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Long-term impacts of warming drive decomposition and accelerate the turnover of labile, not recalcitrant, carbon

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Abstract. Warming is altering the way soils function in ecosystems both directly by changing microbial physiology and indirectly by causing shifts in microbial community composition. Some of these warming-driven changes are short term, but others may persist over time. Here, we took advantage of a long-term (14 yr) warming experiment in a tallgrass prairie to tease apart the influence of short- and long-term warming on litter decomposition. We collected soils originating from warmed and control plots and incubated them with a common litter substrate in a reciprocal design under elevated and ambient growth chamber temperatures. Litter decomposition was 40% higher in soils that were warmed in the field for 14 yr (long-term warming) relative to soils derived from ambient plots. Short-term warming in the laboratory had less of an impact on decomposition—decomposition increased by 12% under laboratory warming. Using a two-pool soil carbon model to explore how different carbon pools may be responding, we found that long-term warming accelerated the turnover of labile, not recalcitrant, carbon in these prairie soils—a result that is likely due to shifts in soil community activity/composition. Taken together, our results offer experimental evidence that warming-induced changes in the soil community that occur over 14 yr of warming have long-lasting effects on carbon turnover.

Key words: carbon turn over; climate change; decomposition; direct and indirect effects; microbial activity; microbial composition; warming.

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INTRODUCTION

Globally, climate change is shifting rates of decomposition and in some cases reducing carbon storage, promoting future positive feedbacks between rising temperatures and reductions in soil carbon storage (Bellamy et al. 2005, Davidson and Janssens 2006, Crowther 2016, Pries et al. 2017, Bond-Lamberty et al. 2018). However, the underlying mechanisms driving these changes remain unclear, and with that, so does the potential for warming to impose sustained impacts on rates of decomposition (Melillo et al. 2017). While increasing temperatures likely alter rates of decomposition directly by shifting microbial extracellular enzyme activity (Lloyd and Taylor 1994, Bradford 2013, Rubenstein et al. 2017), climate also has the potential to drive decomposition via indirect pathways such as shifts in the microbial community including altered composition, abundance, and/or acclimation of soil microbes (Allison et al. 2013, Bradford 2013, Frey et al. 2013, Luo 2014, DeAngelis et al. 2015, Strickland et al. 2015, Melillo et al.

2017, Rubenstein et al. 2017). However, the relative impacts of the short- and long-term drivers of warming-induced shifts in rates of decomposition, while important to our understanding of global carbon storage, are less well understood.

Litter decomposition, in particular, is influenced by multiple drivers including climate, substrate quality and quantity (Meentemeyer 1978, Moore 1999, Raich et al. 2006, Parton et al. 2007, Cornwell 2008, Zhang et al. 2008, Xu et al. 2014, Feng et al. 2017), and the abundance and composition of the decomposer community (Cornelissen 1996, Aerts 1997, Parton et al. 2007). These factors, even as they directly influence decomposition, also feedback and interact with one another. The microbial community plays an important role in determining ecosystem processes such as litter decomposition (Strickland et al. 2009*a*, *b*, Wickings et al. 2012, Allison et al. 2013), and climatic warming can alter the composition of microbial communities (Castro et al. 2010, Luo 2014, Xue et al. 2016). As warming alters the structure and function of soil communities, there are likely to be shifts in ecosystem processes, including litter decomposition (Treseder 2012, Bradford 2013, Karhu 2014). These community change drivers of decomposition may be particularly important as the impacts of warming accumulate over time (Allison et al. 2013, Strickland et al. 2015) and may vary as they cycle through periods of strong and weak effects due to acclimation and/or community shifts (Melillo et al. 2017). Understanding these short-term vs. long-term accumulated effects of temperature on litter decomposition, an important ecosystem process, is critical. Further, the integration of empirically derived data with modeling can help us to predict soil carbon (C) feedbacks under future global change (Li et al. 2014, Rubenstein et al. 2017). Soils store approximately two-thirds of all organic carbon (Jobbágy and Jackson 2000, Schädel et al. 2013), which generally make up three distinct pools whose turnover rates vary from less than a year to thousands of years (Amundson 2001). Modeling approaches allow us to infer the turnover of specific pools of carbon through assimilation across a range of datasets (Wang et al. 2009, Zobitz et al. 2011).

Coupling a long-term field warming manipulation, with a short-term laboratory mesocosm litter decomposition experiment, we explored the mechanisms by which climatic warming may alter rates of litter decomposition in a temperate prairie ecosystem. Already, more than a decade of active warming has changed the composition of both plant (Shi et al. 2015, 2016) and microbial communities (Zhang et al. 2005, Sheik et al. 2011, Zhou et al. 2011, Luo 2014) within an Oklahoma tallgrass prairie. But how do the legacies of these changes to the biotic communities combine with the direct impacts of temperature to drive ecosystem function? Specifically, we examined (1) the short-term role of temperature in regulating rates of decomposition (laboratory temperature manipulation); (2) the long-term, accumulated, role of temperature on decomposition as mediated by the microbial community (field temperature manipulation); and (3) if the temperature-induced patterns we recorded in the short term vs. long term would scale over time (years) by using a discrete two-pool C model (Rey and Jarvis 2006, Schädel et al. 2013, Liang et al. 2015) to estimate microbe-mediated shifts in carbon turnover rate and mean residence time associated with warming.

METHODS

Study site

Soils and litter for these experiments were collected at the Kessler Atmospheric and Ecological Field Station in McClain County, Oklahoma, USA (34°59′ N, 97°31′ W). Soils were of the Nash-Lucien complex with mean annual temperature 16°C and mean annual precipitation 914 mm. All materials were collected from a tallgrass prairie site dominated by the C_4 graminoid *Schizachyrium scoparium* (Michx.) Nash and co-dominated with *Sorghastrum nutans* (L.) Nash under atmospheric warming. A temperature manipulation experiment altering atmospheric and soil temperatures has been ongoing at this site since November of 1999, experimentally warming 2 × 2 m plots using infrared heaters to provide continuous warming. Warmed and ambient control plots are paired in six blocks. To mimic hay harvest, 1 × 1 m subplots nested within the plots are clipped, with aboveground biomass removed once annually at the end of the growing season. These plots experience ~3°C of warming in the warmed plots relative to the ambient plots. More detail about the design of the warming plots can be found in Luo et al. (2001).

Plant soil sampling and incubation

Using a fully factorial mesocosm experiment, litter of *S. scoparium* was decomposed on soils from control and warmed field plots and incubated under one of two temperature conditions set to mimic growing season temperatures in the ambient and warmed field plots, respectively.

In May 2014, we collected soil samples from the clipped subplots within the six control plots and six warmed plots (two clipped plots per warming array). Pairs of a single warmed and control plot were arranged side-by-side in a blocked design. One soil core (2 cm in diameter, 0–15 cm) was collected from each clipped subplot. The soil cores from each of the two clipped subplots associated with each plot were combined to generate a total of 12 soil samples (6 field blocks × 2 warming treatments). Soil samples were sieved to 2 mm. Percent soil organic matter of these soils did not differ between warmed and ambient plots (Appendix S1: Fig. S1).

Standing senesced litter of *S. scoparium* was collected from the prairie community immediately outside of the warming plots in November 2013. Litter was dried at 70°C for ~48 h and then ground to 2.5 mm using a Wiley mill. The ground litter was then autoclaved twice to sterilize it. We used ground litter to: (1) promote litter surface area for microbial colonization, (2) homogenize litter material structure across replicates, (3) remove the physical effects of litter on decomposition (Strickland et al. 2009*b*).

We combined 0.1 g of ground litter with 10 g of field soil from each of the field plots in a 50-mL Falcon tube. Soil and litter were thoroughly mixed. A subset of sixteen 10 g soil samples were also added to Falcon tubes without the addition of litter to control for respiration rates of the soil samples themselves. We added 1.2 mL of deionized water to each sample to bring the samples to ~60% water holding capacity (see de Graaff et al. 2010).

Centrifuge tubes containing the samples were placed in quart size ball jars. The lid of each jar was fitted with a septum, allowing for the periodic removal of air samples; 10 mL of water in the bottom of the jar maintained humidity. Jars were kept in Percival growth chambers, set to maintain temperatures of either 27°C (ambient) or 30°C (warmed) based on summer temperatures within control and warmed field plots, respectively, averaged over the past 5 yr.

CO_2 evolution was measured on days 1, 3, 5, 8, 15, 30, 60, 91, and 120 by removing 10 mL of air from the headspace of each jar using a syringe. Samples were analyzed for CO_2 concentration using a LI-COR 6400 infrared gas analyzer (Li-Cor, Lincoln, Nebraska, USA). After removal of air samples, jars were opened and allowed to air out for 30 min.

Statistical analysis

To isolate CO_2 efflux resulting from decomposition of the added grass litter, as opposed to soil carbon, we calculated litter-evolved CO_2 as CO_2 levels in the soil + litter treatment minus CO_2 levels in the soil-only treatment. This is a standard method for estimating litter C mineralization rates from laboratory incubation studies (Strickland et al. 2009*a*, *b*, Keiser et al. 2011, 2013). Samples were paired for subtraction by field block from which the soil was collected (matched exactly when possible, otherwise paired with the block with the most similar respiration rate for soil + litter treatments), field treatment, and laboratory treatment. To determine the relative importance of short-term (i.e., laboratory incubation temperature) and long-term warming (i.e., origin of the soil microbial community after 14 yr of warming in the field) influences on decomposition rates, we used a two-way ANOVA, blocked by field block, and including both field and laboratory treatments, along with their interaction, as fixed factors to compare CO_2 concentration at each sampling date. We ran an additional ANOVA to examine the impacts of field and laboratory conditions (i.e., physical temperature conditions vs. microbial community responses to long-term warming) and their interaction on cumulative rates of decomposition over the course of the experiment. For this analysis, we again blocked by field block. We calculated type III sums of squares using the car package (Fox and Weisberg 2011).

Soil carbon model

To explore the warming effects on the decomposition of different litter compounds (labile vs.

recalcitrant), we employed an inverse-modeling technique. A litter decomposition model, which includes two pools (i.e., labile and recalcitrant), was used to simulate the litter decomposition.

$$R(t) = K_L f_L C_{tot} e^{-K_L t} + K_R(1 - f_L) C_{tot} e^{-K_R t}$$

where $R(t)$ is CO_2-C emission rate at time t; K_L and K_R are turnover rates of labile and recalcitrant litter, respectively; f_L is the initial fraction of labile litter; C_{tot} is the initial litter C content before incubation.

Bayesian probabilistic inversion technique was used to estimate the distribution of model parameters based on prior knowledge of parameter ranges and incubation data. Four pairs of parameters K_L and K_R (corresponding to the four treatments), and one universal f (f value is universal because identical litter inputs were used for incubation under all four treatments) were used for Bayesian probabilistic inversion.

According to the Bayes' theorem, the posterior probability density function (PDF) $P(\theta|Z)$ of model parameters (θ) for given observations (Z) was estimated from our prior knowledge of PDF $P(\theta)$ and a likelihood function of observations $P(Z|\theta)$ (Liang et al. 2015, Ma et al. 2017)

$$P(\theta|Z) \propto P(Z|\theta)P(\theta).$$

Here, we assumed that the prior PDFs follow uniform distributions. The errors between each observation data and model simulation result independently follow normal distribution with a mean of zero, such that the likelihood function is represented by

$$P(Z|\theta) \propto \exp\left\{ -\sum_{i=1}^{n} \sum_{t \in obs(Z_i)} \frac{[Z_i(t) - X_i(t)]^2}{2\sigma_i^2(t)} \right\}$$

where $Z_i(t)$ and $X_i(t)$ are the observed and modeled values at time t, respectively. The standard deviation of observations is represented by $\sigma_i(t)$. n is the number of datasets in this study, here equaling 4 representing CO_2 efflux from litter decomposition under the four treatments.

To derive the posterior PDFs of parameters, two steps (a proposing step and a moving step) were repeated (Xu et al. 2006, Liang et al. 2015). In the proposing step, a new point θ^{new} was generated based on the previously accepted point θ^{old}

$$\theta^{new} = \theta^{old} + d(\theta_{max} - \theta_{min})/D$$

where θ_{max} and θ_{min} are the maximum and minimum values in the prior PDF, and d is a random value between -0.5 and 0.5. The step length, d, was set to 0.5 to control the proposing step size. In the moving step, the new set of parameter values either were accepted by reducing the sum of the standard deviation from observation and model or were randomly accepted with a probability of 0.05. Four chains of 50,000 simulations were run with an acceptance rate of around 30%. The Gelman-Rubin statistic (Gelman and Rubin 1992, Xu et al. 2006) was used to check the convergence of sampling chains. The first half (i.e., burn-in period) of accepted samples were discarded, and only, the rest were used for further analyses.

RESULTS

Cumulative litter decomposition

Cumulative litter decomposition was significantly promoted by long-term warming impacts (field conditioning of the soil), but not by short-term impacts (laboratory incubation conditions; Fig. 1). Cumulative CO_2 evolution from the decomposing litter was, on average, 40% higher on soils derived from experimentally warmed plots relative to control plots ($F_{1,14} = 7.26$, $P = 0.02$). CO_2 evolution averaged only 12% higher when laboratory incubations were carried out under warmed laboratory conditions and this difference was insignificant ($F_{1,14} = 0.67$, $P = 0.43$). There was no significant interaction between field and laboratory warming treatments ($F_{1,14} = 0.19$, $P = 0.67$). The treatment in which soils from warmed plots were incubated under warmed laboratory conditions had exhibited the highest cumulative CO_2 evolution (Fig. 1).

Litter decomposition over time

The accumulated impacts of long-term warming (warmed or ambient field plots) had a large influence on the rates of decomposition over the first 15 d (Table 1, Fig. 2). However, there was a switch in patterns. By day 30 (through day 90), short-term warming impacts (laboratory incubation temperature) had a larger influence on carbon evolution than field conditioning did—with the ambient laboratory incubation showing

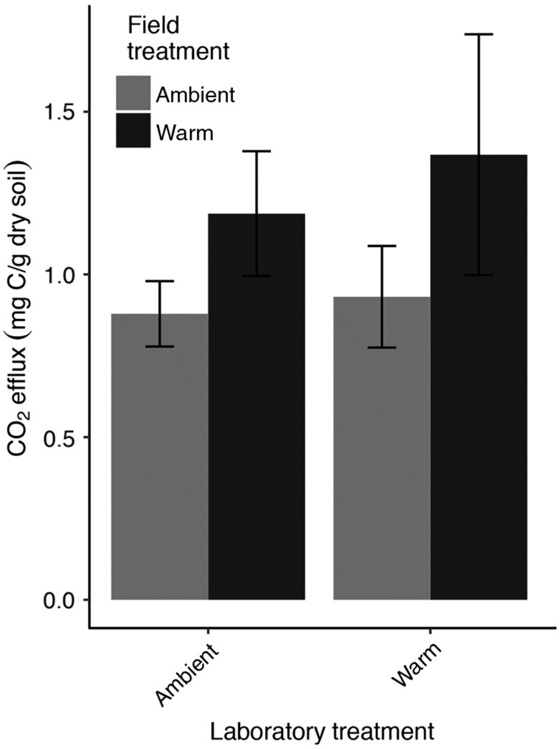

Fig. 1. Mean cumulative CO_2 efflux from litter (± SE) on soils from warmed and ambient field plots incubated in ambient and warmed laboratory conditions.

significantly higher rates of decomposition in the later days of the incubation than under elevated temperatures (Table 1). By the end of the experiment (day 120), decomposition was equally low across all treatments (Table 1).

Two carbon pool model

Soils conditioned under our long-term field warming treatment had a higher modeled labile litter decay rate (K_L)—they were 13% and 23% under ambient and warmed laboratory conditions, respectively. In contrast, short-term laboratory warming had little to no effect on the turnover of labile litter in soils collected from ambient field condition plots (Fig 3a); short-term laboratory warming increased the labile litter decomposition rate of field-warmed soils by only 8%. The turnover rate of recalcitrant litter (K_R) was not well constrained by the incubation data (Fig 3b). Maximum likelihood of the labile carbon content in the litter (f) was 0.32 (±0.02; Appendix S2: Fig. S1), suggesting that labile carbon composes ~32% of the litter.

DISCUSSION

We found that the accumulated long-term effects of warming on decomposition, as mediated by long-term field warming, were far greater than warming impacts over the short term as mediated by laboratory incubation temperature. Our models indicate that much of the difference between long- and short-term litter decomposition is due to shifts turnover rates of the labile, rather than recalcitrant, soil carbon pool under warming.

Prior research at this temperate prairie site found complex and significant impacts of climatic warming cascading through the ecosystem, ultimately increasing rates of carbon cycling (Wan

Table 1. Two-way ANOVA table showing the influence of field temperature (field warming) and laboratory incubation temperature (laboratory warming), along with their interactive effects, on CO_2 evolution for the duration of the experiment (days 1–120).

	Field warming		Laboratory warming		Field × laboratory warming interaction	
Day	*F*	*P*	*F*	*P*	*F*	*P*
1	1.14	0.30	0.00	0.95	0.24	0.63
3	5.61	0.03	2.01	0.18	0.76	0.40
5	9.77	<0.01	1.58	0.23	0.09	0.77
8	6.05	0.03	3.61	0.08	0.30	0.59
15	7.01	0.02	0.48	0.50	1.10	0.31
30	2.05	0.17	4.67	0.05	1.01	0.33
60	3.84	0.07	11.97	<0.01	2.04	0.18
91	0.31	0.59	19.16	<0.01	1.13	0.28
120	0.80	0.39	0.07	0.79	4.62	0.05
Cumulative	7.26	0.02	0.67	0.43	0.19	0.67

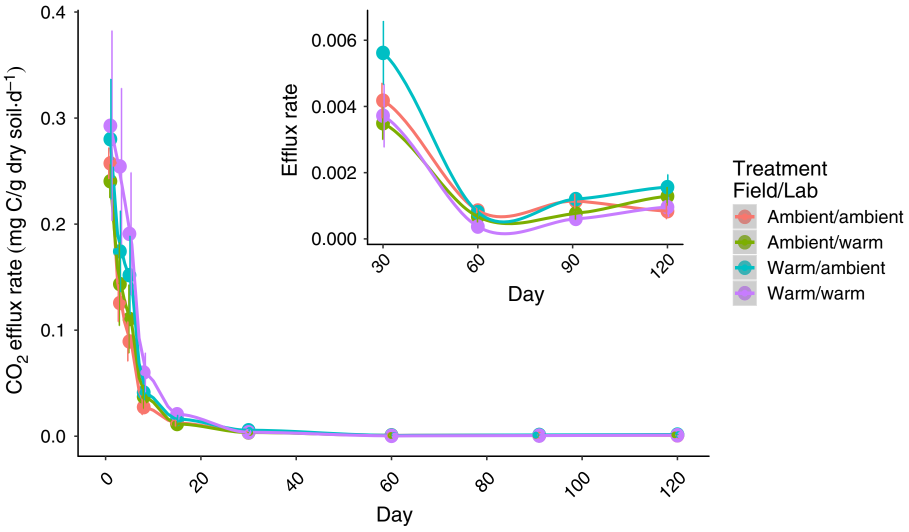

Fig. 2. Rates of CO_2 evolution from litter on soils from ambient and warmed field plots incubated under ambient and warmed laboratory conditions through time (day 1–120). Inset shows CO_2 evolution for days 30–120.

et al. 2005, Zhou et al. 2007, Belay-Tedla et al. 2009). Rates of litter decomposition in this ecosystem are changing, resulting in reductions of labile organic carbon in plots experiencing warmed conditions (Xu et al. 2012*b*). In part, these changes in decomposition can be traced to shifts in the ability of the soil microbial community to decompose soil organic carbon (Xue et al. 2016, Feng et al. 2017). However, even as a picture is emerging regarding the impacts of warming on carbon cycling in terrestrial systems, we still do not fully understand the mechanisms driving these changes. In particular, it is not yet clear to what extent the effects of short- vs. long-term effects warming are and how they impact components of the soil carbon pool, though mounting evidence suggests that the impacts of long-term warming are important and likely changing (Rubenstein et al. 2017).

While it is rare to experimentally tease apart the long-term influence of a shifting microbial community from the short-term impacts of warming on rates of litter decomposition,

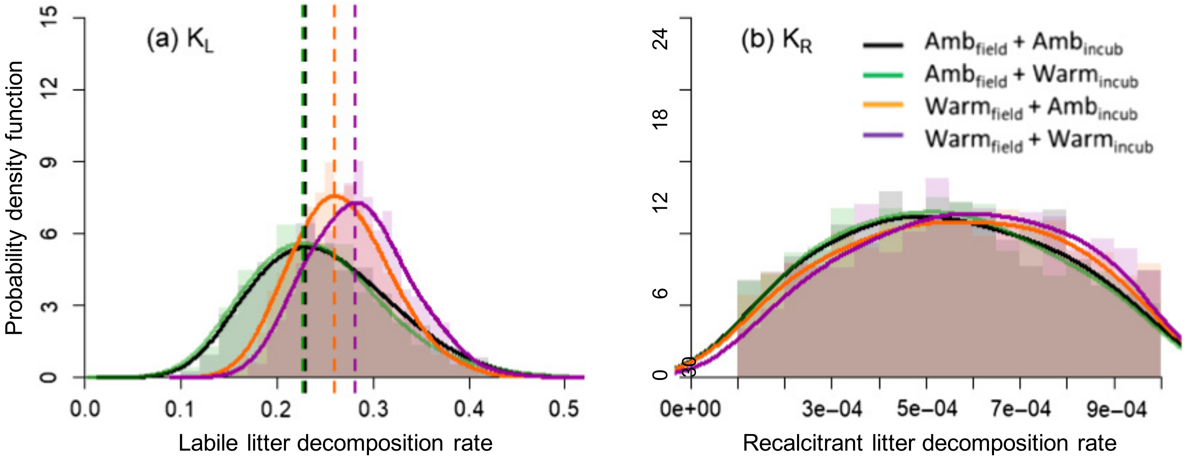

Fig. 3. Probability density distribution of (a) labile litter decomposition rate (K_L) and (b) recalcitrant litter decomposition rate (K_R) under field and laboratory warming treatments.

scientists are beginning to examine the potential for shifting soil microbes to facilitate lasting impacts of climate change. In fact, studies are finding important and lasting footprints of climate conditions in shaping present-day carbon dynamics in ways that sometimes trump the influence of current short-term climate conditions (Strickland et al. 2015, Melillo et al. 2017, Rubenstein et al. 2017). In particular, it seems that acclimation and/or shifts in community composition associated with climate change could potentially drive changes in litter decomposition (Hawkes and Keitt 2015), and that the nature of these changes can cycle through time, creating periods of increased decomposition interspersed with periods of ambient levels of decomposition (Melillo et al. 2017). Our results compliment these findings, pointing to a critical role of climate-mediated structuring of microbial communities in shaping ecosystem carbon dynamics, and suggest important implications for global climate change to drive rates of soil carbon turnover both in the short term, but, perhaps even more importantly, in the long term as mediated by shifts in microbial communities. Importantly, our study suggests such changes in the microbial community under long-term warming may lead to the faster carbon turnover rate, possibly intensifying the positive feedback of soil C dynamics to exacerbate climate change. While we do not expressly explore shifts in the microbial community in this study, and thus cannot point to specifics of how changes in the microbial community alter decomposition, there is good evidence that long-term warming has altered the microbial community in this system (Zhang et al. 2005, Sheik et al. 2011, Zhou et al. 2011, Luo 2014). Our mesocosm study design further allows us to isolate the impacts of climate-induced changes in the soils from the direct impacts of temperature as manipulated in the laboratory. Ultimately, our findings support those of long-term field warming studies that have observed sustained changes in soil carbon cycling as mediated by shifts in microbial communities (Frey et al. 2013, Feng et al. 2017, Melillo et al. 2017). Clearly, soil carbon dynamics will be influenced by warming both spatially and temporally, and these patterns warrant further exploration.

The hypothesis that soil respiration ultimately acclimates to warmer temperatures, with soil respiration initially increasing as a result of warming but then returning to more normal rates in the long term, could be driven by adaptation of the microbial community or by resource depletion (Luo et al. 2001, Bradford et al. 2008, Melillo et al. 2017; but see Hartley et al. 2008, Carey 2016). This acclimation can lead to long-term patterns of decomposition cycling, generating multi-year periods of enhanced decomposition, following by periods of reduced decomposition in-line with ambient levels (Melillo et al. 2017). Here, we found that when isolated from the direct effects of elevated temperature and given a common substrate to decompose, even after 14 yr of experimental warming in the field, microbial communities exposed to elevated temperatures in the field drove faster rates of carbon turnover in our laboratory experiment. While it is difficult to tease apart how these short- and long-term effects of warming vary site to site, our findings of accelerated C turnover on soils from a long-term warming manipulation support other studies that suggest there is a larger role for resource depletion than adaptation in the microbial community when it comes to a dampening of the response of soil respiration to elevated temperature over time (Kirschbaum 2004, Hartley et al. 2007), including findings from our mixed grass prairie system (Xu et al. 2012*a*, Feng et al. 2017).

While long-term warming-mediated shifts in the soil microbial community seemed to be the strongest driver of increased rates of decomposition, we also found short-term impacts of warming on decomposition. These effects became more apparent later in the laboratory incubation. Inversely, the influence of the microbial community was strongest at the beginning of the experiment, while after 120 d we failed to detect a signature of the field treatment (microbial community). Decomposition rates were very low by the end of the experiment, suggesting much of the labile organic matter had already decomposed. Interestingly, higher decomposition rates occurred under ambient laboratory conditions toward the end of the experiment. We suspect this is a result of those treatments having slightly more remaining labile organic material remaining late in the experiment as a result of slightly higher (though not significantly so) rates of decomposition under warmed conditions earlier in the experiment. However, there is also evidence for a shift in the main driver of decomposition, whereby the microbial community is the most important driver of early decomposition but becomes less important through time as labile resources are used up resulting in a convergence of decomposer communities (García-Palacios et al. 2016). This shift could also result from a convergence of microbial community composition among the field soils while under laboratory conditions. However, other studies have found strong evidence that the legacies of past climate conditions on the microbial community can be long lived (Allison et al. 2013). We cannot eliminate the possibility that the addition of litter to our mesocosms may have resulted in some priming of decomposition of the soil organic carbon pool. While it is fairly common to use this sort of mesocosm study to measure litter decomposition by pairing mesocosms with and without litter (Strickland et al. 2009*a*, *b*, Keiser et al. 2011, 2013), a small portion of the calculated CO_2 efflux in our mesocosms may, in fact, be from the mineralization of soil carbon. However, percent organic matter did not differ significantly between soils derived from warmed and ambient plots at the beginning of the mesocosm study (Appendix S1: Fig. S1). As such, though we expect this priming effect to contribute a relatively small amount to overall CO_2 efflux in this study, the magnitude of this priming effect should influence the warmed and ambient field soils to the same extent.

Modeling decomposition of litter using a two-discrete C pool model, including both labile and recalcitrant pools, allowed us to attribute the relative effects of long-term field warming and short-term laboratory warming on the breakdown of labile vs. recalcitrant components of the plant litter detecting changes in C cycling. Such models provide a powerful technique to detect changes in C cycling of fast and slow C pools. Here, we found that changes in the microbial community resulted in the identical litter carbon substrate being perceived as more labile to the altered microbial community originating from the long-term field warming experiment and has resulted in greater carbon loss. Our results suggest that warming over long periods of time alters soil microbial community, which in turn, accelerates litter and soil C decomposition (Crowther et al. 2012, Feng et al. 2017). Thus, the changed microbial community—rather than the short-term impacts of warming—intensifies the positive feedback of soil carbon dynamics to climate change. Past research has suggested that labile and recalcitrant soil carbon pools may be similarly sensitive to warming (Fang et al. 2005), though others have found greater temperature sensitivity of more recalcitrant forms of C (Feng et al. 2017). Our results suggest that while warming will continue to increase rates of decomposition, much of this comes from the increased ability of the warming-altered microbial community to break down labile forms of carbon. In fact, these results may point to a priming effect when labile forms of carbon are added to a warmed system. Our findings suggest the importance of explicitly incorporating changes in the microbial community into models of long-term climate-associated changes in carbon cycling.

CONCLUSIONS

We find that climatic warming has the potential to influence rates of litter decomposition both in the short term and the long term via changes in the soil microbial community. Combining a laboratory-based incubation experiment with a 14-yr field warming experiment, we were able to disentangle these effects to show that, in fact, the indirect impacts of long-term field warming on soils substantially increased rates of decomposition. Further, these indirect impacts of the long-term field experiment were greater than the direct effects of warming on decomposition during the laboratory incubation. These results from combined field, laboratory, and modeling approaches have clear and important implications for terrestrial carbon storage, suggesting the potential for long-lasting increases in rates of labile carbon turnover mediated by climate-induced shifts in the soil microbial community rather than directly by present-day temperature itself.

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DATA AVAILABILITY

Data available in the Oklahoma Biological Survey's Digital Repository: http://biosurvey.ou.edu/souza/Decomp_Data_for_archiving.xlsx

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2715/full