OPINION

Soil carbon loss with warming: New evidence from carbon-degrading enzymes

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Abstract

Climate warming affects soil carbon (C) dynamics, with possible serious consequences for soil C stocks and atmospheric CO_2 concentrations. However, the mechanisms underlying changes in soil C storage are not well understood, hampering long-term predictions of climate C-feedbacks. The activity of the extracellular enzymes ligninase and cellulase can be used to track changes in the predominant C sources of soil microbes and can thus provide mechanistic insights into soil C loss pathways. Here we show, using meta-analysis, that reductions in soil C stocks with warming are associated with increased ratios of ligninase to cellulase activity. Furthermore, whereas long-term (≥5 years) warming reduced the soil recalcitrant C pool by 14%, short-term warming had no significant effect. Together, these results suggest that warming stimulates microbial utilization of recalcitrant C pools, possibly exacerbating long-term climate-C feedbacks.

KEYWORDS

climate-carbon feedback, experimental warming, extracellular enzyme, labile carbon pool, recalcitrant carbon pool, soil carbon storage, soil microorganism, warming duration

1 | INTRODUCTION

Soils store three to four times as much carbon (C) as the atmosphere (Bond-Lamberty & Thomson, 2010; Lal, 2004) and represent the largest natural source of CO_2. Therefore, changes in soil C stocks in response to global warming could substantially alter future climate trajectories (Davidson & Janssens, 2006; Trumbore, Chadwick, & Amundson, 1996). Yet, despite numerous studies in recent decades,

the net effects of climate warming on soil C stocks are still unclear (Knorr, Prentice, House, & Holland, 2005; Smith & Fang, 2010; van Gestel et al., 2018). Several short-term studies found soil C losses with experimental warming (Melillo et al., 2017; Pries, Castanha, Porras, & Torn, 2017; Sistla et al., 2013). If such initial stimulation of soil C decomposition persists, rising temperatures could drive strong positive climate-C feedbacks and accelerate planetary warming (Chen et al., 2015; Karhu et al., 2014). However, it is unclear whether results from short-term experiments can be extrapolated over time. Thus, to improve future predictions of soil C storage, we need to advance the mechanistic understanding of warming effects on soil C dynamics.

Short-term respiratory responses to warming likely represent increased turnover of the labile and readily accessible litter and soil organic matter (SOM; Dorrepaal et al., 2009; Knorr et al., 2005). However, the majority of litter and SOM are protected from microbial attack by complex chemical conformation or by physico-chemical interactions within the soil matrix (Cotrufo et al., 2015; Jenkinson, 1990; Kallenbach, Frey, & Grandy, 2016; Kleber & Johnson, 2010; Schmidt et al., 2011). Therefore, the effects of long-term warming on soil C storage both depend on changes in microbial accessibility of litter and SOM (Schuur et al., 2009; Singh, Bardgett, Smith, & Reay, 2010), and on depolymerization of chemically complex and recalcitrant C pools (Cotrufo, Wallenstein, Boot, Denef, & Paul, 2013; Lehmann & Kleber, 2015).

Cellulases and ligninases are among the most important C-degrading enzymes targeting the degradation of litter and SOM with different qualities (Chen et al., 2017; Jian et al., 2016; Margida, Lashermes, & Moorhead, 2019). Whereas cellulase is associated with decomposition of relatively labile C pools, ligninase is associated with the decomposition of relatively recalcitrant C pools (Sinsabaugh, 2010; Sistla & Schimel, 2013). Thus, the ratio of ligninase to cellulase (ligninase:cellulase) activity can be used to quantify microbial preference in utilizing various pools of litter and SOM (Chen, Luo, García-Palacios, et al., 2018; Romero-Olivares, Allison, & Treseder, 2017; Sinsabaugh, 2010; Yang et al., 2019). A recent meta-analysis showed that warming had differential effects on cellulase and ligninase activities (Chen, Luo, García-Palacios, et al., 2018); however, shifts in C-degrading enzyme activities have not been quantitatively linked to changes in soil C storage. Here, we use meta-analysis to quantify the links between soil C storage and C-degrading enzyme activities under experimental warming, and to synthesize the effects of warming on recalcitrant and labile C pools.

2 | MATERIALS AND METHODS

2.1 | Data collection

We compiled four databases to explore the relationships between C-degrading enzyme activities and soil C storage under experimental warming, and to quantify the effects of warming on labile and recalcitrant C pools (see Supplementary materials and methods in Supporting Information S1). Database 1 included studies that simultaneously reported the effects of warming on soil C-degrading enzyme activities and soil C stocks. If a study reported soil enzyme data but no soil C data, we searched extensively for matching soil C data from papers published by the same research group. Database 2 included studies that reported the effects of warming on enzyme activities of ligninase and cellulase. Database 3 included studies on the effects of warming on recalcitrant C pools, and Database 4 included studies on the effects of warming on labile C pools. A previous version of Database 2 was published by Chen, Luo, Van Groenigen, et al. (2018); the current version has been updated to include 16 observations (six studies) that were published since the previous version was compiled. The other three new databases were created following the same method as used in Chen, Luo, Van Groenigen, et al. (2018). Detailed information about the databases can be found via figshare (https://figshare.com/s/7dd68e1fa45e32b2f9fa) and in the online Supplementary materials, methods and databases in Supporting Information S1.

We searched Web of Science (http://apps.webofknowledge.com/), Google scholar (http://scholar.google.com/) and China National Knowledge Infrastructure (http://www.cnki.net/) for articles that were published before February 2019. The keywords used in the Databases 1 and 2 were (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'. The keywords used in the Databases 3 and 4 were (a) 'climate change' or 'experimental warming' or 'elevated temperature' and (b) 'soil carbon pool' or 'labile carbon' or 'recalcitrant carbon' or 'heavy fraction carbon' or 'light fraction carbon' or 'dissolved carbon' or 'occluded carbon' or 'aromatic carbon' or 'phenolic' or 'hydrolysable carbon'.

To be included in our datasets, articles had to report experimental warming protocols, particularly warming duration. We only considered experiments that lasted at least 1 year, and we made a distinction between short-term (<5 years) and long-term (≥5 years) experiments. Treatment replicates and standard deviations needed to be reported. Environmental and site variables (Tables S1 and S2) were tabulated if these were reported. In total, 68 articles were selected based on these criteria (see Supplementary references lists and Figure S1 in Supporting Information S1).

2.2 | Description of environmental and experimental variables

For each study in our dataset, we recorded a wide range of environmental variables, including latitude (with a range from 20.45°N to 76.55°N), longitude (149.57°W to 144.73°E), elevation (5–4,763 m), climatic variables (mean annual temperature [MAT, −12 to 27°C], mean annual precipitation (MAP, 122–2048 mm), vegetation type (http://www.worldclim.org/, including farmland, grassland, forest, heathland and tundra) and soil type (http://www.fao.org/about/en/, including Phaeozems, Histosols, Luvisols, Podzols, Cambisols,

Chernozems, Oxisols, Andosols, Entisol, Arensol, Cryosols, Mollisols and Gelisols). Regarding the warming protocols, we recorded the magnitude (i.e., the average temperature difference between the warming and control plots, with a range from 0.3 to 5.1°C), duration (in years, from 1 to 23 years as continuous variable) and methods (open top chambers, infrared heaters, greenhouses, heating cables and curtains). When critical information was not reported in the article, we tried to obtain this information by contacting the corresponding author.

2.3 | Carbon-degrading enzymes

For the purpose of our analysis, ligninase activity represented the activities of peroxidases (EC1.11.1.7) or phenol oxidases (EC1.10.3.2) or polyphenol oxidases (EC1.14.18.1) or the average of their activities if two or three of them were reported simultaneously (Table S3). These enzymes are oxidative in nature and can effectively accelerate the breakdown of relatively recalcitrant molecules such as lignin, phenol and other aromatics (Sinsabaugh, 2010). Cellulase activity represented the activities of β-1,4-glucosidases (EC3.2.1.21) or β-1,4-xylosidases (EC3.2.1.37) or β-1,4-D-cellobiohydrolases (EC3.2.1.91) or their average. Cellulases breaks down cellulose, hemicellulose and several related polysaccharides into monosaccharides such as beta-glucose, or short polysaccharides and oligosaccharides. The ratio of ligninase:cellulase activities is an effective proxy of microbial substrate preference (Romero-Olivares et al., 2017; Sinsabaugh, 2010; Yang et al., 2019), with higher ratios indicating relatively greater investment in decomposition of chemically recalcitrant C pools (Chen, Luo, García-Palacios, et al., 2018; Ren et al., 2017; Romero-Olivares et al., 2017). Detailed information on the enzyme assays can be found in the online supplementary materials and methods in Supporting Information S1.

2.4 | Soil carbon pools

Soil organic C can be broadly divided into chemically labile and recalcitrant pools, which differ in rates of microbial mineralization and in residence time (Chen, Luo, Van Groenigen, et al., 2018; Cotrufo et al., 2013; Davidson & Janssens, 2006; Kögel-Knabner & Rumpel, 2018). Labile C is the fraction with the shortest mean residence time (days to years), and includes, for example, simple root exudates, fresh plant detritus with relative small particle size and living or dead cells (necromass) that can easily be decomposed (Kolář et al., 2009; Strosser, 2010). Soil labile C pools serve as readily available energy sources for soil microorganisms, thereby contributing to enhanced nutrient cycling in soils. In the present study, pool sizes of labile C were estimated from: (a) active C pools with short residence time, determined by soil incubations and inverse modeling (Carrillo, Pendall, Dijkstra, Morgan, & Newcomb, 2011; Feng et al., 2017); (b) readily hydrolysable or oxidizable C or dissolved organic C or water- or K_2SO_4-extractable C (Bhattacharyya et al., 2013) and (c)

light fraction C, determined by physical soil fractionation (Song et al., 2012; von Lützow et al., 2007). Detailed information on the measurements and proxies of labile C pools can be found in the online supplementary materials and methods in Supporting Information S1.

Recalcitrant C pools consist of organic material resistant to decomposition, with mean residence times of years to decades or longer. (Davidson & Janssens, 2006; Kleber, 2010). The nature of recalcitrant compounds ranges from simple halogenated hydrocarbons to complex polymers, such as lignin. Recalcitrant C pools can be made biodegradable by enzymes capable of deconstructing these compounds. In the present study, soil recalcitrant C pools include (a) passive C pools, determined from soil incubation and data-assimilation (Feng et al., 2017); (b) non-readily oxidizable C (Bhattacharyya et al., 2013) or non-readily hydrolysable C (Belay-Tedla, Zhou, Su, Wan, & Luo, 2009; Bhattacharyya et al., 2013; Zhao et al., 2014); (c) phenolic, lignin or other aromatic or occluded large C compounds (Jassey et al., 2013; Schnecker, Borken, Schindlbacher, & Wanek, 2016); and (d) heavy C fractions, determined by physical fractionation (Song et al., 2012; von Lützow et al., 2007). Detailed information on the measurements and proxies of recalcitrant C pools can be found in the online supplementary materials and methods in Supporting Information S1.

2.5 | Data analysis

We used meta-analysis to synthesize the effects of experimental warming on (a) the ratio of ligninase:cellulase activities and (b) the changes in soil recalcitrant and labile C pools. This was done by calculating the logarithmic response ratio (lnR), a metric commonly used in meta-analysis (Chen et al., 2015; Hedges, Gurevitch, & Curtis, 1999; Zhao et al., 2017):

$$\ln R = \ln (X_T/X_A), \tag{1}$$

where X_T and X_A are the arithmetic mean values of the variables in the experimental warming and ambient treatments, respectively. The variances (ϑ) of lnR was calculated as:

$$\vartheta = \frac{SD_T^2}{N_T X_T} + \frac{SD_A^2}{N_A X_A}, \tag{2}$$

where N_T and N_A are the number of replicates, and SD_T and SD_A are the standard deviations for experimental warming and ambient treatments, respectively.

Articles were included as a random factor in the meta-analysis, since some articles contributed multiple observations. A mixed-effects meta-analysis was conducted using the function rma.mv in the R package 'metafor' (Viechtbauer, 2010). The effect size was back-transformed to percentage change to ease interpretation. Using the R package 'glmulti', we performed a model selection analysis to calculate the relative importance of all predictors in determining treatment effects, closely following the methods used by Chen, Luo, García-Palacios, et al. (2018), Chen, Luo, Van Groenigen, et al. (2018).

Briefly, the relative importance for a specific variable was calculated as the sum of the Akaike weights for all models containing this variable; this sum was considered as the overall support for each variable across all potential models. A threshold value of 0.8 was set to identify the most important variables (Terrer, Vicca, Hungate, Phillips, & Prentice, 2016; van Groenigen et al., 2017).

3 | RESULTS

The response of ligninase:cellulase activities was negatively correlated with warming-induced changes in soil C storage. Specifically, one unit increase in the lnR of ligninase:cellulase caused 0.09 unit decrease in the lnR of soil C storage (Database 1; Figure 1a). The relative importance of the lnR for lignase:cellulase supported the removal of other predictors, such as environmental and site variables (latitude, elevation, MAT and MAP), experimental warming protocols (warming methods, warming duration and warming magnitude) and ecosystem types (Figure 1b).

Averaged across all studies on C-degrading enzyme activities (Database 2), experimental warming significantly increased the ratio of ligninase:cellulase activities by 13% (95% confidence interval: 4%–23%). Whereas long-term (≥5 years) experimental warming significantly increased the ratio of ligninase:cellulase by 39%, short-term warming (<5 years) had no effect (Figure 2).
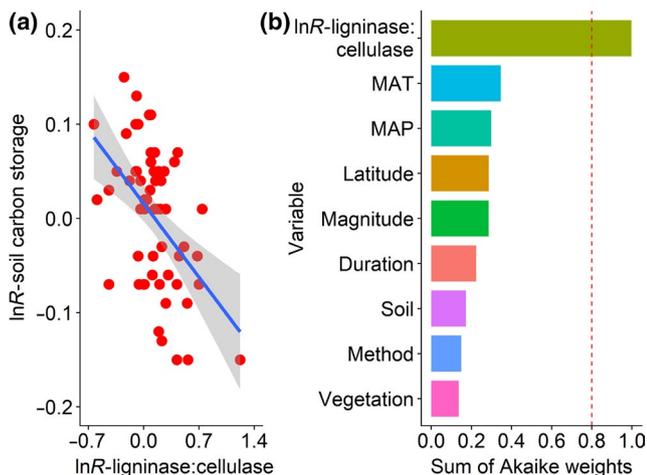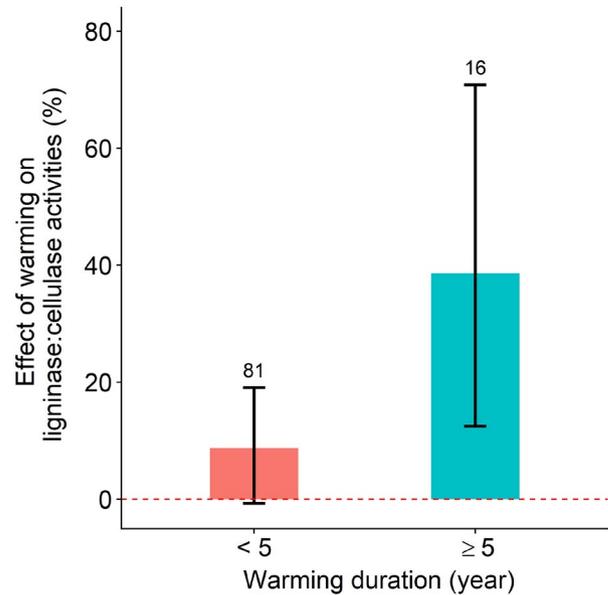
FIGURE 2 Effects of experimental warming duration on lignase:cellulase activities. Data were grouped into warming duration of shorter or longer than 5 years. Error bars indicate the 95% confidence interval. Numbers above the error bars indicate sample sizes for each group. Warming effects are considered significant if the confidence interval does not include zero. Warming responses of lignase:cellulase activities are significantly different between short-term and long-term studies (*p* = .036) [Colour figure can be viewed at wileyonlinelibrary.com]

FIGURE 1 (a) Relation between warming-induced shifts in ligninase:cellulase activities and corresponding changes in soil carbon storage. (b) Relative importance of variables regulating the effects of experimental warming on soil carbon storage. Results are based on studies that simultaneously reported warming responses of soil carbon (C) storage and soil C-degrading enzyme activities. Warming-induced shifts in ligninase:cellulase activities are negatively correlated with changes in soil C storage (R^2 = .237; *p* < .001; *n* = 58). Regression line in panel (a) shows the linear regression; the shaded grey area represents the confidence interval. lnR-Lig:Cell, log-transformed response ratio of ligninase:cellulase activities. Duration, magnitude and method all refer to aspects of the warming treatment; detailed information on these variables can be found in Section 2. MAT, mean annual temperature; MAP, mean annual precipitation [Colour figure can be viewed at wileyonlinelibrary.com]
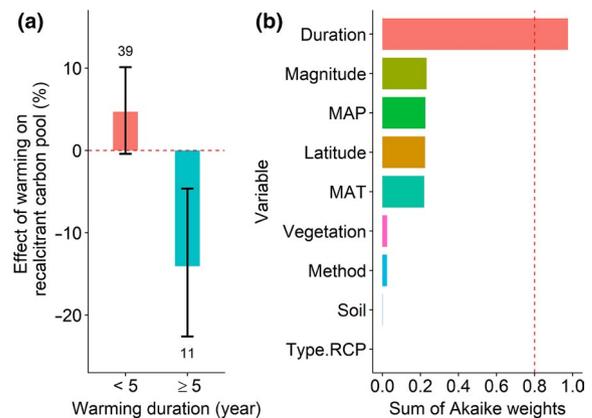
FIGURE 3 (a) Effects of experimental warming duration on the recalcitrant carbon (C) pool. (b) Relative importance of variables regulating the effects of experimental warming on the soil recalcitrant C pool. Data were grouped into warming duration of shorter or longer than 5 years. Error bars indicate the 95% confidence interval. Numbers above the error bars indicate sample sizes for each group. Warming effects are considered significant if the confidence interval does not include zero. There is a significant difference between short-term and long-term studies for warming responses of the recalcitrant C pool (*p* = .001). Duration, magnitude and method indicate aspects of the warming treatment; detailed information on these variables can be found in Section 2. MAT, mean annual temperature; MAP, mean annual precipitation. Type. RCP, distinguishes between various proxies for the recalcitrant C pool; detailed information can be found in Section 2 [Colour figure can be viewed at wileyonlinelibrary.com]

Long-term experimental warming significantly decreased soil recalcitrant C pools by 14%, while no effect was observed for short-term warming (Figure 3a). Whereas warming responses of the recalcitrant C pool were best predicted by warming duration (Figure 3b), none of the predictors reached the threshold of 0.8 for the effects of warming on the labile C pool (Figure S2). Consistent with this analysis, warming responses of the soil labile C pool did not depend on experiment duration (Figure S3).

4 | DISCUSSION

Our finding of a warming-induced increase in ligninase activity relative to cellulase activity indicates soil microbes decompose more chemically complex and recalcitrant C pools (e.g., lignin) to fuel their metabolic processes (Romero-Olivares et al., 2017; Sinsabaugh, 2010). Indeed, several recent studies found that warming favors microbial functional communities degrading old and recalcitrant C pools (Cheng et al., 2017; Feng et al., 2017; Woodcroft et al., 2018; Xue et al., 2016).

Importantly, warming-induced increases in ligninase:cellulase activity were negatively correlated with warming responses of soil C storage. We propose three possible explanations for this result. First, the decomposition of complex structural macromolecules with warming duration may increase microbial accessibility to protected litter and SOM, such as lignin-encrusted C-compounds that are liberated by enzymatic depolymerization prior to the microbial utilization (Cotrufo et al., 2013; Lehmann & Kleber, 2015). This will accelerate the degradation of litter and SOM, leading to further soil C losses.

Second, microbial C use efficiency (CUE), the ratio of C allocated for growth versus respiration (Manzoni, Taylor, Richter, Porporato, & Ågren, 2012), is different for the degradation of cellulose- and lignin-like substrates (Cotrufo et al., 2013). Indeed, reported CUE values for cellulose are much higher than for lignin (Bahri et al., 2008; Dijkstra et al., 2011) because additional energy is required for the depolymerization of lignin-like substrates. This suggests that more C could be respired by stimulating the degradation of lignin- than cellulose-like substrates (Lehmann & Kleber, 2015). This interpretation agrees well with our recent finding that warming-stimulation of ligninase activity is positively correlated with warming-stimulation of soil respiration (Chen, Luo, García-Palacios, et al., 2018).

Third, warming-induced shifts from cellulase to ligninase activities could increase soil N availability because many N-containing molecules are physically and chemically shielded by the lignified macromolecules (Averill & Waring, 2018; Chen, Luo, Van Groenigen, et al., 2018; Plaza, Courtier-Murias, Fernández, Polo, & Simpson, 2013). Enhanced N availability could amplify the effects of warming on microbial-mediated litter and SOM decomposition (Chen et al., 2016; Kuzyakov & Blagodatskaya, 2015). For example, alleviation of N limitation has caused large and rapid C losses in tundra, even for the historically accumulated old C pool (Mack, Schuur, Bret-Harte, Shaver, & Chapin, 2004; Xue et al., 2016).

Our results suggest that progressive shifts from cellulase to ligninase activities stimulate soil C loss with experimental warming, causing positive climate-C feedbacks. These results are align with multiple studies showing that long-term warming decreases soil C storage more than short-term warming (Bardgett, Freeman, & Ostle, 2008; Hopkins, Torn, & Trumbore, 2012; Trivedi et al., 2016). Our findings are also consistent with results from a long-term warming experiment at Harvard Forest (MA, USA), where 18 years of experimental warming quadrupled ligninase activity but did not affect cellulase activity. These divergent changes in enzyme activities were accompanied with soil C losses and reductions in soil lignin abundance (Melillo et al., 2017; Pold, Melillo, & DeAngelis, 2015). Similarly, Feng et al. (2017) showed that 12 years experimental warming substantially enhanced degradation of recalcitrant C pools and increased microbial genes involved in degrading complex C-molecules.

Shifts in microbial C-degrading enzyme activities with continued warming are consistent with previous explanations for continued soil C loss with long-term warming, such as shifts and adaptations in microbial community and physiology (Melillo et al., 2017; Metcalfe, 2017), changes in microbial CUE (Tucker, Bell, Pendall, & Ogle, 2013), and increased microbial accessibility to litter and SOM (Bailey et al., 2018; Doetterl et al., 2015). The key roles of C-degrading enzymes in regulating soil C storage are also in line with results from a recent meta-analysis showing that increases in soil C stocks with long-term N enrichment were negatively correlated with N-effects on ligninase activity (Chen, Luo, Van Groenigen, et al., 2018).

Our interpretation that prolonged warming could weaken soil C storage is further supported by the decreased chemical recalcitrant C pool size with long-term warming. After the initial microbial assimilation of readily accessible C pools with warming, soil microorganisms can acclimate to C starvation through utilization of chemical recalcitrant C pools. This change in microbial preference of C substrates can be facilitated by shifts from microbial cellulase to ligninase activities (Crowther & Bradford, 2013). For example, warming decreased the abundance of lignin-derived compounds but increased ligninase activity in a mixed temperate forest (Feng, Simpson, Wilson, Williams, & Simpson, 2008). Microbial utilization of recalcitrant C pools could substantially accelerate overall soil C loss because depolymerization of these recalcitrant macromolecules increases microbial accessibility to litter and SOM previously protected by recalcitrant C pools (Lehmann & Kleber, 2015; Paustian et al., 2016; Schmidt et al., 2011).

The moderate correlation between warming effects on soil C stocks and ligninase:cellulase activities (Figure 1a) indicates that warming effects on soil C storage cannot be fully explained by soil enzyme responses alone. Indeed, soil C stocks are determined by the balance between plant litter that is decomposed

and transformed into SOM versus the amount that is mineralized (Cotrufo et al., 2015; Jenkinson, 1990; Kallenbach et al., 2016; Kleber & Johnson, 2010). Thus, other soil processes, for example, warming-induced changes in litter input, root exudation, the formation of stable SOM from microbial products and C leaching could also contribute to changes in soil C storage with warming (Liang, Amelung, Lehmann, & Kästner, 2019; Pausch & Kuzyakov, 2018), while those process are not considered in this meta-analysis. Moreover, even though the enzymes considered in this meta-analysis can indirectly affect the decomposition of bulk soil C, they are mostly involved in the decomposition of plant litter and particulate SOM (Lavallee, Soong, & Cotrufo, 2019). Thus, whereas warming-induced shifts in ligninase:cellulase activity play an important role in determining soil C dynamics with warming, it is still unclear what part of the soil C pool will be affected by these shifts over time frames longer than the spans of the experiments in our dataset.

Including microbial processes can improve the performance of Earth System Models (ESMs; Allison, Wallenstein, & Bradford, 2010; Wieder, Bonan, & Allison, 2013), but the representation of microbial processes in these models vary and are disputed (Sulman et al., 2018; Treseder et al., 2012). Microbial parameters are typically estimated from short-term studies and it is still unclear to what extent these parameters can be extrapolated to longer time scales. Indeed, microbial responses to warming change over time (Ballantyne & Billings, 2018; Walker et al., 2018), for example, the progressive shifts from cellulase to ligninase activities identified in this meta-analysis. Thus, keeping microbial parameters constant with warming duration may lead to inaccurate ESM predictions. A recent study by Chen, Chen, and Luo (2019) demonstrated that including data-driven and dynamic (i.e., variable over time) microbial parameters into the Terrestrial Ecosystem model improved model performance of soil C dynamics considerably. Nonetheless, enzyme-mediated SOM decomposition is usually assumed to be a first-order kinetic relationship (Chen et al., 2019), and ESMs typically lack the biological, physical and chemical protection of SOM as discussed above (Dwivedi et al., 2019). We suggest that future studies should seek to advance ESMs by considering temporal shifts in C-degrading enzyme activities as well as the enzyme-associated destabilization of soil C pools with prolonged warming.

Our analysis highlights three important research gaps. First, to the best of our knowledge, there are no studies that measured soil enzyme activity over warming duration (i.e., for multiple years) at the same experimental site. Thus, to increase our understanding of temporal dynamics in enzyme responses, we strongly encourage researchers to repeat enzyme measurements in ongoing warming experiments. Second, the microbial mechanisms underlying shifts in enzyme activities are still unclear. This lack of mechanistic understanding hampers incorporating microbial mechanisms in the models. Thus, we suggest that future research quantifies the relation between microbial community composition, gene expression and the production

and activity of soil enzymes. Finally, we note that the studies in our dataset used a wide range of assay methods for enzymes and soil C pools. Although our meta-analysis suggests that warming effects on recalcitrant soil C pools did not depend on assay methods for C extraction, uniform research techniques would facilitate comparisons between experiments. Thus, we suggest that multi-site comparison studies conducting measurements in the same laboratory using the same methods will help us understand the role of enzymes in controlling SOM formation and transformation processes.

5 | CONCLUSION

This meta-analysis underscores the key role of microbial enzyme and substrate interactions in driving soil C dynamics with long-term climate warming. Specifically, our results suggest that increases in ligninase activity relative to cellulase activity will catalyze the degradation of chemical recalcitrant C. This shift in enzyme activity may also increase microbial accessibility of litter and SOM, leading to accelerated soil C loss with prolonged warming. However, enzyme-mediated decomposition processes are poorly represented in C decomposition models and field observations. Therefore, to improve our predictions of soil C storage with climate change, future research needs to identify the microbial and molecular mechanisms underlying the shifts in soil C-degrading enzyme activities and their controlling factors.

CONFLICT OF INTEREST
The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS
JC, KJvG and YL designed the study. JC, YZ and YJ collected the data. JC and KJvG conducted the meta-analysis and wrote the manuscript, with substantial contributions from all co-authors. LE, JEO, ZL, PEL, BAH, RLS and UJ contributed substantially to the comments and revisions.

DATA AVAILABILITY STATEMENT
Databases from this paper are available from the online supplementary files and figshare (https://figshare.com/s/7dd68e1fa45e32b2f9fa).

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REFERENCES

Allison, S. D., Wallenstein, M. D., & Bradford, M. A. (2010). Soil-carbon response to warming dependent on microbial physiology. *Nature Geoscience*, 3(5), 336–340. https://doi.org/10.1038/ngeo846

Averill, C., & Waring, B. (2018). Nitrogen limitation of decomposition and decay: How can it occur? *Global Change Biology*, 24(4), 1417–1427. https://doi.org/10.1111/gcb.13980

Bahri, H., Rasse, D. P., Rumpel, C., Dignac, M. F., Bardoux, G., & Mariotti, A. (2008). Lignin degradation during a laboratory incubation followed by 13C isotope analysis. *Soil Biology and Biochemistry*, 40(7), 1916–1922. https://doi.org/10.1016/j.soilbio.2008.04.002

Bailey, V. L., Bond-Lamberty, B., DeAngelis, K., Grandy, A. S., Hawkes, C. V., Heckman, K., … Wallenstein, M. D. (2018). Soil carbon cycling proxies: Understanding their critical role in predicting climate change feedbacks. *Global Change Biology*, 24(3), 895–905. https://doi.org/10.1111/gcb.13926

Ballantyne, I. F., & Billings, S. A. (2018). Model formulation of microbial CO_2 production and efficiency can significantly influence short and long term soil C projections. *The ISME Journal*, 12(6), 1395–1403. https://doi.org/10.1038/s41396-018-0085-1

Bardgett, R. D., Freeman, C., & Ostle, N. J. (2008). Microbial contributions to climate change through carbon cycle feedbacks. *The ISME Journal*, 2(8), 805–814. https://doi.org/10.1038/ismej.2008.58

Belay-Tedla, A., Zhou, X., Su, B., Wan, S., & Luo, Y. (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(1), 110–116. https://doi.org/10.1016/j.soilbio.2008.10.003

Bhattacharyya, P., Roy, K. S., Neogi, S., Dash, P. K., Nayak, A. K., Mohanty, S., … Rao, K. S. (2013). Impact of elevated CO_2 and temperature on soil C and N dynamics in relation to CH_4 and N_2O emissions from tropical flooded rice (*Oryza sativa* L.). *Science of the Total Environment*, 461, 601–611. https://doi.org/10.1016/j.scitotenv.2013.05.035

Bond-Lamberty, B., & Thomson, A. (2010). Temperature-associated increases in the global soil respiration record. *Nature*, 464(7288), 579–582. https://doi.org/10.1038/nature08930

Carrillo, Y., Pendall, E., Dijkstra, F. A., Morgan, J. A., & Newcomb, J. M. (2011). Response of soil organic matter pools to elevated CO_2 and warming in a semi-arid grassland. *Plant and Soil*, 347(1–2), 339–350. https://doi.org/10.1007/s11104-011-0853-4

Chen, J. I., Luo, Y., García-Palacios, P., Cao, J., Dacal, M., Zhou, X., … van Groenigen, K. J. (2018). Differential responses of carbon-degrading enzyme activities to warming: Implications for soil respiration. *Global Change Biology*, 24(10), 4816–4826. https://doi.org/10.1111/gcb.14394

Chen, J. I., Luo, Y., Li, J., Zhou, X., Cao, J., Wang, R.-W., … Zhou, L. (2017). Costimulation of soil glycosidase activity and soil respiration by nitrogen addition. *Global Change Biology*, 23(3), 1328–1337. https://doi.org/10.1111/gcb.13402

Chen, J., Luo, Y., Van Groenigen, K. J., Hungate, B. A., Cao, J., Zhou, X., & Wang, R. W. (2018). A keystone microbial enzyme for nitrogen control of soil carbon storage. *Science Advances*, 4(8), eaaq1689. https://doi.org/10.1126/sciadv.aaq1689

Chen, J. I., Luo, Y., Xia, J., Jiang, L., Zhou, X., Lu, M., … Cao, J. (2015). Stronger warming effects on microbial abundances in colder regions. *Scientific Reports*, 5, 18032. https://doi.org/10.1038/srep18032

Chen, J. I., Luo, Y., Xia, J., Wilcox, K. R., Cao, J., Zhou, X., … Wang, R.-W. (2016). Warming effects on ecosystem carbon fluxes are modulated by plant functional types. *Ecosystems*, 1–12. https://doi.org/10.1007/s10021-016-0035-6

Chen, Y., Chen, J., & Luo, Y. (2019). Data-driven ENZYme (DENZY) model represents soil organic carbon dynamics in forests impacted by nitrogen deposition. *Soil Biology and Biochemistry*, 138, 107575. https://doi.org/10.1016/j.soilbio.2019.107575

Cheng, L., Zhang, N., Yuan, M., Xiao, J., Qin, Y., Deng, Y. E., … Zhou, J. (2017). Warming enhances old organic carbon decomposition through altering functional microbial communities. *The ISME Journal*, 11(8), 1825–1835. https://doi.org/10.1038/ismej.2017.48

Cotrufo, M. F., Soong, J. L., Horton, A. J., Campbell, E. E., Haddix, M. L., Wall, D. H., & Parton, W. J. (2015). Formation of soil organic matter via biochemical and physical pathways of litter mass loss. *Nature Geoscience*, 8(10), 776–779. https://doi.org/10.1038/ngeo2520

Cotrufo, M. F., Wallenstein, M. D., Boot, C. M., Denef, K., & Paul, E. (2013). The Microbial Efficiency-Matrix Stabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: Do labile plant inputs form stable soil organic matter? *Global Change Biology*, 19(4), 988–995. https://doi.org/10.1111/gcb.12113

Crowther, T. W., & Bradford, M. A. (2013). Thermal acclimation in widespread heterotrophic soil microbes. *Ecology Letters*, 16(4), 469–477. https://doi.org/10.1111/ele.12069

Davidson, E. A., & Janssens, I. A. (2006). Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature*, 440(7081), 165–173. https://doi.org/10.1038/nature04514

Dijkstra, P., Thomas, S. C., Heinrich, P. L., Koch, G. W., Schwartz, E., & Hungate, B. A. (2011). Effect of temperature on metabolic activity of intact microbial communities: Evidence for altered metabolic pathway activity but not for increased maintenance respiration and reduced carbon use efficiency. *Soil Biology and Biochemistry*, 43(10), 2023–2031. https://doi.org/10.1016/j.soilbio.2011.05.018

Doetterl, S., Stevens, A., Six, J., Merckx, R., Van Oost, K., Casanova Pinto, M., … Boeckx, P. (2015). Soil carbon storage controlled by interactions between geochemistry and climate. *Nature Geoscience*, 8(10), 780–783. https://doi.org/10.1038/ngeo2516

Dorrepaal, E., Toet, S., Van Logtestijn, R. S. P., Swart, E., Van De Weg, M. J., Callaghan, T. V., & Aerts, R. (2009). Carbon respiration from subsurface peat accelerated by climate warming in the subarctic. *Nature*, 460(7255), 616–619. https://doi.org/10.1038/nature08216

Dwivedi, D., Tang, J., Bouskill, N., Georgiou, K., Chacon, S. S., & Riley, W. J. (2019). Abiotic and biotic controls on soil organo-mineral interactions: Developing model structures to analyze why soil organic matter persists. *Reviews in Mineralogy and Geochemistry*, 85(1), 329–348. https://doi.org/10.2138/rmg.2019.85.11

Feng, W., Liang, J., Hale, L. E., Jung, C. G., Chen, J. I., Zhou, J., … Luo, Y. (2017). Enhanced decomposition of stable soil organic carbon and microbial catabolic potentials by long-term field warming. *Global Change Biology*, 23(11), 4765–4776. https://doi.org/10.1111/gcb.13755

Feng, X., Simpson, A. J., Wilson, K. P., Williams, D. D., & Simpson, M. J. (2008). Increased cuticular carbon sequestration and lignin oxidation in response to soil warming. *Nature Geoscience*, 1(12), 836–839. https://doi.org/10.1038/ngeo361

Hedges, L. V., Gurevitch, J., & Curtis, P. S. (1999). The meta-analysis of response ratios in experimental ecology. *Ecology*, 80(4), 1150–1156. https://doi.org/10.1890/0012-9658(1999)080[1150:TMAORR]2.0.CO;2

Hopkins, F. M., Torn, M. S., & Trumbore, S. E. (2012). Warming accelerates decomposition of decades-old carbon in forest soils.

Proceedings of the National Academy of Sciences of the United States of America, 109(26), E1753–E1761. https://doi.org/10.1073/pnas.1120603109

Jassey, V. E. J., Chiapusio, G., Binet, P., Buttler, A., Laggoun-Défarge, F., Delarue, F., … Gilbert, D. (2013). Above- and belowground linkages in Sphagnum peatland: Climate warming affects plant-microbial interactions. *Global Change Biology*, 19(3), 811–823. https://doi.org/10.1111/gcb.12075

Jenkinson, D. S. (1990). The turnover of organic carbon and nitrogen in soil. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 329(1255), 361–368. https://doi.org/10.1098/rstb.1990.0177

Jian, S., Li, J., Chen, J. I., Wang, G., Mayes, M. A., Dzantor, K. E., … Luo, Y. (2016). Soil extracellular enzyme activities, soil carbon and nitrogen storage under nitrogen fertilization: A meta-analysis. *Soil Biology and Biochemistry*, 101, 32–43. https://doi.org/10.1016/j.soilbio.2016.07.003

Kallenbach, C. M., Frey, S. D., & Grandy, A. S. (2016). Direct evidence for microbial-derived soil organic matter formation and its ecophysiological controls. *Nature Communications*, 7, 13630. https://doi.org/10.1038/ncomms13630

Karhu, K., Auffret, M. D., Dungait, J. A. J., Hopkins, D. W., Prosser, J. I., Singh, B. K., … Hartley, I. P. (2014). Temperature sensitivity of soil respiration rates enhanced by microbial community response. *Nature*, 513(7516), 81–84. https://doi.org/10.1038/Nature13604

Kleber, M. (2010). What is recalcitrant soil organic matter? *Environmental Chemistry*, 7(4), 320–332. https://doi.org/10.1071/EN10006

Kleber, M., & Johnson, M. G. (2010). Advances in understanding the molecular structure of soil organic matter: Implications for interactions in the environment. *Advances in Agronomy*, 106, 77–142. https://doi.org/10.1016/S0065-2113(10)06003-7

Knorr, W., Prentice, I. C., House, J. I., & Holland, E. A. (2005). Long-term sensitivity of soil carbon turnover to warming. *Nature*, 433(7023), 298–301. https://doi.org/10.1038/nature03226

Kögel-Knabner, I., & Rumpel, C. (2018). Advances in molecular approaches for understanding soil organic matter composition, origin, and turnover: A historical overview. *Advances in Agronomy*, 149, 1–48. https://doi.org/10.1016/bs.agron.2018.01.003

Kolář, L., Kužel, S., Horáček, J., Čechová, V., Borová-Batt, J., & Peterka, J. (2009). Labile fractions of soil organic matter, their quantity and quality. *Plant, Soil and Environment*, 55(6), 245–251. https://doi.org/10.17221/87/2009-PSE

Kuzyakov, Y., & Blagodatskaya, E. (2015). Microbial hotspots and hot moments in soil: Concept & review. *Soil Biology and Biochemistry*, 83, 184–199. https://doi.org/10.1016/j.soilbio.2015.01.025

Lal, R. (2004). Soil carbon sequestration impacts on global climate change and food security. *Science*, 304(5677), 1623–1627. https://doi.org/10.1126/science.1097396

Lavallee, J. M., Soong, J. L., & Cotrufo, M. F. (2019). Conceptualizing soil organic matter into particulate and mineral-associated forms to address global change in the 21st century. *Global Change Biology*. https://doi.org/10.1111/gcb.14859

Lehmann, J., & Kleber, M. (2015). The contentious nature of soil organic matter. *Nature*, 528(7580), 60–68. https://doi.org/10.1038/nature16069

Liang, C., Amelung, W., Lehmann, J., & Kästner, M. (2019). Quantitative assessment of microbial necromass contribution to soil organic matter. *Global Change Biology*, 25(11), 3578–3590. https://doi.org/10.1111/gcb.14781

Mack, M. C., Schuur, E. A. G., Bret-Harte, M. S., Shaver, G. R., & Chapin, F. S. (2004). Ecosystem carbon storage in arctic tundra reduced by long-term nutrient fertilization. *Nature*, 431(7007), 440–443. https://doi.org/10.1038/nature02887

Manzoni, S., Taylor, P., Richter, A., Porporato, A., & Ågren, G. I. (2012). Environmental and stoichiometric controls on microbial carbon-use efficiency in soils. *New Phytologist*, 196(1), 79–91. https://doi.org/10.1111/j.1469-8137.2012.04225.x

Margida, M. G., Lashermes, G., & Moorhead, D. L. (2019). Estimating relative cellulolytic and ligninolytic enzyme activities as functions of lignin and cellulose content in decomposing plant litter. *Soil Biology and Biochemistry*, 141, 107689. https://doi.org/10.1016/j.soilbio.2019.107689

Melillo, J. M., Frey, S. D., Deangelis, K. M., Werner, W. J., Bernard, M. J., Bowles, F., … Grandy, A. (2017). Long-term pattern and magnitude of soil carbon feedback to the climate system in a warming world. *Science*, 358(6359), 101–105. https://doi.org/10.1126/science.aan2874

Metcalfe, D. B. (2017). Microbial change in warming soils. *Science*, 358(6359), 41–42. https://doi.org/10.1126/science.aap7325

Pausch, J., & Kuzyakov, Y. (2018). Carbon input by roots into the soil: Quantification of rhizodeposition from root to ecosystem scale. *Global Change Biology*, 24(1), 1–12. https://doi.org/10.1111/gcb.13850

Paustian, K., Lehmann, J., Ogle, S., Reay, D., Robertson, G. P., & Smith, P. (2016). Climate-smart soils. *Nature*, 532(7597), 49–57. https://doi.org/10.1038/nature17174

Plaza, C., Courtier-Murias, D., Fernández, J. M., Polo, A., & Simpson, A. J. (2013). Physical, chemical, and biochemical mechanisms of soil organic matter stabilization under conservation tillage systems: A central role for microbes and microbial by-products in C sequestration. *Soil Biology and Biochemistry*, 57, 124–134. https://doi.org/10.1016/j.soilbio.2012.07.026

Pold, G., Melillo, J. M., & Deangelis, K. M. (2015). Two decades of warming increases diversity of a potentially lignolytic bacterial community. *Frontiers in Microbiology*, 6. https://doi.org/10.3389/fmicb.2015.00480

Pries, C. E. H., Castanha, C., Porras, R. C., & Torn, M. S. (2017). The whole-soil carbon flux in response to warming. *Science*, 355(6332), 1420–1423. https://doi.org/10.1126/science.aal131

Ren, C., Zhao, F., Shi, Z., Chen, J. I., Han, X., Yang, G., … Ren, G. (2017). Differential responses of soil microbial biomass and carbon-degrading enzyme activities to altered precipitation. *Soil Biology and Biochemistry*, 115, 1–10. https://doi.org/10.1016/j.soilbio.2017.08.002

Romero-Olivares, A. L., Allison, S. D., & Treseder, K. K. (2017). Decomposition of recalcitrant carbon under experimental warming in boreal forest. *PLoS ONE*, 12(6), e0179674. https://doi.org/10.1371/journal.pone.0179674

Schmidt, M. W. I., Torn, M. S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I. A., … Trumbore, S. E. (2011). Persistence of soil organic matter as an ecosystem property. *Nature*, 478(7367), 49–56. https://doi.org/10.1038/nature10386

Schnecker, J., Borken, W., Schindlbacher, A., & Wanek, W. (2016). Little effects on soil organic matter chemistry of density fractions after seven years of forest soil warming. *Soil Biology and Biochemistry*, 103, 300–307. https://doi.org/10.1016/j.soilbio.2016.09.003

Schuur, E. A., Vogel, J. G., Crummer, K. G., Lee, H., Sickman, J. O., & Osterkamp, T. (2009). The effect of permafrost thaw on old carbon release and net carbon exchange from tundra. *Nature*, 459(7246), 556–559. https://doi.org/10.1038/nature08031

Singh, B. K., Bardgett, R. D., Smith, P., & Reay, D. S. (2010). Microorganisms and climate change: Terrestrial feedbacks and mitigation options. *Nature Reviews Microbiology*, 8(11), 779–790. https://doi.org/10.1038/nrmicro2439

Sinsabaugh, R. L. (2010). Phenol oxidase, peroxidase and organic matter dynamics of soil. *Soil Biology and Biochemistry*, 42(3), 391–404. https://doi.org/10.1016/j.soilbio.2009.10.014

Sistla, S. A., Moore, J. C., Simpson, R. T., Gough, L., Shaver, G. R., & Schimel, J. P. (2013). Long-term warming restructures Arctic tundra without changing net soil carbon storage. *Nature*, 497(7451), 615–618. https://doi.org/10.1038/nature12129

Sistla, S. A., & Schimel, J. P. (2013). Seasonal patterns of microbial extracellular enzyme activities in an arctic tundra soil: Identifying direct and indirect

effects of long-term summer warming. *Soil Biology and Biochemistry*, 66, 119–129. https://doi.org/10.1016/j.soilbio.2013.07.003

Smith, P., & Fang, C. (2010). Carbon cycle: A warm response by soils. *Nature*, 464(7288), 499–500. https://doi.org/10.1038/464499a

Song, B., Niu, S., Zhang, Z., Yang, H., Li, L., & Wan, S. (2012). Light and heavy fractions of soil organic matter in response to climate warming and increased precipitation in a temperate steppe. *PLoS ONE*, 7(3), e33217. https://doi.org/10.1371/journal.pone.0033217

Strosser, E. (2010). Methods for determination of labile soil organic matter: An overview. *Journal of Agrobiology*, 27(2), 49–60. https://doi.org/10.2478/s10146-009-0008-x

Sulman, B. N., Moore, J. A. M., Abramoff, R., Averill, C., Kivlin, S., Georgiou, K., ... Classen, A. T. (2018). Multiple models and experiments underscore large uncertainty in soil carbon dynamics. *Biogeochemistry*, 141(2), 109–123. https://doi.org/10.1007/s10533-018-0509-z

Terrer, C., Vicca, S., Hungate, B. A., Phillips, R. P., & Prentice, I. C. (2016). Mycorrhizal association as a primary control of the CO_2 fertilization effect. *Science*, 353(6294), 72–74. https://doi.org/10.1126/science.aaf4610

Treseder, K. K., Balser, T. C., Bradford, M. A., Brodie, E. L., Dubinsky, E. A., Eviner, V. T., ... Waldrop, M. P. (2012). Integrating microbial ecology into ecosystem models: Challenges and priorities. *Biogeochemistry*, 109(1–3), 7–18. https://doi.org/10.1007/s10533-011-9636-5

Trivedi, P., Delgadobaquerizo, M., Trivedi, C., Hu, H., Anderson, I. C., Jeffries, T. C., ... Singh, B. K. (2016). Microbial regulation of the soil carbon cycle: Evidence from gene–enzyme relationships. *The ISME Journal*, 10(11), 2593–2604. https://doi.org/10.1038/ismej.2016.65

Trumbore, S. E., Chadwick, O. A., & Amundson, R. (1996). Rapid exchange between soil carbon and atmospheric carbon dioxide driven by temperature change. *Science*, 272(5260), 393–396. https://doi.org/10.1126/science.272.5260.393

Tucker, C. L., Bell, J., Pendall, E., & Ogle, K. (2013). Does declining carbon-use efficiency explain thermal acclimation of soil respiration with warming? *Global Change Biology*, 19(1), 252–263. https://doi.org/10.1111/gcb.12036

van Gestel, N., Shi, Z., van Groenigen, K. J., Osenberg, C. W., Andresen, L. C., Dukes, J. S., ... Hungate, B. A. (2018). Predicting soil carbon loss with warming. *Nature*, 554(7693), E4–E5. https://doi.org/10.1038/nature25745

Van Groenigen, K. J., Osenberg, C. W., Terrer, C., Carrillo, Y., Dijkstra, F., Heath, J., ... Hungate, B. A. (2017). Faster turnover of new soil carbon inputs under increased atmospheric CO_2. *Global Change Biology*, 23(10), 4420–4429. https://doi.org/10.1111/gcb.13752

Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software*, 36(3), 1–48. https://doi.org/10.18637/jss.v036.i03

Von Lützow, M., Kögel-Knabner, I., Ekschmitt, K., Flessa, H., Guggenberger, G., Matzner, E., & Marschner, B. (2007). SOM fractionation methods: Relevance to functional pools and to stabilization mechanisms. *Soil Biology and Biochemistry*, 39(9), 2183–2207. https://doi.org/10.1016/j.soilbio.2007.03.007

Walker, T. W. N., Kaiser, C., Strasser, F., Herbold, C. W., Leblans, N. I. W., Woebken, D., ... Richter, A. (2018). Microbial temperature sensitivity and biomass change explain soil carbon loss with warming. *Nature Climate Change*, 8(10), 885–889. https://doi.org/10.1038/s41558-018-0259-x

Wieder, W. R., Bonan, G. B., & Allison, S. D. (2013). Global soil carbon projections are improved by modelling microbial processes. *Nature Climate Change*, 3(10), 909–912. https://doi.org/10.1038/nclimate1951

Woodcroft, B. J., Singleton, C. M., Boyd, J. A., Evans, P. N., Emerson, J. B., Zayed, A. A. F., ... Tyson, G. W. (2018). Genome-centric view of carbon processing in thawing permafrost. *Nature*, 560(7716), 49. https://doi.org/10.1038/s41586-018-0338-1

Xue, K., Yuan, M. M., Shi, Z. J., Qin, Y., Deng, Y. E., Cheng, L., ... Zhou, J. (2016). Tundra soil carbon is vulnerable to rapid microbial decomposition under climate warming. *Nature Climate Change*, 6(6), 595–600. https://doi.org/10.1038/nclimate2940

Yang, S., Yao, F., Ye, J. I., Fang, S., Wang, Z., Wang, R., ... Zou, H. (2019). Latitudinal pattern of soil lignin/cellulose content and the activity of their degrading enzymes across a temperate forest ecosystem. *Ecological Indicators*, 102, 557–568. https://doi.org/10.1016/j.ecolind.2019.03.009

Zhao, C., Zhu, L., Liang, J., Yin, H., Yin, C., Li, D., ... Liu, Q. (2014). Effects of experimental warming and nitrogen fertilization on soil microbial communities and processes of two subalpine coniferous species in Eastern Tibetan Plateau, China. *Plant and Soil*, 382(1–2), 189–201. https://doi.org/10.1007/s11104-014-2153-2

Zhao, F., Ren, C., Shelton, S., Wang, Z., Pang, G., Chen, J., & Wang, J. (2017). Grazing intensity influence soil microbial communities and their implications for soil respiration. *Agriculture, Ecosystems & Environment*, 249, 50–56. https://doi.org/10.1016/j.agee.2017.08.007

SUPPORTING INFORMATION

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