Science of the Total Environment 912 (2024) 169059

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Changing soil available substrate primarily caused by fertilization management contributed more to soil respiration temperature sensitivity than microbial community thermal adaptation

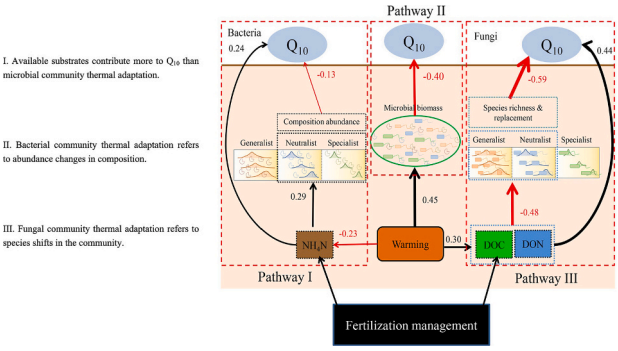
Zhibin Guo [a,c], Chang-An Liu [b,*], Keke Hua [a,c], Daozhong Wang [a,c,*], Pingping Wu [a,c], Shuixia Wan [a,c], Chuanlong He [a,c], Linchuan Zhan [a,c], Ji Wu [a,c,*]

[a] Soil and Fertilizer Research Institute, Anhui Academy of Agricultural Sciences, Hefei, Anhui 230031, China
[b] CAS Key Laboratory of Tropical Plant Resources and Sustainable Use, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun town, Mengla County, Yunnan Province 666303, China
[c] Key Laboratory of Nutrient Cycling and Resources Environment of AnHui Province, Hefei, Anhui 230031, China

HIGHLIGHTS

- Available substrates contribute more to Q_{10} than microbial community thermal adaptation.
- Bacterial community thermal adaptation refers to changes in bacterial abundances.
- Fungal community thermal adaptation refers to shifts in community species.

GRAPHICAL ABSTRACT



ARTICLE INFO

Editor: Elena Paoletti

Keywords:
Soil respiration
Microbial community thermal adaptation
Q_{10} of soil respiration
Dissolved organic carbon
Available nitrogen

ABSTRACT

Substrate depletion and microbial community thermal adaptation are major mechanisms that regulate the temperature sensitivity (Q_{10}) of soil microbial respiration. Traditionally, the Q_{10} of soil microbial respiration is measured using laboratory incubation, which has limits in the continuous input of available substrates and the time scale for microbial community thermal adaptation. How the available substrate and the soil microbial community regulate the Q_{10} of soil microbial respiration under natural warming conditions remains unclear. To fill this gap in knowledge, a long-term field experiment was conducted consisting of two years of soil respiration observations combined with a soil available substrate and microbial community thermal adaptation analysis under seasonal warming conditions. The Q_{10} of soil respiration was calculated using the square root method, and it was more affected by the available substrate than by microbial community thermal adaptation. Fertilization management has a stronger effect on soil available substrate than temperature. As the temperature increased, NH_4-N proved itself to be important for the bacterial community in the process of Q_{10} regulation, while dissolved organic carbon and nitrogen were key factors for the fungal community. Based on the niche breadth of microbial

* Corresponding authors.
E-mail addresses: liuchangan@xtbg.ac.cn (C.-A. Liu), wangdaozhong11@126.com (D. Wang), 120794518@qq.com (J. Wu).

https://doi.org/10.1016/j.scitotenv.2023.169059
Received 11 September 2023; Received in revised form 28 November 2023; Accepted 30 November 2023
Available online 6 December 2023

community composition, the changing Q_{10} of the soil respiration was not only closely associated with the specialist community, but also the generalist and neutralist communities. Furthermore, bacterial community thermal adaptation primarily occurred through shifts in the abundances of specialists and neutralists, while changes in species richness and species replacement occurred for the fungal generalists and neutralists. This work indicates that changing available nitrogen and DOC primarily caused by fertilization management contributed more in regulating the Q_{10} of soil microbial respiration than microbial community thermal adaptation, and there are different mechanisms for bacterial and fungal community thermal adaptation under warming.

1. Introduction

Soil heterotrophic respiration, the primary process whereby carbon is released by soil microorganisms to the atmosphere, constitutes an important component of the global carbon cycle. It is significantly influenced by temperature, and rising temperature results in increased soil heterotrophic respiration (Nissan et al., 2023). Temperature sensitivity (Q_{10}) is a common method for describing proportional changes in soil heterotrophic respiration in response to warming (Bååth, 2018; Li et al., 2020; Yang et al., 2022a). As Q_{10} values may vary greatly, it is important to specify Q_{10} changes to accurately estimate the amount of carbon released into the atmosphere during a specific period under warming conditions.

The Q_{10} of soil heterotrophic respiration is not constant. In previous research, Q_{10} showed a clear decrease with increasing temperature (Bååth, 2018; Wang et al., 2019). The mechanisms responsible for this decrease were microbial thermal adaptation and substrate depletion (Kirschbaum, 2004, 2013; Bradford et al., 2019; X. Guo et al., 2020; Z. Guo et al., 2020; Moinet et al., 2021). These two mechanisms are directly and indirectly linked to soil microbial properties, and may contribute to different levels of soil carbon loss under warming. While microbial thermal adaptation results in a decreased loss of soil labile carbon, substrate depletion mechanism means more carbon release. Therefore, knowledge of soil microbial communities under warming is vital for understanding the Q_{10} of soil heterotrophic respiration and its mechanisms.

Soil microbial communities generally acclimate to warming through physiological changes (Crowther and Bradford, 2013), genetic adaptation (Bennett et al., 1990; Bennett and Lenski, 1997), and shifts in the microbial community (Donhauser et al., 2020). Physiological changes result in short-term acclimation to warming for existing microbial taxa, while genetic adaptation and community shifts lead to species that are inherently adapted to higher temperature conditions outcompeting or replacing less well-adapted species (Donhauser et al., 2020). The outcomes of these species interactions under warming change the structure and functions of microbial communities. As one of the cornerstones of ecology, niche-based processes contribute to the structure of microbial communities and can be used to generate predictions about how species will respond to climatic changes, such as warming (Levine and HilleRisLambers, 2009; Post et al., 2009; Qin et al., 2023). For example, warming can enhance environmental filtering and lead to distinct patterns in the distribution of soil microbial niches (He et al., 2023; Qin et al., 2023). Therefore, generalist and specialist strategies based on the niche breadth provide a basis for predicting how microbial communities will respond to changes in soil environmental factors (Lennon et al., 2012). Irrespective of the above mechanisms, previous research has demonstrated that higher temperatures result in lower Q_{10} values of soil microbial respiration and vice versa with decreasing temperature in a phenomenon termed community thermal adaptation (Bååth, 2018; Nottingham et al., 2021).

The thermal adaptation of a microbial community depends on the temperature change regime, including the magnitude of the temperature change and its duration (Bååth, 2018; Zhang et al., 2023). For example, one- to two-month laboratory incubation at 25 °C had no significant impact on the Q_{10} of microbial respiration in comparison with incubation at 5 °C, while increasing the temperature to approximately 30 °C resulted in rapid community thermal adaptation (Barcenas-moreno et al., 2009; Birgander et al., 2013). This means that short-term laboratory studies are not sufficient to explore microbial community adaptations to warming due to the negative effects of a disrupted soil structure on the soil microbial community structure and the depletion of the available substrate during the pre-incubation processing of soil samples (Lin et al., 2019; Mason-Jones et al., 2020; Podrebarac et al., 2021; Li et al., 2022; Feng and Wang, 2023). In contrast, available substrate was mostly sufficiently for the microbial communities in surface soils, and field conditions with longer time scales and large temperature shifts result in microbial thermal adaptation (Rousk et al., 2012; Schindlbacher et al., 2015; Carey et al., 2016; Cui et al., 2023).

Field experiments can be used for the Q_{10} analysis of soil microbial respiration and related mechanisms (Bååth, 2018; X. Guo et al., 2020; Z. Guo et al., 2020; Nottingham et al., 2022). However, in previous research smaller temperature increases under field conditions did not lead to microbial community thermal adaptation, which is strongly determined by the peak seasonal temperature (Rijkers et al., 2023). Thus, a field experiment lasting several months across several seasons should not only overcome the above mentioned drawbacks of laboratory incubation, but also provide an opportunity to study the mechanisms influencing the Q_{10} of soil heterotrophic respiration under warming. Another advantage of field experiment is the fertilization management in the agroecosystem, which was widely adopted for improving the productivity and nutritional quality of food crops (Ishfaq et al., 2023). Fertilization management changes soil substrate availability and soil microbe, and subsequently regulates the response of soil respiration to temperature (X. Guo et al., 2020; Z. Guo et al., 2020; Numa et al., 2021). According to the report of Numa et al. (2021), the response of soil respiration to warming is governed by substrate availability as microbial biological processes dominate when substrate is non-limiting. Therefore, in this study a long-term field experiment with different fertilization managements was conducted to provide a stable soil environment, diverse levels of substrate availability and reduce the impact of artificial management on soil microbial properties (X. Guo et al., 2020; Z. Guo et al., 2020). This aim of this study is to answer the following questions: (i) which is more important for the Q_{10} of soil heterotrophic respiration, microbial community thermal adaptation or the changes of available substrate caused by fertilization management in the agroecosystem? (ii) What are the differences in community thermal adaptation between soil bacteria and fungi? In this study, the microbial community thermal adaptation is assessed by measuring four community parameters under warming: community similarity, species replacement, species richness difference, and the niche structure. The available substrate consisted of dissolved organic carbon and available nitrogen, and the in-situ soil respiration was observed in winter and in summer. It was predicted that microbial community thermal adaptation was more important than the changing available substrate caused by fertilization management in the regulation of the Q_{10} of respiration in the agroecosystem. Moreover, it was hypothesized that decreasing Q_{10} values under warming were closely linked with the community thermal adaptation of microbial specialists based on niche theory (Tilman, 2004; von Meijenfeldt et al., 2023) and the commonly accepted associations between microbial living strategies and the Q_{10} of microbial respiration (Li et al., 2021; Yang et al., 2022a).

2. Materials and methods

2.1. Study site and soil sampling

This research was conducted based on a long-term field experiment (32°14′N, 116°37′E) that began in 1982 and was located in the Mengcheng county, Anhui Province, China. The soil at the study site is a vertisol (IUSS Working Group, 2014; Li et al., 2011). In the current research, four treatments were selected that indicated (1) the control (CK), with no crops and no fertilization; (2) crops without fertilization (NF); (3) crops with long-term mineral fertilization (NPK); and (4) crops with mineral fertilization plus the return of wheat straw to the cropland (WS). The crops were a winter wheat and soybean rotation. In both NPK and WS treatments, the number of nitrogen, phosphorus and potassium was 180 kg ha^{-1}, 90 kg ha^{-1} and 135 kg ha^{-1} respectively, while another 7500 kg ha^{-1} of wheat straw was returned into cropland for WS. For the mineral fertilizers and crop straw, they were all used as basal fertilizers with conventional tillage in annual mid-October before winter wheat sowing. In the soybean growth season, there was no fertilization practice.

Soil samples were collected from the 5–15 cm upper soil layer in January, February, May, and June of 2015, just after the measurement of the soil physicochemical and microbial properties. Each treatment had three replicates. As the season changed from winter to summer, the temperature increased from 4.1 °C in January to 27.1 °C in June (Table 1). After removing plant debris and stones and sieving through a 2-mm sieve, soil samples were divided into two subsamples. One was stored at 4 °C for the determination of the microbial biomass, the soil water content, NH_4-N, NO_3-N, dissolved organic carbon (DOC), and dissolved organic nitrogen (DON), and the other subsample was stored at −80 °C for microbial total DNA extraction.

2.2. Respiration measurement and the Q_{10} calculation

According to Wang et al. (2021a), soil respiration at the seedling and harvest stages of winter wheat largely originates from soil microbes. In the present study, the soil heterotrophic respiration (CO_2) was measured twice a week using the static closed chamber method (Hutchinson and Livingston, 1993; Zhang et al., 2017) in January and February, the seedling time of winter wheat, as well as in May and June, the harvest time of winter wheat, in both 2014 and 2015. The soil temperature was measured at depth of 5 cm. Prior to the measurement of soil heterotrophic respiration, a rectangular polyvinyl carbonate (PVC) chamber base was inserted into the cropland soil at a depth of 10 cm, and the plants in and around the chamber base were removed. Soil air samples were collected using a sampling chamber with a size of 30 cm × 15 cm × 30 cm and 60-mL airtight syringes. After collection, the samples were immediately transferred into pre-evacuated vials (40 mL) and analyzed using a gas chromatograph (Agilent 7890A, USA) equipped with a flame ionization detector to detect CO_2.

Table 1
Temperature (°C) at the 5-cm soil layer under seasonal warming in the CK, NF, WS, and NPK treatments.

Year	Treatments	January	February	May	June
2014	CK	4.17 ± 0.17	5.47 ± 0.20	23.40 ± 0.55	26.63 ± 0.43
	NF	4.43 ± 0.07	5.47 ± 0.03	24.00 ± 0.32	26.47 ± 0.27
	WS	4.70 ± 0.06	5.40 ± 0.06	23.20 ± 0.32	26.50 ± 0.30
	NPK	4.53 ± 0.15	5.33 ± 0.03	23.73 ± 0.35	26.27 ± 0.33
2015	CK	5.57 ± 0.30	6.77 ± 0.12	21.57 ± 0.38	26.00 ± 0.29
	NF	5.47 ± 0.33	6.87 ± 0.13	21.37 ± 0.22	25.90 ± 0.15
	WS	6.07 ± 0.12	6.97 ± 0.09	21.57 ± 0.32	26.60 ± 0.32
	NPK	5.63 ± 0.29	6.87 ± 0.12	21.07 ± 0.27	26.10 ± 0.26

The temperature sensitivity of soil respiration (Q_{10}) was calculated using the square root model. Specifically, the T_{min} (theoretical minimum temperature for soil microbial respiration) for each treatment was calculated according to Bååth (2018), as follows:

$$\sqrt{Rs} = a \times (T - T_{min}), \quad (1)$$

where Rs is the rate of soil respiration at a given soil temperature (mg m^{-2} h^{-1}) of T (°C), T_{min} (°C) is the minimum temperature for microbial respiration, and *a* is a slope parameter related to the absolute respiration rate.

The temperature sensitivity of soil respiration (Q_{10}) was calculated using the following equation:

$$Q_R = [(T + R - T_{min})/(T - T_{min})]^2 \quad (2)$$

where Q_R is the temperature sensitivity of soil respiration for a given temperature range of R, and T is the lowest temperature for comparison. Tmin was calculated using Eq. (1). In this study, the temperature ranges of R were 0–10 °C and 15–25 °C.

2.3. Analysis of the soil physicochemical properties

The soil water content, DOC, DON, and available nitrogen were determined according to Bao (2005). Briefly, the soil water content was measured after drying for 24 h at 105 °C. The soil DOC and DON contents were determined using a total organic carbon (TOC) analyzer after the extraction of fresh soil samples with 0.5 M potassium sulfate (K_2SO_4). The soil nitrate-N (NO_3^-N) and ammonium-N (NH_4 − N) were measured using a continuous flow analytical system with 50 mL of a 2 M KCl extraction solution and 5 g of fresh soil. The soil microbial biomass carbon (MBC) was measured using the fumigation-extraction method after soil sampling.

2.4. Analysis of the microbial properties

The soil DNA extraction method was described in detail in our previous research (Guo et al., 2022). Briefly, 0.5 g fresh soil stored at −80 °C was used for the soil DNA extraction using an MP Fast DNA™ SPIN Kit (MP Biomedicals, Solon, OH, USA). Subsequently, the concentrated and purified DNA was used for the analysis of soil bacteria and fungi after amplification with the primer pairs 515F/806R and ITS5/ITS2, respectively (Caporaso et al., 2011; Bellemain et al., 2010; Schmidt et al., 2013). After being purified and mixed in equimolar ratios, the collected sequencing libraries of 16S and ITS1 DNA were sequenced on an Illumina HisSeq Platform at Novogene Bioinformatics Technology Co., Ltd. (Beijing, China), and the raw sequence data were collected. The raw data were processed using QIIME1 and UCHIME, and the obtained high-quality sequences of bacteria and fungi with ≥97 % similarity were gathered into the same operational taxonomic units (OTUs) using UPARSE software (Caporaso et al., 2010; Edgar et al., 2011; Edgar, 2013). The alpha and beta diversity of the soil bacterial and fungal community were then calculated based on a 97 % OTU similarity of the obtained sequences. Soil bacterial and fungal taxa were annotated using the Ribosomal Database Project (RDP) classifier and the UNITE database, respectively (Wang et al., 2007; Kõljalg et al., 2013). The bacterial and fungal sequence data were deposited in the National Center for Biotechnology Information (NCBI) under the accession numbers PRJNA909425 and PRJNA909421, respectively.

According to previous research on the niche breadth of soil microbes, the soil bacterial and fungal community composition of each treatment was classified into generalist, neutralist, and specialist categories using

the spaa package in R software (Levins, 1968; Pandit et al., 2009; Zhang et al., 2018; Jiao et al., 2020). The bacterial and fungal community thermal adaptation of each treatment was assessed based on changes in the beta diversity across various temperatures that was partitioned into community compositional similarity, species replacement, and richness differences using the adespatial package in R software (Shen et al., 2020).

2.5. Statistical analysis

Two-way ANOVA (ANOVA) was used to test the effects of fertilization regime, temperature and their interaction on soil DOC, DON, NO_3^-N, $NH_4 - N$, soil respiration and its temperature sensitivity (Q_{10}) using SAS 9.4 software (SAS Institute, Cary, NC, USA). A Spearman's correlation analyses among the temperature, the soil available substrate, the microbial community thermal adaptation, and the Q_{10} were performed and plotted using the "linkET", "ggplot2", and "dplyr" packages of R 4.1.0, with significance observed at $P < 0.05$. To test the significance of each environmental factor to the microbial community structure, the "envfit" function in R was used.

Structural equation modeling (SEM) was used to analyze the direct and indirect associations between the soil temperature, available substrate, microbial community thermal adaptation, and the Q_{10} of soil respiration using Amos 17.0 (IBM, SPSS, USA). Two goodness of fit parameters were selected: the Chi-squared test (χ^2; the model showed good fit when $0 \leq \chi^2/df \leq 2$ and $0.05 < P \leq 1.00$) and the root mean square error of approximation (RMSEA; the model showed good fit when $0 \leq RMSEA \leq 0.05$ and $0.10 < P \leq 1.00$ and acceptable fit when $0.05 < RMSEA \leq 0.08$ and $0.05 < P \leq 0.10$) (Delgado-Baquerizo et al., 2017). The final model included the standardized total effects of the soil available substrate, temperature, microbial biomass, and community thermal adaptation on the Q_{10} values. Based on previous knowledge that (1) soil temperature can drive the Q_{10} of soil respiration by regulating the movement of the available substrate across different soil horizons (Podrebarac et al., 2021); (2) temperature can enhance environmental filtering and trigger changes in community composition due to an influx of warm-adapted species based on niche theory (He et al., 2023; Qin et al., 2023); and (3) available substrate depletion plays a significant role in the process of changes in the Q_{10} (Kirschbaum, 2004, 2013; Moinet et al., 2021), this study constructed a conceptual model of hypothetical relationships.

3. Results

3.1. Q_{10} of soil respiration and temperature regimes

Soil respiration was significantly affected by fertilization management and temperature (Table 2). Based on the F value of two-way ANOVA test, the influence of temperature was stronger than fertilization management. To determine the Q_{10} of soil heterotrophic respiration, the square root curves of the soil respiration under each treatment were obtained by fitting curves using the square root relationship, and the T_{min} was then obtained (Fig. 1a). The T_{min} of microbial activity was similar between 2014 and 2015 for each treatment at −14.53 °C and −14.75 °C for NF, respectively, −29.53 °C and −30.52 °C for NPK, respectively, −17.44 °C and −19.82 °C for WS, respectively, and −9.27 °C and −10.40 °C for CK, respectively. The calculation of the respiratory $Q10_{0-10}$ and $Q10_{15-25}$ revealed that both fertilization management and temperature significantly changed the Q_{10} of soil respiration (Fig. 1b and Table 2). Therein, temperature has a stronger impact on the Q_{10} than fertilization management, and the Q_{10} in summer was significantly lower than that in winter in all treatments.

3.2. Soil microbial community composition and beta diversity

Soil microbial alpha diversities were measured (Table S1). For the community composition, based on the niche breadth of each OTU, the bacterial and fungal generalists were both significantly less abundant ($P < 0.05$) than the specialists and neutralists (Fig. 2; Table S2), and the relative abundances of the specialists and neutralists combined for both bacteria and fungi accounted >99.00 % of the total. For soil bacteria, the abundance of generalists ranged from 0.08 % to 0.23 %, that of specialists ranged from 32.00 % to 60.28 %, and that of neutralists ranged from 37.39 % to 67.18 %, while the relative abundances of fungal generalists, specialists, and neutralists were 0.36 %–0.99 %, 67.99 %–90.48 %, and 8.98 %–31.13 %, respectively.

For the soil bacterial beta diversity with different niche breadths, the highest community similarity was observed in the generalists, while the lowest was found in the neutralists, for which the averaged values in all treatments ranged from 0.79 to 0.86 and from 0.45 to 0.50, respectively (Fig. 3). Among the generalists, specialists, and neutralists, the highest levels of species replacement and species richness differences were both found in the neutralists and ranged from 0.33 to 0.41 and from 0.09 to 0.18, respectively.

Soil fungal community similarities for the generalists, specialists, and neutralists were all lower than those of bacteria, but with higher species replacement and species richness differences. For fungal generalists, the beta diversity was 0.33–0.47 for community similarity, 0.35–0.47 for species replacement, and 0.17–0.23 for species richness differences, while the beta diversity values of community similarity, species replacement, and species richness differences were 0.35–0.48, 0.37–0.48, and 0.12–0.15 for specialists, respectively, and 0.15–0.19, 0.63–0.67, and 0.14–0.21 for neutralists, respectively (Fig. 4).

3.3. Factors driving the Q_{10} of soil respiration

Soil available substrates were significantly influenced by fertilization management and temperature except for DON (Table 2), and the contribution of available substrates combined with microbial biomass carbon and alpha diversity, including Shannon diversity and species richness, was 85.68 % for soil respiration (Fig. 5). Pearson's correlation analysis indicated that there were significant ($P < 0.05$) linkages between the Q_{10} of soil respiration and temperature, NH_4-N, MBC, bacterial specialists, and bacterial neutralists (Fig. 6a; Tables S3 and S4). In

Table 2
Two-way ANOVA test on the effect of fertilization regime (FR) and temperature (Tem) on the DOC, DON, NO_3^-N, $NH_4 - N$, soil respiration (SR) and its temperature sensitivity (Q_{10}).

Variables		FR		Tem		FR × Tem	
		F value	P	F value	P	F value	P
SR	2014	35.42***	<0.001	213.24***	<0.001	13.26***	<0.001
	2015	26.75***	<0.001	187.24***	<0.001	24.10***	<0.001
Q_{10}		79.77***	<0.001	246.58***	<0.001	35.39***	<0.001
DOC		23.81***	<0.001	10.97***	<0.001	8.04***	<0.001
DON		1.08	0.37	0.94	0.43	0.72	0.69
NO_3^-N		23.17***	<0.001	10.65***	<0.001	2.80*	<0.02
$NH_4 - N$		48.11***	<0.001	14.20***	<0.001	0.84*	0.02

"*", "**", "***" indicate that $P < 0.05$, $P < 0.01$ and $P < 0.001$, respectively.

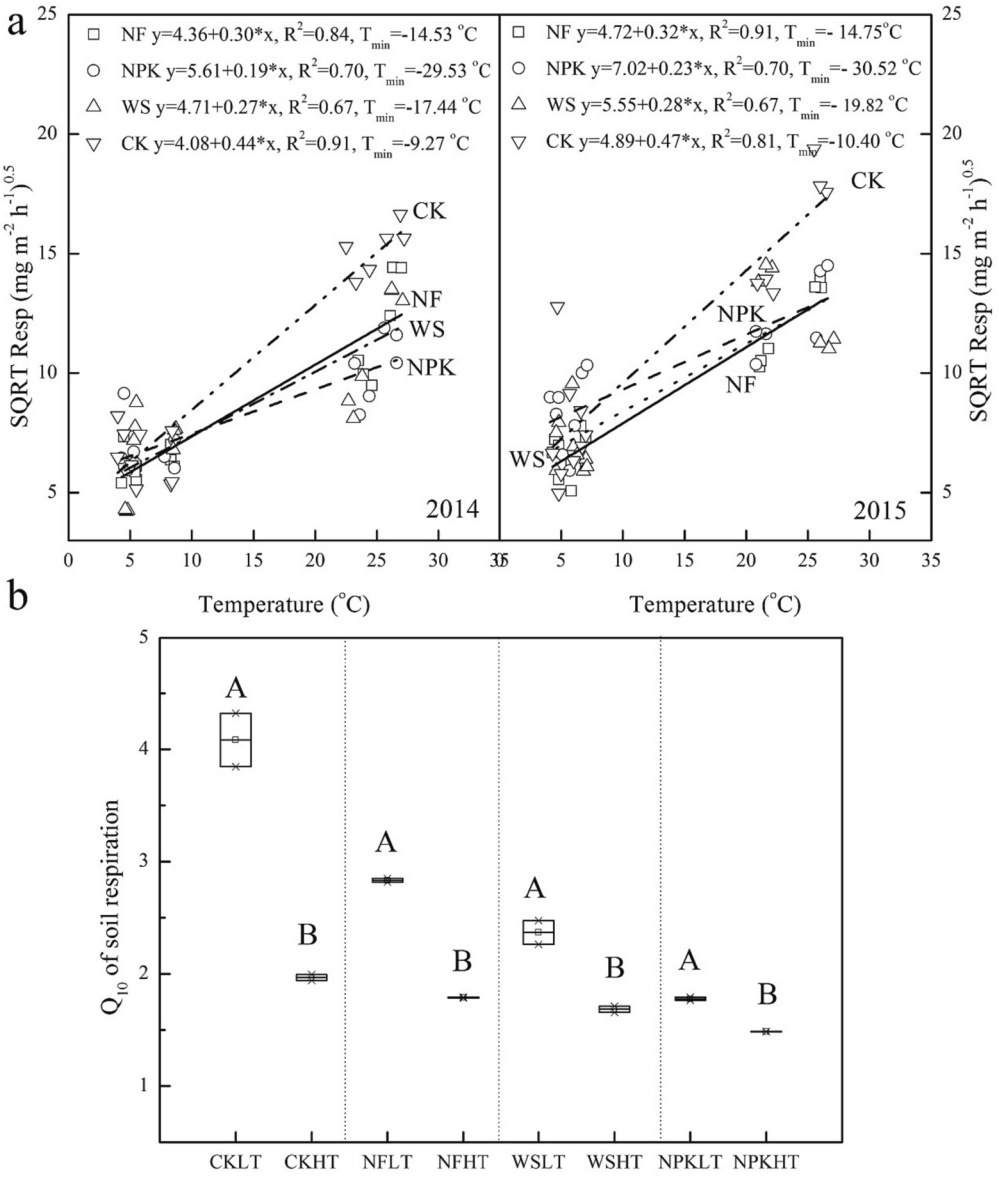


Fig. 1. T_{min} value for each treatment in 2014 and 2015 based on field observations of soil respiration (a); the temperature sensitivity of soil respiration at temperatures of 0–10 °C (LT) and 15–25 °C (HT) (b) under the NF, WS, NPK, and CK treatments. Different uppercase letters in the figure indicate significant differences at the $P < 0.05$ level. CK: control; NF: crops without fertilization; NPK: crops with long-term mineral fertilization; WS: crops with mineral fertilization plus the return of wheat straw to the cropland.

addition, there were significant and close relationships ($P < 0.05$) between the Q_{10} of soil respiration and the beta diversity of fungal generalists and neutralists (Fig. 6b).

A SEM analysis was used to discriminate the direct and indirect effects of soil available substrate (C and nitrogen availabilities), microbial biomass, bacterial and fungal community composition, and community structure on the temperature sensitivity (Q_{10}) of soil heterotrophic respiration (Fig. 7). This analysis showed that soil bacteria and fungi both had negative impacts on the Q_{10}. In contrast, there were positive relationships between the Q_{10} and the DOC, DON and $NH_4 - N$ contents. The NH_4-N, temperature, and MBC limited the contributions of bacterial specialists and neutralists to the Q_{10}, while DOC and DON regulated the Q_{10} via changing the beta diversity of fungal generalists and neutralists. Specifically, 29.65 %, 10.87 %, 26.14 %, and 7.25 % of the total variance in the Q_{10} was explained by the individual factors of temperature, NH_4-N, MBC, and bacterial generalists and neutralists, respectively, while 41.82 %, 12.50 %, and 40.42 % was explained by the individual factors of DOC, DON, and the fungal beta diversity of generalists and neutralists, respectively (Figs. 7).

4. Discussion

Under field condition, soil respiration consists of heterotrophic respiration from soil microbe and autotrophic respiration from plants. To determine whether soil respiration could be used to interpretate soil microbial respiration directly, we firstly analyzed the contribution of microbial properties and soil water content, DOC, DON, NH_4-N, NO_3-N, temperature to soil respiration, and find that up to 85.68 % of soil respiration could be explained, which means soil respiration under changing temperature in our research was mainly caused by soil microbe and soil available substrate variation. Furthermore, we also analyzed the contributions of soil water content, temperature, DON, DOC, NH_4-N and NO_3-N to bacterial and fungal community structure to characterize the community thermal adaptation as temperature changing under field condition, and found that more than half of their community variations could be explained (Fig. S1). Therein, temperature

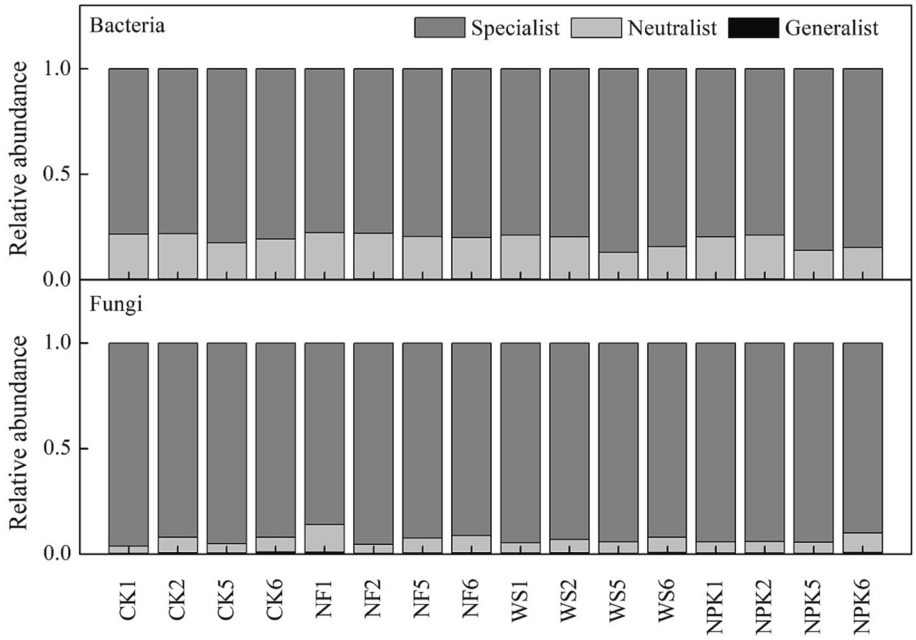


Fig. 2. Relative abundances of bacterial and fungal generalists, specialists, and neutralists under the CK, NF, WS and NPK treatments. CK: control; NF: crops without fertilization; NPK: crops with long-term mineral fertilization; WS: crops with mineral fertilization plus the return of wheat straw to the cropland.

was the primary factor in structuring soil bacterial and fungal community in CK, NF, WS, and NPK (Fig. S2). These results provide evidence that microbial community shift is driven direct response to temperature, and showing that the community change coincided closely with increases in thermal adaptation of the community.

4.1. Available substrate, temperature, fertilization management and the Q_{10} of soil respiration

Inconsistent with the first hypothesis, the findings showed that the soil available substrates were significantly affected by temperature, and contributed more to the Q_{10} of soil respiration than the MBC and microbial community thermal adaptation. These results may be referred to the warming processes under field conditions, which generally lead to an exchange of available carbon and nitrogen between different soil layers (Podrebarac et al., 2021). Thus, there are limitations to investigating the mechanisms of changes in Q_{10} using laboratory incubation experiments (García-Palacios et al., 2021; Chen et al., 2023). It is necessary to consider the continuous input of substrate during warming incubation (Feng and Wang, 2023).

Furthermore, we also found that fertilization management has a stronger effect on soil DOC and NH_4-N than temperature (Table 2), and the key factors in the microbial processes of the Q_{10} regulation were NH_4-N for bacterial community and DOC and DON for fungal community, respectively. These results indicated that available nitrogen as important as DOC should be considered in the microbial process of soil respiration measurement using laboratory incubation, and fertilization management was more important than temperature in regulating the Q_{10} under field conditions. Being consistent with previous research that reported nitrogen addition changed the sensitivity of microbial respiration to warming, we further found that a positive relationship existed between soil NH_4-N and the Q_{10} (Wang et al., 2018; Yang et al., 2022b; Zheng et al., 2022; Chen and Chen, 2023; Zheng et al., 2023). From this perspective, increasing the number of environmental and anthropogenic factors considered, such as the interactive effect of temperature and changes of DOC and available nitrogen caused by fertilization management on the Q_{10} in the agroecosystem, is vital to predict changes in soil carbon stocks under global warming (Wang et al., 2018; Chen et al., 2023; Rillig et al., 2023; Zhang et al., 2023).

4.2. Ecological niche processes and microbial community thermal adaptation

In the present study, the microbial community composition was categorized as generalist, neutralist, or specialist according to the variation in the niche breadth of each OTU. This method can be used to making predictions about how a microbial community composition will respond to environmental and climate changes, as well as the sensitivity of the microbial community composition to these changes (Lennon et al., 2012; Qin et al., 2023). Microbial specialists are K-strategists with high carbon use efficiency, and there is a close association between Q_{10} and K-strategists (Li et al., 2021; Yang et al., 2022a; von Meijenfeldt et al., 2023). The present study quantified the contribution of microbial specialists to the Q_{10} of soil microbial respiration. It was found that not only bacterial specialists, but also bacterial neutralists, fungal generalists, and fungal neutralists, were significantly closely related to the Q_{10}. These results partially agreed with the second hypothesis that indicated that the microbial community thermal adaptation processes were complicated and that the community level of thermal adaptation should be focused on instead of the thermal adaptation of individual species (Tian et al., 2022).

This study supported the findings of previous studies, showing that the approaches of bacterial and fungal communities to thermal adaptation were different regarding the regulation of Q_{10} (Nottingham et al., 2022). Abundances change for bacteria, and alpha and beta diversities shift for fungi during community thermal adaptation processes. Different community thermal adaptation regimes may be attributed to bacteria having a larger proportion of the overall microbial biomass and a higher optimum temperature for bacterial activity and growth than that of fungi. For example, in previous research, soil bacteria accounted for 70 %–90 % of the total microbial biomass (Bardgett and Van Der Putten, 2014), and this biomass increased along with warming up to the optimum temperature of 27–30 °C (Bardgett and Van Der Putten, 2014; Rijkers et al., 2022). Another important reason for this is the short-period generation of bacteria, which means that the thermal adaptation of specific bacteria can increase quickly through a large number of generations within a few weeks or months (Bååth, 1998; Tian et al., 2022). In comparison to bacteria, soil fungi have hypha, larger bodies, and greater plasticity, all of which improve their resistance to

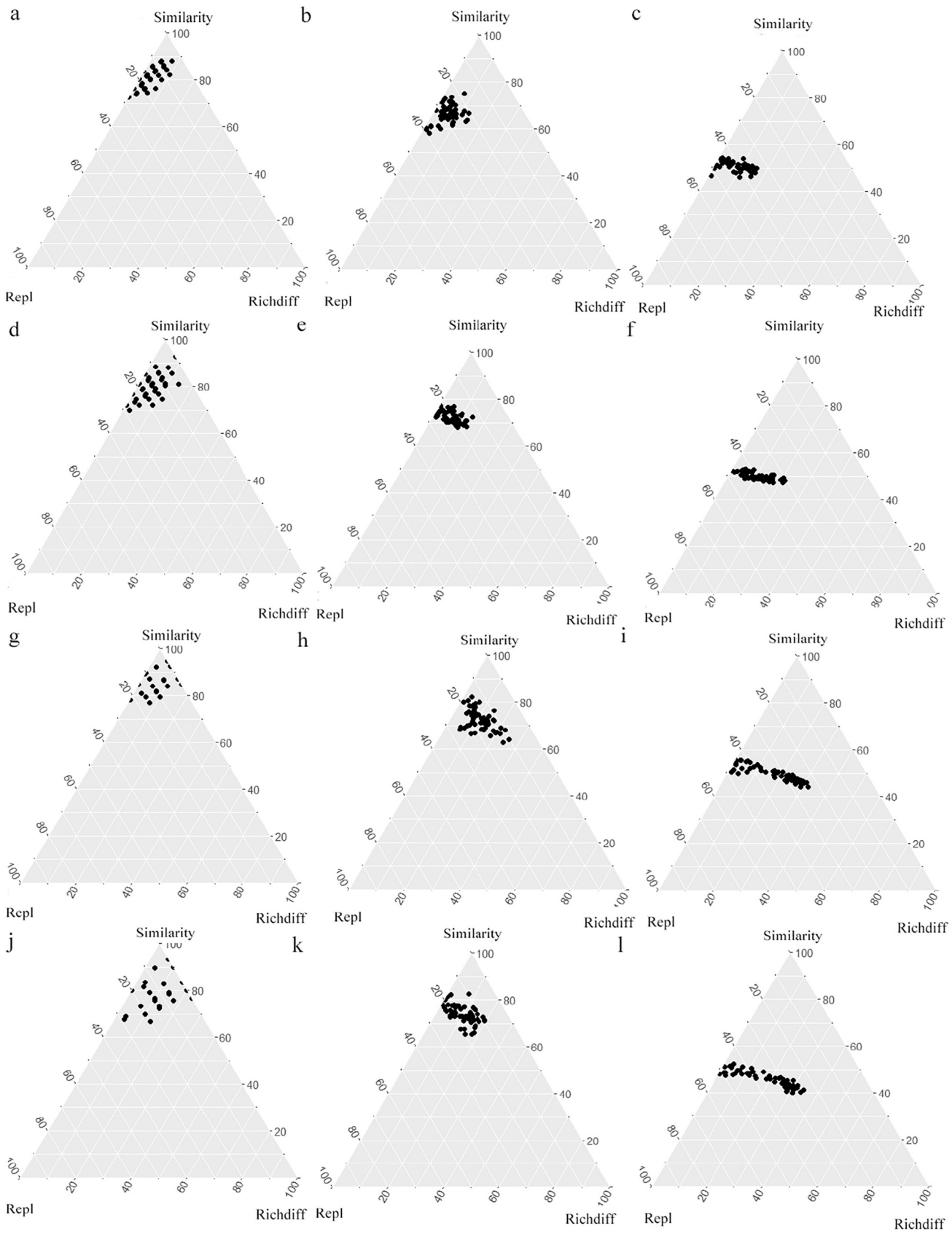


Fig. 3. Ternary plot of the beta diversity, including the community similarity, species replacement (Repl), and species richness difference (Richdiff) of bacterial generalists, specialists, and neutralists under NF (generalist: a, specialist: b, and neutralist: c), CK (generalist: d, specialist: e, and neutralist: f), WS (generalist: g, specialist: h, and neutralist: i), and NPK (generalist: j, specialist: k, and neutralist: l) treatments. CK: control; NF: crops without fertilization; NPK: crops with long-term mineral fertilization; WS: crops with mineral fertilization plus the return of wheat straw to the cropland.

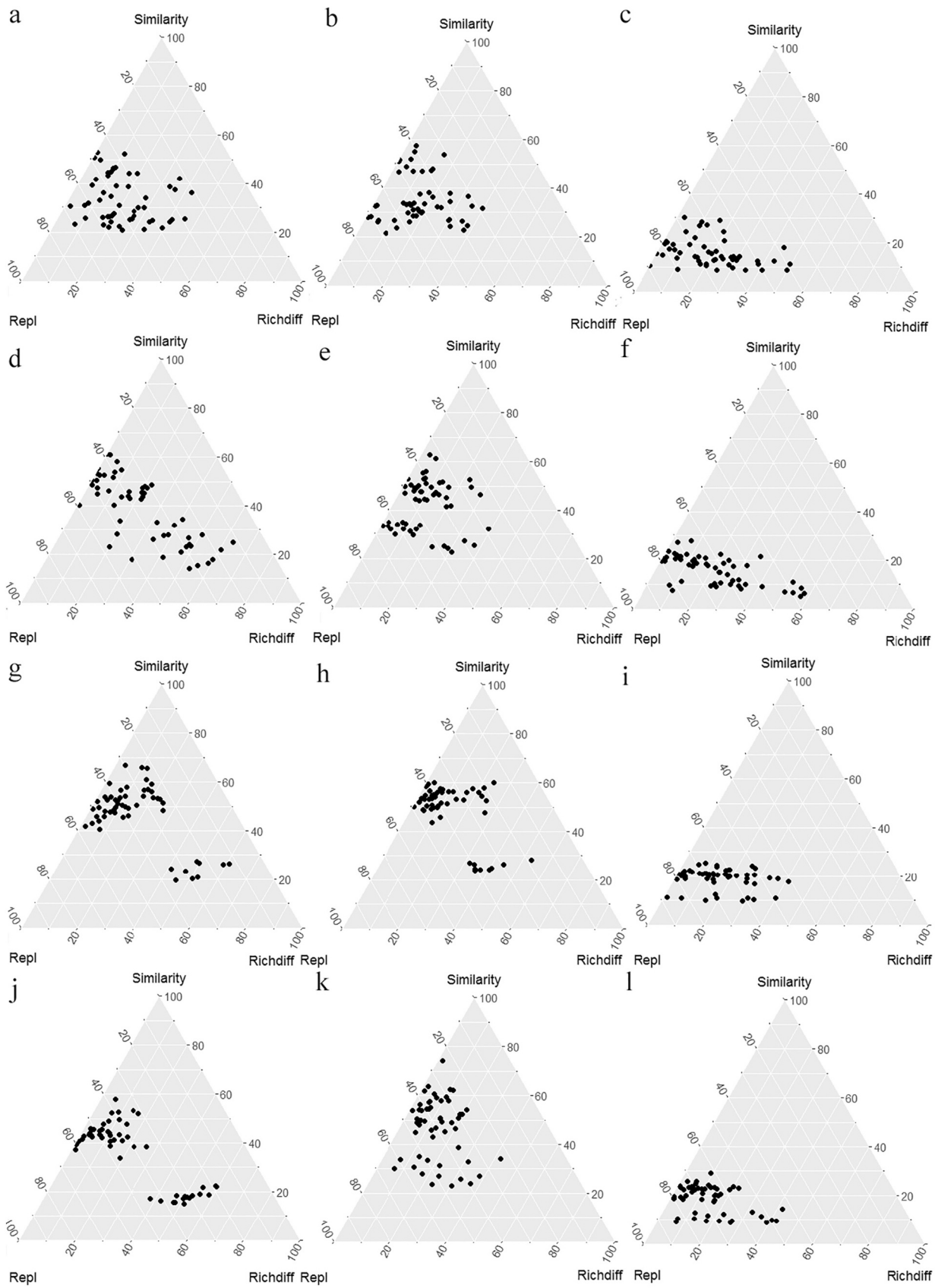


Fig. 4. Ternary plot of the community similarity, species replacement (Repl), and species richness difference (Richdiff) of soil fungal generalists, specialists and neutralists under the NF (a, b, and c), CK (d, e, and f), WS (g, h, and i) and NPK (j, k and l) treatments. CK: control; NF: crops without fertilization; NPK: crops with long-term mineral fertilization; WS: crops with mineral fertilization plus the return of wheat straw to the cropland.

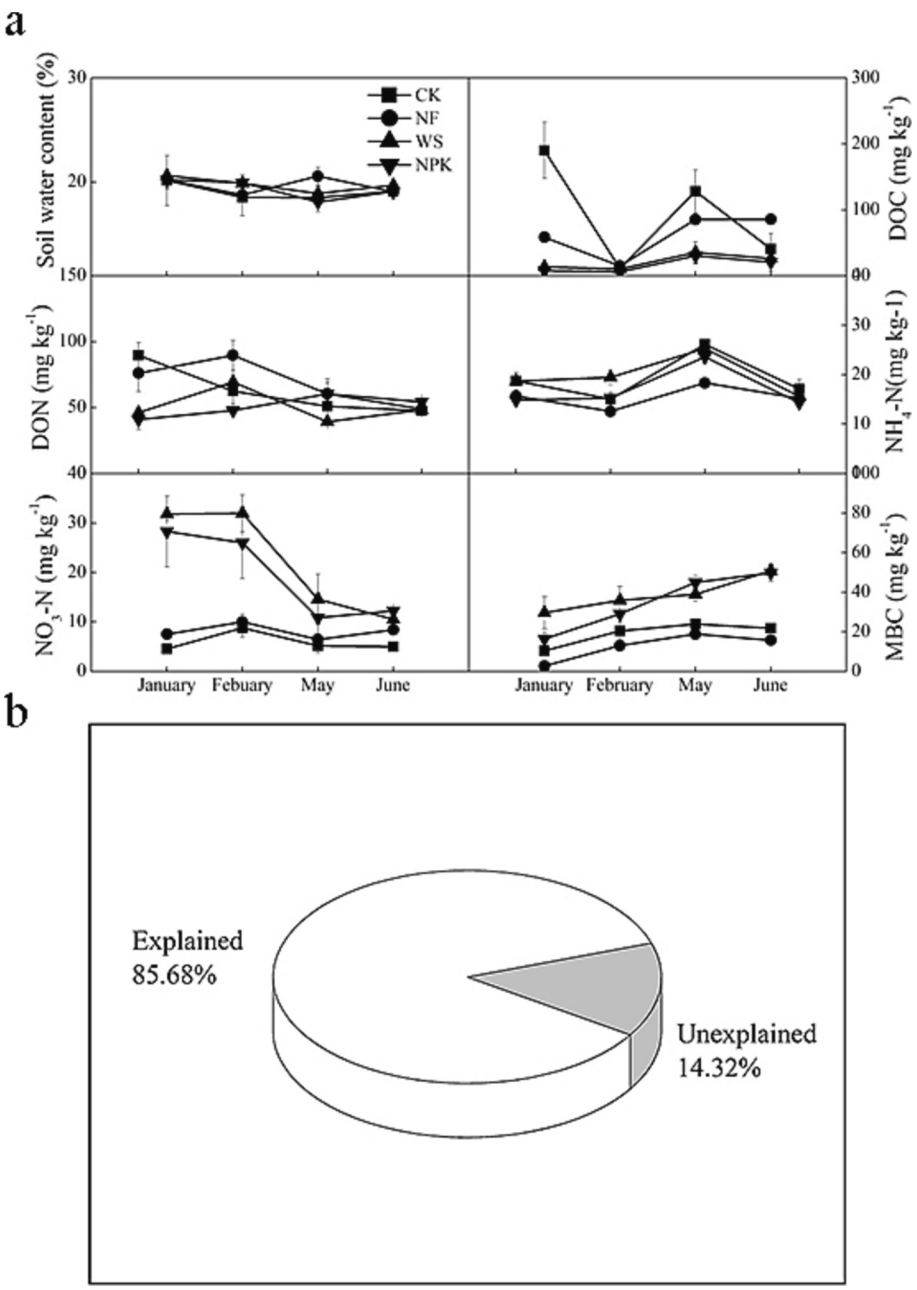


Fig. 5. (a) Soil water content (%), dissolved organic carbon (DOC: mg kg^{-1}) and nitrogen (DON: mg kg^{-1}), NH_4-N (mg kg^{-1}), NO_3-N (mg kg^{-1}), and microbial biomass carbon (MBC: mg kg^{-1}) under seasonal warming in the CK, NF, WS, and NPK treatments. (b) the contribution of soil water content, DOC, DON, NH_4-N, NO_3-N, temperature, MBC, microbial Shannon diversity and species richness on soil respiration. CK: control; NF: crops without fertilization; NPK: crops with long-term mineral fertilization; WS: crops with mineral fertilization plus the return of wheat straw to the cropland.

environmental changing, such as warming (Alster et al., 2021). However, their optimum temperature is lower (Feng et al., 2022), and the optimum growth temperatures among various fungal species are different (Gavito et al., 2005; Yuste et al., 2011; Voyles et al., 2017; Fukasawa, 2018). Consequently, some fungal species may be replaced by others under warming conditions.

4.3. Implications and limitations

Niche theory provides insight into the outcome of species interactions and generates predictions about how species will respond to future climate scenarios (Post et al., 2009). To our knowledge, this is the first study focusing on the community thermal adaptation to the Q_{10} of soil respiration based on the niche breadth of the microbial community composition. Similar to the r-K selection used for soil microbial community composition, the niche-based method is not only reliable for determining the functional traits of the community along environmental factor gradients (Lennon et al., 2012), but also overcomes some drawbacks of the former method. For example, the r-K selection for the microbial community classification was difficult and primarily resulted in broad groupings. In some cases, a contrary categorization of the microbial community composition was the result. For example, the Proteobacteria phylum is classified as representative of r-strategists in the publication of Fierer et al. (2007), but its subphylums, including Alphaproteobacteria, Gammaproteobacteria and Deltaproteobacteria, are classified as K-strategists in other studies (Wang et al., 2021b; Yang et al., 2022a).

However, the present study has a number of limitations. For

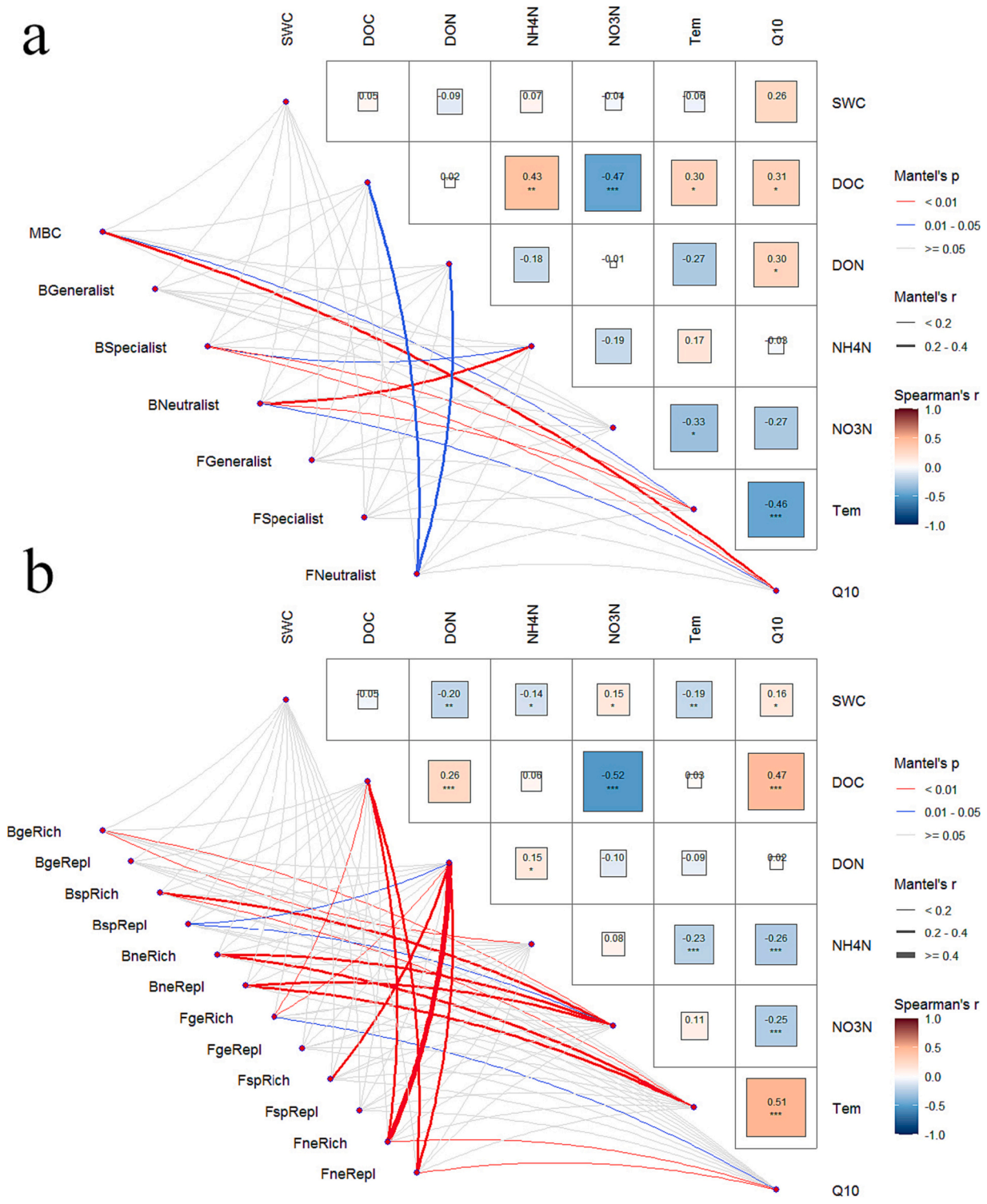


Fig. 6. Spearman's correlation analysis between the temperature sensitivity (Q_{10}) of soil respiration and microbial biomass carbon (MBC), the relative abundances (a) and beta diversity (b) of bacterial and fungal generalists, specialists, and neutralists. Red, blue, and white lines represent significance at the 0.01 and 0.05 levels and nonsignificance ($P > 0.05$), respectively. The line width corresponds to the strength of the relationship (Spearman's r value). Pairwise comparisons of soil properties, temperature, soil respiration, and its Q_{10} are demonstrated in the right panel. The correlation coefficients ranging from negative to positive are indicated by color intensity ranging from blue to red. The statistical results are labeled as "***" at $P < 0.001$, "**" at $P < 0.01$, and "*" at $P < 0.05$. SWC: soil water content; DOC: dissolved organic carbon; DON: dissolved organic nitrogen.

example, this research was conducted based on field conditions. Although the different roles played by NH_4-N, DOC, and DON in bacterial and fungal community construction under warming are known, without further experiments under controlled conditions, it is difficult to clearly determine how the different substrates regulated the Q_{10} of soil respiration by changing bacterial and fungal community thermal adaptations. Another limitation was that the results of the present study were presented based on site-level datasets in agricultural system. The

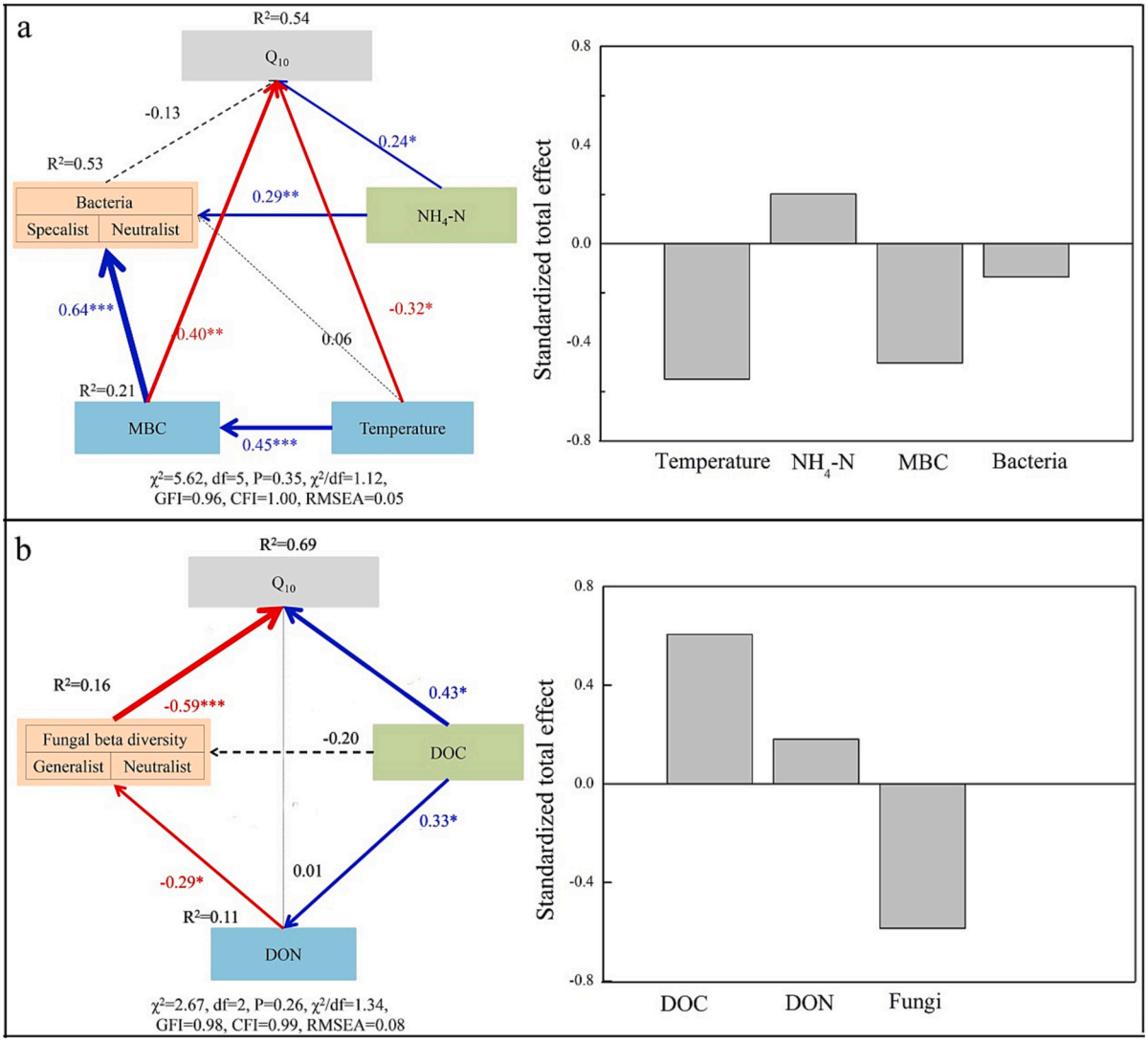


Fig. 7. Effects of bacterial community composition, fungal beta diversity, dissolved organic carbon, NH_4-N, microbial biomass carbon (MBC), and their standardized total effects on the temperature sensitivity (Q_{10}) of soil respiration evaluated using the structural equation model (SEM). The bacterial community includes the specialists and neutralists, while the fungal beta diversity consists of generalists and neutralists. Red and blue arrows indicate significant negative and positive relationships, respectively, while the gray dashed arrows represent nonsignificant pathways. The arrow thickness represents the strength of the relationship. The numbers adjacent to the arrows and the variances represent standardized path coefficients and the percentages (R^2) of variance explained by the model. "***," "**," and "*" indicate significant differences at the $P < 0.001$, $P < 0.01$, and $P < 0.05$ levels, respectively.

characteristics of site-level field experiments are related to agricultural management practices as well as local climatic and environmental conditions. Thus, these local-level results have limits and cannot be generalized to regional or continental scales. For example, some research conducted in subtropical forest has pointed out that available phosphorus but not nitrogen controlled soil respiration and its temperature sensitivity, and the microbial mechanisms were not community thermal adaptation but referred to the nutrients availability-induced changes in communities and microbial resource-allocation strategies (Mou et al., 2023; Wang et al., 2023; Yang et al., 2023). The reasons for the difference between our results and researches conducted in subtropical forest may be referred to fertilization management, vegetation traits and plant growth conditions (Boone et al., 1998; Haaf et al., 2021). Thus, more studies based on various land use categories and vegetable traits are required to provide support for our findings.

5. Conclusion

In summary, the available substrate contributed more to regulating the Q_{10} of soil heterotrophic respiration than microbial community thermal adaptation. Fertilization management has a stronger effect on soil available substrate than temperature. Under warming conditions, NH_4-N was important for the bacterial community in the process of Q_{10} regulation, while DOC and DON were important for the fungal community. Based on the niche breadth, the changing Q_{10} of soil respiration was not only closely associated with the specialist community, but also with the generalist and neutralist communities. Furthermore, bacterial community thermal adaptation primarily occurred through shifts in the abundances of specialists and neutralists, while changes in the species richness and species replacement occurred in the fungal generalist and neutralist communities during thermal adaptation.

CRediT authorship contribution statement

Zhibin Guo: Writing – original draft. **Chang-An Liu:** Writing – review & editing, Conceptualization. **Keke Hua:** Investigation, Formal analysis, Data curation. **Daozhong Wang:** Writing – review & editing, Supervision. **Pingping Wu:** Investigation, Data curation. **Shuixia Wan:**

Methodology, Data curation. **Chuanlong He:** Methodology, Investigation. **Linchuan Zhan:** Investigation, Data curation. **Ji Wu:** Writing – review & editing, Supervision, Funding acquisition.

Declaration of competing interest

The authors declare no competing interests.

Data availability

Data will be made available on request.

Acknowledgements

This work was supported by the projects of the international cooperation project (G2023019005L), Natural Science Foundation of China (Grant numbers 41501323), the Anhui Provincial Natural Science Foundation (Grant number 2008085MD108), and the Science and Technology Major Project of Anhui Province (Grant number 201903a06020028). We also thank Pro. Kazuyuki Inubushi of Tokyo University of Agriculture and Hirohiko Nagano of Niigata University for their valuable suggestions during the revising process, and LetPub (www.letpub.com) for its linguistic assistance during the preparation of this manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2023.169059.

References

Alster, C.J., Allison, S.D., Johnson, N.G., Glassman, S.I., Treseder, K.K., 2021. Phenotypic plasticity of fungal traits in response to moisture and temperature. ISME Commun. 1 (1), 1–8.
Bååth, E., 1998. Growth rates of bacterial communities in soils at varying pH: a comparison of the thymidine and leucine incorporation techniques. Microb. Ecol. 36, 316–327.
Bååth, E., 2018. Temperature sensitivity of soil microbial activity modeled by the square root equation as a unifying model to differentiate between direct temperature effects and microbial community adaptation. Glob. Chang. Biol. 24 (7), 2850–2861.
Bao, S., 2005. Soil Agro Chemistrical Analysis (the 3rd edition). China Agriculture Press, Beijing.
Barcenas-moreno, G.E.M.A., Gomez-brandon, M.A.R.I.A., Rousk, J., Baath, E., 2009. Adaptation of soil microbial communities to temperature: comparison of fungi and bacteria in a laboratory experiment. Glob. Chang. Biol. 15 (12), 2950–2957.
Bardgett, R.D., Van Der Putten, W.H., 2014. Belowground biodiversity and ecosystem functioning. Nature 515 (7528), 505–511.
Bellemain, E., Carlsen, T., Brochmann, C., Coissac, E., Taberlet, P., Kauserud, H., 2010. ITS as an environmental DNA barcode for fungi: an in silico approach reveals potential PCR biases. BMC Microbial. 10, 1–9.
Bennett, A.F., Lenski, R.E., 1997. Evolutionary adaptation to temperature. VI. Phenotypic acclimation and its evolution in Escherichia coli. Evolution 51 (1), 36–44.
Bennett, A.F., Dao, K.M., Lenski, R.E., 1990. Rapid evolution in response to high-temperature selection. Nature 346 (6279), 79–81.
Birgander, J., Reischke, S., Jones, D.L., Rousk, J., 2013. Temperature adaptation of bacterial growth and 14C-glucose mineralisation in a laboratory study. Soil Biol. Biochem. 65, 294–303.
Boone, R.D., Nadelhoffer, K.J., Canary, J.D., Kaye, J.P., 1998. Roots exert a strong influence on the temperature sensitivityof soil respiration. Nature 396 (6711), 570–572.
Bradford, M.A., McCulley, R.L., Crowther, T., Oldfield, E.E., Wood, S.A., Fierer, N., 2019. Cross-biome patterns in soil microbial respiration predictable from evolutionary theory on thermal adaptation. Nat. Ecol. Evol. 3 (2), 223–231.
Caporaso, J.G., Kuczynski, J., Stombaugh, J., Bittinger, K., Bushman, F.D., Costello, E.K., Fierer, N., Gonzalez Pena, A., Goodrich, J.K., Gordon, J.I., Huttley, G.A., Kelley, S.I., Knights, D., Koenig, J.E., Ley, R.E., Lozupone, C.A., McDonald, D., Muegge, B.D., Pirrung, M., Reeder, J., Sevinsky, J.R., Turnbaugh, P.J., Walters, W.A., Widmann, J., Yatsunenko, T., Zaneveld, J., Knight, R., 2010. QIIME allows analysis of high-throughput community sequencing data. Nat. Methods 7 (5), 335–336.
Caporaso, J.G., Lauber, C.L., Walters, W.A., Berg-Lyons, D., Lozupone, C.A., Turnbaugh, P.J., Fierer, N., Knight, R., 2011. Global patterns of 16S rRNA diversity at a depth of millions of sequences per sample. Proc. Natl. Acad. Sci. U.S.A. 108, 4516–4522.
Carey, J.C., Tang, J., Templer, P.H., Kroeger, K.D., Crowther, T.W., Burton, A.J., Dukes, J.S., Emmett, B., Frey, S.D., Heskel, M.A., Jiang, L.F., Machmuller, M.B., Mohan, J., Panetta, A.M., Reich, P.B., Reinsch, S., Wang, X., Allison, S.D., Bamminger, C., Bridgham, S., Collins, S.L., de Dato, G., Eddy, W.C., Enquist, B.J., Estiarte, M., Harte, J., Henderson, A., Johnson, B.R., Larsen, K.S., Luo, Y., Marhan, S., Melillo, J.M., Penuelas, J., Pfeifer-Meister, L., Poll, C., Rastetter, E., Reinmann, A.B., Reynolds, L.L., Schmidt, I.K., Shaver, G.R., Strong, A.L., Susseela, V., Tietema, A., 2016. Temperature response of soil respiration largely unaltered with experimental warming. PNAS 113 (48), 13797–13802.
Chen, C., Chen, H.Y., 2023. Mapping global nitrogen deposition impacts on soil respiration. Sci. Total Environ. 871, 161986.
Chen, J., Zhang, Y., Kuzyakov, Y., Wang, D., Olesen, J.E., 2023. Challenges in upscaling laboratory studies to ecosystems in soil microbiology research. Glob. Chang. Biol. 29, 569–574.
Crowther, T.W., Bradford, M.A., 2013. Thermal acclimation in widespread heterotrophic soil microbes. Ecol. Lett. 16 (4), 469–477.
Cui, Y., Peng, S., Delgado-Baquerizo, M., Rillig, M.C., Terrer, C., Zhu, B., Jing, X., Chen, J., Li, J., Feng, J., He, Y., Fang, L., Moorhead, D.L., Sinsabaugh, R.L., Peñuelas, J., 2023. Microbial communities in terrestrial surface soils are not widely limited by carbon. Glob. Chang. Biol. 29 (15), 4412–4429.
Delgado-Baquerizo, M., Bissett, A., Eldridge, D.J., Maestre, F.T., He, J.Z., Wang, J.T., Hamonts, K., Liu, Y.R., Singh, B.K., Fierer, N., 2017. Palaeoclimate explains a unique proportion of the global variation in soil bacterial communities. Nat. Ecol. Evol. 1 (9), 1339–1347.
Donhauser, J., Niklaus, P.A., Rousk, J., Larose, C., Frey, B., 2020. Temperatures beyond the community optimum promote the dominance of heat-adapted, fast growing and stress resistant bacteria in alpine soils. Soil Biol. Biochem. 148, 107873.
Edgar, R.C., 2013. UPARSE: highly accurate OTU sequences from microbial amplicon reads. Nat. Methods 10 (10), 996–998.
Edgar, R.C., Haas, B.J., Clemente, J.C., Quince, C., Knight, R., 2011. UCHIME improves sensitivity and speed of chimera detection. Bioinformatics 27 (16), 2194–2200.
Feng, X., Wang, S., 2023. Plant influences on soil microbial carbon pump efficiency. Glob. Chang. Biol. 29 (14), 3854–3856.
Feng, Y., Zhang, J., Berdugo, M., Guirado, E., Guerra, C.A., Egidi, E., Wang, J.T., Singh, B.K., Delgado-Baquerizo, M., 2022. Temperature thresholds drive the global distribution of soil fungal decomposers. Glob. Chang. Biol. 28 (8), 2779–2789.
Fierer, N., Bradford, M.A., Jackson, R.B., 2007. Toward an ecological classification of soil bacteria. Ecology 88 (6), 1354–1364.
Fukasawa, Y., 2018. Temperature effects on hyphal growth of wood-decay basidiomycetes isolated from Pinus densiflora deadwood. Mycoscience 59 (3), 259–262.
García-Palacios, P., Crowther, T.W., Dacal, M., Hartley, I.P., Reinsch, S., Rinnan, R., Rousk, J., den Hoogen, J., Ye, J.S., Bradford, M.A., 2021. Evidence for large microbial-mediated losses of soil carbon under anthropogenic warming. Nat. Rev. Earth Environ. 2 (7), 507–517.
Gavito, M.E., Olsson, P.A., Rouhier, H., Medina-Peñafiel, A., Jakobsen, I., Bago, A., Azcón-Aguilar, C., 2005. Temperature constraints on the growth and functioning of root organ cultures with arbuscular mycorrhizal fungi. New Phytol. 168 (1), 179–188.
Guo, X., Gao, Q., Yuan, M., Wang, G., Zhou, X., Feng, J., Shi, Z., Hale, L., Wu, L., Zhou, A., Tian, R., Liu, F., Wu, B.O., Chen, L., Jung, C.G., Niu, S., Li, D., Xu, X., Jiang, L., Escalas, A., Wu, L., He, Z., Van Nostrand, J.D., Ning, D., Liu, X., Yang, Y.F., Schuur, A.G., Konstatinidis, K.T., Cole, J.R., Penton, R., Luo, Y., Tiedje, J.M., Zhou, J., 2020a. Gene-informed decomposition model predicts lower soil carbon loss due to persistent microbial adaptation to warming. Nat. Commun. 11 (1), 4897.
Guo, Z., Wan, S., Hua, K., Yin, Y., Chu, H., Wang, D., Guo, X., 2020b. Fertilization regime has a greater effect on soil microbial community structure than crop rotation and growth stage in an agroecosystem. Appl. Soil Ecol. 149, 103510.
Guo, Z., Liu, C.A., Hua, K., Wang, D., Wan, S., He, C., Zhan, L., 2022. Temporal variation of management effects on soil microbial communities. Geoderma 418, 115828.
Haaf, D., Six, J., Doetterl, S., 2021. Global patterns of geo-ecological controls on the response of soil respiration to warming. Nat. Clim. Chang. 11 (7), 623–627.
He, Q., Wang, S., Feng, K., Michaletz, S.T., Hou, W., Zhang, W., Li, F., Zhang, Y., Wang, D., Peng, X., Yang, X., Deng, Y., 2023. High speciation rate of niche specialists in hot springs. ISME J. 17, 1303–1314.
Hutchinson, G.L., Livingston, G.P., 1993. Use of chamber systems to measure trace gas fluxes. In: Agricultural Ecosystem Effects on Trace Gases and Global Climate Change, 55, pp. 63–78.
Ishfaq, M., Wang, Y., Xu, J., Hassan, M.U., Yuan, H., Liu, L., He, B., Ejaz, I., White, P.J., Cakmak, I., Chen, W.S., Wu, J.C., van der Werf, W., Li, C., Zhang, F., Li, X., 2023. Improvement of nutritional quality of food crops with fertilizer: a global meta-analysis. Agron. Sustain. Dev. 43 (6), 74.
IUSS Working Group, 2014. World reference base for soil resources 2014. In: International soil classification system for naming soils and creating legends for soil maps.
Jiao, S., Yang, Y., Xu, Y., Zhang, J., Lu, Y., 2020. Balance between community assembly processes mediates species coexistence in agricultural soil microbiomes across eastern China. ISME J. 14 (1), 202–216.
Kirschbaum, M.U., 2013. Seasonal variations in the availability of labile substrate confound the temperature dependence of organic matter decomposition. Soil Biol. Biochem. 57, 568–576.
Kirschbaum, M.U., 2004. Soil respiration under prolonged soil warming: are rate reductions caused by acclimation or substrate loss? Glob. Chang. Biol. 10 (11), 1870–1877.
Kõljalg, U., Nilsson, R.H., Abarenkov, K., Tedersoo, L., Taylor, A.F.S., Bahram, M., Bates, S.T., Bruns, T.D., Bengtsson-Palme, J., Callaghan, T.M., Douglas, B., Drenkhan, T., Eberhardt, U., Dueñas, M., Grebenc, T., Griffith, G.W., Hartmann, M., Kirk, P.M., Kohout, P., Larsson, E., Lindahl, B.D., Lücking, R., Martín, M.P.,

Matheny, P.B., Nguyen, N.H., Niskanen, T., Oja, J., Peay, K.G., Peintner, U., Peterson, M., Põldmaa, K., Saag, L., Saar, I., Schüßler, A., Scott, J.A., Senés, C., Smith, M.E., Suija, A., Taylor, D.L., Telleria, M.T., Weiss, M., Larsson, K.H., 2013. Towards a unified paradigm for sequence-based identification of fungi. Mol. Ecol. 22, 5271–5277.
Lennon, J.T., Aanderud, Z.T., Lehmkuhl, B.K., Schoolmaster Jr., D.R., 2012. Mapping the niche space of soil microorganisms using taxonomy and traits. Ecology 93 (8), 1867–1879.
Levine, J.M., HilleRisLambers, J., 2009. The importance of niches for the maintenance of species diversity. Nature 461 (7261), 254–257.
Levins, R., 1968. Evolution in Changing Environments: Some Theoretical Explorations. Princeton University Press.
Li, C., Xiao, C., Guenet, B., Li, M., Xu, L., He, N., 2022. Short-term effects of labile organic C addition on soil microbial response to temperature in a temperate steppe. Soil Biol. Biochem. 167, 108589.
Li, D., Zhang, G., Gong, Z., 2011. On taxonomy of Shajiang black soils in China. Soils 43 (4), 623–629.
Li, H., Yang, S., Semenov, M.V., Yao, F., Ye, J., Bu, R., Ma, R., Lin, J., Kurganova, I., Wang, X., Deng, Y., Kravchenko, I., Jiang, Y., Kuzyakov, Y., 2021. Temperature sensitivity of SOM decomposition is linked with a K-selected microbial community. Glob. Chang. Biol. 27 (12), 2763–2779.
Li, J., Pei, J., Pendall, E., Fang, C., Nie, M., 2020. Spatial heterogeneity of temperature sensitivity of soil respiration: a global analysis of field observations. Soil Biol. Biochem. 141, 107675.
Lin, Y., Ye, G., Kuzyakov, Y., Liu, D., Fan, J., Ding, W., 2019. Long-term manure application increases soil organic matter and aggregation, and alters microbial community structure and keystone taxa. Soil Biol. Biochem. 134, 187–196.
Mason-Jones, K., Vrehen, P., Koper, K., Wang, J., van der Putten, W.H., Veen, G.C., 2020. Short-term temperature history affects mineralization of fresh litter and extant soil organic matter, irrespective of agricultural management. Soil Biol. Biochem. 150, 107985.
Moinet, G.Y., Dhami, M.K., Hunt, J.E., Podolyan, A., Liáng, L.L., Schipper, L.A., Whitehead, D., Nunez, J., Nascente, A., Millard, P., 2021. Soil microbial sensitivity to temperature remains unchanged despite community compositional shifts along geothermal gradients. Glob. Chang. Biol. 27 (23), 6217–6231.
Mou, Z., Kuang, L., Zhang, J., Li, Y., Wu, W., Liang, C., Hui, D., Lambers, H., Sardans, J., Penuelas, J., Liu, J., Ren, H., Liu, Z., 2023. Nutrient availability and stoichiometry mediate microbial effects on soil carbon sequestration in tropical forests. Soil Biol. Biochem. 186, 109186.
Nissan, A., Alcolombri, U., Peleg, N., Galili, N., Jimenez-Martinez, J., Molnar, P., Holzner, M., 2023. Global warming accelerates soil heterotrophic respiration. Nat. Commun. 14 (1), 3452.
Nottingham, A., Scott, J.J., Saltonstall, K., Broders, K., Montero-Sanchez, M., Püspök, J., Bååth, E., Meir, P., 2022. Microbial diversity decline and community response are decoupled from increased respiration in warmed tropical forest soil. Nat. Microbiol. 7, 1650–1660.
Nottingham, A.T., Hicks, L.C., Meir, P., Salinas, N., Zimmermann, M., Bååth, E., 2021. Annual to decadal temperature adaptation of the soil bacterial community after translocation across an elevation gradient in the Andes. Soil Biol. Biochem. 158, 108217.
Numa, K.B., Robinson, J.M., Arcus, V.L., Schipper, L.A., 2021. Separating the temperature response of soil respiration derived from soil organic matter and added labile carbon compounds. Geoderma 400, 115128.
Pandit, S.N., Kolasa, J., Cottenie, K., 2009. Contrasts between habitat generalists and specialists: an empirical extension to the basic metacommunity framework. Ecology 90 (8), 2253–2262.
Podrebarac, F.A., Billings, S.A., Edwards, K.A., Laganière, J., Norwood, M.J., Ziegler, S. E., 2021. Soil profile connectivity can impact microbial substrate use, affecting how soil CO_2 effluxes are controlled by temperature. Biogeosciences 18 (16), 4755–4772.
Post, E., Brodie, J., Hebblewhite, M., Anders, A.D., Maier, J.A., Wilmers, C.C., 2009. Global population dynamics and hot spots of response to climate change. BioScience 59 (6), 489–497.
Qin, C., Pellitier, P.T., Van Nuland, M.E., Peay, K.G., Zhu, K., 2023. Niche modelling predicts that soil fungi occupy a precarious climate in boreal forests. Glob. Ecol. Biogeogr. 32, 1127–1139.
Rijkers, R., Rousk, J., Aerts, R., Sigurdsson, B.D., Weedon, J.T., 2022. Optimal growth temperature of Arctic soil bacterial communities increases under experimental warming. Glob. Chang. Biol. 28 (20), 6050–6064.
Rijkers, R., Dekker, M., Aerts, R., Weedon, J.T., 2023. Maximum summer temperatures predict the temperature adaptation of Arctic soil bacterial communities. Biogeosciences 20 (4), 767–780.
Rillig, M.C., van der Heijden, M.G., Berdugo, M., Liu, Y.R., Riedo, J., Sanz-Lazaro, C., Moreno-Jimenez, E., Romero, F., Tedersoo, L., Delgado-Baquerizo, M., 2023. Increasing the number of stressors reduces soil ecosystem services worldwide. Nat. Clim. Chang. 13 (5), 478–483.
Rousk, J., Frey, S.D., Bååth, E., 2012. Temperature adaptation of bacterial communities in experimentally warmed forest soils. Glob. Chang. Biol. 18 (10), 3252–3258.
Schindlbacher, A., Schnecker, J., Takriti, M., Borken, W., Wanek, W., 2015. Microbial physiology and soil CO2 efflux after 9 years of soil warming in a temperate forest–no indications for thermal adaptations. Glob. Chang. Biol. 21 (11), 4265–4277.
Schmidt, P.A., Bálint, M., Greshake, B., Bandow, C., Römbke, J., Schmitt, I., 2013. Illumina metabarcoding of a soil fungal community. Soil Biol. Biochem. 65, 128–132.
Shen, C., Gunina, A., Luo, Y., Wang, J., He, J.Z., Kuzyakov, Y., Hemp, A., Classen, A.T., Ge, Y., 2020. Contrasting patterns and drivers of soil bacterial and fungal diversity across a mountain gradient. Environ. Microbiol. 22 (8), 3287–3301.
Tian, W., Sun, H., Zhang, Y., Xu, J., Yao, J., Li, J., Li, B., Nie, M., 2022. Thermal adaptation occurs in the respiration and growth of widely distributed bacteria. Glob. Chang. Biol. 28 (8), 2820–2829.
Tilman, D., 2004. Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. PNAS 101 (30), 10854–10861.
von Meijenfeldt, F.B., Hogeweg, P., Dutilh, B.E., 2023. A social niche breadth score reveals niche range strategies of generalists and specialists. Nat. Ecol. Evol. 7 (5), 768–781.
Voyles, J., Johnson, L.R., Rohr, J., Kelly, R., Barron, C., Miller, D., Minster, J., Rosenblum, E.B., 2017. Diversity in growth patterns among strains of the lethal fungal pathogen Batrachochytrium dendrobatidis across extended thermal optima. Oecologia 184, 363–373.
Wang, Q., Garrity, G.M., Tiedje, J.M., Cole, J.R., 2007. Naive Bayesian classifier for rapid assignment of rRNA sequences into the new bacterial taxonomy. Appl. Environ. Microbiol. 73 (16), 5261–5267.
Wang, Q., Liu, S., Wang, Y., Tian, P., Sun, T., 2018. Influences of N deposition on soil microbial respiration and its temperature sensitivity depend on N type in a temperate forest. Agric. For. Meteorol. 260, 240–246.
Wang, Q., Zhao, X., Chen, L., Yang, Q., Chen, S., Zhang, W., 2019. Global synthesis of temperature sensitivity of soil organic carbon decomposition: latitudinal patterns and mechanisms. Funct. Ecol. 33 (3), 514–523.
Wang, X., Li, S., Zhu, B., Homyak, P.M., Chen, G., Yao, X., Yang, Y., 2023. Long-term nitrogen deposition inhibits soil priming effects by enhancing phosphorus limitation in a subtropical forest. Glob. Chang. Biol. 29, 4081–4093.
Wang, Y., Zhang, Y., Li, X., Dong, W., Hu, C., Zhang, Y., 2021a. Partitioning nocturnal respirations and their respective δ13C signatures in a wheat–maize rotation. Agric. For. Meteorol. 307, 108490.
Wang, Z., Wang, Z., Li, T., Wang, C., Dang, N., Wang, R., Jiang, Y., Wang, H., Li, H., 2021b. N and P fertilization enhanced carbon decomposition function by shifting microbes towards an r-selected community in meadow grassland soils. Ecol. Indic. 132, 108306.
Yang, S., Wu, H., Wang, Z., Semenov, M.V., Ye, J., Yin, L., Wang, X., Kravchenko, I., Semenov, V., Kuzyakov, Y., Jiang, Y., Li, H., 2022a. Linkages between the temperature sensitivity of soil respiration and microbial life strategy are dependent on sampling season. Soil Biol. Biochem. 172, 108758.
Yang, X., Duan, P., Hicks, L., Wang, K., Li, D., 2023. Mechanisms underlying the responses of microbial carbon and nitrogen use efficiencies to nitrogen addition are mediated by topography in a subtropical forest. Sci. Total Environ. 880, 163236.
Yang, Y., Li, T., Pokharel, P., Liu, L., Qiao, J., Wang, Y., An, S.S., Chang, S.X., 2022b. Global effects on soil respiration and its temperature sensitivity depend on nitrogen addition rate. Soil Biol. Biochem. 174, 108814.
Yuste, J.C., Penuelas, J., Estiarte, M., Garcia-Mas, J., Mattana, S., Ogaya, R., Pujol, O.M., Sardans, J., 2011. Drought-resistant fungi control soil organic matter decomposition and its response to temperature. Glob. Chang. Biol. 17 (3), 1475–1486.
Zhang, J., Zhang, B., Liu, Y., Guo, Y., Shi, P., Wei, G., 2018. Distinct large-scale biogeographic patterns of fungal communities in bulk soil and soybean rhizosphere in China. Sci. Total Environ. 644, 791–800.
Zhang, X., Zhang, J., Zheng, C., Guan, D., Li, S., Xie, F., Chen, J., Hang, X., Jiang, Y., Deng, A., Afreh, D., Zhang, W., 2017. Significant residual effects of wheat fertilization on greenhouse gas emissions in succeeding soybean growing season. Soil Tillage Res. 169, 7–15.
Zhang, Y., Li, J.T., Xu, X., Chen, H.Y., Zhu, T., Xu, J.J., Xu, X.N., Li, J.Q., Liang, C., Li, B., Fang, C.M., Nie, M., 2023. Temperature fluctuation promotes the thermal adaptation of soil microbial respiration. Nat. Ecol. Evol. 7 (2), 205–213.
Zheng, M., Zhang, T., Luo, Y., Liu, J., Lu, X., Ye, Q., Wang, S., Huang, J., Mao, Q.G., Mo, J.G., Zhang, W., 2022. Temporal patterns of soil carbon emission in tropical forests under long-term nitrogen deposition. Nat. Geosci. 15 (12), 1002–1010.
Zheng, X., Zhang, Y., Zhang, Y., Cui, Y., Wu, J., Zhang, W., Wang, D., Zou, J., 2023. Interactions between nitrogen and phosphorus in modulating soil respiration: a meta-analysis. Sci. Total Environ. 905, 167346.