RESEARCH ARTICLE

Effects of soil organism interactions and temperature on carbon use efficiency in three different forest soils

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HIGHLIGHTS

- Three typical forest soils and three soil organisms were collected.
- Interactions among soils and organisms were examined by incubation experiment.
- Biotic factors mainly affect microbial CUE by changing biomass.
- Temperature regulates microbial CUE by affecting microbial respiration.

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GRAPHICAL ABSTRACT

ABSTRACT

Microbial carbon use efficiency (CUE) affects the soil C cycle to a great extent, but how soil organisms and the abiotic environment combine to influence CUE at a regional scale remains poorly understood. In the current study, microcosms were used to investigate how microbial respiration, biomass, and CUE responded to biotic and abiotic factors in natural tropical, subtropical, and temperate forests. Soil samples from the forests were collected, sterilized, and populated with one or a combination of three types of soil organisms (the fungus *Botrytis cinerea*, the bacterium *Escherichia coli*, and the nematode *Caenorhabditis elegans*). The microcosms were then kept at the mean soil temperatures of the corresponding forests. Microbial respiration, biomass, and CUE were measured over one-month incubation period. The results showed that microbial biomass and CUE were significantly higher, but microbial respiration lower in the subtropical and temperate forest soils than in tropical forest soil. Biotic factors mainly affected CUE by their effect on microbial biomass, while temperature affected CUE by altering respiration. Our results indicate that temperature regulates the interactive effects of soil organisms on microbial biomass, respiration, and CUE, which would provide a basis for understanding the soil C cycle in forest ecosystems.

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1 Introduction

Soil contains the largest carbon (C) pool in terrestrial ecosystems (Lal, 2004). Carbon emissions from the soil

make a significant contribution to the atmospheric CO₂ concentration and therefore to global climate change (Melillo et al., 2017; Fang et al., 2018). The terrestrial C cycle is a vital biogeochemical cycle in which forest soils are especially important (Tang et al., 2018; Piao et al., 2020; Sanders-DeMott et al., 2020). Processes belowground are sensitive to environmental changes (Reinsch et al., 2017), and as such, soil C emissions are affected by the biotic and abiotic factors that contribute to these environmental changes (Wu et al.,

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2014; Eberwein et al., 2015; Estruch et al., 2020). The variance observed in soil respiration models, which are a function of soil C emissions, is mainly explained by abiotic factors such as temperature, moisture, and C content of the soil (Kane et al., 2003; Rodeghiero and Cescatti, 2010; Li et al., 2020; Zhou et al., 2020). The influence of abiotic factors on soil C emissions has been extensively documented (Mancinelli et al., 2010; Butterly et al., 2019), however, the effect of biotic factors in different forest ecosystems has not been as well understood (Geisen et al., 2019).

Soil organisms regulate soil C storage and CO₂ efflux via their decomposition activities (Moore et al., 2015; Zhu et al., 2016; Luo et al., 2020). CO₂ efflux from the soil is altered by physiological and behavioral changes made by individual microbial populations (Hiscox et al., 2010; Crowther et al., 2011) and also by compositional changes in the microbial community (Crowther et al., 2015; Wu et al., 2019). Fungi, bacteria, and nematodes make substantial contributions to biogeochemical cycles as critical components of soil food webs (Bardgett and van der Putten, 2014; Crowther et al., 2019). Previous studies have concluded that CO₂ efflux from the soil may be increased by the interactions between wood-decaying fungi (Maynard et al., 2017) and by nematodes feeding on microorganisms (Fu et al., 2005). Although the dynamics of CO₂ efflux from the soil have been attributed to changes in soil organism diversity and/or community composition, little is known on the effects of soil organisms and their interactions on soil CO₂ efflux.

Carbon use efficiency (CUE) has been used as a tool to gain an understanding of C storage and emission in ecosystems (Milcu et al., 2012; Wu et al., 2019); it is defined as the ratio of growth to total C uptake by organisms (Stefano et al., 2012; Tucker et al., 2012). Frequently used as a quantitative indicator reflecting C assimilation capacity and sequestration potential of soils, CUE is also important in the prediction of C feedback between soil organisms and the abiotic environment (Delucia et al., 2007; Davidson et al., 2014; McGee et al., 2019). A high CUE implies that soil organisms release less C into the atmosphere, which is conducive for the stability and long-term retention of C in the soil (Stefano et al., 2012; Dillaway and Kruger, 2014).

The effects of soil organisms, as the only factor, on CUE have been well documented (Sinsabaugh et al., 2013; Fang et al., 2020). However, the effects of their interactions with abiotic factors such as temperature, an important factor in soil respiration, on microbial CUE are yet to be established (Davidson et al., 2014; Maynard et al., 2017). In the current study, changes in microbial respiration, biomass, and CUE as a result of the interactions among the fungal, bacterial, and nematode populations in three forest soils (tropical, subtropical, and temperate) in Yunnan Province, China, were examined. The region was divided into the various ecosystem types according to geologic uplift, which is appropriate for the detection of interactions among soil organisms at a regional scale. We hypothesized that (1) interactions among soil organisms would affect microbial CUE due to changes in

microbial biomass; and (2) microbial respiration would be different in the three forest soils due to their different mean annual temperatures, which would affect microbial CUE. To test these hypotheses, we conducted a laboratory incubation experiment with different combinations of forest soil types and soil organism populations.

2 Materials and methods

2.1 Soil collection and pretreatment

In July 2018, we collected surface soil (0–10 cm) in three forests in Yunnan Province, China. The forests were located in Xishuangbanna (E101°25', N21°41'), Ailao Mountain (E100°54'–101°29', N24°00'–24°44'), and Shangrila (E100°02', N27°13'). Xishuangbanna has a tropical climate and a mean annual temperature of 21.5°C. Ailao Mountain has a subtropical climate and a mean annual temperature of 11.6°C and Shangrila has a temperate climate and a mean annual temperature of 5.9°C. At each site, ten 10 × 10 m² plots were established, in which nine 10 × 10 × 10 cm³ soil cores were collected. The soil samples from each location were mixed and analyzed for background organic C content, total nitrogen content, and pH which were found to be: 35.88 g kg⁻¹, 2.85 g kg⁻¹, and 6.30, respectively, for Xishuangbanna; 123.35 g kg⁻¹, 6.97 g kg⁻¹ and 3.97, respectively, for Ailao Mountain; and 93.54 g kg⁻¹, 5.23 g kg⁻¹ and 4.70, respectively, for Shangrila.

After plant debris and gravel were removed, each soil was mixed, passed through a 2-mm sieve, and stored at 4°C. A quantity of fresh soil (45.03 to 62.12 g, equivalent to 30 g of dry soil) was transferred into a 500-mL glass bottle with 24 bottles for each forest soil. After soil moisture was adjusted to 60% of maximum water holding capacity, the bottles were placed in a high-pressure steam sterilizer (121°C) for 60 min to eliminate the original organisms in the soil. Respiration in the bottles was then measured to determine the presence of microorganisms that survived steam sterilization and was found to be very low, indicating that most but not all of the organisms had been removed. Respiration and biomass values for these “pretreatment” bottles were subtracted from all of the respiration and biomass values obtained following treatment in the study.

Each bottle was covered with a cap with a 2-mm-diameter hole in the center. A 2-mm-diameter PVC pipe was inserted a short distance into the hole, and the connection of the pipe to the hole was sealed with an adhesive. The PVC pipe was connected to a three-way valve outside the bottle. When the three-way valve was opened, gas could be exchanged in the bottle; when the valve was closed, a closed environment would be maintained inside the bottle.

2.2 Experimental design and incubation conditions

Three widely distributed soil organisms were selected for use in the experiment: the fungus *Botrytis cinerea*, the bacterium

Escherichia coli, and the bacterivore nematode *Caenorhabditis elegans*. *B. cinerea* was obtained from the Soil Ecology Laboratory, Nanjing Agricultural University. *E. coli* and *C. elegans* were obtained from the State Key Laboratory for Conservation and Utilization of Bio-Resources in Yunnan. These organisms were added to the forest soils in the bottles in eight different combinations to create microcosms in a full factorial design: no organism, fungus alone, bacterium alone, nematode alone, fungus + bacterium, fungus + nematode, bacterium + nematode, and fungus + bacterium + nematode. The combination of all three organisms represented different communities in the incubation experiment, which reflects the interactions among organisms in the three forest soils. Each microcosm was replicated thrice, such that there were 24 bottles for each forest soil and 72 bottles in total. The *B. cinerea* and *E. coli* were added to the soil as previously described (Crowther et al., 2011; Maynard et al., 2017). In brief, *B. cinerea* was grown on potato dextrose agar medium, and *E. coli* was grown on lysogeny broth medium. *B. cinerea* and *E. coli* were added to the soil in the microcosms as 1.1-cm-diameter disks that had been removed from the solid media. Two disks of the indicated microorganism were added per microcosm for treatments with *B. cinerea* only and *E. coli* only, and one disk of each kind of indicated microorganism was added per microcosm for treatments that included two or three species. For treatments with *C. elegans*, 30 nematodes in a small volume of water (about 0.2 mL) were added per microcosm. The number of nematodes added was based on a previous study in the region (Li et al., 2009) and other incubation studies (Fu et al., 2005; Crowther et al., 2011).

After the organisms were added to the soils in the microcosms, the microcosms were covered with caps and the three-way valves were closed to maintain a closed environment. The microcosms were then placed in constant temperature incubators whose temperatures corresponded to the mean annual temperatures of the corresponding soils (21.5°C for tropical, 11.6°C for subtropical, and 5.9°C for temperate soils). Incubation lasted for a month as was the case in a similar trial (Maynard et al., 2017). After the commencement of incubation, the CO₂ content of the atmosphere in each bottle was measured every two days with a gas chromatograph (GC9310, Shanghai, China). Gas was sampled with a 5-mL syringe that was connected to the three-way valve; the valve was opened to collect the sample and was then closed. The closed three-way valve was then connected to a new 5-mL syringe, the valve opened, and the new syringe was used to inject 5-mL of free-air CO₂ into the bottle to maintain the pressure balance. Also, the three-way valves were opened for an hour (this was done immediately after gas sampling) to allow gas exchange between the bottles and the exterior environment to prevent the CO₂ content in the bottles from increasing to levels that would influence the activities of organisms. After one hour of gas exchange, another 5-mL sample of gas was collected from each bottle and assessed for CO₂.

After incubation, the soil samples were assessed for

biomass C content measured with a TOC analyzer (Elementar, Langensfeld, Germany) and the chloroform fumigation extraction method (Zhou et al., 2009).

2.3 Microbial respiration and CUE determination

The respiratory rates (μg CO₂ g⁻¹ soil d⁻¹) were determined as follows (Wu et al., 2014):

$$R_t = \frac{M}{V_0} \cdot \frac{C_{t+2}V_{t+2} - C_tV_t}{2} \cdot \frac{1}{m} \cdot \frac{P}{P_0} \cdot \frac{T_0}{T_a}$$

where $M = 44 \text{ g mol}^{-1}$; $V_0 = 22.4 \text{ L mol}^{-1}$; $C = \text{ppm}$ (1×10^{-6}); $V = \text{gas volume (mL)}$ in the bottles; $m = 30 \text{ g}$; $P = 80.735 \text{ kPa}$ (atmospheric pressure in Kunming City, Yunnan Province, China); $P_0 = 101.325 \text{ kPa}$ (normal atmospheric pressure); $T_0 = 273 \text{ K}$; and $T_a = \text{temperature of incubation (273 + } T \text{) K}$. Because the respiration from soil fauna is usually small, all CO₂ emissions in this study were attributed to soil microorganisms.

Respiration (μg C g⁻¹ soil) was determined as follows (Wu et al., 2014):

$$R = \sum_{i=1}^n (R_i \cdot t) \cdot \frac{12}{44}$$

CUE was determined as follows: (Maynard et al., 2017; Fang et al., 2020):

$$\text{CUE} = \frac{B}{B + R}$$

where $B = \text{content of biomass C (}\mu\text{g C g}^{-1}\text{soil)}$; and $R = \text{content of respiration C (}\mu\text{g C g}^{-1}\text{soil)}$. The value of CUE ranges from 0 to 1; with a higher value indicating a higher CUE.

Predicted respiration, biomass, and CUE in incubated soil organism communities were determined as follows (Maynard et al., 2017):

$$R_p = R_b + R_f + R_n$$

$$B_p = B_b + B_f + B_n$$

$$\text{CUE}_p = \frac{B_p}{B_p + R_p}$$

where R_b/B_b , R_f/B_f , and $R_n/B_n = \text{respiration/biomass of bacteria, fungi, and nematodes, when incubated individually}$.

Proportional change in respiration, biomass, and CUE were determined as follows:

$$R^* = \frac{R - R_p}{R_p}$$

$$B^* = \frac{B - B_p}{B_p}$$

$$\text{CUE}^* = \frac{\text{CUE} - \text{CUE}_p}{\text{CUE}_p}$$

Proportional changes >0 indicate that the interactions among

soil organisms increased soil respiration, biomass, or CUE. Proportional changes < 0 indicate that interactions among soil organisms decreased soil respiration, biomass, or CUE. Proportional changes $= 0$ indicate that interactions among soil organisms did not affect soil respiration, biomass, or CUE (Maynard et al., 2017).

2.4 Statistical analysis

One-way analyses of variance (ANOVA) were used to assess the effects of different combinations of organisms on respiration, biomass, and CUE in each forest soil (tropical, subtropical, and temperate). In the figures, mean values with different letters are significantly different at $P < 0.05$. Three-way ANOVAs were used to assess the effects of *B. cinerea*, *E. coli*, *C. elegans*, and their interactions on respiration, biomass, and CUE in the forest soils. Regression analysis was used to analyze the relationships between population richness (number of species added) and respiration, biomass, and CUE. Pearson correlation analysis was used to determine relationships among respiration, biomass, and CUE vs. temperature against soil physicochemical properties. SPSS 16.0 (SPSS, Inc., Chicago, USA) was used for statistical analysis. The random forest modeling (package randomForest in R) was used to quantitatively assess the effects of abiotic (temperature and respiration) and biotic (microbial biomass) variables on CUE.

3 Results

3.1 Microbial respiration, biomass, and CUE in different forest soils

Microbial respiration in the tropical forest soils did not show any significant differences among treatments (Fig. 1A). In the subtropical forest soil, microbial respiration in the fungus treatment was higher than in the bacterium, nematode, and bacterium + nematode treatments (Fig. 1B). In the temperate forest soil, microbial respiration in fungus + bacterium treatment was higher than nematode, bacterium + nematode, and fungus + nematode treatments (Fig. 1C). There also appeared to be no respiration occurring in temperate forest soil incubated with the nematodes. Among the treatments, microbial biomass was lowest with the fungus + bacterium + nematode treatment in all three forest soils (Fig. 1D–F). In subtropical and temperate forest soils, microbial CUE was significantly lower in the fungus + bacterium + nematode treatment than in the other treatments (Fig. 1H, I).

The mean microbial respiration for all treatments within a soil was significantly higher in the tropical forest soil than in the subtropical and temperate forest soils (Fig. 2A). The mean microbial biomass and CUE in the tropical soil were significantly lower than in the subtropical and temperate soils (Fig. 2B, C). The random forest modeling showed that 42.97% of the variation observed in CUE was a result of microbial respiration and temperature while 36.95% was

attributed to microbial biomass (Fig. 2D). Microbial biomass was not correlated with any of the abiotic factors (Table 1). Microbial respiration was correlated with temperature and C/N ($P = 0.007$ and 0.045 , respectively) while CUE was correlated only with temperature ($P < 0.001$). (Table 1).

3.2 Microbial respiration, biomass, and CUE in different population combinations

In soil treatments with one and two species, microbial respiration was significantly higher in the tropical forest soil than in the temperate forest soil (Fig. 3A, B). Microbial respiration did not significantly differ in the 3-species treatment (Fig. 3C). Microbial biomass was significantly higher with the 1-species treatment in subtropical soils compared to tropical and temperate soils. (Fig. 3D). In the 2-species treatment, microbial biomass was lowest in the tropical forest soil than in the other two soils (Fig. 3E). The CUE was significantly lower in the tropical forest soil containing one and two species than in the other two soils (Fig. 3G, H). No significant differences were observed in the 3-species treatments among the soils across all variables. There were no significant increases or decreases in microbial respiration with increases in the number of species in all soil types. Microbial biomass declined significantly with an increase in species number in the tropical and subtropical forest soils (Fig. 4D, E) but not in the temperate forest soil (Fig. 4F). CUE declined as species number increased in the subtropical and temperate forest soils (Fig. 4H, I).

The three-way ANOVA revealed that the fungus + bacterium and bacterium + nematode treatments significantly affected microbial biomass, while fungus + nematode, bacterium + nematode, and fungus + bacterium + nematode treatments significantly affected CUE in the three forest soils (Table 2). The interactive effects of the bacterium + nematode treatment tended to decrease microbial biomass, while the fungus + bacterium treatment increased microbial biomass and respiration (Fig. 5). All four of the interactive effects increased the CUE in the tropical forest soil and decreased or negligibly affected the CUE in the subtropical and temperate forest soils (Fig. 5).

4 Discussion

4.1 Biotic factors affected CUE by changing biomass

Previous studies have examined the effects of microorganisms on soil respiration, but few have delineated the relationships among respiration, biomass, and CUE (Graaff et al., 2015; Fang et al., 2020). The current study revealed that with an increase in the population diversity of soil organisms, microbial biomass and CUE declined, which suggests that the increase in population diversity may reduce CUE by reducing biomass. The changes in microbial biomass can be attributed to the interactions among soil organisms as evidenced by the effects of the bacterium + nematode treatment which

Fig. 1 Microbial respiration (A–C), biomass (D–F), and carbon use efficiency (CUE) (G–I) for all organism-addition treatments in the tropical, subtropical, and temperate forest soils. The seven organism-addition treatments are indicated on the x-axis. Values are means $\pm$ SE ($n = 3$). In each panel, means with different letters are significantly different at $P < 0.05$.

Fig. 2 Microbial respiration (A), biomass (B), carbon use efficiency (C), and importance of abiotic and biotic factors (D) averaged across all organism-addition treatments in the tropical, subtropical, and temperate forest soils. Values are means $\pm$ SE ($n = 21$). In each panel, means with different letters are significantly different at $P < 0.05$.

decreased microbial biomass in all three forest soils. This is in agreement with other work that has shown a negative correlation between microbial biomass and species richness (Nielsen et al., 2011; Li et al., 2020). On the other hand, it has been reported that soil biota composition rather than species richness regulated soil C sequestration and emission, indicating that community composition and population diversity may have different effects on the soil carbon cycle (De Deyn, 2013). This suggests that the effects of population diversity on microbial respiration could be a consequence of functional compositional changes in the soil community.

We also found that biotic factors rarely affected microbial respiration, i.e., microbial respiration was influenced by biotic factors in only three of the twenty-one treatment combinations; this may indicate that the biotic factors affected CUE by changing biomass. We speculate that the effects of species diversity on microbial respiration were marginal in our incubation experiment since microbial respiration in the three forest soils did not follow any particular trend with changes in species diversity. Maynard et al., (2017) reported that biotic factors contributed more to the variation in CUE than abiotic factors and that interactions among microorgan-

Table 1 Correlation coefficients (r values) and P values ($n = 3$) for relationships among soil respiration, biomass, and CUE vs. soil physicochemical properties.

Factors	Temperature		SOC		DOC		TN		TP		AP		C/N	
	r	P	r	P	r	P	r	P	r	P	r	P	r	P
Respiration	1.000	0.007	-0.758	0.452	-0.988	0.098	-0.695	0.511	-0.993	0.077	0.843	0.361	0.997	0.045
Biomass	-0.843	0.361	0.988	0.098	0.921	0.255	0.970	0.157	0.907	0.277	-0.432	0.715	0.885	0.309
CUE	-1.000	<0.001	0.751	0.459	0.986	0.106	0.687	0.518	0.991	0.085	-0.849	0.354	0.997	0.053

Notes: SOC = soil organic carbon; DOC = dissolved organic carbon; TN = total nitrogen; TP = total phosphorus; AP = available phosphorus; C/N = SOC/TN.

Fig. 3 Microbial respiration (A–C), biomass (D–F), and carbon use efficiency (G–I) as affected by the number of species added to the tropical, subtropical, and temperate forest soils. Values are means $\pm$ SE. $n = 3$ when one or three species were added and $n = 9$ when two species were added. In each panel, means with different letters are significantly different at $P < 0.05$.

isms reduced CUE, which is similar to what was observed in the current study. This could have been caused by differences in functional composition where the *C. elegans*, a bacterivore, altered the microbial biomass due to its feeding behavior and consequently affected CUE (Fu et al., 2005). The current work points to biotic influence on CUE mediated by changes in biomass rather than respiration in the forest soils studied.

4.2 Abiotic factors affected CUE by changing respiration

Microbial respiration and CUE but not microbial biomass were significantly correlated to temperature in the three forest soils

as shown in the correlation analysis. Microbial CUE declined as temperature increased in the current study probably because an increase in temperature led to an increase in respiration and a subsequent decrease in CUE (Stefano et al., 2012; Tucker et al., 2012). In a study involving multiple sites in the Italian Alps, Rodeghiero and Cescatti (2010) fitted soil respiration, temperature, and other environmental variables into a simple logistic model and found that mean soil annual temperature explained most of the intersite variation in soil respiration, this is consistent with our finding that temperature and microbial respiration accounted for over 40% of the variation seen in CUE.

Fig. 4 Relationships between the number of species added and microbial respiration (A–C), biomass (D–F), and carbon use efficiency (G–I) in the tropical, subtropical, and temperate forest soils. $n = 3$ when one or three species were added and $n = 9$ when two species were added. Linear regression statistics are indicated.

As indicated in a recent review (Wu et al., 2019) as well as earlier studies (Chambers et al., 2004; Delucia et al., 2007), plant and microbial CUEs are lower in tropical ecosystems compared to temperate ones. These CUE variations among different ecosystems can be at least partially explained by temperature (Geyer et al., 2016). In other work, for example, temperature was considered the main factor affecting respiration and decomposition rates in soil (Giardina and Ryan, 2000; Davidson and Janssens, 2006; Jing et al., 2015), which is in line with our findings. We would also like to point out that C/N affected microbial respiration in this study. Since

soil nutrient traits can affect CUE due to different substrates for microorganisms in different soils. Additional studies with other forest types and for longer incubation durations are necessary to verify this inference.

5 Conclusions

Our assessment of the effects of abiotic and biotic factors on soil respiration, microbial biomass, and microbial CUE indicates that these factors affected CUE differently at a regional scale. Temperature mainly affected CUE by changing

Fig. 5 The proportional changes in microbial respiration (pink symbols), biomass (green symbols), and carbon use efficiency (orange symbols) in the tropical (A), subtropical (B), and temperate (C) forest soils. $n = 3$ when one or three species were added and $n = 9$ when two species were added.

Table 2 The effects of fungus (*Botrytis cinerea*), bacterium (*Escherichia coli*), nematode (*Caenorhabditis elegans*) and their interactions on microbial respiration, biomass, and carbon use efficiency (CUE) as indicated by a three-way analysis of variances ($n = 3$).

Factors	Forest soil	Fungus		Bacterium		Nematode		Fungus × Bacterium		Fungus × Nematode		Bacterium × Nematode		Fungus × Bacterium × Nematode	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Respiration	Tropical	0.89	0.359	4.11	0.060	0.15	0.703	1.80	0.199	0.01	0.910	1.77	0.202	0.23	0.640
	Subtropical	24.89	<0.001	0.35	0.561	0.00	0.961	1.96	0.180	1.15	0.300	0.43	0.520	1.98	0.178
	Temperate	10.85	0.005	11.30	0.004	3.11	0.097	0.34	0.568	0.39	0.543	1.13	0.303	1.75	0.205
Biomass	Tropical	0.62	0.442	23.46	<0.001	16.08	0.001	8.23	0.011	9.24	0.008	36.59	<0.001	3.37	0.085
	Subtropical	0.45	0.511	0.32	0.579	0.75	0.398	19.16	<0.001	6.10	0.025	10.33	0.005	0.38	0.545
	Temperate	20.02	<0.001	3.03	0.101	2.48	0.135	19.17	<0.001	0.12	0.737	40.47	<0.001	10.61	0.005
CUE	Tropical	2.80	0.114	3.95	0.064	2.59	0.127	3.54	0.078	12.11	0.003	8.98	0.009	6.53	0.021
	Subtropical	3.43	0.083	8.82	0.009	9.28	0.008	62.49	<0.001	61.28	<0.001	71.97	<0.001	8.59	0.010
	Temperate	63.72	<0.001	60.09	<0.001	80.64	<0.001	203.81	<0.001	221.7	<0.001	210.4	<0.001	58.91	<0.001

respiration, while biotic factors affected CUE mainly by changing microbial biomass in the different forest soils. The modifying effects of biotic and abiotic factors on the soil carbon cycle appear to be dependent on forest ecosystem type. This provides new insights that could be expanded in future studies of belowground biodiversity and ecosystem function.

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Author contributions

JPW and SMW conceived and designed the experiments. All authors analyzed the data and jointly wrote the manuscript.

Competing financial interests

The authors declare no competing financial interests.

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