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A Meta-analysis of the Effects of Warming and Elevated CO_2 on Soil Microbes

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Abstract: Soil microbes play important roles in terrestrial ecosystem carbon and nitrogen cycling. Climatic warming and elevated CO_2 are two aspects of climatic change. In this study, we used a meta-analysis approach to synthesise observations related to the effects of warming and elevated CO_2 on soil microbial biomass and community structure. Ecosystem types were mainly grouped into forests and grasslands. Warming methods included open top chambers and infrared radiators. Experimental settings included all-day warming, daytime warming and nighttime warming. Warming increased soil actinomycetes and saprotrophic fungi, while elevated CO_2 decreased soil gram-positive bacteria (G^+). Mean annual temperature and mean annual precipitation were negatively correlated with warming effects on gram-negative bacteria (G^-) and total phospholipid fatty acid (PLFA), respectively. Elevation was positively correlated with the warming effect on total PLFA, bacteria, G^+ and G^-. Grassland exhibited a positive response of total PLFA and actinomycetes to warming, while forest exhibited a positive response in the ratio of soil fungi to bacteria (F/B ratio) to warming. The open top chamber method increased G^-, while the infrared radiator method decreased the F/B ratio. Daytime warming rather than all-day warming increased G^-. Our findings indicated that the effects of warming on soil microbes differed with ecosystem types, warming methods, warming times, elevation and local climate conditions.

Key words: ecosystem types; elevated CO_2; increased temperature; response ratio; warming methods

1 Introduction

Soil microbes play important roles in terrestrial ecosystem carbon and nitrogen cycling (Zhou et al., 2012). There are several major soil microbial taxa, including fungi, gram-positive bacteria (G^+), gram-negative bacteria (G^-), actinomycetes, arbuscular mycorrhizal fungi (AMF), and saprotrophic fungi (SF). Most soil microbial biomass is composed of fungi and bacteria (Baath and Anderson, 2003). Different soil microbial taxa have different functions (Hu et al., 2001). Human activity has resulted in an increase in the atmospheric carbon dioxide (CO_2) concentration and the global surface temperature has increased since the Industrial Revolution (IPCC, 2013). Elevated CO_2 and warming will most likely alter soil microbial communities (Kanerva et al., 2008; Rinnan et al., 2007).

Phospholipid fatty acid (PLFA) analysis is one of the most commonly used methods to determine soil microbial community composition. Based on the PLFA analysis, soil fungi, total bacteria, G^+, G^-, actinomycetes, AMF, SF and other soil taxa can be determined (Bardgett, et al., 1996; Frostegard, et al., 1993). The change of soil total PLFA can reflect changes of soil microbial biomass for soil biota from

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all taxa (Zhang et al., 2014). The changes in soil fungi, total bacteria, G^+, G^-, actinomycetes, AMF and SF can be used to reflect the changes in soil microbial biomass for a specific taxon, respectively (Zhang et al., 2014). The changes in soil fungi to bacteria ratio (F/B ratio) and the ratio of G^+ to G^- (G^+/G^- ratio) can be used to reflect the changes in soil microbial community structure (Fu and Shen, 2017b). Soil microbial taxa can have inconsistent responses to experimental warming with regard to ecosystem types and climatic conditions. Elevated temperature can either increase (Shen et al., 2014), decrease (Allison and Treseder, 2008; Ma et al., 2011) or have a negligible effect on soil fungi and bacteria (Liu et al., 2014; Schindlbacher et al., 2011). Elevated temperature can also have inconsistent effects on soil G^+, G^-, actinomycetes and AMF (Li et al., 2013; Rousk et al., 2013). Elevated temperature can increase (Zhang et al., 2004), reduce (Zhang et al., 2014) or have a negligible effect (Gutknecht et al., 2012; Zhang et al., 2013) on soil F/B ratio. Elevated temperature effects on the soil G^+/G^- ratio have been found to vary with landscape types, including increases in an alpine swamp meadow and forest ecosystem on the Tibetan Plateau, reductions in an alpine meadow and steppe on the Tibetan Plateau and a tundra ecosystem in the Changbai Mountain, and no obvious effect in a subarctic tundra (Rinnan et al., 2007; Wang et al., 2014; Zhang et al., 2014; Zhao et al., 2014).

There are inconsistent results on the relationship between warming duration and warming effects on soil microbial biomass, with either no relationship (Bai et al., 2013; Zhang et al., 2015) or a negative relationship (Blankinship et al., 2011). In addition, findings on the relationships between elevated CO_2 duration and elevated CO_2 effects on soil microbial biomass were also inconsistent, with either negative (Blankinship et al., 2011) or positive correlations (Ross et al., 2013). Several meta-analyses have indicated that soil microbial biomass in forest soils responded more strongly to warming than the microbial biomass in grassland soils (Bai et al., 2013; Lu et al., 2013), whereas Zhang et al. (2015) have found that microbial biomass in grassland soils responded more strongly to warming than that in forest soils. Therefore, it remains unclear whether treatment durations are related to treatment effects on soil microbes or whether soil microbial biomass in forest soils can respond more strongly to warming than microbial biomass in grassland soils.

To better understand these conflicting results, we compiled the data from 28 published warming and/or elevated CO_2 studies related to soil microbial community composition derived from PLFA analyses. All of the 28 studies were based on field experiments. No previous meta-analyses have examined the relationship between the effect of warming on soil microbes and elevation. The main objectives of this study were to: 1) examine the general effects of warming or elevated CO_2 on soil microbes; 2) test whether warming duration or warming magnitude can affect responses of soil microbes to warming; 3) check whether elevated CO_2 duration or elevated CO_2 magnitude can influence responses of soil microbes to elevated CO_2; and 4) investigate whether responses of soil microbes to warming can vary with ecosystem types or elevation.

2 Methods

2.1 Data compilation

The relevant articles published prior to 2017 were found using the Web of Science and the China National Knowledge Infrastructure. The compiled database included soil total PLFA, fungi, bacteria, G^+, G^-, actinomycetes, AMF, SF, the F/B ratio and the G^+/G^- ratio.

Our criteria for selecting relevant articles or subsets of data from articles included: 1) only field experimental studies were used; 2) for experiments with multiple factors, only the data from warming or elevated CO_2 treatments compared to a control were adopted; 3) at least one of the variables considered here was measured; 4) for experiments with multiple observations at different times from the same study site, only the latest results were adopted, considering that the observations included in the meta-analysis should be independent (Hedges et al., 1999); and (5) multiple soil depths, treatment magnitudes or ecosystem types were treated as independent variables.

We extracted the data (means, standard deviations or standard errors, and sample sizes) using the GetData software if the studies provided the data in figures (Fu and Shen, 2017c; Fu et al., 2015). Only one study analyzed the interactive effects of warming and elevated CO_2 on the soil microbial community (Andresen et al., 2014). Therefore, we did not analyze the interactive effects of warming and elevated CO_2.

All 28 studies were grouped according to ecosystem type, which included forest, grassland, shrubland and tundra ecosystems (Table 1). Experimental durations (i.e., from the beginning of warming or elevated CO_2 treatment to the soil sampling time) were calculated in years. The main warming methods included open top chamber and infrared radiator. There were all-day warming, daytime warming and nighttime warming treatments in different studies. Warming magnitudes ranged from 0.1°C to 4°C (including 23 levels) and mean annual temperatures ranged from –7.3°C to 16.3°C. The increased CO_2 concentrations ranged from 36 ppm to 360 ppm (including 8 levels). The elevated CO_2 methods employed in the experiments included regular FACE techniques, greenhouses and open-top chambers.

2.2 Statistical analyses

We used the METAWIN 2.1 software (Sinauer Associates Inc., Sunderland, MA, USA) to perform this meta-analysis. We treated the natural logarithm of the response ratio (R) as the effect size (Hedges et al., 1999).

Table 1 Basic information for the 28 studies included in the meta-analysis

Authors	Year	Journal	Title	*MAT* (℃)	*MAP* (mm)	Elevation (m)	Latitude	Longitude	Vegetation types
Wang et al.	2011	Chinese Journal of Applied and Environmental Biology	Microbial communities of alpine meadow soil in the Eastern Qinghai-Tibetan Plateau subjected to experimental warming and grazing	1.1	752.4	3561	32.45	102.37	Grassland
Schindlbacher et al.	2011	Soil Biology & Biochemistry	Experimental warming effects on the microbial community of a temperate mountain forest soil	5.7	1480	910	47.58	11.64	Forest
Andresen et al.	2014	PLoS ONE	Bacteria and fungi respond differently to multifactorial climate change in a temperate heathland, traced with 13C-glycine and FACE CO_2	8	600		55.88	11.97	Tundra
Rinnan et al.	2007	Global Change Biology	Fifteen years of climate change manipulations alter soil microbial communities in a subarctic heath ecosystem	–0.4	245.5	450	68.35	18.82	Tundra
Rousk et al.	2013	Global Change Biology	Investigating the long-term legacy of drought and warming on the soil microbial community across five European shrubland ecosystems				56.38	10.95	Shrubland
							46.88	19.72	Shrubland
							40.60	8.15	Shrubland
							52.40	5.92	Shrubland
							53.05	–3.47	Shrubland
Zhou et al.	2012	Nature Climate Change	Microbial mediation of carbon-cycle feedbacks to climate warming	16.3	914		34.98	–97.52	Grassland
Zhao et al.	2014	Plant and Soil	Effects of experimental warming and nitrogen fertilization on soil microbial communities and processes of two subalpine coniferous species in Eastern Tibetan Plateau, China	8.9	919.5	1820	31.68	103.88	Forest
Zhang et al.	2014	PLoS ONE	Responses of soil microbial communities to experimental warming in alpine grasslands on the Qinghai-Tibet Plateau	–3.8	290.9	4635	34.82	92.93	Grassland
Zhang et al.	2011	Soil Biology & Biochemistry	Soil microbial community changes and their linkages with ecosystem carbon exchange under asymmetrically diurnal warming	2.1	383	1324	42.03	116.28	Grassland
Shen et al.	2014	Pedosphere	Soil microbial responses to experimental warming and nitrogen addition in a temperate steppe of Northern China	2.1	383	1324	42.03	116.28	Grassland
Zhang et al.	2013	Oecologia	Soil microbial responses to warming and increased precipitation and their implications for ecosystem C cycling	2.1	383	1324	42.03	116.28	Grassland
Wang et al.	2014	Acta Ecologica Sinica	Effects of warming on soil microbial community structure in Changbai Mountain tundra	–7.3	1600	2028			Tundra
Gutknecht et al.	2012	Global Change Biology	Microbial communities and their responses to simulated global change fluctuate greatly over multiple years				37.67	–122.37	Grassland
Xu et al.	2015	Soil Biology & Biochemistry	Labile, recalcitrant, microbial carbon and nitrogen and the microbial community composition at two Abies faxoniana forest elevations under elevated temperatures	2.7	813	3000			Forest
Maestre et al.	2015	Frontiers in Microbiology	Warming reduces the cover and diversity of biocrust-forming mosses and lichens, and increases the physiological stress of soil microbial communities in a semi-arid *Pinus halepensis* plantation	14.6	315		38.54	–49.00	Forest
Zhang et al.	2015	European Journal of Soil Science	Depth-related responses of soil microbial communities to experimental warming in an alpine meadow on the Qinghai-Tibet Plateau	–3.8	383	4635	34.85	92.93	Grassland
De Long et al.	2016	Ecosystems	Contrasting responses of soil microbial and nematode communities to warming and plant functional group removal across a post-fire boreal forest successional gradient						Forest
Yoshitake et al.	2015	Ecological Research	Soil microbial response to experimental warming in cool temperate semi-natural grassland in Japan	7.1	2128		36.13	137.42	Grassland

Continued

Authors	Year	Journal	Title	*MAT* (℃)	*MAP* (mm)	Elevation (m)	Latitude	Longi-tude	Vegetation types
Kao-Kniffin et al.	2013	Microbial Ecology	A microbial link between elevated CO_2 and methane emissions that is plant species-specific						Grassland
Feng et al.	2010	Global Change Biology	Altered microbial community structure and organic matter composition under elevated CO_2 and N fertilization in the duke forest				35.97	–79.08	Forest
Kasurinen et al.	2005	Global Change Biology	Below-ground responses of silver birch trees exposed to elevated CO_2 and O_3 levels during three growing seasons		307.33	120	62.65	27.05	Forest
Kanerva et al.	2008	Soil Biology & Biochemistry	Changes in soil microbial community structure under elevated changes in soil microbial community structure under elevated tropospheric O_3 and CO_2				60.82	23.47	Grassland
Ebersberger et al.	2004	Plant and Soil	Effects of long term CO_2 enrichment on microbial community structure in calcareous grassland	8.75	900	520	47.55	7.57	Grassland
Janus et al.	2005	Microbial Ecology	Elevated atmospheric CO_2 alters soil microbial communities associated with trembling aspen (Populus tremuloides) roots				45.57	–84.67	Forest
Hagedorn et al.	2013	Soil Biology & Biochemistry	Nine years of CO_2 enrichment at the alpine treeline stimulates soil respiration but does not alter soil microbial communities				47.47	7.50	Forest
Manninen et al.	2010	Soil Biology & Biochemistry	Plant and soil microbial biomasses in *Agrostis capillaris* and *Lathyrus pratensis* monocultures exposed to elevated O_3 and CO_2 for three growing seasons				60.82	23.47	Grassland
Chung et al.	2007	Global Change Biology	Plant species richness, elevated CO_2, and atmospheric nitrogen deposition alter soil microbial community composition and function						Grassland
Guenet et al.	2012	Geoderma	The impact of long-term CO_2 enrichment and moisture levels on soil microbial community structure and enzyme activities						Grassland

MAT mean annual temperature; *MAP* mean annual precipitation.

$$\ln R = \ln\left(\frac{\overline{X}_t}{\overline{X}_c}\right) = \ln\left(\overline{X}_t\right) - \ln\left(\overline{X}_c\right) \qquad (1)$$

where $\overline{X}_t$ and $\overline{X}_c$ are the mean values of the treatments and control, respectively.

We used the inverse of the pooled variance ($1/v$) as the weighting factor (w) for each study,

$$v = \frac{S_t^2}{n_t \overline{X}_t^2} + \frac{S_c^2}{n_c \overline{X}_c^2} \qquad (2)$$

where n_t and n_c are the sample sizes of the treatments and control, respectively; and S_t^2 and S_c^2 are the standard deviations of the treatments and control, respectively.

Then, we obtained the mean effect size ($\ln \overline{R}$) derived from all observations,

$$\ln \overline{R} = \frac{\sum_{i=1}^{m} w_i \ln R_i}{\sum_{i=1}^{m} w_i} \qquad (3)$$

where $\ln R_i$ and w_i are $\ln R$ and w of the ith observation, respectively.

A fixed effects model was used to examine whether warming or elevated atmospheric CO_2 had a significant effect on each variable across all studies. Mean effect sizes were generated and 95% bias-corrected bootstrap confidence intervals (CI) were estimated. If the 95% bias- corrected bootstrap CI did not include zero, the response of the variable to warming or elevated atmospheric CO_2 was considered significant (Fu and Shen, 2017a). Both of the common rank correlation tests, Kendall's tau and Spearman Rank-Order correlation, for publication bias were performed, and all the rank correlations were non-significant. The mean effect size of each variable was transformed to the percentage change as $(e^{\mathrm{Log_e}\overline{R}} - 1) \times 100\%$ (Fu and Shen, 2016).

We used a fixed effects model with a grouping variable to compare responses among vegetation types, warming times and warming methods. For a specific group, the mean effect size was calculated using only the data of that group. If the 95% bias-corrected bootstrap CI did not bracket zero for a specific group, the response of that specific variable to warming or elevated atmospheric CO_2 was considered significant.

We used a random effects model with a continuous variable (> 15 observations) to test the correlations of the effect sizes of warming or elevated CO_2 with experimental duration or magnitude. If the regression coefficient (i.e., slope) was significant, then this independent variable could explain significantly the variation among the effect sizes of the treatments.

3 Results

Different soil microbe taxa may have different sensitivities to elevated temperature and CO_2. Warming significantly increased soil actinomycetes by 11.1% and saprotrophic fungi by 13.8%, whereas warming did not significantly change soil total PLFA, fungi, bacteria, G^+, G^-, AMF, F/B ratio or G^+/G^- ratio (Fig. 1). Elevated CO_2 only significantly decreased soil G^+ by 6.6% (Fig. 2).

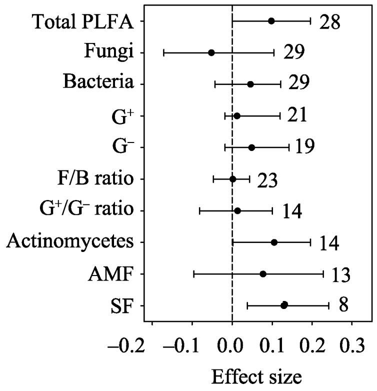

Fig. 1 Warming effects on soil microbial biomass

Note: G^+: gram-positive bacteria, G^-: gram-negative bacteria, F/B ratio: the ratio of soil fungi to bacteria, G^+/G^- ratio: the ratio of G^+ to G^-, AMF: arbuscular mycorrhizal fungi, SF: saprotrophic fungi. The error bars indicate effect sizes and 95% bootstrap confidence intervals. The sample size for each variable is shown next to the bar.

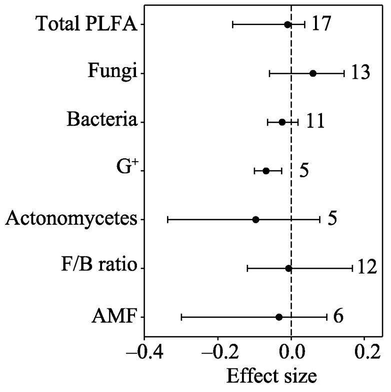

Fig. 2 Elevated CO_2 effects on soil microbial biomass

Note: Related descriptions as shown in Fig. 1.

Warming duration and magnitude were not correlated with warming effects on soil total PLFA, fungi, bacteria, G^+, G^- or F/B ratio (Table 2). Increased CO_2 duration ($Q_M = 1.20$, $p = 0.274$, $n = 17$) and magnitude ($Q_M = 0.74$, $p = 0.389$, $n = 17$) were not correlated with elevated CO_2 effects on soil total PLFA.

Mean annual air temperature and mean annual precipitation were negatively correlated with warming effect on soil G^- and soil total PLFA, respectively (Table 2). Elevation was positively correlated with warming effect on soil total PLFA, bacteria, G^+ and G^- (Table 2).

Table 2 Relationships between warming effects on soil microbial biomass and relevant variables

Variables	Slope	*p*	Q_M	Q_E	Q_T	*n*
Warming duration						
Total PLFA	–0.01	0.633	0.23	29.21	29.44	28
Fungi	0.01	0.568	0.33	24.81	25.13	28
Bacteria	0.01	0.394	0.73	29.67	30.39	29
G^+	0.03	0.417	0.66	20.04	20.69	20
G^-	0.01	0.849	0.04	18.21	18.25	18
F/B ratio	–0.01	0.471	0.52	18.79	19.31	22
Warming magnitude						
Total PLFA	–0.02	0.819	0.05	27.44	27.49	24
Fungi	0.05	0.517	0.42	22.01	22.43	26
Bacteria	0.01	0.887	0.02	27.36	27.38	26
G^+	0.01	0.904	0.01	22.38	22.39	21
G^-	0.03	0.580	0.31	19.21	19.52	19
F/B ratio	–0.01	0.815	0.05	16.16	16.21	19
Mean annual air temperature						
Total PLFA	–0.01	0.451	0.57	18.44	19.00	20
Fungi	–0.01	0.366	0.82	14.80	15.62	20
Bacteria	–0.01	0.269	1.22	17.68	18.90	21
G^+	–0.01	0.166	1.92	22.23	24.16	20
G^-	**–0.02**	**0.014**	6.09	19.75	25.84	18
F/B ratio	–0.0021	0.633	0.23	16.55	16.78	19
Mean annual precipitation						
Total PLFA	**–0.0002**	**0.019**	5.54	24.16	29.70	19
Fungi	–0.0002	0.077	5.15	19.67	24.82	19
Bacteria	–0.0001	0.244	1.36	19.22	20.58	20
G^+	–0.0002	0.109	2.57	19.34	21.91	20
G^-	–0.0002	0.208	1.58	18.43	20.01	18
F/B ratio	0.0000	0.597	0.28	14.33	14.61	18
Elevation						
Total PLFA	**0.0001**	**0.031**	4.63	16.81	21.45	17
Fungi	0.00	0.366	0.82	15.94	16.76	17
Bacteria	**0.0001**	**0.018**	5.63	15.45	21.09	17
G^+	**0.0001**	**0.010**	6.63	19.30	25.93	17
G^-	**0.0001**	**0.034**	4.51	19.65	24.16	16

Note: Slope: regression coefficients; *P*: the statistical probability; *n*: the number of the observations used in the meta-analysis; Q_T: Total heterogeneity of the effect sizes of treatments among all studies; Q_M: the variation that can be explained by the continuous randomized-effects model; Q_E: The residual error; A significant slope ($P < 0.05$) indicates that an independent variable can explain the variation among effect sizes. G^+: gram-positive bacteria, G^-: gram-negative bacteria, F/B ratio: the ratio of soil fungi to bacteria.

Warming increased soil total PLFA by 29.5% and actinomycetes by 19.9% in grasslands, whereas soil total PLFA and actinomycetes in forests did not change under warming (Fig. 3). The OTC method increased G^- by 19.3%, while the

IR method did not affect G^- (Fig. 4). The IR method decreased the F/B ratio by 6.8%, while the OTC method did not affect the F/B ratio (Fig. 4). Daytime warming increased G^- by 10.7%, while all-day warming did not affect G^- (Fig. 5).

4 Discussion

Elevated CO_2 may affect the soil microbial community considering the decrease in soil gram-positive bacteria (G^+) found in our study, which was likely attributed to the following mechanisms. First, elevated CO_2 generally increases ratios of soil carbon to nitrogen and litter carbon to nitrogen (de Graaff et al., 2006; Luo et al., 2006; Yang et al., 2011), while soil gram-positive bacteria decreases with increasing ratios of soil carbon to nitrogen and litter carbon to nitrogen (Huang et al., 2014; Lange et al., 2014). Second, elevated CO_2 generally decreases soil nitrogen availability (de Graaff et al., 2006) and soil bacterial growth may be suppressed in nitrogen-limited systems (Hu et al., 2001).

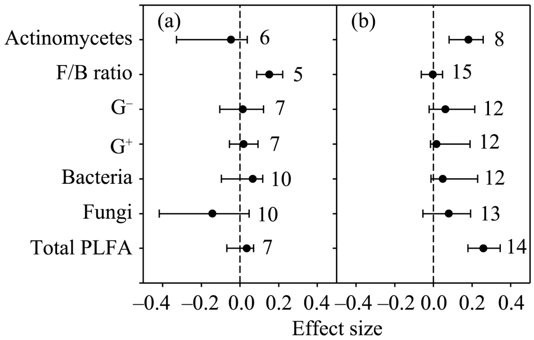

Fig. 3 Warming effects on soil microbial biomass for (a) forest and (b) grassland

Note: Related descriptions as shown in Fig. 1.

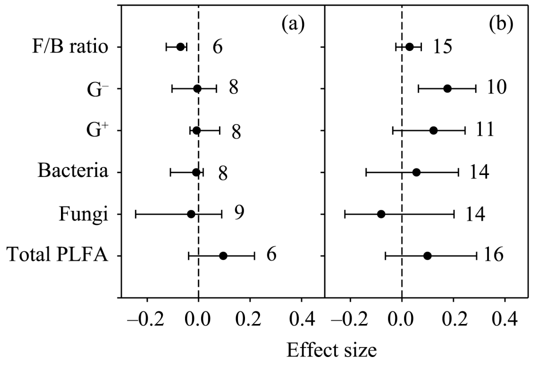

Fig. 4 Effects of (a) infrared radiator and (b) open top chamber on soil microbial biomass

Note: Related descriptions as shown in Fig. 1.

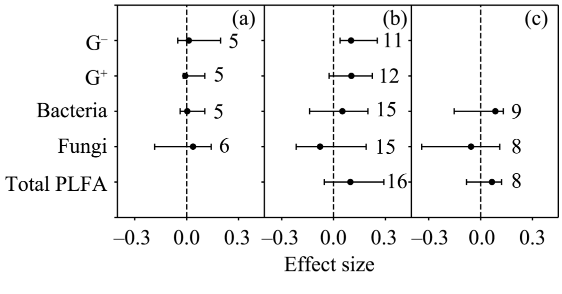

Fig. 5 Effects of (a) all-day, (b) daytime and (c) nighttime warming on soil microbial biomass

Note: Related descriptions as shown in Fig. 1.

Our findings implied that soil microbes might have stronger responses to warming in colder and drier areas, and the responses of soil microbes to warming increased with increasing elevation. These findings were in line with some previous studies (Chen et al., 2015; Zhang et al., 2015). Therefore, the temperature sensitivity of soil microbes may increase with increasing elevation, and decreasing temperature and water availability. Our findings were also in agreement with a previous meta-analysis which showed that daytime warming had a stronger positive effect on soil microbial abundance than all-day warming (Chen et al., 2015).

Our findings supported a previous study which showed that warming increased soil microbial biomass carbon and nitrogen in alpine grasslands but not in forests on the Tibetan Plateau (Zhang et al., 2015). This phenomenon may be attributed to the following mechanisms. First, the positive effects of warming on soil microbial total PLFA decreased with increasing mean annual precipitation (Table 2) and the grasslands had a lower mean annual precipitation than the forests in our meta-analysis (most <800 mm vs. >800 mm). Second, the positive effects of warming on soil microbial total PLFA increased with increasing elevation (Table 2) and the grasslands had a higher average elevation than the forests in our meta-analysis (3994 m vs. 2535 m). In addition, warming increased the F/B ratio by 16.4% in forests but not in grasslands (Fig.3). Therefore, forest and grassland soil microbes appear to have different sensitivities to elevated temperature.

Our findings also supported recent a meta-analysis which indicated that warming effects on soil microbial biomass varied between the OTC and IR methods (Chen, et al., 2015). The finding that warming effects on the F/B ratio varied between the OTC and IR methods can be attributed to the following mechanisms. First, the F/B ratio decreased with increasing soil nitrogen availability (Zhang et al., 2005), and the increased magnitude of soil nitrogen availability caused by the IR method was greater than that caused by the OTC method (Bai et al., 2013). Second, the IR and OTC methods resulted in different magnitudes of increases in plant belowground biomass and decreases in soil moisture (Lu et al., 2013), which in turn caused different changes in the soil F/B ratios between the IR and OTC methods (Gutknecht et al., 2012).

5 Conclusions

Warming increased soil actinomycetes and saprotrophic fungi, while elevated CO_2 decreased soil gram-positive bacteria (G^+). Mean annual temperature and mean annual precipitation were negatively correlated with the warming effect on gram-negative bacteria (G^-) and total phospholipid fatty acid (PLFA), respectively. Elevation was positively correlated with the warming effect on total PLFA, bacteria, G^+ and G^-. Grassland exhibited a positive response of total PLFA and actinomycetes to warming, while forest exhibited a positive response in the ratio of soil fungi to bacteria (F/B ratio) to warming. The open top chamber method increased G^-, while the infrared radiator method decreased the F/B ratio. Daytime warming, rather than all-day warming, increased G^-. Therefore, the sensitivities of soil microbial communities to warming varied with ecosystem types, warming methods and warming times. In colder and drier areas, soil microbial biomass appeared to have a higher temperature sensitivity. The temperature sensitivity of soil microbial biomass also increased with increasing elevation.

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整合分析增温和增 CO_2 对土壤微生物的影响

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摘 要：土壤微生物在陆地生态系统碳氮循环中起着重要作用。气候变暖和 CO_2 浓度增加是气候变化的两个重要方面。本研究整合分析了实验增温和 CO_2 浓度增加对土壤微生物量和群落结构的影响。生态系统类型主要包括森林生态系统和草地生态系统。增温方法包括开顶式增温小室和热红外增温。增温时间有全天增温、白天增温和晚上增温。实验增温增加了土壤放线菌和腐生真菌，而 CO_2 浓度增加减少了土壤革兰氏阳性细菌。实验增温对土壤革兰氏阴性细菌和总的磷脂脂肪酸量的影响随着年均温和年降水量的增加而减少。实验增温对土壤总的磷脂脂肪酸量、细菌含量、革兰氏阳性和阴性细菌的量的影响随着海拔的升高而增加。实验增温增加了草地生态系统的土壤总的磷脂脂肪酸量和放线菌含量，并增加了森林生态系统的土壤真菌和细菌的比值。开顶式增温小室增加了土壤革兰氏阴性细菌，而红外增温减少了土壤真菌和细菌的比值。白天增温增加了土壤革兰氏阴性细菌，而全天增温没有改变土壤革兰氏阴性细菌。因此，实验增温对土壤微生物的影响与生态系统类型、实验增温方法、增温时间、海拔和当地的气候条件有关。

关键词：生态系统类型；CO_2 浓度增加；增温；响应比；增温方法