Fig. 3b). Yet unlike fungal biomass, C:N ratios were not retained as predictors of decomposition rates during model simplification, suggesting that differences in nitrogen availability across the 36 inoculum discs did not drive observed differences in decomposition rates.

Following model simplification, we used standardized coefficients to compare the relative influence of the retained predictors on decomposition rates. The standardized coefficient for contemporary temperature (mean std. coeff.±SE = 0.62 ± 0.071, $p < 0.001$) was approximately 3.8-times larger than that of historical temperature alone (mean std. coeff.±SE = 0.16 ± 0.072, $p = 0.026$). That is, a one standard deviation change in contemporary temperature during decomposition had an approximately 3.8-times greater influence on decomposition rates than a one standard deviation change in historical temperature. While clearly smaller than the effect of contemporary temperature, it is notable that the effect of historical temperature was approximately equivalent to that of initial fungal biomass (mean std. coeff.±SE = 0.22 ± 0.072, $p = 0.002$). When we consider the dual legacy effects of historical temperature (i.e. by summing coefficients for biomass and historical temperature, thereby simulating a one standard deviation change in each), the effect on decomposition is approximately two-thirds the size of a similar change in contemporary temperature.

4. Discussion

We explored the relative importance of direct and indirect effects of temperature on the functioning of microbial communities. We evaluated two competing hypotheses: one which emphasized

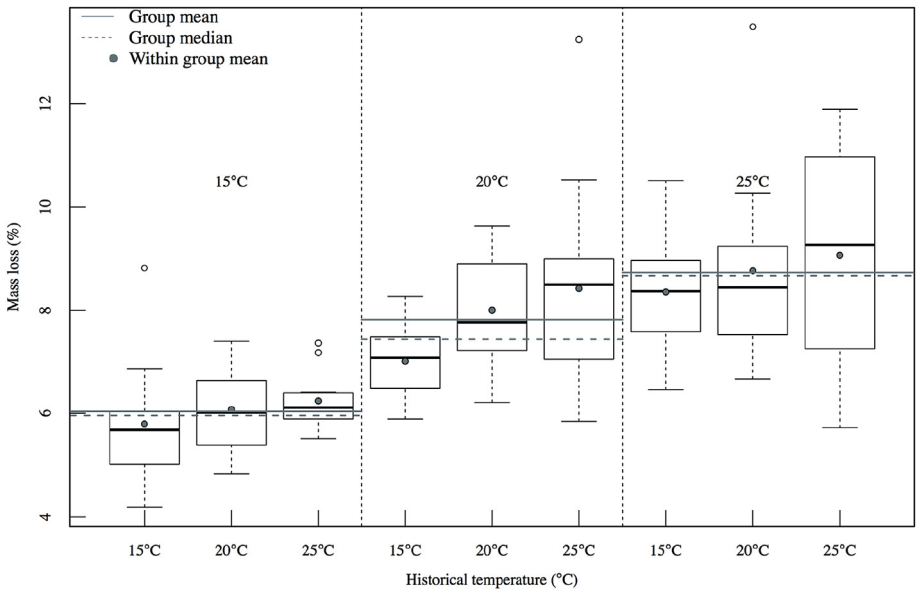

Fig. 2. Mass loss (percent loss of original mass; y-axis) in the second incubation period is plotted against contemporary and historical temperature groups. Historical temperature is shown in the x-axis, while contemporary temperature groups are ordered within the figure and separated by vertical dotted lines. Within each contemporary temperature group, the solid horizontal line represents the contemporary group mean; the dashed line represents the contemporary group median. Within each contemporary temperature/historical temperature combination, a dot represents the group mean and the solid line represents the group median. The top and bottom of the whiskers represent maximum and minimum values, respectively. Outliers are represented by open circles. Decomposition rates increase with increasing contemporary temperature, while variation within contemporary temperature groups on the basis of historical temperature demonstrates the additional significance of historical temperature in determining decomposition rates. Samples within a contemporary temperature group should be equivalent if historical temperature had no significant effect on microbial community function. Yet exposure to higher historical temperature led to faster decomposition under the same contemporary temperature, an effect which was evident in all three contemporary temperature groups.

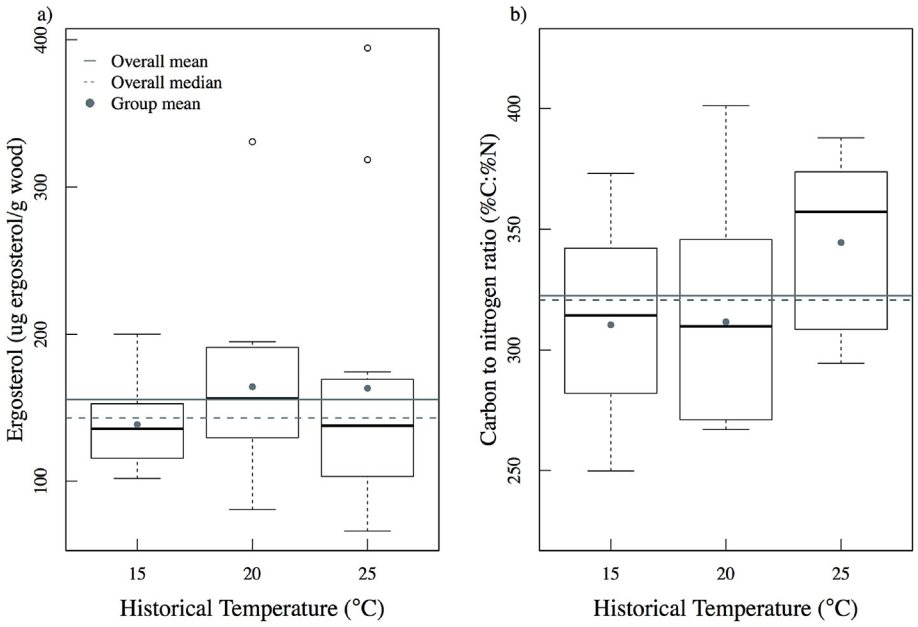

Fig. 3. Historical temperature effects on fungal biomass and wood quality, which determined starting conditions for the second incubation period. a) Ergosterol (μg ergosterol per g dry wood) by historical temperature. Values range from 66 to 394 μg. Across all samples, the solid line represents mean, and the dashed line represents the median. Within each historical temperature group, a dot represents the group mean, and the solid line represents the group median. The top and bottom of the whiskers represent maximum and minimum values, respectively. Outliers are represented by open circles. Ergosterol levels did not vary significantly based on historical temperature, but ergosterol was a significant predictor of decomposition rates. b) C:N ratios by historical temperature. Samples previously incubated at 25 °C have significantly higher C:N ratios (0.10%N) than samples previously incubated at 15 °C (0.12%N); however, C:N ratios were not significant predictors of decomposition rates in the second incubation period.

only the direct effect of temperature on decomposition, and an alternate hypothesis which proposed that direct temperature effects are modified by historical temperature effects that act indirectly to shape functioning. Our results partially support the second hypothesis by suggesting that both direct and indirect effects of temperature are important determinants of wood decomposition rates. However, in contrast to expected trade-offs under thermal adaptation (Barcenas-Moreno et al., 2009; Birgander et al., 2013; Bradford, 2013), we found that communities from historically warmer temperatures always decomposed wood fastest, regardless of the contemporary temperature. Theory and empirical evidence (Barcenas-Moreno et al., 2009; Birgander et al., 2013; Keiser and Bradford, 2017) suggests that we would have instead expected a temperature shift (i.e., an interaction between historical and contemporary temperature). That is, communities from historically warm conditions would decompose wood fastest in warm contemporary conditions; at cooler contemporary conditions, these same communities would decompose wood more slowly than communities adapted to cooler conditions.

Had we observed the temperature shift in functioning expected under Hypothesis 2, we should have detected it as an interaction between historical and contemporary temperature. Empirical evidence has suggested that fungi demonstrate a shift towards higher optimum growth rates after previous exposure to high temperatures (Barcenas-Moreno et al., 2009). Similarly, for leaf litter, the decomposition activity of communities sourced from warmer conditions also appears to exhibit a shift to the right, with communities from warmer conditions only decomposing litter fastest under warm conditions (Strickland et al., 2015; Keiser and Bradford, 2017). Yet in Birgander et al. (2013), optimum growth rate of bacteria was found to be sensitive to previous incubation temperature, whereas mineralization rates did not increase at higher temperatures in response to previous incubation. Whereas growth rates, mineralization rates, and decomposition rates should all presumably be linked, it is not immediately clear given our results and those of Birgander et al. (2013) that the response of decomposition rates to temperature change will always track the response of fungal growth rates. Given that growth rates seems most obviously to link to biogeochemical process rates (Rousk, 2016), it will be important for biogeochemical understanding and prediction to discern under what conditions microbial growth rate might be uncoupled from organic matter decomposition rates.

In our study, communities established under warmer conditions went on to decompose wood at faster rates than communities established under cooler conditions, regardless of contemporary temperature during decomposition. Nevertheless, the direct effect of contemporary temperature was dominant and nearly 4-times greater than the indirect effect of historical temperature. However, if we consider the indirect effects of historical temperature together with the influence of inoculum fungal biomass, we find that combined these indirect effects have approximately two-thirds the impact of direct temperature. Further, an increase of 1 °C in historical temperature resulted, on average, in a 1% increase in mass loss. Given that the average mass loss observed during our incubations was <10%, an additional 1% loss is a substantive effect size. Overall, our findings therefore point to the potential for indirect effects of prior conditions, as mediated by impacts on fungal community biomass and functional properties, to be important determinants of contemporary biogeochemical rates.

Our results are consistent with the theoretical expectation of the mechanisms underpinning decomposition: specifically, that both the amount of enzymes and the direct effect of temperature on enzyme-catalysis are likely to play a dominant role in regulating decomposition rates (Hättenschwiler et al., 2005; Gessner et al., 2010; Crowther et al., 2012). Predictably, we find that increased incubation temperature and higher fungal biomass result in more rapid decomposition. Notably, the fungal biomass effects did not appear driven by historical temperatures. This suggests that unidentified factors such as priority effects, which also drive community structure and function (Fukami et al., 2010), likely

contributed to the indirect effects we observed.

Three potential mechanisms might have driven the observed indirect legacy effect of historical temperature. These include physiological acclimation, evolutionary shifts within a static community, or changes in community composition (i.e., species sorting) (Birgander et al., 2013; Bradford, 2013). We can only speculate as to whether one or all of these mechanisms drove our observations, although physiological acclimation is unlikely to account for these changes since we established a "next-generation" community to measure decomposition rates and permitted a 2-week acclimation period. The most reasonable explanations would seem to include shifts, during the first incubation period, in community properties such as taxonomic or phylogenetic diversity, trait expression, and/or the relative abundance of taxa that vary in their decomposition potentials (Allison and Martiny, 2008; Barcenas-Moreno et al., 2009; Fukami et al., 2010). Connections between shifts in ecosystem processes and microbial communities have been established in previous work. For example, Treseder et al. (2012) found that changes in temperature resulted in significant changes to microbial community composition, and Strickland et al. (2009) showed that distinct microbial communities mineralize carbon at significantly different rates. However, we did not resolve the specific change(s) in microbial communities that might underlie these effects. A potentially fruitful way forward might be to consider temperature-sensitive trait responses and associated trade-offs, in order to establish whether they may explain the indirect effects we observed (Crowther et al., 2014).

Prior work suggests that broad-scale climate can drive biogeographic differences in the potential rates of decomposition mediated by microbial communities (Rinnan et al., 2009; Karhu et al., 2014; Averill et al., 2016). Our study highlights that historical climate has the capacity to shape microbial communities in a manner that influences contemporary decomposition rates (Strickland et al., 2015). This finding has implications for how microbial-mediated process rates are likely to respond to seasonal fluctuations in temperature and longer-term climatic change (Allison et al., 2010; Frey et al., 2013; Tang and Riley, 2015). In an era of significant environmental change, it is increasingly important that we clarify how climatic changes will directly influence process rates, and how indirect changes to community composition and structure may amplify or ameliorate these influences (Manning et al., 2006; Reich, 2010; Sistla et al., 2013; Karhu et al., 2014; Keiser and Bradford, 2017). Our study demonstrates that rising temperature may have a dual effect on microbial communities: directly, higher temperature stimulates increased decomposition; indirectly, previous exposure to higher temperatures results in additionally elevated decomposition rates.

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