Apparent thermal acclimation of soil heterotrophic respiration mainly mediated by substrate availability

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Running title: Substrate availability mediates thermal acclimation of R_H

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Abstract

Multiple lines of existing evidence suggest that increasing CO_2 emission from soils in response to rising temperature could accelerate global warming. However, in experimental studies, the initial positive response of soil heterotrophic respiration (R_H) to warming often weakens over time (referred to apparent thermal acclimation). If the decreased R_H is driven by thermal adaptation of soil microbial community, the potential for soil carbon (C) losses would be reduced substantially. In the meanwhile, the response could equally be caused by substrate depletion, and would then reflect the gradual loss of soil C. To address uncertainties regarding the causes of apparent thermal acclimation, we carried out sterilization and inoculation experiments using the soil samples from an alpine meadow with 6-years of warming and nitrogen (N) addition. We demonstrate that substrate depletion, rather than microbial adaptation, determined the response of R_H to long-term warming. Furthermore, N addition appeared to alleviate the apparent acclimation of R_H to warming. Our study provides strong empirical support for substrate availability being the cause of the apparent acclimation of soil microbial respiration to temperature. Thus, these mechanistic insights could facilitate efforts of biogeochemical modelling to accurately project soil C stocks in the future climate.

Keywords: heterotrophic respiration, warming, nitrogen addition, microbial adaptation, substrate depletion

Introduction

Globally, soils up to two-meter depth store about 3 times as much carbon (C, 2200-2500 Pg) as Earth's atmosphere (Scharlemann *et al*., 2014; Jackson *et al*., 2017). The loss of soil organic carbon (SOC) via microbial decomposition, referred to as heterotrophic respiration (R_H), has been increasing in response to climatic warming (Crowther *et al*., 2016; Bond-Lamberty *et al*., 2018), representing positive feedback that would further contribute to rising global surface temperatures. The positive warming-C cycle feedback has been embedded in the Earth system models to predict C stocks in terrestrial ecosystems (Cox *et al.*, 2000; Wieder *et al*., 2015; IPCC, 2021). However, a wealth of long-term field manipulative experiments showed that the initial positive response of soil respiration to warming may decline over time (Luo *et al*., 2001; Melillo *et al*., 2002; Hartley *et al*., 2008; Bradford, 2013; Walker *et al*., 2018). Thus, when measurements are made at a common temperature, R_H rates are lower in previously warmed soils than in soils from control plots. This phenomenon is referred to apparent thermal acclimation, indicating that soil C stocks may be less vulnerable to climate change than currently feared. Therefore, a deeper understanding of soil microbial decomposition in response to warming is imperative to improve the accuracy and precision of model projections of terrestrial C-climate feedback in the future (Luo, 2007; García-Palacios *et al*., 2021).

Two main mechanistic explanations have been proposed to interpret the decreased trend of soil microbial respiration over time (Fig. 1). Firstly, shifts in microbial community composition, population dynamic, and physiological

71 acclimation following warming may attenuate SOC decomposition (Zhang *et al*.,
72 2005; Allison *et al*., 2010; Bradford *et al*., 2019). For example, a decade of soil
73 warming induced a shift of microbial community towards Gram-positive bacteria and
74 decreased the relative abundance of fungi (Frey *et al*., 2008; Melillo *et al*., 2017).
75 Meanwhile, the reduction of microbial growth efficiencies and carbon-use efficiency
76 at warmer temperatures could decrease microbial respiration (Crowther & Bradford,
77 2013; Li *et al*., 2019). Alternatively, substrate (especially the labile soil C pool
78 representing readily bioavailable C components to microbes) depletion caused by
79 enhanced microbial activity may weaken the positive effect of warming on microbial
80 respiration over time (Knorr *et al*., 2005; Tucker *et al*., 2013; Pold *et al*., 2017). While
81 substrate depletion reflects the gradual loss of soil C, and rates of C release would be
82 dependent on the availability of SOM to decomposers, thermal adaptation would
83 imply a reduction in microbial activity prior to C being released. Thus, these two
84 hypotheses have very different implications for feedbacks of C cycle to climate
85 change. For this reason, uncertainties related to the importance of microbial
86 adaptation vs. substrate depletion in regulating the feedbacks of R_H to warming limit
87 our confidence in projecting long-term soil C dynamics in response to climate change
88 (Bradford *et al*., 2016; Ye *et al*., 2019).
89 Several attempts had been made to clarify the role of microbial adaptation and
90 substrate depletion on R_H to climate warming. Laboratory incubation studies with
91 long-term warmed soils, which measured mass-specific respiration rate under
92 saturated substrate condition with sucrose amendment, showed that shifts in microbial

93 physiology and community mediated the response of R_H to warming (Bradford *et al*.,
94 2008). However, in a 3-year grassland experiment with soil warming and shading
95 treatments, Hartley *et al*. (2007) found that substrate availability was the key driver
96 involved in apparent thermal acclimation of R_H; by reducing differences in substrate
97 availability between previously warmed and control soils, the legacy effects were lost.
98 In addition, the result of a 26-year soil warming experiment, conducted in a mid-
99 latitude hardwood forest, suggested that the rate of soil C loss was modulated by
100 diverse factors at different warming phases, including depletion of microbial
101 accessible C pools at the early phase, reductions in microbial biomass and shifts in
102 microbial community composition and C use efficiency at the middle phase, and a
103 decrease in the relative abundance of recalcitrant C pool, representing that soil
104 organic matter is not readily available to microbes either because of its intrinsic
105 chemical stability or protected in the soil matrix physically (Dungait *et al*., 2012), at
106 the late phase (Melillo *et al*., 2017). However, it is still uncertain whether and how
107 substrate availability and microbial community influence the response of R_H to
108 warming.

109 To reduce the uncertainties, we evaluate the roles of microbial community and
110 substrate depletion in causing apparent thermal acclimation of R_H by using a
111 sterilizing-inoculating method in alpine meadow soils of the northeastern Qinghai-
112 Tibetan Plateau. Soils in this region have high SOC density but are among the most
113 vulnerable regions to global warming (Ding *et al*., 2016; Crowther *et al*., 2016). Soil
114 samples were taken from a 6-year experiment with warming and nitrogen (N)

addition. N addition can alter plant growth rates, the C:N ratio, and then the amount of new C entering the soils (Vitousek *et al*., 1997; Xia & Wan, 2008). Therefore, it provided further opportunity to investigate the importance of substrate availability in determining the respiration rates. We tested the following two main hypotheses: (1) previous experience of 6-years of warming would cause apparent thermal acclimation by reducing R_H in warmed soils compared with controls when both incubated at a common temperature, and (2) the apparent thermal acclimation was mediated by microbial adaptation and substrate depletion jointly.

Materials and Methods

Site description and sample collection

The soil warming and N addition experiment was established in a typical alpine meadow ecosystem (36°42' N, 100°47' E) in the Qinghai Lake basin, northeastern Qinghai-Tibetan Plateau in 2011. The elevation of this experimental site is about 3200 m. Mean annual temperature (MAT) and precipitation (MAP) range from -4.6 to 1 °C and 291 to 575 mm, respectively. Soil temperature ranges from 6.3 to 20.5 °C across the growing season. Mean annual evaporation is about 800 to 2000 mm in 2011-2017. Both maximum temperature and precipitation were found in July. The dominated vegetation includes *Kobresia tibetica*, *Triglochin maritimum*, *Blysmus sinocompressus*, and *Carex heterostachya*.

The field experiment included 12 plots, each 4 m × 4 m, that were grouped into 3 blocks. The four plots within each block were randomly assigned to one of four

137 treatments: (i) control (CK) – no warming and no N addition; (ii) warming (W) –
138 increasing soil temperature by about 1.4 °C using open-top chamber (OTC, 60°
139 inclination of the panels, 0.5-m tall, and 2.08-m basal diameter); (iii) N addition (N) –
140 adding NH_4NO_3 at a rate of 1 g m^{-2} a^{-1} twice a year based on the reported atmospheric
141 N deposition rate in the study area (Lü & Tian, 2007); and (iv) the combination of
142 warming and N addition (WN).

143 Soils were sampled in July 2017 and three soil cores (3 cm in diameter and 15
144 cm in depth) were taken from each plot. The surface soils were used since microbial
145 activity and then heterotrophic respiration rate are greatest in this layer (Bradford *et*
146 *al*., 2008). All soil samples were transported with dry ice to the laboratory in East
147 China Normal University for analysis. Soil samples were sieved through 2-mm
148 screen, and roots, large litter fragments and stones were removed. For each plot, the
149 homogenized soils were divided into three subsamples: (1) one was stored at 4 °C for
150 incubation experiments; (2) another was air-dried to measure soil physical and
151 chemical properties; and (3) the last one was frozen at -20 °C to measure soil
152 microbial properties.

153 *Soil and microbial analyses*

154 Soil water holding capacity (WHC) was determined by wetting a subsample for
155 12 h, and then draining it through filter paper for 12 h. The saturated gravimetric
156 water content (100% WHC) was calculated by drying the subsample at 105 °C for 24
157 h. The soil total C and N contents were measured using an elemental analyzer
158 (Elementar, Vario Max, Germany).

Soil microbial community composition was determined by phospholipid fatty acid (PLFA) analysis. Briefly, the PLFAs were extracted from a subsample of 8 g freeze-drying soils following the mild alkaline methyl esterification method (Bossio & Scow, 1998), and identified by gas chromatography and mass spectrometry (Thermo ISQ TRACE GC system Ultra ISQ, Germany). The fatty acids were quantified by the standard of FAME 19:0. Soil bacteria (i15:0, a15:0, i16:0, i17:0, a17:0 16:1ω7c, cy17:0, 18:1ω7c, cy19:0) and fungi (18:1ω9 and 18:2ω6,9) were classified as different microbial communities based on the results of the PLFA analysis (Frostegård & Bååth, 1996; Liu *et al*., 2021).

Experimental incubations

To investigate variation in soil heterotrophic respiration (R_H) and its temperature sensitivity *(*Q_{10}) affected by warming and N addition, 12 wet soil samples (4 treatments × 3 replicates) were set up to measure the R_H for 10-day incubation. Specifically, 30 g (dry weight equivalent) of each homogenized subsample were placed in 150 mL polyethylene plastic bottles. All soil samples were adjusted to 60% water-holding capacity (WHC) through adding deionized water, since 50-70% WHC was treated as optimum range for soil incubation (Paul *et al*., 2001). Soil water content in each bottle was measured and adjusted based on weight at intervals of 2-3 days. Before starting the incubations, soils were pre-incubated at 20 °C for 24 hours to activate the microbes and minimize disturbance of microbial activities (Hamdi *et al.*, 2011). After pre-incubations, all soil samples were placed in a varying temperature incubator that automatically regulated temperature to increase from 5 to

25 °C and then decrease from 25 to 5 °C in 24 h. The incubation temperature spanned the full temperature range (6.3 to 20.5 °C) experienced by soils across the growing season at our study site. The CO_2 emission rate from soil was measured ranging from 5 to 25 °C using an automatic temperature to control soil flux system (PRI-8800; Pre-Eco, Beijing, China). Each soil sample was measured every hour over the measuring period, with a total of about 120 measurements for each treatment. Briefly, sample bottles were placed in a 16-hole water bath and the temperature was controlled automatically. The CO_2 concentration of each bottle was measured by a CO_2 analyzer (Li-7000, LI-COR, Lincoln, NE, USA) every second, and the total measuring time for each sample was 180 seconds. The R_H was calculated by the following equation (Liu *et al*., 2018; Wang *et al*., 2018):

$$R_H = \frac{C \times V \times \alpha \times \beta}{22.4 \times m} \quad (1)$$

where R_H is the rate of soil heterotrophic respiration (μg C-CO_2 g^{-1} d^{-1}); C is the slope of CO_2 concentration; V is the volume of the gas tube and bottle (mL); m is the soil weight (g); α is the conversion coefficient for CO_2 mass (from CO_2 to C); and β is the conversion coefficient for time (from seconds to days).

Q_{10} values were calculated using the following exponential equations (Lloyd & Taylor, 1994; Luo & Zhou, 2006):

$$R_H = A \times e^{bT} \quad (2)$$

$$Q_{10} = e^{10b} \quad (3)$$

where T is the incubation temperature (°C), and A and b are the exponential parameters that represent the intercept and slope of the line, respectively.

To distinguish the effects of soil substrate and microbial community on R_H variation, soil sterilization and inoculation experiments were used in the further incubations (Fig. S1). A subset of soil samples from three treatments (CK, W, and WN) were sterilized by γ-irradiation of 25 kGy for about 24 h (Marschner & Bredow, 2002; McNamara *et al.*, 2003). To investigate the effects of soil substrate on R_H variation, sterilized soils from different treatments were inoculated with the same microbes (Table S1). Specifically, the irradiated soil samples of CK and W were inoculated by replacing 5% of the sterilized soil with non-sterile soil of CK, with these treatments abbreviated to CK-CK(S) and CK-W(S), respectively. Then these soil samples were filled back into bottles after homogenization. Meanwhile, the irradiated soil samples of W and WN treatments were inoculated with non-sterile soil of W, which were termed as W-W(S) and W-WN(S). By contrast, in the experiment investigating the effects of soil microbial community on R_H variation, sterilized soils of CK were inoculated with non-sterile soils from CK and W, with these treatments abbreviated to CK(M)-CK and W(M)-CK. The other two treatments: W(M)-W and WN(M)-W were produced by using the similar configuration steps (Table S1). All these samples were adjusted to soil moisture of 60% WHC using sterile deionized water before incubation. We measured the R_H using the PRI-8800 system, and calculated the Q_{10} values using equations 1-3. The soil heterotrophic respiration rate at 20 °C (R_{20}) was used as an index of substrate lability (Craine *et al*., 2010).

Statistical analysis

Two-way analysis of variance (ANOVA) was used to test for significant

differences in all measured data among different treatments. Differences were assessed by post-hoc tests using Fisher's protected least significant difference (LSD), and the significance level was set at 0.05. Exponential regressions were used to investigate the relationship between R_H and incubated temperature for each treatment (SigmaPlot, version 12.5, SysStat Software, Inc.). Using linear regression, we evaluated whether other soil and microbial variables, such as soil C/N ratio and fungi biomass, explained significant variation in R_{20} and Q_{10}. All these statistical analyses were conducted by IBM SPSS Statistics 23 (IBM Crop, Armonk, NY, USA).

Results

Effects of warming and N addition on R_H

Soil heterotrophic respiration (R_H) increased exponentially with the incubation temperature in all treatments (Fig. 2). The R_H in warming (W), N addition (N) and their combination (WN) was significantly lower than that in the control (CK). Warming decreased the R_H in those plots without N addition, but increased it in N addition plots, showing an interaction between warming and N addition ($P < 0.01$, Figs. 2a and b, Table S2). On average, the respiration rates at 20 °C (R_{20}) were 20.2, 19.4, and 25.3 μg C-CO_2 g^{-1} d^{-1} under W, N, and WN treatments, respectively, representing decreases of 24.3%, 27.3%, and 5.2% compared with the control. However, the temperature sensitivity (Q_{10}) of R_H showed no significant changes among different treatments (Figs. 2c and d).

We regressed R_{20} against soil substrates and microbial properties among

247 treatments, observing a positive relationship between R_{20} and soil C:N ratio ($r^2 = 0.35$,
248 $P < 0.05$, Fig. 3a) and a negative relationship between R_{20} and fungi biomass ($r^2 =$
249 0.33, $P < 0.05$, Fig. 3b).

250 *Soil substrate and microbial community regulating the R_H*

251 To quantify the role of substrate availability on the variation of R_H, the sterilized
252 soils from CK and W treatments were inoculated with microbes of CK, having two
253 treatments: CK-CK(S) and CK-W(S). The R_H and R_{20} of CK-CK(S) were significantly
254 higher than those in the CK-W(S) ($P < 0.05$), but Q_{10} showed no significant
255 differences ($P > 0.05$, Fig. 4c). When the sterilized soils from W and WN treatments
256 were inoculated with microbes of W treatment (W-W(S), W-WN(S)), the R_H and R_{20}
257 of W-W(S) was significantly lower than those in the W-WN(S) with no significant
258 difference in Q_{10} (Fig. 4d). The retention of differences between different *in situ*
259 treatments following sterilization and inoculation showed that soil substrates largely
260 regulated the variation of R_H.

261 To identify the influence of soil microbial community on the response of R_H to
262 warming, we inoculated microbes of CK and W treatments to the sterilized soils of the
263 control, which were named as CK(M)-CK and W(M)-CK, respectively. The R_{20} and
264 Q_{10} showed no significant difference between CK(M)-CK and W(M)-CK (Fig. 5c).
265 When microbes of W and WN treatments were inoculated to the sterilized soils of W
266 treatment (abbreviated as W(M)-W and WN(M)-W, respectively), the R_{20} in WN(M)-
267 W was slightly higher than that in the W(M)-W with no significant difference in the
268 Q_{10} (Fig. 5d). Again, these results showed that microbial community had little

influence on the response of R_H to warming.

Discussion

In this study, our results demonstrate that the reduction in soil R_H caused by experimental warming in an alpine meadow was largely caused by substrate depletion, rather than microbial thermal adaptation. On average, when measured at a common temperature, the reduction in the R_H in the warmed treatments was about 32% compared to the control (Fig. 2). This is in broad agreement with previous findings on apparent thermal acclimation (Eliasson *et al*., 2005; Carey *et al*., 2016; Chen *et al*., 2016a). The respiration rate at a common assay temperature (i.e., 20 °C in this study) was significantly correlated with soil C/N ratio and fungi biomass (Fig. 3), suggesting that the warming-induced reduction in R_H may be dictated to changes in soil substrate and/or microbial communities (i.e., substrate limitation and microbial adaptation, Hartley *et al*., 2007; Bradford *et al*., 2008; Melillo *et al*., 2017).

Taking advantage of the sterilizing-inoculating experiments, we further clarified the effects of microbial community and substrate limitation in determining the apparent thermal acclimation of R_H. If the adaptation of the microbial community explained the differences in respiration rates across the treatments, inoculation of the sterilized control soil with the warmed community should have reduced respiration rates. However, a non-significant increase in respiration was observed for the sterilized control soils inoculated with warmed microbes. Similarly, inoculation of the warmed soils with microbes from the warmed and N addition treatment should have

increased respiration, but a small statistically significant decrease in respiration was observed (Figs. 4 and 5). Therefore, it does not appear that the adaptation of the microbial community controls respiration rates. This empirical investigation suggests that the lower R_H from the warmed soils is regulated by substrate depletion, rather than the microbial adaptation.

N addition also reduced heterotrophic respiration (Fig. 2), likely resulting from the decrease in soil pH, microbial biomass, and extracellular enzyme activity (Zhou *et al*., 2014; Chen *et al*., 2018; Xing *et al*., 2022). Furthermore, our sterilization-reinoculation experiments suggest that this negative effect was driven by a substrate availability. This could be related to reductions in decomposition rates of more recalcitrant organic matter, which also decreased the availability of labile C (Janssens *et al*., 2010; Tian *et al*., 2019; Widdig *et al*., 2020). However, the data also suggest that N addition appeared to alleviate the apparent acclimation of R_H to warming. The R_H in the warming combined with N addition treatment was higher than that in each single factor (Fig. 2), suggesting that there existed significant interaction between warming and N addition that reduced the effects of warming on substrate availability (Zhou *et al*., 2016; Yue *et al*., 2017). A field manipulative experiment conducted in Tibetan alpine meadow demonstrated that warming significantly increased N losses via enhanced NO_3^- leaching and N_2O emissions (Zhang *et al*., 2020), alleviating the limiting effect of N addition on microbial activity. Since alpine ecosystems are characterized by limited soil mineral N (Chen *et al*., 2016b), N addition likely also stimulates plant productivity and C inputs to soil, and then moderates the substrate

depletion induced by warming. Therefore, the interactive effects of multiple global change factors on soil microbial respiration should include a more detailed understanding of the mechanisms underlying variation in substrates (Zhou *et al*., 2016; Song *et al*., 2019), and deserves the further study.

Experimentally determining the relative importance of microbial community and substrate depletion in regulating apparent thermal acclimation of R_H is extremely difficult due to their tight coupling (Walker *et al*., 2018). Since our sterilization and inoculation experiments were designed to differentiate the effects of microbial community and substrate limitation, it should be noted that sterilization and inoculation might alter soil C substrate to some degree (Figs. 2, 4 and 5). However, sterilization and inoculation did not eliminate the impacts of low substrate availability induced by 6-year warming, as evidenced by a lower R_H in the sterilized soils from warmed treatments inoculated with the control microbes than that in sterilized soils from the control inoculated with the same microbial community (Figs. 4 and 5). Our results therefore demonstrate that substrate depletion can explain the reduction in respiration rates. Despite this, no effect was observed on soil C content and components (e.g., labile and recalcitrant C pools). This finding is actually consistent with the results from warming experiments (Lu *et al.*, 2013; Guan *et al*., 2018; Li *et al*., 2020) and demonstrates that it is remarkably difficult to measure a "small change in a big number" such as a warming effect on the amount of C stored in soils, likely due to these changes being less than the measurement errors (Smith, 2004; Hartley *et al*., 2007). Currently, there is large uncertainty in the projected soil C changes under

warming, and future research is needed to probe how climate change affects the measurable and biophysically defined sub-SOM pools using isotopic, biomarker, and fractionation approaches (Hartley *et al*., 2021; Lugato *et al*., 2021; Georgiou *et al*., 2022).

Having eliminated microbial community composition as a key determinant of differences in rates of heterotrophic respiration in these soils, again it indicates that the differences in the R_{20} were caused by the depletion of labile SOC pools in response to sustained warming (Knorr *et al*., 2005; Hartley *et al*., 2007). Therefore, our data suggest that there remains the potential for C loss in response to warming, and it thus becomes critical to understand the soil properties that regulate how much soil C stocks are vulnerable to being released in the long-term (Crowther *et al*., 2016; Hartley *et al*., 2021). Most Earth system models (ESMs) are heavily dependent on the short-term temperature responses of soil respiration (Q_{10}) to infer long-term changes in global C stocks (Davidson *et al*., 2006; Jones *et al*., 2011; Li *et al*., 2020). Our evidence that microbial adaptation does not cause the apparent thermal acclimation of heterotrophic respiration in soil warming experiments suggests that C stocks will be lost as the world warms, and it is critical that soil C vulnerability is reflected in the process-based models that are used in future climate change projections.

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Figure legends

Figure 1 Proposed mechanisms to interpret the thermal acclimation of soil heterotrophic respiration (R_H). Microbial adaptation (a) results from a shift in soil microbial population, community composition, and physiological activities in response to soil warming, and then attenuates the SOC decomposition rate. Substrate depletion (b) involves a decrease in the soil labile C pool in response to sustained warming, leading to a subsequent reduction in the rate of R_H.

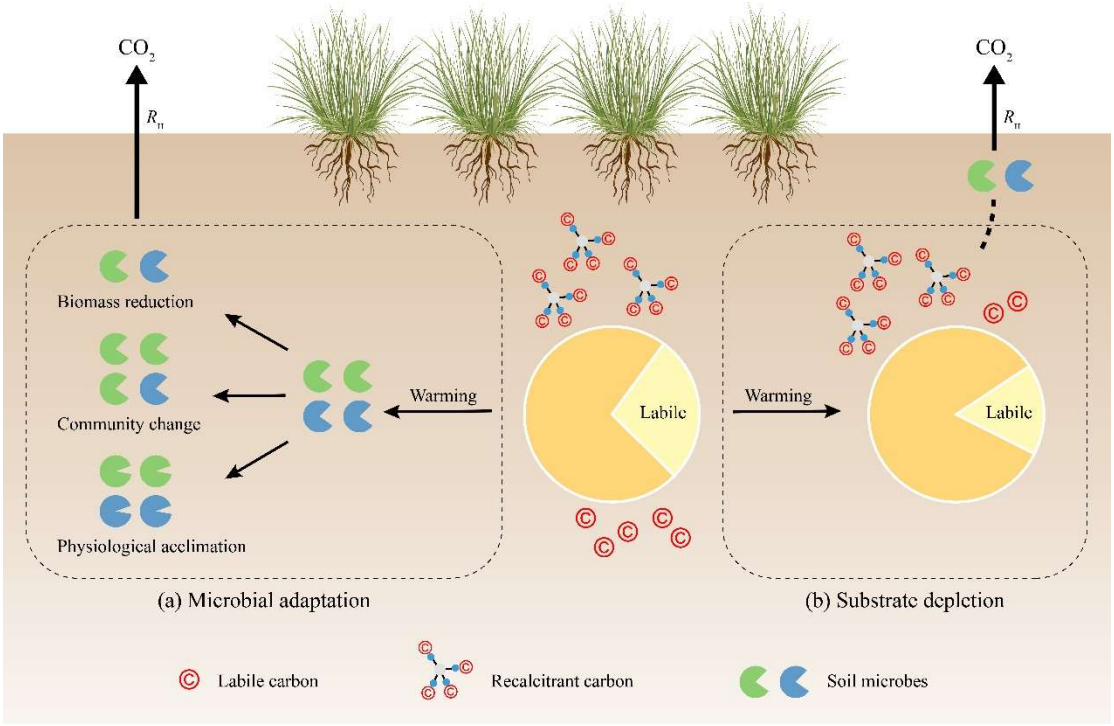
Figure 2 The response of heterotrophic respiration rates (R_H) to incubated temperature in different treatments (a and b), including control (C), warming (W), N addition (N), and the combination of warming and N addition (WN). This relationship was modeled as an exponential function of soil temperature: $R_H = \alpha [\exp (\beta \times \text{temperature})]$, where α is respiration rate at 0 °C and β is temperature sensitivity of respiration (Q_{10}). Effects of warming, nitrogen addition, and their combination on the respiration rate at 20 °C (R_{20}, c) and temperature sensitivities (Q_{10}, d). Different letters over the bars indicate significant differences among different treatments at $P = 0.05$ level.

Figure 3 Relationships between soil heterotrophic respiration rate at 20 °C (R_{20}) and soil C:N ratio (a) and fungi biomass (b).

Figure 4 The heterotrophic respiration rates (R_H, a and b), respiration rate at 20 °C (R_{20}, c) and temperature sensitivities (Q_{10}, d) in different sterilized samples inoculated with the same microbial community. CK-CK(S) and CK-W(S) represents soil microbial community of CK were inoculated to the sterilized soil

samples of CK and W, respectively (a). W-W(S) and W-WN(S) represents soil microbial community of W were inoculated to the sterilized soil samples of W and WN, respectively (b).

Figure 5 The heterotrophic respiration rates (R_H, a and b), respiration rate at 20 °C (R_{20}, c) and temperature sensitivities (Q_{10}, d) in the same sterilized soil samples inoculated with different soil microbial communities. CK(M)-CK and W(M)-CK represents the sterilized soil samples of CK inoculated with microbial community of CK and W, respectively. W(M)-W and WN(M)-W represents the sterilized soil samples of W inoculated with microbial community of W and WN respectively.



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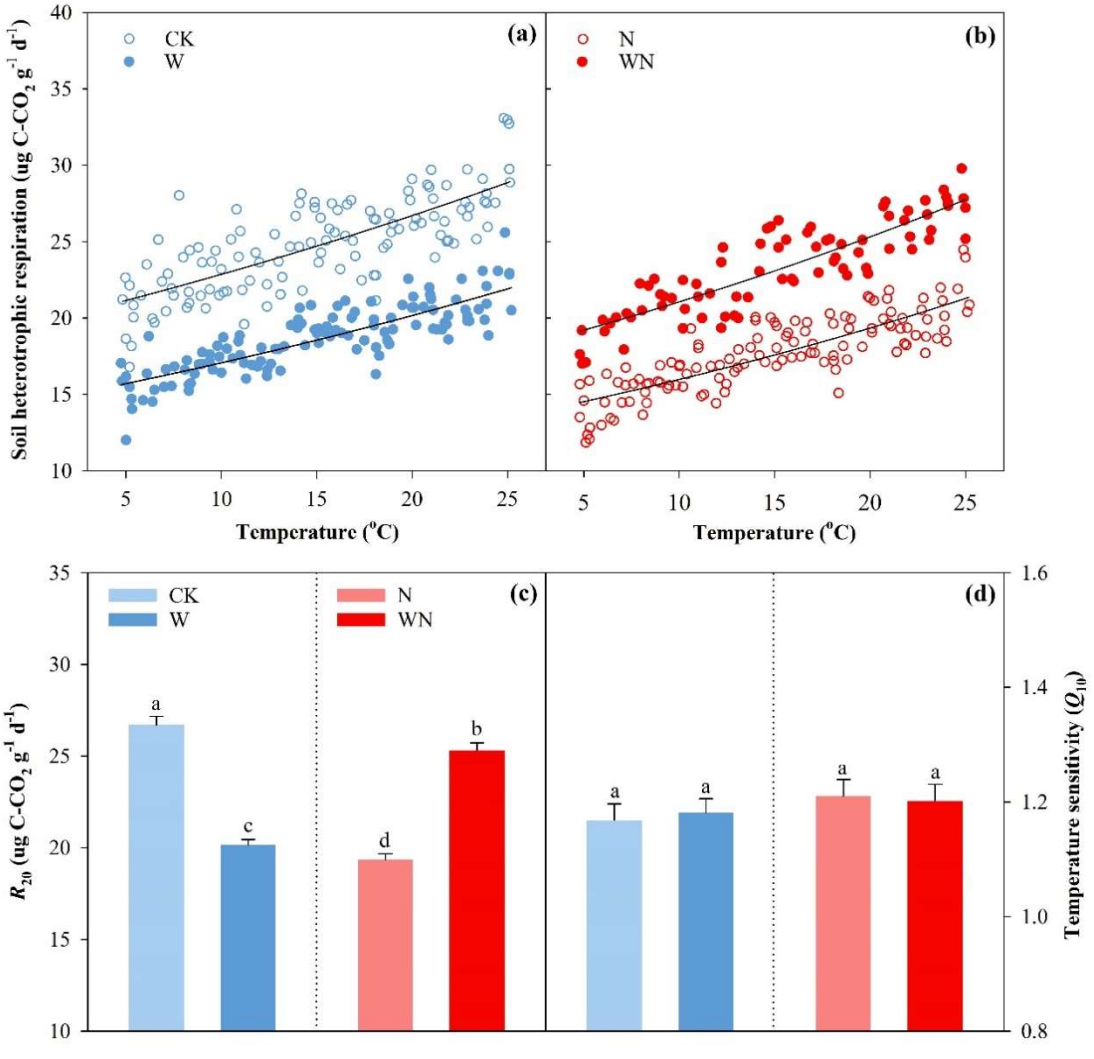
596 Figure 1



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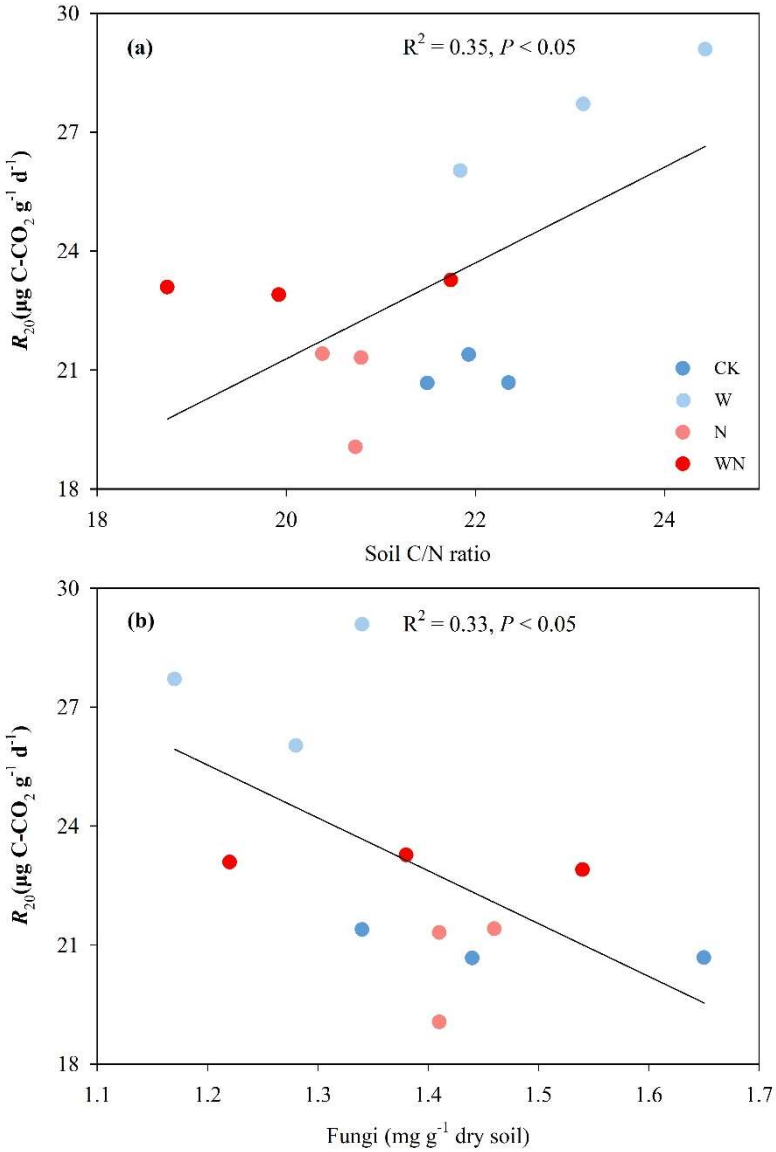

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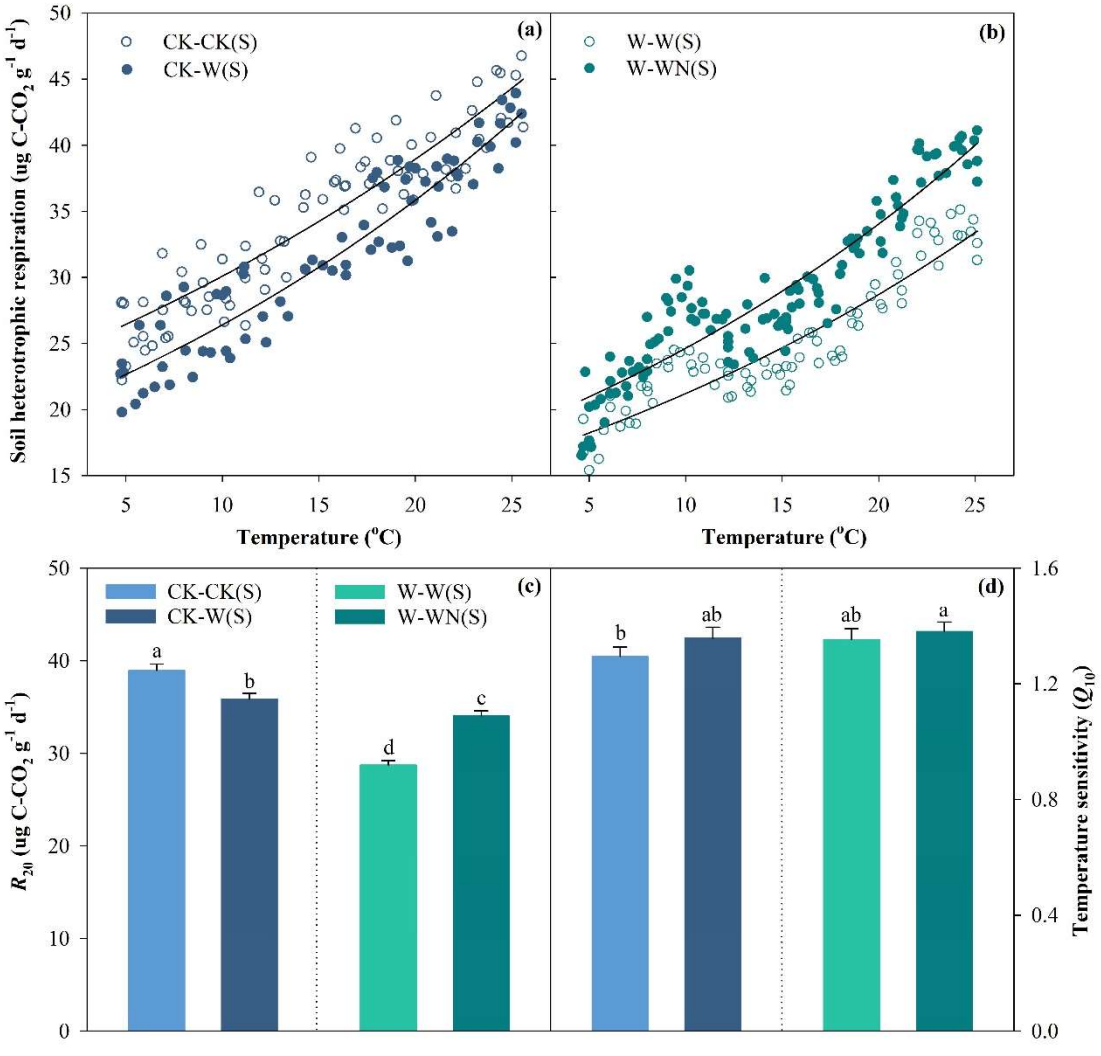
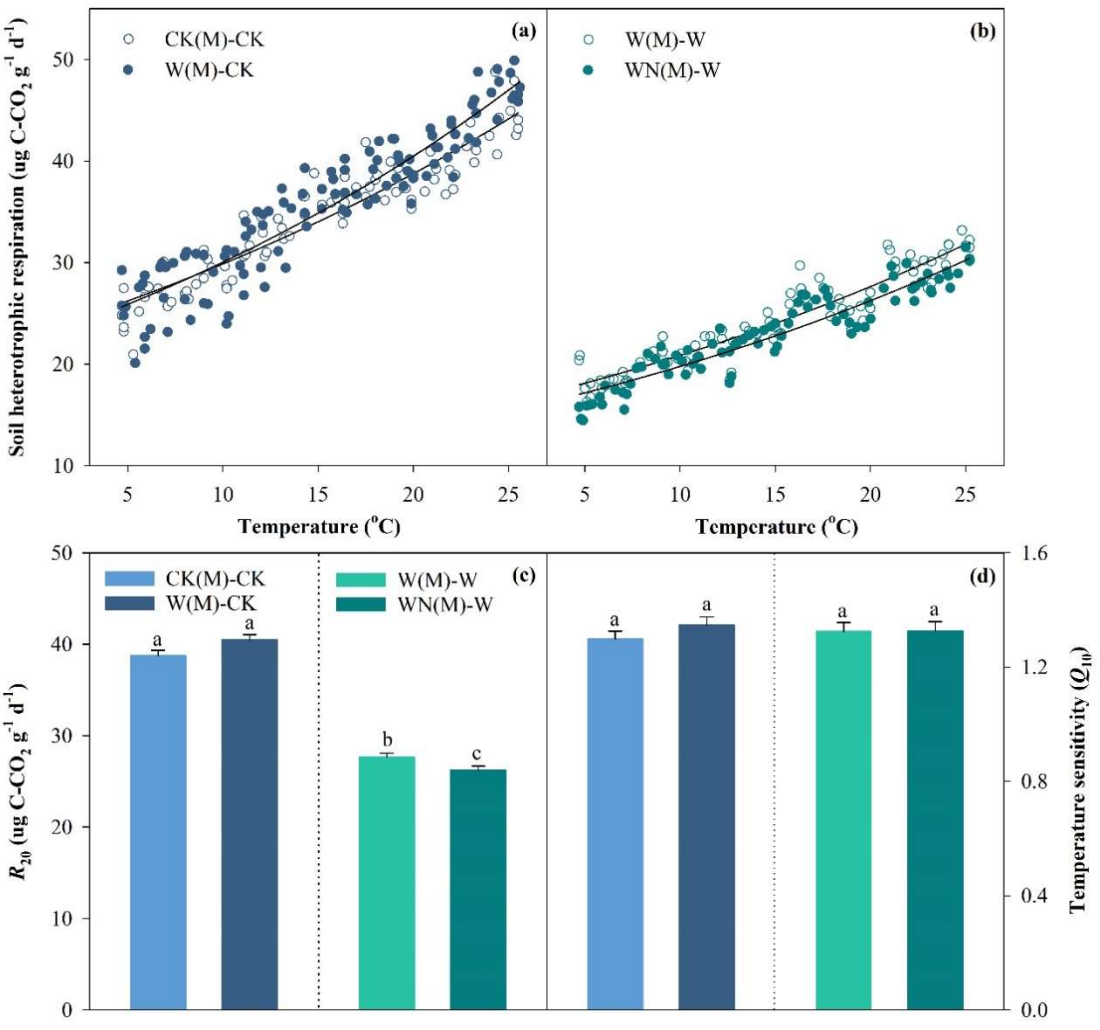

(a)
CK-CK(S)
CK-W(S)
(b)
W-W(S)
W-WN(S)
Soil heterotrophic respiration (ug C-CO2 g-1 d-1)
Temperature (°C)
(c)
(d)
R20 (ug C-CO2 g-1 d-1)
Temperature sensitivity (Q10)
a
b
c
d
ab

Figure 4



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604 Figure 5