Received: 28 September 2017 | Accepted: 11 June 2018
DOI: 10.1111/gcb.14394

PRIMARY RESEARCH ARTICLE

WILEY Global Change Biology

Differential responses of carbon-degrading enzyme activities to warming: Implications for soil respiration

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Funding information
US National Science Foundation, Grant/Award Number: 1137293 and OIA-1301789; National Natural Science Foundation of

Abstract

Extracellular enzymes catalyze rate-limiting steps in soil organic matter decomposition, and their activities (EEAs) play a key role in determining soil respiration (SR). Both EEAs and SR are highly sensitive to temperature, but their responses to climate warming remain poorly understood. Here, we present a meta-analysis on the response of soil cellulase and ligninase activities and SR to warming, synthesizing data from 56 studies. We found that warming significantly enhanced ligninase activity by 21.4% but had no effect on cellulase activity. Increases in ligninase activity were positively correlated with changes in SR, while no such relationship was found for cellulase. The warming response of ligninase activity was more closely related to the responses of SR than a wide range of environmental and experimental methodological factors. Furthermore, warming effects on ligninase activity increased with experiment duration. These results suggest that soil microorganisms sustain long-term increases in SR with warming by gradually increasing the degradation of the recalcitrant carbon pool.

China, Grant/Award Number: 41701292; United States Department of Energy, Grant/Award Number: DE-SC00114085; US Department of Energy

KEYWORDS
cellulase activity, decomposition, extracellular enzyme activity, global warming, ligninase activity, recalcitrant carbon pool, soil microorganisms, soil respiration

1 | INTRODUCTION

The average global surface temperature is predicted to increase between 1 and 4°C by the end of the twenty-first century (Collins & Knutti, 2013; O'neill et al., 2017). Rising temperatures have cascading impacts on ecosystem carbon (C) budgets, and these can cause both positive and negative C cycle–climate feedbacks (Carey et al., 2016; Chen, Sang, Zhang, & Hu, 2016; Chen, Zhou et al., 2017; Karhu et al., 2014; Paustian et al., 2016; Peñuelas et al., 2017; Yang et al., 2018). Soil respiration (SR) represents the largest C flux from soils to the atmosphere (Bradford et al., 2016; Tucker, Bell, Pendall, & Ogle, 2013) and is primarily driven by the microbial decomposition of soil organic matter (SOM). However, we know little about the mechanisms underlying the response of SR to climate warming (Chen, Luo, Xia, Wilcox et al., 2016; Conant et al., 2011; Van Gestel et al., 2018). It is specific that there is a lack of information regarding the degree to which soil extracellular enzymes (EEs), which catalyze the rate-limiting step in SOM decomposition (Allison, Wallenstein, & Bradford, 2010; Jing et al., 2014; Sinsabaugh, 2010; Stone et al., 2012), are affected by warming. These enzymes, primarily produced by microbes, are considered proximate agents of SR because they lower the activation energy of key reactions and speed up the breakdown of polymers (Chen, Luo et al., 2017; Chen et al., 2018; Janssens et al., 2010; Suseela, Tharayil, Xing, & Dukes, 2014). Although the rates at which these enzymes are produced and degraded are sensitive to temperature (Allison & Treseder, 2008; German, Marcelo, Stone, & Allison, 2012; Papanikolaou, Britton, Helliwell, & Johnson, 2010; Steinweg, Dukes, Paul, & Wallenstein, 2013), it is still unclear how warming responses of enzymes affect SR.

Cellulose and lignin are the two most abundant SOM compounds, and microbially mediated decomposition of these materials composes a main source of SR (Carreiro, Sinsabaugh, Repert, & Parkhurst, 2000; Chen et al., 2018; Janssens et al., 2010; Waldrop, Zak, Sinsabaugh, Gallo, & Lauber, 2004). Cellulose and hemicellulose comprise the main composition of primary plant cell walls. Hydrolysis of cellulose and hemicellulose is mainly catalyzed by cellulase, including β-1,4-glucosidase (BG), β-1,4-xylosidase (BX), and β-D-cellobiosidase (CBH) (Carreiro et al., 2000; Chen, Luo et al., 2017; Jian et al., 2016). The aromatic C polymer lignin is found in secondary plant cell walls, where it covers and shields cellulose from microbial decay. Oxidation and degradation of phenolic-containing recalcitrant compounds are facilitated by ligninase, that is, peroxidase (PER), phenol oxidase (PO), and polyphenol oxidase (PPO; Dashtban, Schraft, Syed, & Qin, 2010; Romero-Olivares, Allison, & Treseder, 2017; Sinsabaugh et al., 2008; Zhou et al., 2012). The critical roles of cellulase and ligninase in mediating SOM decomposition suggest that climate warming may affect SR through its effects on EEAs, yet we still lack direct evidence.

Cellulase and ligninase are synthesized by specific groups of microorganisms (Burns et al., 2013; Carreiro et al., 2000; Wang et al., 2012), and it may take years for microbial communities to adapt to environmental changes (Deangelis et al., 2015). Thus, responses of cellulase and ligninase activities to warming may vary over time. Because warming methods differ in their effects on soil temperature and moisture (Chen et al., 2015, Lu et al., 2013), soil microbial community (Chen et al.,2015), and belowground C allocation (Rustad et al., 2001; Schindlbacher, Schnecker, Takriti, Borken, & Wanek, 2015), they may differ in their effects on EEAs as well. Including cellulase and ligninase activities in soil C models may improve future predictions of soil C stocks (Ali et al., 2015; Luo, Chen, Chen, & Feng, 2017; Moorhead, Sinsabaugh, Hill, & Weintraub, 2016). However, warming effects on cellulase and ligninase activities, as well as the underlying mechanisms, are still unclear.

To address this knowledge gap, we conducted a meta-analysis of the responses of cellulase and ligninase activities to warming and their links with SR responses. More specifically, our study seeks (a) to quantify the effects of warming on cellulase and ligninase activities, (b) to investigate the factors affecting the responses of cellulase and ligninase activities to warming, and (c) to test whether the responses of cellulase and ligninase activities to warming are linked with changes in SR.

2 | MATERIALS AND METHODS

2.1 | Data collection

We extracted results for enzyme activities of ligninase and cellulase under warming experiments conducted in the field. We used Web of Science (http://apps.webofknowledge.com/), Google Scholar (http://scholar.google.com/), and China National Knowledge Infrastructure (http://www.cnki.net/) for an exhaustive search of journal articles published before June 2018, using the following key words : (a) "climate change" or "experimental warming" or "elevated temperature" and (b) "cellulase," or "ligninase," or "glucosidase," or "xylosidase," or "cellobiosidase," or "peroxidase," or "phenol oxidase," or "polyphenol oxidase," and (c) "terrestrial" or "soil" or "land."

To be included in our dataset, experiments had to meet several criteria: (a) the warming treatment lasted at least 1 year; (b) vegetation, soil physicochemical parameters, and climate were similar between control and warming treatments; (c) sample size and standard deviations were reported; and (d) warming protocols (i.e., warming method, warming magnitude, warming time, and warming season) were clearly described. All studies in our dataset measured enzyme activity for warmed and control soils at the same incubation temperature (i.e., temperature differences between treatments occurred only in the field and not during the incubation). As such, differences in enzyme activity between warmed and control soils were not related to the temperature sensitivity of enzymes, but reflect warming effects on enzyme production by soil microbes. We found 56 articles that met our requirements (see Supporting information Dataset and Figure S1).

For each study in our dataset, we extracted information on cellulase and ligninase activities (Supporting information Table S1). If a paper reported multiple warming responses (e.g., in multifactor experiments or studies applying more than one warming protocol), each experiment was included separately in our dataset. If one paper reported two or three kinds of cellulase or ligninase, then their sum values were considered as the overall responses of cellulase and ligninase activities. We also recorded a wide range of environmental variables, including latitude, longitude, elevation, climatic variables (mean annual temperature (MAT), mean annual precipitation (MAP)), sampling date, sampling temperature, vegetation type (http://www.worldclim.org/), and soil type (http://www.fao.org/about/en/). Regarding the warming protocols, we recorded the magnitude (i.e., the average temperature difference between the warming and control plots), duration (in years), and methods (open top chamber (OTC), infrared heater (IH), green house (GH), heating cable, and curtain). We also recorded SR, soil C:N, microbial biomass, and the ratio of fungal to bacterial abundance for both control and warming treatments when these data were reported. When warming responses of SR were not available, we used responses of heterotrophic respiration or weight loss in litter bag experiments as proxy values. To extract data from figures, we used Engauge Digitizer 4.1 (http://digitizer.sourceforge.net). When some critical information was not reported in the article, we tried to obtain this information by contacting the corresponding author.

2.2 | Data analysis

We used meta-analysis to evaluate the effects of warming on cellulase, ligninase, individual enzyme activity, and other ancillary variables (García-Palacios et al., 2014; Hedges, Gurevitch, & Curtis, 1999; Van Groenigen, Qi, Osenberg, Luo, & Hungate, 2014; Zhao et al., 2017). The effects of warming on EEAs were evaluated using the natural logarithm of the response ratio (ln*R*):

$$\ln R = \ln\left(\frac{\overline{X_W}}{\overline{X_C}}\right) = \ln(\overline{X_W}) - \ln(\overline{X_C}), \quad (1)$$

with $\overline{X_W}$ and $\overline{X_C}$ as the arithmetic mean concentrations in the warming and control treatments, respectively. The variances (ν) of ln*R* were calculated as follows:

$$\nu = \frac{S_W^2}{n_W \overline{X_W^2}} + \frac{S_C^2}{n_C \overline{X_C^2}}, \quad (2)$$

with n_W and n_C as the number of replicates and S_W and S_C as the *SDs* for warming and control treatments, respectively.

The overall effect and the 95% confidence interval were calculated using the "rma.mv" function in the R package "metafor" (Viechtbauer, 2010). Because incubation temperature for enzyme measurements varied among studies, we included "incubation temperature" as a random factor in the meta-analysis. Because several papers contributed more than one response ratio, we also included the variable "paper" as a random factor (Chen et al., 2018; Terrer, Vicca, Hungate, Phillips, & Prentice, 2016; Van Groenigen et al., 2017). The effects of warming were considered significant if the 95% confidence interval did not overlap with zero. The results for the analyses on ln*R* were back-transformed and reported as percentage change with warming (i.e., $100 \times (e^{\ln R} - 1)$) to ease interpretation.

The meta-analytic models were selected using the same approach as in Chen et al. (2018), Terrer et al. (2016), and Van Groenigen et al. (2017). In brief, we analyzed all potential combinations of the studied factors in a mixed-effects metaregression model using the "glmulti" package in R (Bangert-Drowns, Hurley, & Wilkinson, 2004; Calcagno & De Mazancourt, 2010). The importance of a specific predictor was expressed as the sum of Akaike weights for models that included this factor, which can be considered as the overall support for each variable across all models. A cutoff of 0.8 was set to differentiate between important and nonessential predictors.

3 | RESULTS

Across the whole dataset, warming significantly enhanced ligninase activity by an average of 21.4%. It is specific that warming significantly increased activities of PER by 18.4%, PO by 13.5%, and PPO by 28.6%. In contrast, warming had no effect on cellulase activity (Figure 1a) or any of the individual cellulase enzymes BG, BX, and CBH. The responses of cellulase and ligninase activities to warming were normally distributed (Figure 1b,c), and they were independent of the sample size (Supporting information Figure S2).

None of the variables tested for the effects of warming on cellulase activity reached the threshold value (0.8) of the summed Akaike weights (Figure 2a). In contrast, effects of warming on ligninase activity were best explained by warming duration and warming method (Figure 2b). Linear regression analysis confirmed that ln*R* of ligninase activity was positively correlated with warming duration, while no such relationship was found for cellulase activity (Figure 3a,b). Regarding warming methods, warming did not affect cellulase activity for any of the warming methods (Figure 3a). In contrast, OTC, GH, and IH significantly increased ligninase activity by 15.5%, 31.4%, and 22.3%, respectively, while cables had no effect on ligninase activity (Figure 3b).

Warming significantly increased microbial biomass-specific ligninase activity (i.e., the ratio of ligninase activity to total microbial abundance) by 40.6% (Supporting information Figure S3a). This increase was weakly positively correlated with warming-induced changes in the ratio of fungal to bacterial abundance (Supporting information Figure S3b). At last, our analyses suggest that warming

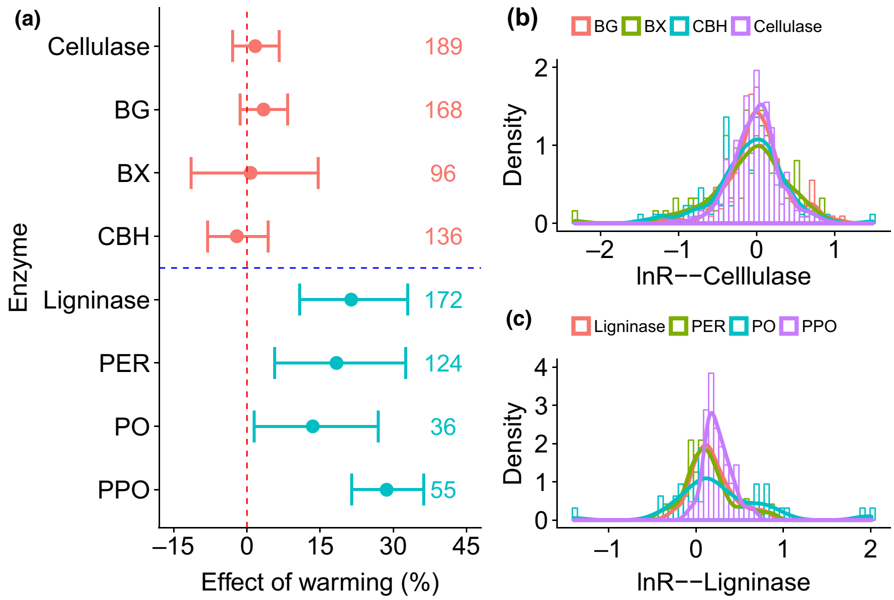

FIGURE 1 (a) Effects of warming on cellulase and ligninase activities indicated with the mean percentage of change in warming vs. control plots. Distribution of the log-transformed response ratios (lnR) of (b) cellulase and (c) ligninase activities to experimental warming. Error bars represent 95% confidence intervals. The sample size for each variable is shown in the right column of the figure. PER, peroxidase; PO, phenol oxidase; PPO, polyphenol oxidase; BG, β-1,4-glucosidase; BX, β-1,4-xylosidase; CBH, β-D-cellobiosidase [Colour figure can be viewed at wileyonlinelibrary.com]

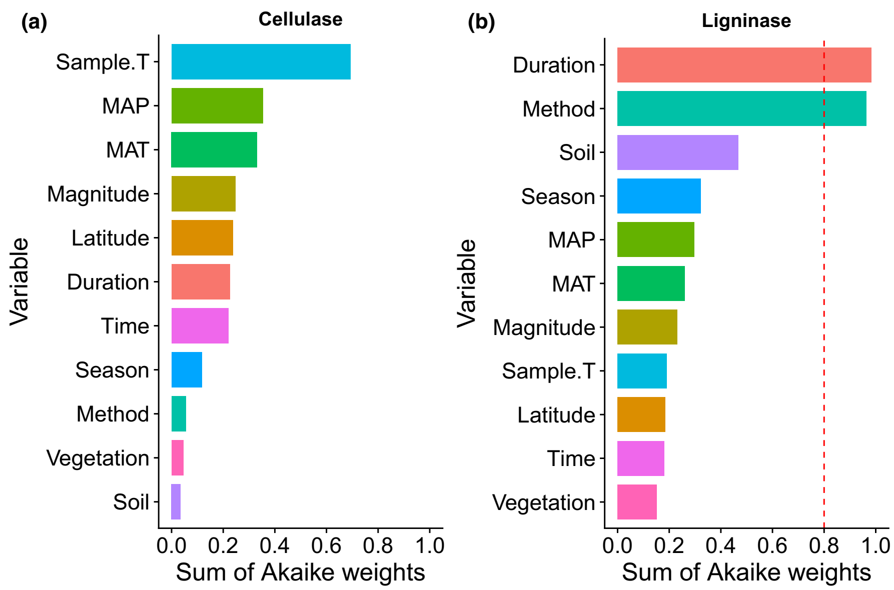

FIGURE 2 Model-averaged importance of the predictors of warming effects on soil (a) cellulase and (b) ligninase activities. The importance is based on the sum of Akaike weights derived from model selection using corrected Akaike's information criteria. Cutoff is set at 0.8 to differentiate between important and nonessential predictors. MAT, mean annual temperature; MAP, mean annual precipitation; Sample.*T*, sampling temperature; time, daily warming regime (i.e., day, night, or diurnal warming); season, annual warming regime (i.e., growing season, nongrowing season, or whole-year warming) [Colour figure can be viewed at wileyonlinelibrary.com]

had stronger positive effects on biomass-specific ligninase activity for long-term than short-term studies, while this relationship was not observed for biomass-specific cellulase activity (Supporting information Figure S4a and S4b).

Warming on average increased SR by 15.8% (95% CI: 6.3%–26.1%) in our dataset. We found no relationship between the responses of cellulase activity and the responses of SR to warming (Figures 4a). However, the warming response of SR was positively correlated with the response of ligninase activity and the positive relationship held when analyzed for PER, PO, and PPO individually (Figure 4b; Supporting information Figure S5). To compare the relative importance of cellulase and ligninase activities in explaining the response of SR to warming, we limited our model selection analysis to studies that simultaneously reported the effects of warming on cellulase and ligninase activities and SR. Effects of warming on SR were best predicted by the responses of ligninase activity over a wide range of ecosystem types, climatic variables, and warming protocols (Figure 4c). Experiment duration had no significant impact on SR responses to warming, either in the subset of studies that reported responses of both enzymes (Figure 4c) or across the entire dataset.

4 | DISCUSSION

Our results show that warming significantly enhanced ligninase activity and that warming responses are positively correlated with warming duration. In contrast, warming does not affect cellulase activity.

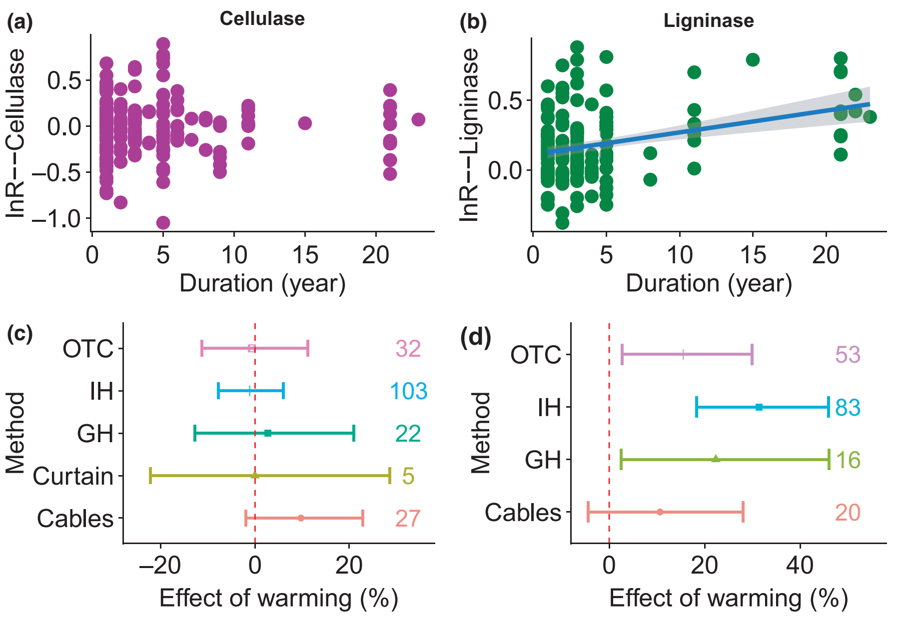

FIGURE 3 Relationships between warming-induced changes in (a) cellulase and (b) ligninase activities and warming duration. Effects of warming on (c) cellulase and (d) ligninase activities for various warming methods. The response of ligninase activity was positively correlated with warming duration ($y = 0.016x + 0.113$, $R^2 = 0.117$, $p < 0.001$, $F = 22.590$, $n = 172$). Error bars represent 95% confidence intervals. OTC, open top chamber; IH, infrared heater; GH, green house. The sample size for each variable is shown in the right column of the figure [Colour figure can be viewed at wileyonlinelibrary.com]

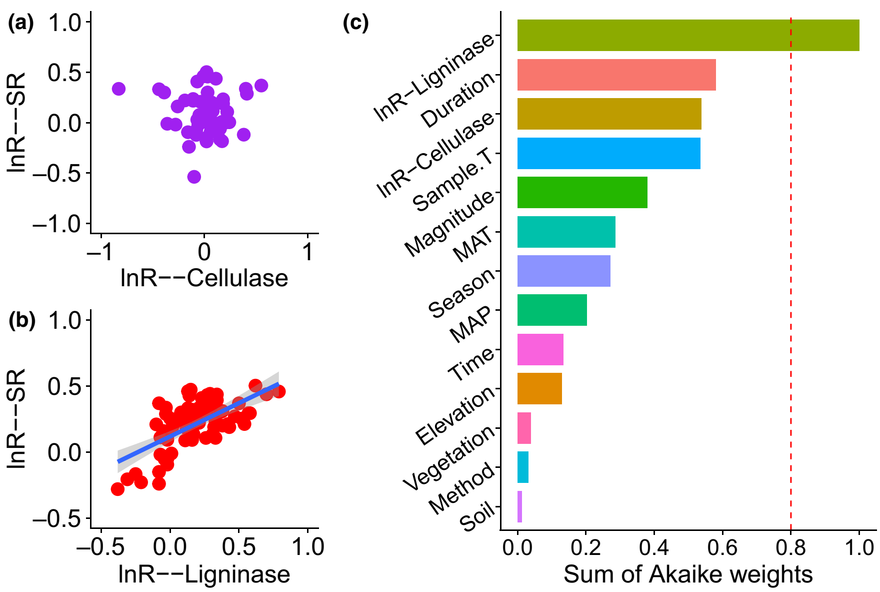

FIGURE 4 Relationships between the effect of warming (ln*R*) on soil respiration (SR) and ln*R* of (a) cellulase and (b) ligninase activities. (c) Model-averaged importance of the predictors of warming effects on SR. The warming response of SR was positively correlated with the warming response of ligninase activity ($y = 0.528x + 0.108$, $R^2 = 0.467$, $p < 0.001$, $F = 61.260$, $n = 72$). Model selection analysis is limited to studies that simultaneously reported the responses of ligninase, cellulase, and SR. The importance is based on the sum of Akaike weights derived from model selection using corrected Akaike's information criteria. Cutoff is set at 0.8 to differentiate between important and nonessential predictors. MAT, mean annual temperature; MAP, mean annual precipitation; time, daily warming regime (i.e., day, night, or diurnal warming); season, annual warming regime (i.e., growing season, nongrowing season, or whole-year warming); Sample.*T*, sampling temperature [Colour figure can be viewed at wileyonlinelibrary.com]

Why does warming have differential effects on cellulase and ligninase activities? We propose three possible mechanisms. First, the enzyme responses reflect warming-induced changes in substrate availability. Enzyme activity can be described by the Michaelis–Menten relationship, which primarily depends on substrate availability (Davidson & Janssens, 2006; Sinsabaugh et al., 2008). Initial stimulation of SR by warming depletes easily hydrolyzable substrates (Allison, Mcguire, & Treseder, 2010; Luo, Wan, Hui, & Wallace, 2001), limiting the positive response of cellulase activity to increasing temperatures (Davidson & Janssens, 2006; Stone et al., 2012; Weedon, Aerts, Kowalchuk, & Van Bodegom, 2014). At the same time, warming-induced declines in easily hydrolyzable C pools can lead to microbial C starvation (Crowther & Bradford, 2013; Fenner et al., 2006; Melillo et al., 2017; Metcalfe, 2017). Under these circumstances, soil microbial communities may adapt to utilize previously inaccessible recalcitrant C pools to fuel their metabolic activities. Microbial utilization of recalcitrant substrates such as phenol requires depolymerization, a process catalyzed by ligninase (De Gonzalo, Colpa, Habib, & Fraaije, 2016; Jassey, Chiapusio, Gilbert, Toussaint, & Binet, 2012; Sinsabaugh, 2010).

Second, warming may increase ligninase activity through its effect on soil N availability. Warming-induced redistribution of N from soils to vegetation could progressively lead to microbial N limitation, particularly in high C:N regions (Bai et al., 2013; Beier et al., 2008; Melillo et al., 2011). In that case, soil microorganisms are expected to invest C and energy to acquire N through decomposition of N-containing molecules (Chen, Luo et al., 2017; Sinsabaugh et al., 2008), which are often physically or chemically protected by other aromatic macromolecules such as lignin (Hobbie, 2008; Weedon et al., 2012; Zhao et al., 2014). This explanation is supported by the positive correlation between warming effects on ligninase activity and soil C:N, while no clear relationship is found for the responses of cellulase activity (Supporting information Figure S6). At last, warming-induced changes in soil microclimate (Domínguez, Holthof, Smith, Koller, & Emmett, 2017; Zhou et al., 2013), fresh C input (Bhattacharyya, Roy, Neogi, Dash et al., 2013; Xue et al., 2016; Yin et al., 2013), and plant community composition (Kardol, Cregger, Campany, & Classen, 2010; Steinauer et al., 2015) can all cause substantial changes in microbial communities as well.

Increased ligninase production with warming might reflect shifts in the microbial community composition. Indeed, several studies suggest that warming-induced changes in soil microbial community composition cause differential responses of cellulase and ligninase activities (Deangelis et al., 2015; Pold, Grandy, Melillo, & Deangelis, 2017). This explanation is also consistent with studies showing that fungi are main contributors to ligninase production (De Gonzalo et al., 2016; Kinnunen, Maijala, Jarvinen, & Hatakka, 2017) and that experimental warming increases fungal abundance (A'bear, Jones, Kandeler, & Boddy, 2014; Delarue et al., 2015). However, warming may also directly or indirectly cause physiological adaptation of soil microorganisms to increase enzyme production (Manzoni, Taylor, Richter, Porporato, & Gren, 2012; Nie et al., 2013; Schindlbacher et al., 2015), even when warming decreases total microbial biomass (Pold et al., 2017; Sistla & Schimel, 2013; Sorensen et al., 2018). This is consistent with recent findings that experimental warming tends to decrease microbial C use efficiency (Manzoni et al., 2012; Tucker et al., 2013).

Why does the effect of warming on ligninase activity increase over time? Soil microorganisms can adjust their community composition or alter their C utilization strategies to adapt to warming, but it requires several years or even decades for significant changes in their community composition to occur (Deangelis et al., 2015; Feng et al., 2017; Rousk, Smith, & Jones, 2013). Furthermore, warming-induced N limitation may take several years to manifest (Bai et al., 2013; Melillo et al., 2011). In addition, long-term warming could also restructure plant community and alter litter quality toward decay resistance (e.g., high lignin content) (Melillo et al., 2011; Talbot, Yelle, Nowick, & Treseder, 2012), thereby promoting the microbial production of ligninase.

Regardless of the mechanism underlying the differential warming response of ligninase and cellulase, our results suggest that warming-induced shifts in cellulase and ligninase activities could help to sustain long-term increases in SR with warming (Lin, Zhu, & Cheng, 2015; Romero-Olivares et al., 2017; Souza et al., 2017). This is because warming responses of ligninase activity exert far larger control over SR than a broad range of environmental and experimental variables. These results suggest that responses of SR to warming are largely modulated by a single group of lignin-modifying enzymes, which contributes to sustained positive responses of SR to long-term climate warming.

Warming methods constituted the second important predictor of the warming effects on ligninase activity. Cables only warm soils and are reported to have negative effects on microbial biomass, litter inputs, and root exudates (Rustad et al., 2001; Schindlbacher et al., 2015). It is similar that a recent meta-analysis shows that cables generally decrease total microbial, fungal, and bacterial abundance, while other warming methods increase microbial abundance (Chen et al., 2015). We hypothesize that these negative responses suppressed microbial activity and microbial enzymatic production (Chen et al., 2015, Hanson et al., 2017). In addition, high warming magnitude and large reductions in soil moisture in cable experiments may decrease microbial C use efficiency (Schindlbacher et al., 2011, 2012), which could potentially suppress microbial cellulase and ligninase production.

Model projections of soil C dynamics often lack representation of EEA-regulated SOM decomposition (Davidson & Janssens, 2006; Luo et al., 2016; Wieder, Bonan, & Allison, 2013). However, our finding that warming-induced shifts in cellulase and ligninase activities may facilitate sustained increases in SR under long-term climate warming highlights the need for a closer integration of enzymatic decomposition into soil biogeochemical models. It is unfortunate that responses of SR and EEAs to long-term climate warming remain understudied, as experiment duration is often constrained by funding availability. If the relationship between ligninase and warming duration holds across a wide range of land ecosystems, our results suggest that ecosystem climate–carbon feedbacks could be stronger than previously assumed.

ACKNOWLEDGEMENTS

First, we would like to thank the authors whose work is included in this meta-analysis, especially those who supplied us with additional data. Second, we would like to thank Robert Sinsabaugh and three anonymous reviewers for their valuable comments on an earlier version of this manuscript. This study was supported by the National Natural Science Foundation of China (41701292), China Postdoctoral Science Foundation (2017M610647, 2018T111091), the Natural Science Basic Research Plan in Shaanxi Province (2017JQ3041), the

State Key Laboratory of Loess and Quaternary Geology (SKLLQG1602), the Key Laboratory of Aerosol Chemistry and Physics (KLACP-17-02), Institute of Earth Environment, and Chinese Academy of Sciences. Contributions from Dr. Luo's Eco-lab to this study were financially supported by US Department of Energy grant DE-SC00114085 and US National Science Foundation grants EF 1137293 and OIA-1301789. This work was also supported by NSFC-Yunnan United Fund (U1302267) and the National Science Fund for Distinguished Young Scholars (31325005).

DATA ACCESSIBILITY

The data associated with this paper are available from the online supplementary file.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Chen J, Luo Y, García-Palacios P, et al. Differential responses of carbon-degrading enzyme activities to warming: Implications for soil respiration. *Glob Change Biol*. 2018;24:4816–4826. https://doi.org/10.1111/gcb.14394