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14 Differential responses of carbon-degrading enzymes activities to warming:

15 implications for soil respiration

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17 Running title: Carbon-degrading enzyme responses to warming

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## 55 **Abstract**

56 Extracellular enzymes catalyze rate-limiting steps in soil organic matter  
57 decomposition, and their activities (EEAs) play a key role in determining soil

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58 respiration (SR). Both EEAs and SR are highly sensitive to temperature, but their  
59 responses to climate warming remain poorly understood. Here, we present a  
60 meta-analysis on the response of soil cellulase and ligninase activities and SR to  
61 warming, synthesizing data from 56 studies. We found that warming significantly  
62 enhanced ligninase activity by 21.4% but had no effect on cellulase activity. Increases  
63 in ligninase activity were positively correlated with changes in SR, while no such  
64 relationship was found for cellulase. The warming response of ligninase activity was  
65 more closely related to the responses of SR than a wide range of environmental and  
66 experimental methodological factors. Furthermore, warming effects on ligninase  
67 activity increased with experiment duration. These results suggest that soil  
68 microorganisms sustain long term increases in SR with warming by gradually  
69 increasing the degradation of the recalcitrant carbon pool.

70

## 71 **KEYWORDS**

72 Extracellular enzyme activity, Decomposition, Soil microorganisms, Soil respiration,  
73 Recalcitrant carbon pool, Ligninase activity, Cellulase activity, Global warming

## 74 **1 | INTRODUCTION**

75 The average global surface temperature is predicted to increase between 1 and 4°C by  
76 the end of the 21<sup>st</sup> century (Collins & Knutti, 2013, O'Neill et al., 2017). Rising  
77 temperatures have cascading impacts on ecosystem carbon (C) budgets, and these can  
78 cause both positive and negative C cycle–climate feedbacks (Carey et al., 2016, Chen  
79 et al., 2016a, Chen et al., 2017a, Karhu et al., 2014, Paustian et al., 2016, Peñuelas et  
80 al., 2017, Yang et al., 2018). Soil respiration (SR) represents the largest C flux from  
81 soils to the atmosphere (Bradford et al., 2016, Tucker, Bell, Pendall, & Ogle, 2013),  
82 and is primarily driven by the microbial decomposition of soil organic matter (SOM).  
83 However, we know little about the mechanisms underlying the response of SR to  
84 climate warming (Chen et al., 2016b, Conant et al., 2011, van Gestel et al., 2018).  
85 Specifically, there is a lack of information regarding the degree to which soil  
86 extracellular enzymes (EEs), which catalyze the rate-limiting step in SOM  
87 decomposition (Allison, Wallenstein, & Bradford, 2010a, Jing et al., 2014,

88 Sinsabaugh, 2010, Stone et al., 2012), are affected by warming. These enzymes,  
89 primarily produced by microbes, are considered proximate agents of SR because they  
90 lower the activation energy of key reactions and speed up the breakdown of polymers  
91 (Chen et al., 2017b, Chen et al., 2018, Janssens et al., 2010, Suseela, Tharayil, Xing,  
92 & Dukes, 2014). Although the rates at which these enzymes are produced and  
93 degraded are sensitive to temperature (Allison & Treseder, 2008, German, Marcelo,  
94 Stone, & Allison, 2012, Papanikolaou, Britton, Helliwell, & Johnson, 2010, Steinweg,  
95 Dukes, Paul, & Wallenstein, 2013), it is still unclear how warming responses of  
96 enzymes affect SR.

97 Cellulose and lignin are the two most abundant SOM compounds, and  
98 microbially mediated decomposition of these materials composes a main source of SR  
99 (Carreiro, Sinsabaugh, Repert, & Parkhurst, 2000, Chen et al., 2018, Janssens et al.,  
100 2010, Waldrop et al., 2004). Cellulose and hemicellulose comprise the main  
101 composition of primary plant cell walls. Hydrolysis of cellulose and hemicellulose is  
102 mainly catalyzed by cellulase, including  $\beta$ -1,4-glucosidase (BG),  $\beta$ -1,4-xylosidase  
103 (BX) and  $\beta$ -D-cellobiosidase (CBH) (Carreiro, Sinsabaugh, Repert, & Parkhurst, 2000,  
104 Chen et al., 2017b, Jian et al., 2016). The aromatic C polymer lignin is found in  
105 secondary plant cell walls, where it covers and shields cellulose from microbial decay.  
106 Oxidation and degradation of phenolic-containing recalcitrant compounds are  
107 facilitated by ligninase, that is, peroxidase (PER), phenol oxidase (PO) and  
108 polyphenol oxidase (PPO) (Dashtban, Schraft, Syed, & Qin, 2010, Romero-Olivares,  
109 Allison, & Treseder, 2017, Sinsabaugh et al., 2008, Zhou et al., 2012). The critical  
110 roles of cellulase and ligninase in mediating SOM decomposition suggest that climate  
111 warming may affect SR through its effects on EEAs, yet we still lack direct evidence.

112 Cellulase and ligninase are synthesized by specific groups of microorganisms  
113 (Burns et al., 2013, Carreiro, Sinsabaugh, Repert, & Parkhurst, 2000, Wang et al.,  
114 2012), and it may take years for microbial communities to adapt to environmental  
115 changes (DeAngelis et al., 2015). Thus, responses of cellulase and ligninase activities  
116 to warming may vary over time. Because warming methods differ in their effects on  
117 soil temperature and moisture (Chen et al., 2015, Lu et al., 2013), soil microbial

118 community (Chen et al., 2015) and belowground C allocation (Rustad et al., 2001,  
119 Schindlbacher et al., 2015), they may differ in their effects on EEAs as well.  
120 Including cellulase and ligninase activities in soil C models may improve future  
121 predictions of soil C stocks (Ali et al., 2015, Luo, Chen, Chen, & Feng, 2017,  
122 Moorhead, Sinsabaugh, Hill, & Weintraub, 2016). However, warming effects on  
123 cellulase and ligninase activities as well as the underlying mechanisms are still  
124 unclear.

125 To address this knowledge gap, we conducted a meta-analysis of the responses of  
126 cellulase and ligninase activities to warming and their links with SR responses. More  
127 specifically, our study seeks : (1) to quantify the effects of warming on cellulase and  
128 ligninase activities, (2) to investigate the factors affecting the responses of cellulase  
129 and ligninase activities to warming, and (3) to test whether the responses of cellulase  
130 and ligninase activities to warming are linked with changes in SR.

131

## 132 **2 | MATERIALS AND METHODS**

### 133 **2.1 | Data collection**

134 We extracted results for enzyme activities of ligninase and cellulase under warming  
135 experiments conducted in the field. We used Web of Science  
136 (<http://apps.webofknowledge.com/>), Google Scholar (<http://scholar.google.com/>) and  
137 China National Knowledge Infrastructure (<http://www.cnki.net/>) for an exhaustive  
138 search of journal articles published before June 2018, using the following key words :  
139 (1) “climate change” or “experimental warming” or “elevated temperature” and (2)  
140 “cellulase”, or “ligninase”, or “glucosidase”, or “xylosidase”, or “cellobiosidase”, or  
141 “peroxidase”, or “phenol oxidase”, or “polyphenol oxidase”, and (3) “terrestrial” or  
142 “soil” or “land”.

143 To be included in our dataset, experiments had to meet several criteria: (1) the  
144 warming treatment lasted at least one year; (2) vegetation, soil physicochemical  
145 parameters and climate were similar between control and warming treatments; (3)  
146 sample size and standard deviations were reported; (4) warming protocols (i.e.,  
147 warming method, warming magnitude, warming time and warming season) were

148 clearly described. All studies in our dataset measured enzyme activity for warmed and  
149 control soils at the same incubation temperature (i.e., temperature differences between  
150 treatments occurred only in the field, and not during the incubation). As such,  
151 differences in enzyme activity between warmed and control soils were not related to  
152 the temperature sensitivity of enzymes, but reflect warming effects on enzyme  
153 production by soil microbes. We found 56 articles that met our requirements (see  
154 Dataset and Figure S1).

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

175

## 176 **2.2 | Data analysis**

177 We used meta-analysis to evaluate the effects of warming on cellulase, ligninase,  
178 individual enzyme activity and other ancillary variables (García-Palacios et al., 2014,  
179 Hedges, Gurevitch, & Curtis, 1999, Van Groenigen et al., 2014, Zhao et al., 2017).  
180 The effects of warming on EEAs were evaluated using the natural log of the response  
181 ratio ( $\ln R$ ):

$$183 \quad \ln R = \ln\left(\frac{\overline{X}_W}{\overline{X}_C}\right) = \ln(\overline{X}_W) - \ln(\overline{X}_C) \quad (1),$$

184  
185 with  $\overline{X}_W$  and  $\overline{X}_C$  as the arithmetic mean concentrations in the warming and control  
186 treatments, respectively. The variances ( $\nu$ ) of  $\ln R$  were calculated by:

$$187 \quad \nu = \frac{S_W^2}{n_W \overline{X}_W^2} + \frac{S_C^2}{n_C \overline{X}_C^2} \quad (2),$$

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

192 The overall effect and the 95% confidence interval were calculated using the  
193 “rma.mv” function in the R-package “metafor” (Viechtbauer, 2010). Because  
194 incubation temperature for enzyme measurements varied among studies, we included  
195 “Incubation temperature” as a random factor in the meta-analysis. Because several  
196 papers contributed more than one response ratio, we also included the variable “paper”  
197 as a random factor (Chen et al., 2018, Terrer et al., 2016, van Groenigen et al., 2017).  
198 The effects of warming were considered significant if the 95% confidence interval did  
199 not overlap with zero. The results for the analyses on  $\ln R$  were back-transformed and  
200 reported as percentage change with warming (that is,  $100 \times (e^{\ln R} - 1)$ ) to ease  
201 interpretation.

202 The meta-analytic models were selected by using the same approach as in Chen  
203 et al. (2018), Terrer et al. (2016) and van Groenigen et al. (2017). Briefly, we analyzed  
204 all potential combinations of the studied factors in a mixed-effects meta-regression

205 model using the “glmulti” package in R (Bangert-Drowns, Hurley, & Wilkinson, 2004,  
206 Calcagno & de Mazancourt, 2010). The importance of a specific predictor was  
207 expressed as the sum of Akaike weights for models that included this factor, which  
208 can be considered as the overall support for each variable across all models. A cut-off  
209 of 0.8 was set to differentiate between important and non-essential predictors.

210

### 211 **3 | RESULTS**

212 Across the whole dataset, warming significantly enhanced ligninase activity by an  
213 average of 21.4%. Specifically, warming significantly increased activities of PER by  
214 18.4%, PO by 13.5% and PPO by 28.6%. In contrast, warming had no effect on  
215 cellulase activity (Figure 1a), or any of the individual cellulase enzymes BG, BX and  
216 CBH. The responses of cellulase and ligninase activities to warming were normally  
217 distributed (Figure 1b and 1c), and they were independent of the sample size (Figure  
218 S2).

219 None of variables tested for the effects of warming on cellulase activity reached  
220 the threshold value (0.8) of the summed Akaike weights (Figure 2a). In contrast,  
221 effects of warming on ligninase activity were best explained by warming duration and  
222 warming method (Figure 2b). Linear regression analysis confirmed that  $\ln R$  of  
223 ligninase activity was positively correlated with warming duration, while no such  
224 relationship was found for cellulase activity (Figure 3a and 3b). Regarding warming  
225 methods, warming did not affect cellulase activity for any of the warming methods  
226 (Figure 3a). In contrast, OTC, GH and IH significantly increased ligninase activity by  
227 15.5%, 31.4% and 22.3%, respectively; while cables had no effect on ligninase  
228 activity (Figure 3b).

229 Warming significantly increased microbial biomass specific ligninase activity (i.e.  
230 the ratio of ligninase activity to total microbial abundance) by 40.6% (Figure S3a).  
231 This increase was weakly positively correlated with warming-induced changes in the  
232 ratio of fungal to bacterial abundance (Figure S3b). Finally, our analyses suggest that  
233 warming had stronger positive effects on biomass specific ligninase activity for  
234 long-term than short-term studies, while this relationship was not observed for



235 biomass specific cellulase activity (Figure S4a and S4b).

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

#### 249 **4 | DISCUSSION**

250 Our results show that warming significantly enhanced ligninase activity, and that  
251 warming responses are positively correlated with warming duration. In contrast,  
252 warming does not affect cellulase activity. Why does warming have differential  
253 effects on cellulase and ligninase activities? We propose three possible mechanisms.  
254 First, the enzyme responses reflect warming-induced changes in substrate availability.  
255 Enzyme activity can be described by the Michaelis–Menten relationship, which  
256 primarily depends on substrate availability (Davidson & Janssens, 2006, Sinsabaugh  
257 et al., 2008). Initial stimulation of SR by warming depletes easily hydrolysable  
258 substrates (Allison, McGuire, & Treseder, 2010b, Luo, Wan, Hui, & Wallace, 2001),  
259 limiting the positive response of cellulase activity to increasing temperatures  
260 (Davidson & Janssens, 2006, Stone et al., 2012, Weedon, Aerts, Kowalchuk, & van  
261 Bodegom, 2014). At the same time, warming-induced declines in easily hydrolysable  
262 C pools can lead to microbial C starvation (Crowther & Bradford, 2013, Fenner et al.,  
263 2006, Melillo et al., 2017, Metcalfe, 2017). Under these circumstances, soil microbial  
264 communities may adapt to utilize previously inaccessible recalcitrant C pools to fuel

265 their metabolic activities. Microbial utilization of recalcitrant substrates such as  
266 phenol requires depolymerization, a process catalyzed by ligninase (De Gonzalo,  
267 Colpa, Habib, & Fraaije, 2016, Jassey et al., 2012, Sinsabaugh, 2010).

268 Second, warming may increase ligninase activity through its effect on soil N  
269 availability. Warming-induced redistribution of N from soils to vegetation could  
270 progressively lead to microbial N limitation, particularly in high C:N regions (Bai et  
271 al., 2013, Beier et al., 2008, Melillo et al., 2011). In that case, soil microorganisms are  
272 expected to invest C and energy to acquire N through decomposition of N-containing  
273 molecules (Chen et al., 2017b, Sinsabaugh et al., 2008), which are often physically or  
274 chemically protected by other aromatic macromolecules such as lignin (Hobbie, 2008,  
275 Weedon et al., 2012, Zhao et al., 2014). This explanation is supported by the positive  
276 correlation between warming effects on ligninase activity and soil C:N, while no clear  
277 relationship is found for the responses of cellulase activity (Figure S6). Finally,  
278 warming-induced changes in soil microclimate (Domínguez et al., 2017, Zhou et al.,  
279 2013), fresh C input (Bhattacharyya et al., 2013a, Xue et al., 2016, Yin et al., 2013)  
280 and plant community composition (Kardol, Cregger, Company, & Classen, 2010,  
281 Steinauer et al., 2015) can all cause substantial changes in microbial communities as  
282 well.

283 Increased ligninase production with warming might reflect shifts in the microbial  
284 community composition. Indeed, several studies suggest that warming-induced  
285 changes in soil microbial community composition cause differential responses of  
286 cellulase and ligninase activities (DeAngelis et al., 2015, Pold, Grandy, Melillo, &  
287 DeAngelis, 2017). This explanation is also consistent with studies showing that fungi  
288 are main contributors to ligninase production (De Gonzalo, Colpa, Habib, & Fraaije,  
289 2016, Kinnunen, Maijala, JArvinen, & Hatakka, 2017), and that experimental  
290 warming increases fungal abundance (A'Bear, Jones, Kandeler, & Boddy, 2014,  
291 Delarue et al., 2015). However, warming may also directly or indirectly cause  
292 physiological adaptation of soil microorganisms to increase enzyme production  
293 (Manzoni et al., 2012, Nie et al., 2013, Schindlbacher et al., 2015), even when  
294 warming decreases total microbial biomass (Pold, Grandy, Melillo, & DeAngelis,

295 2017, Sistla & Schimel, 2013, Sorensen et al., 2018). This is consistent with recent  
296 findings that experimental warming tends to decrease microbial C use efficiency  
297 (Manzoni et al., 2012, Tucker, Bell, Pendall, & Ogle, 2013).

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

308 Regardless of the mechanism underlying the differential warming response of  
309 ligninase and cellulase, our results suggest that warming-induced shifts in cellulase  
310 and ligninase activities could help to sustain long-term increases in SR with warming  
311 (Lin, Zhu, & Cheng, 2015, Romero-Olivares, Allison, & Treseder, 2017, Souza et al.,  
312 2017). This is because warming responses of ligninase activity exert far larger control  
313 over SR than a broad range of environmental and experimental variables. These  
314 results suggest that responses of SR to warming are largely modulated by a single  
315 group of lignin-modifying enzymes, which contributes to sustained positive responses  
316 of SR to long-term climate warming.

317 Warming methods constituted the second important predictor of the warming  
318 effects on ligninase activity. Cables only warm soils and are reported to have negative  
319 effects on microbial biomass, litter inputs and root exudates (Rustad et al., 2001,  
320 Schindlbacher et al., 2015). Similarly, a recent meta-analysis shows that cables  
321 generally decrease total microbial, fungal and bacterial abundance, while other  
322 warming methods increase microbial abundance (Chen et al., 2015). We hypothesize  
323 that these negative responses suppressed microbial activity and microbial enzymatic  
324 production (Chen et al., 2015, Hanson et al., 2017). In addition, high warming

325 magnitude and large reductions in soil moisture in cable experiments may decrease  
326 microbial C use efficiency (Schindlbacher et al., 2011, Schindlbacher et al., 2012),  
327 which could potentially suppress microbial cellulase and ligninase production.

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

338

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354

355 **DATA ACCESSIBILITY**

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

357

358 **SUPPORTING INFORMATION**

359 Additional Supporting Information may be found online in the supporting information  
360 tab for this article.

361

362 **CONFLICT of INTEREST**

363 The authors declare no conflict of interest.

364

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## 764 **Figure captions**

765

766 **FIGURE 1** (a) Effects of warming on cellulase and ligninase activities indicated with  
767 the mean percentage of change in warming vs. control plots. Distribution of the  
768 log-transformed response ratios (lnR) of (b) cellulase and (c) ligninase activities to  
769 experimental warming. Error bars represent 95% confidence intervals. The sample  
770 size for each variable is shown in the right column of the figure. PER, peroxidase; PO,  
771 phenol oxidase; PPO, polyphenol oxidase; BG,  $\beta$ -1,4-Glucosidase; BX,  
772  $\beta$ -1,4-Xylosidase; CBH,  $\beta$ -D-Cellobiosidase.

773

774 **FIGURE 2** Model-averaged importance of the predictors of warming effects on soil  
775 (a) cellulase and (b) ligninase activities. The importance is based on the sum of  
776 Akaike weights derived from model selection using corrected Akaike's Information  
777 Criteria. Cutoff is set at 0.8 in order to differentiate between important and  
778 non-essential predictors. MAT, mean annual temperature; MAP, mean annual  
779 precipitation; Sample.T, sampling temperature; Time, daily warming regime (i.e., day,  
780 night, or diurnal warming); Season, annual warming regime (i.e. growing season,  
781 non-growing season or whole-year warming).

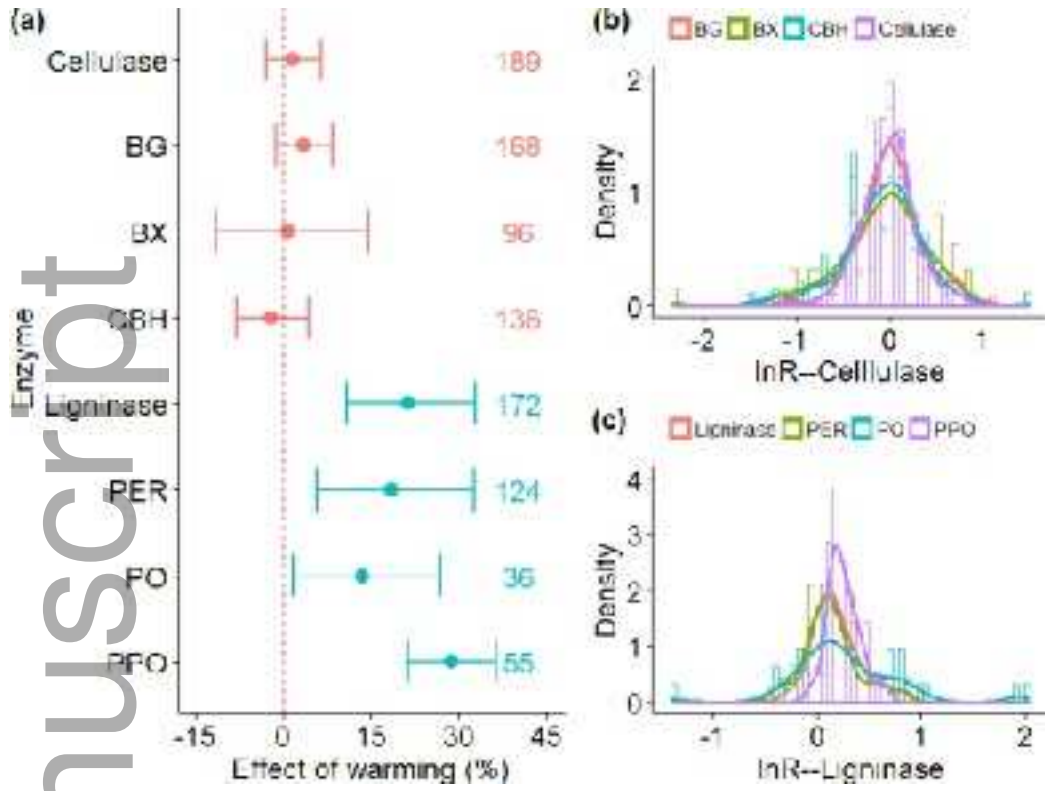
782

783 **FIGURE 3** Relationships between warming-induced changes in (a) cellulase and (b)  
784 ligninase activities and warming duration. Effects of warming on (c) cellulase and (d)  
785 ligninase activities for various warming methods. The response of ligninase activity  
786 was positively correlated with warming duration ( $y = 0.016x + 0.113$ ,  $R^2 = 0.117$ ,  $p <$   
787  $0.001$ ,  $F = 22.590$ ,  $n = 172$ ). Error bars represent 95% confidence intervals. OTC,  
788 open top chamber; IH, infrared heater; GH, green house. The sample size for each  
789 variable is shown in the right column of the figure.

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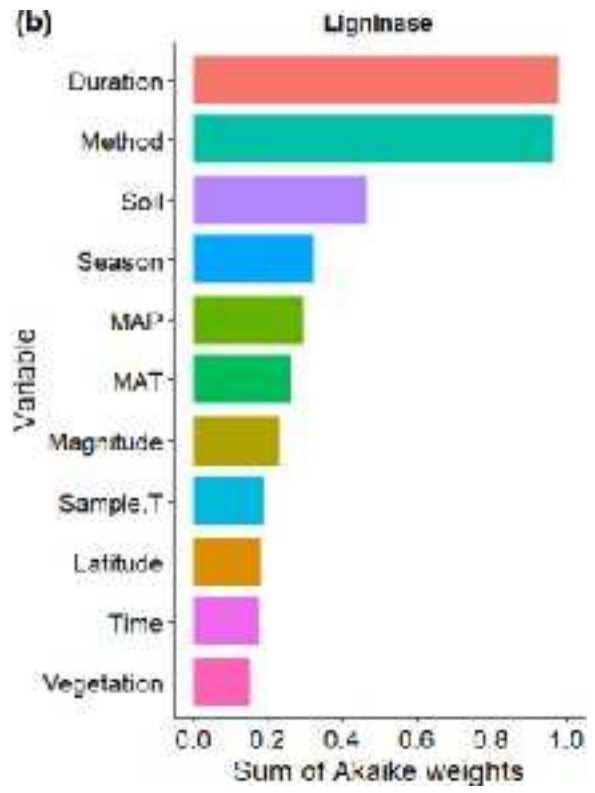
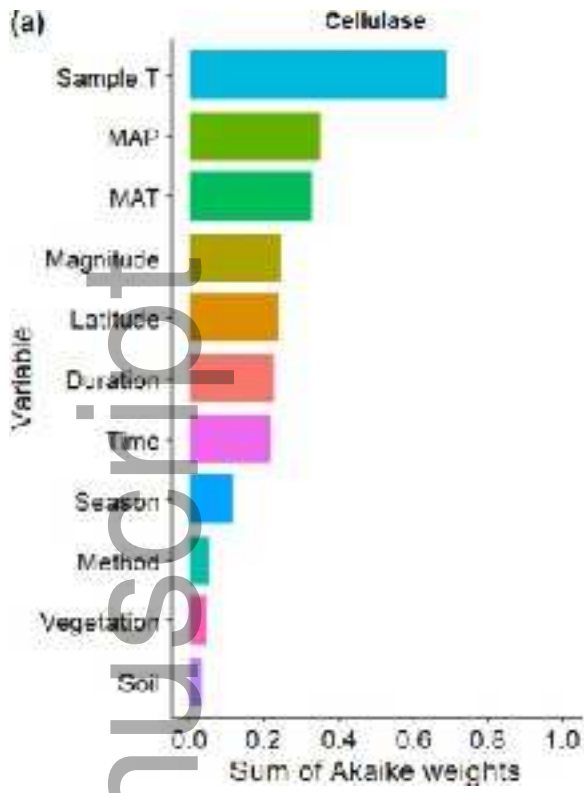
791

792 **FIGURE 4** Relationships between the effect of warming (lnR) on soil respiration (SR)  
793 and lnR of (a) cellulase and (b) ligninase activities. (c) Model-averaged importance of  
794 the predictors of warming effects on SR. The warming response of SR was positively  
795 correlated with the warming response of ligninase activity ( $y = 0.528x + 0.108$ ,  $R^2 =$   
796  $0.467$ ,  $p < 0.001$ ,  $F = 61.260$ ,  $n = 72$ ). Model selection analysis is limited to studies  
797 that simultaneously reported the responses of ligninase, cellulase and SR. The  
798 importance is based on the sum of Akaike weights derived from model selection using  
799 corrected Akaike's Information Criteria. Cutoff is set at 0.8 to differentiate between  
800 important and non-essential predictors. MAT, mean annual temperature; MAP, mean  
801 annual precipitation; Time, daily warming regime (i.e., day, night, or diurnal  
802 warming); Season, annual warming regime (i.e. growing season, non-growing season  
803 or whole-year warming); Sample.T, sampling temperature.



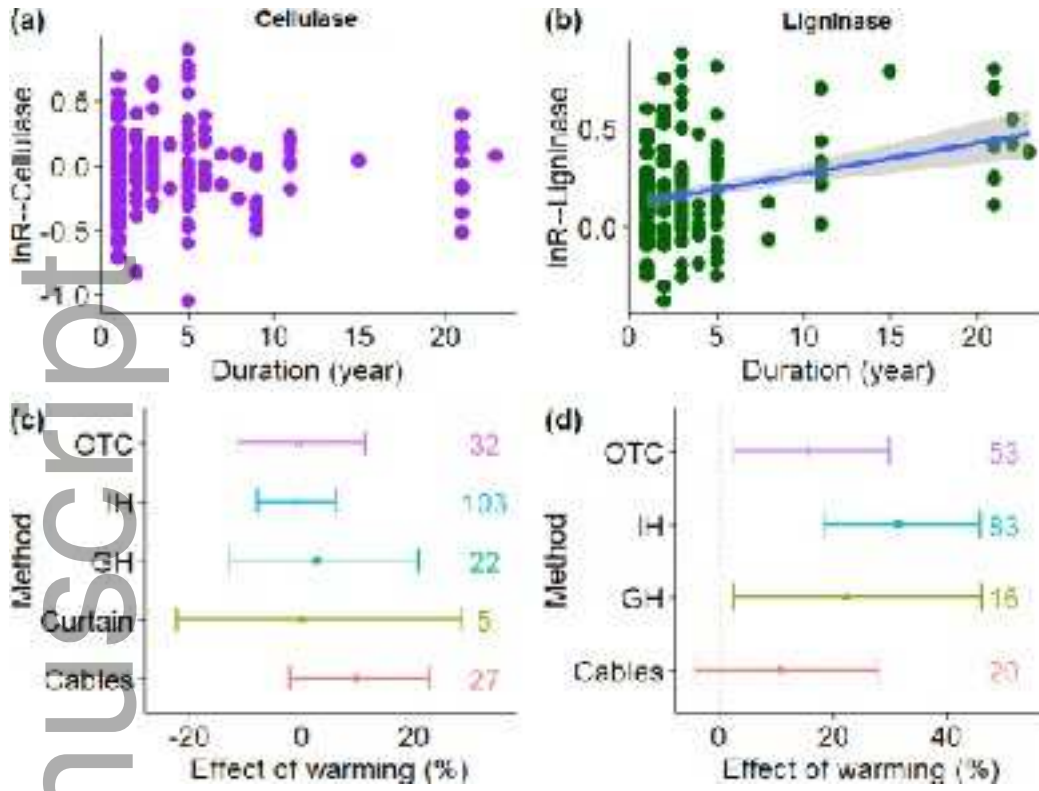
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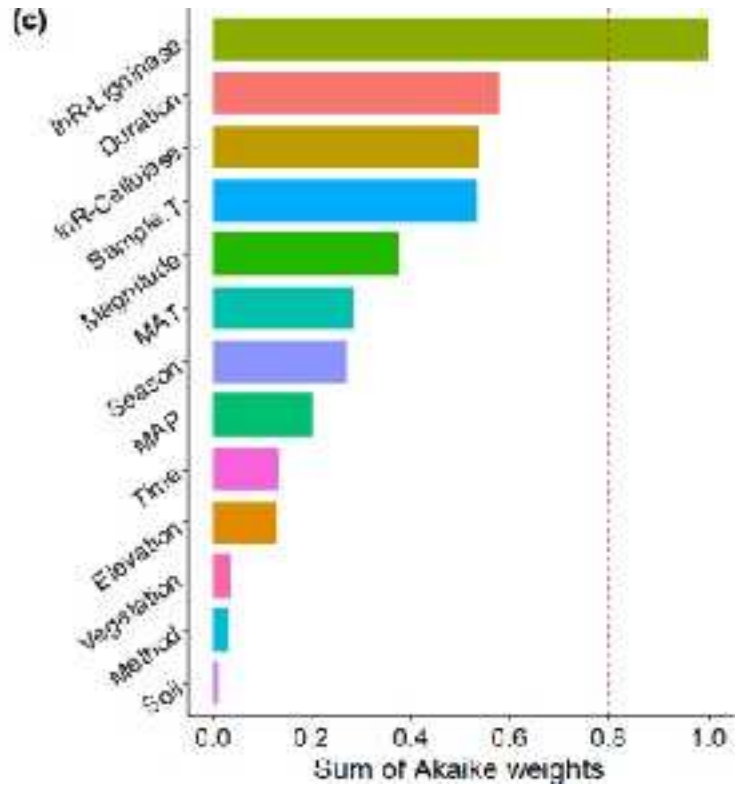
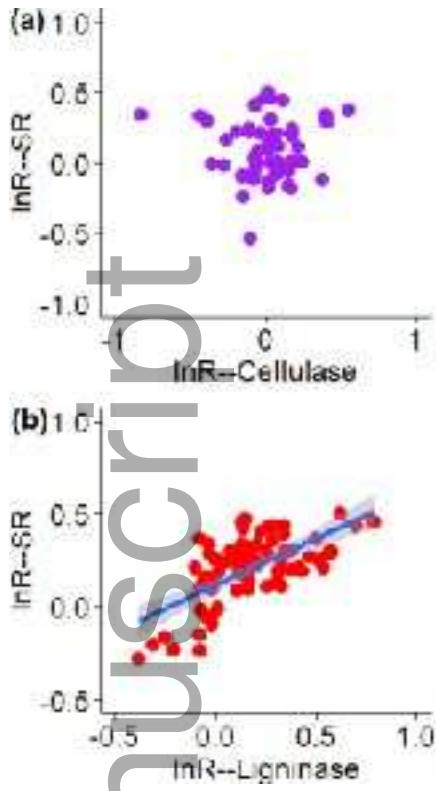


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