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 turnover; 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.
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 C4 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. 2009b).

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.

CO2 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 CO2 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 CO2 efflux resulting from decomposition of the added grass litter, as opposed to soil carbon, we calculated litter-evolved CO2 as CO2 levels in the soil + litter treatment minus CO2 levels in the soil-only treatment. This is a standard method for estimating litter C mineralization rates from laboratory incubation studies (Strickland et al. 2009a, 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 CO2 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 \( f \) (the 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 (\( \theta \)) 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

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

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 \( \theta_{new} \) was generated based on the previously accepted point \( \theta_{old} \)

\[ \theta_{new} = \theta_{old} + d(\theta_{max} - \theta_{min})/D \]

where \( \theta_{max} \) and \( \theta_{min} \) 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...
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 ($\pm$0.02; Appendix S2: Fig. S1), suggesting that labile carbon composes $\sim$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...
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. 2012b). 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. 2. Rates of CO₂ 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 CO₂ evolution for days 30–120.

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. 2012a, 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. 2009a, 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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LITERATURE CITED

Aerts, R. 1997. Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. Oikos 79:439–449.

Allison, S. D., Y. Lu, C. Weihe, M. L. Goulden, A. C. Martiny, K. K. Treseder, and J. B. H. Martiny. 2013. Microbial abundance and composition influence litter decomposition response to environmental change. Ecology 94:714–725.

Amundson, R. 2001. The carbon budget in soils. Annual Review Earth Planet Sciences 29:535–562.

Belay-Tedla, A., X. Zhou, B. Su, S. Wan, and Y. Luo. 2009. Labile, recalcitrant, and microbial carbon and nitrogen pools of a tallgrass prairie soil in the US Great Plains subjected to experimental warming and clipping. Soil Biology and Biochemistry 41:110–116.

Bellamy, P. H., P. J. Loveland, R. I. Bradley, R. M. Lark, and G. J. D. Kirk. 2005. Carbon losses from all soils across England Wales 1978–2003. Nature 437:245–248.

Bond-Lamberty, B., V. L. Bailey, M. Chen, C. M. Gough, and R. Vargas. 2018. Globally rising soil heterotrophic respiration over recent decades. Nature 560:80–83.

Bradford, M. A. 2013. Thermal adaptation of decomposer communities to warming soils. Frontiers in Microbiology 4:art333.

Bradford, M. A., C. A. Davies, S. D. Frey, T. R. Mad- dox, J. M. Melillo, J. E. Mohan, J. F. Reynolds, K. K. Treseder, and M. D. Wallenstein. 2008. Thermal adaptation of soil microbial respiration to elevated temperature. Ecology Letters 11:1316–1327.

Carey, J. C., et al. 2016. Temperature response of soil respiration largely unaltered with experimental warming. Proceedings of the National Academy of Sciences USA 113:13797–13802.

Castro, H. F., A. T. Classen, E. E. Austin, R. J. Norby, and C. W. Schadt. 2010. Soil microbial community responses to multiple experimental climate change drivers. Applied and Environmental Microbiology 76:999–1007.

Cornelissen, J. H. C. 1996. An experimental comparison of leaf decomposition rates in a wide range of temperate plant species and types. Journal of Ecology 84:573–582.

Cornwell, W. K., et al. 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. Ecology Letters 11:1065–1071.

Crowther, T. W., et al. 2016. Quantifying global soil carbon losses in response to warming. Nature 540:104–108.

Crowther, T. W., A. Littleboy, T. H. Jones, and L. Boddy. 2012. Interactive effects of warming and invertebrate grazing on the outcomes of competitive fungal interactions. FEMS Microbiology Ecology 81:419–426.

Davidson, E. A., and I. A. Janssens. 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440:165.

DeAngelis, K. M., G. Pold, B. D. Topcuoglu, L. T. A. van Diepen, R. M. Varney, J. L. Blanchard, J. Melillo, and S. D. Frey. 2015. Long-term forest soil warming alters microbial communities in temperate forest soils. Frontiers in Microbiology 6:104.

de Graaff, M. A., A. T. Classen, H. F. Castro, and C. W. Schadt. 2010. Labile soil carbon inputs mediate the soil microbial community composition and plant residue decomposition rates. New Phytologist 188:1055–1064.

Fang, C., P. Smith, J. B. Moncrieff, and J. U. Smith. 2005. Similar response of labile and resistant soil organic matter pools to changes in temperature. Nature 433:57–59.

Feng, W., et al. 2017. Enhanced decomposition of stable soil organic carbon and microbial catabolic potentials by long-term field warming. Global Change Biology 23:4765–4776.

Fox, J. and S. Weisberg. 2011. An R companion to applied regression, second edition. Sage Publications, Thousand Oaks, California, USA.

Frey, S. D., J. Lee, J. M. Melillo, and J. Six. 2013. The temperature response of soil microbial efficiency and its feedback to climate. Nature Climate Change 3:395.

Garcia-Palacios, P., E. A. Shaw, D. H. Wall, and S. Hättenschwiler. 2016. Temporal dynamics of biotic and abiotic drivers of litter decomposition. Ecology Letters 19:554–563.

Gelman, A., and D. B. Rubin. 1992. Inference from iterative simulation using multiple sequences. Statistical Science 7:457–472.

Hartley, I. P., A. Heinemeyer, and P. Ineson. 2007. Effects of three years of soil warming and shading on the rate of soil respiration: substrate availability and not thermal acclimation mediates observed response. Global Change Biology 13:1761–1770.

Hartley, I. P., D. W. Hopkins, M. H. Garnett, M. Sommerkorn, and P. A. Woomer. 2008. Soil microbial respiration in arctic soils does not acclimate to temperature. Ecology Letters 11:1092–1100.
Hawkes, C. V., and T. H. Keitt. 2015. Resilience vs. historical contingency in microbial responses to environmental change. Ecology Letters 18:612–625.

Jobbágy, E. G., and R. B. Jackson. 2000. The vertical distribution of soil organic carbon and its relation to climate and vegetation. Ecological Applications 10:423–436.

Karhu, K., et al. 2014. Temperature sensitivity of soil respiration rates enhanced by microbial community response. Nature 513:81–84.

Keiser, A. D., J. D. Knoepp, and M. A. Bradford. 2013. Microbial communities may modify how litter quality affects potential decomposition rates as tree species migrate. Plant and Soil 372:167–176.

Keiser, A. D., M. S. Strickland, N. Fierer, and M. A. Bradford. 2011. The effect of resource history on the functioning of soil microbial communities is maintained across time. Biogeoosciences 8:1477–1486.

Kirschbaum, M. U. F. 2004. Soil respiration under prolonged soil warming: Are rate reductions caused by acclimation or substrate loss? Global Change Biology 10:1870–1877.

Li, J., G. Wang, S. D. Allison, M. A. Mayes, and Y. Luo. 2014. Soil carbon sensitivity to temperature and carbon use efficiency compared across microbial-ecosystem models of varying complexity. Biogeochemistry 119:67–84.

Liang, J., D. Li, Z. Shi, J. M. Tiedje, J. Zhou, E. A. G. Schuur, K. T. Konstantinidis, and Y. Luo. 2015. Methods for estimating temperature sensitivity of soil organic matter based on incubation data: a comparative evaluation. Soil Biology & Biochemistry 80:127–135.

Lloyd, J., and J. A. Taylor. 1994. On the temperature dependence of soil respiration. Functional Ecology 8:315–323.

Luo, C., et al. 2014. Soil microbial community responses to a decade of warming as revealed by comparative metagenomics. Applied and Environmental Microbiology 80:1777–1786.

Luo, Y., S. Wan, D. Hui, and L. L. Wallace. 2001. Acclimatization of soil respiration to warming in a tall grass prairie. Nature 413:622.

Ma, S., J. Jiang, Y. Huang, Z. Shi, R. M. Wilson, D. Ricciuto, S. D. Sebestyen, P. J. Hanson, and Y. Luo. 2017. Data-constrained projections of methane fluxes in a northern Minnesota peatland in response to elevated CO2 and warming. Journal of Geophysical Research: Biogeosciences 122:2841–2861.

Meentemeyer, V. 1978. Macroclimate and lignin control of litter decomposition rates. Ecology 59:465–472.

Melillo, J. M., S. D. Frey, K. M. DeAngelis, W. J. Werner, M. J. Bernard, F. P. Bowles, G. Pold, M. A. Knorr, and A. S. Grandy. 2017. Long-term pattern and magnitude of soil carbon feedback to the climate system in a warming world. Science 358:101–105.

Moore, T. R., et al. 1999. Litter decomposition rates in Canadian forests. Global Change Biology 5:75–82.

Parton, W., et al. 2007. Global-scale similarities in nitrogen release patterns during long-term decomposition. Science 315:361–364.

Pries, C. E. H., C. Castanha, R. C. Porras, and M. S. Torn. 2017. The whole-soil carbon flux in response to warming. Science 355:1420–1423.

Raich, J. W., A. E. Russell, K. Kitayama, W. J. Parton, and P. M. Vitousek. 2006. Temperature influences carbon accumulation in moist tropical forests. Ecology 87:76–87.

Rey, A. N. A., and P. Jarvis. 2006. Modelling the effect of temperature on carbon mineralization rates across a network of European forest sites (FORCAST). Global Change Biology 12:1894–1908.

Rubenstein, M. A., T. W. Crowther, D. S. Maynard, J. S. Schilling, and M. A. Bradford. 2017. Decoupling direct and indirect effects of temperature on decomposition. Soil Biology and Biochemistry 112:110–116.

Schädel, C., Y. Luo, R. D. Evans, S. Fei, and S. M. Schaeffer. 2013. Separating soil CO2 efflux into C-pool-specific decay rates via inverse analysis of soil incubation data. Oecologia 171:721–732.

Sheik, C. S., W. H. Beasley, M. S. Elshahed, X. Zhou, Y. Luo, and L. R. Krumholz. 2011. Effect of warming and drought on grassland microbial communities. The ISME Journal 5:1692–1700.

Shi, Z., R. Sherry, X. Xu, O. Hararuk, L. Souza, L. Jiang, J. Xia, J. Liang, and Y. Luo. 2015. Evidence for long-term shift in plant community composition under decadal experimental warming. Journal of Ecology 103:1131–1140.

Shi, Z., X. Xu, L. Souza, K. Wilcox, L. Jiang, J. Liang, J. Xia, P. García-Palacios, and Y. Luo. 2016. Dual mechanisms regulate ecosystem stability under decade-long warming and hay harvest. Nature Communications 7:11973.

Strickland, M. S., A. D. Keiser, and M. A. Bradford. 2015. Climate history shapes contemporary leaf litter decomposition. Biogeochemistry 122:165–174.

Strickland, M. S., C. Lauber, N. Fierer, and M. A. Bradford. 2009a. Testing the functional significance of microbial community composition. Ecology 90:441–451.

Strickland, M. S., E. Osburn, C. Lauber, N. Fierer, and M. A. Bradford. 2009b. Litter quality is in the eye of the beholder: initial decomposition rates as a function of inoculum characteristics. Functional Ecology 23:627–636.
Treseder, K. K., et al. 2012. Integrating microbial ecology into ecosystem models: challenges and priorities. Biogeochemistry 109:7–18.

Wan, S., D. Hui, L. L. Wallace, and Y. Lou. 2005. Direct and indirect effects of experimental warming on ecosystem carbon processes in a tallgrass prairie. Global Biogeochemical Cycles 19:2.

Wang, Y. P., C. M. Trudinger, and I. G. Enting. 2009. A review of applications of model-data fusion to studies of terrestrial carbon fluxes at different scales. Agriculture for Meteorology 149:1829–1842.

Wickings, K., A. S. Grandy, S. C. Reed, and C. C. Cleveland. 2012. The origin of litter chemical complexity during decomposition. Ecology Letters 15:1180–1188.

Xu, X., Y. Luo, and J. Zhou. 2012a. Carbon quality and the temperature sensitivity of soil organic carbon decomposition in a tallgrass prairie. Soil Biology and Biochemistry 50:142–148.

Xu, X., J. P. Schimel, P. E. Thornton, X. Song, F. Yuan, and S. Goswami. 2014. Substrate and environmental controls on microbial assimilation of soil organic carbon: a framework for Earth system models. Ecology Letters 17:547–555.

Xu, X., R. A. Sherry, S. Niu, J. Zhou, and Y. Luo. 2012b. Long-term experimental warming decreased labile soil organic carbon in a tallgrass prairie. Plant and Soil 361:307–315.

Xu, T., L. White, D. Hui, and Y. Luo. 2006. Probabilistic inversion of a terrestrial ecosystem model: analysis of uncertainty in parameter estimation and model prediction. Global Biogeochemical Cycles. https://doi.org/10.1029/2005GB002468

Xue, K., et al. 2016. Warming alters expressions of microbial functional genes important to ecosystem functioning. Frontiers in Microbiology 7:668.

Zhang, D., D. Hui, Y. Luo, and G. Zhou. 2008. Rates of litter decomposition in terrestrial ecosystems: global patterns and controlling factors. Journal of Plant Ecology 1:85–93.

Zhang, W., K. M. Parker, Y. Luo, S. Wan, L. L. Wallace, and S. Hu. 2005. Soil microbial responses to experimental warming and clipping in a tallgrass prairie. Global Change Biology 11:266–277.

Zhou, J., et al. 2011. Microbial mediation of carbon-cycle feedbacks to climate warming. Nature Climate Change 2:106–110.

Zhou, X., S. Wan, and Y. Luo. 2007. Source components and interannual variability of soil CO2 efflux under experimental warming and clipping in a grassland ecosystem. Global Change Biology 13:761–775.

Zobitz, J. M., A. R. Desai, D. J. P. Moore, and M. A. Chadwick. 2011. A primer for data assimilation with ecological models using Markov Chain Monte Carlo (MCMC). Oecologia 167:599–611.

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