Title page

Microbial assemblies associated with temperature sensitivity of soil respiration along an altitudinal gradient

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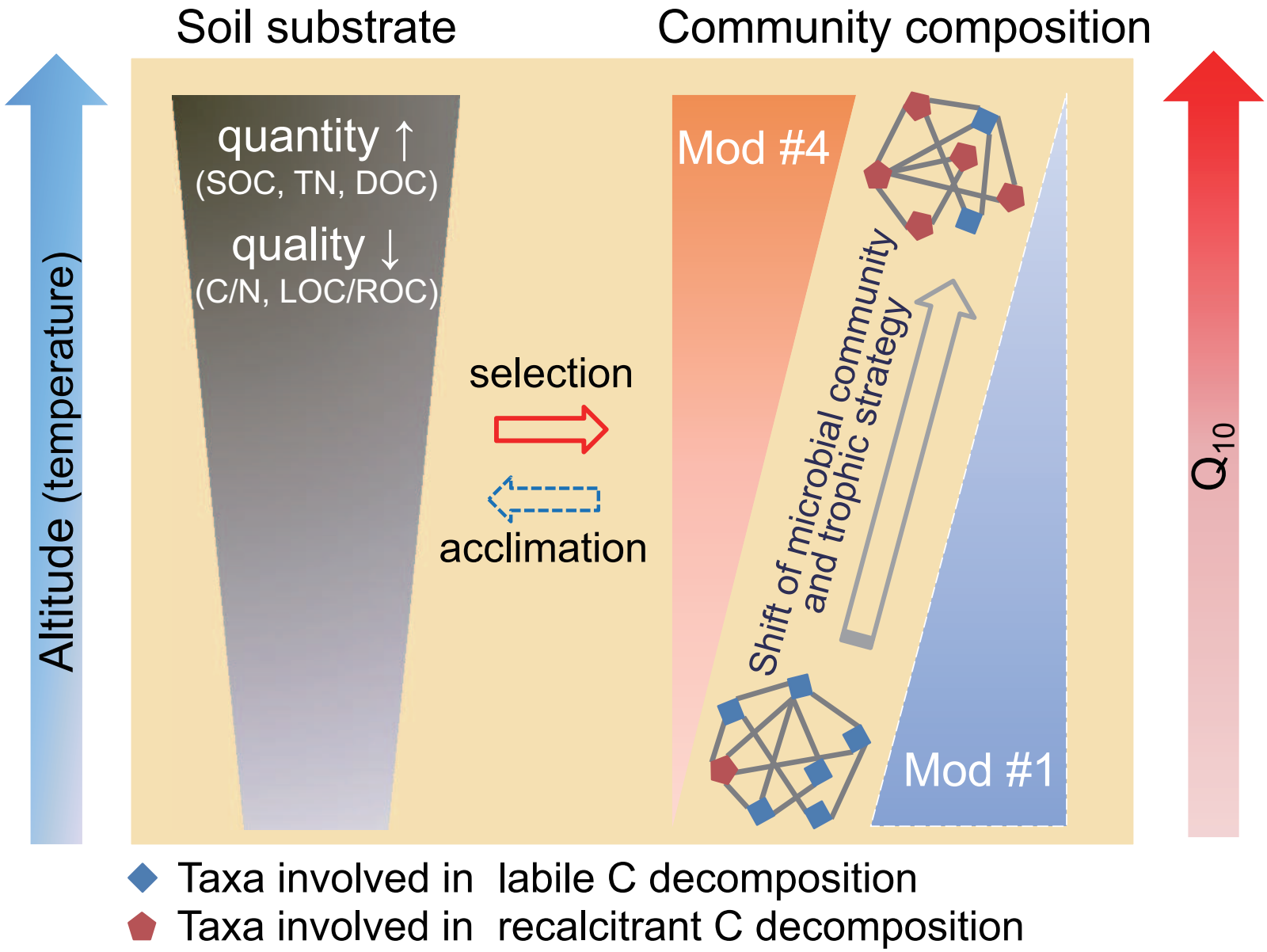
Graphical Abstract



Highlights

- Soil microbial communities drove changes in Q_{10} of soil respiration
- Microbial assemblies with distinct C utilization strategies varied with altitude
- The major co-occurring microbial assemblies were important predictors of Q_{10}

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Abstract

Identifying the drivers of the response of soil microbial respiration to warming is integral to accurately forecasting the carbon-climate feedbacks in terrestrial ecosystems. Microorganisms are the fundamental drivers of soil microbial respiration and its response to warming; however, the specific microbial communities and properties involved in the process remain largely undetermined. Here, we identified the associations between microbial community and temperature sensitivity (Q_{10}) of soil microbial respiration in alpine forests along an altitudinal gradient (from 2974 to 3558 m) from the climate-sensitive Tibetan Plateau. Our results showed that changes in microbial community composition accounted for more variations of Q_{10} values than a wide range of other factors, including soil pH, moisture, substrate quantity and quality, microbial biomass, diversity and enzyme activities. Specifically, co-occurring microbial assemblies (i.e., ecological clusters or modules) targeting labile carbon consumption were negatively correlated with Q_{10} of soil microbial respiration, whereas microbial assemblies associated with recalcitrant carbon decomposition were positively correlated with Q_{10} of soil microbial respiration. Furthermore, there were progressive shifts of microbial assemblies from labile to recalcitrant carbon consumption along the altitudinal gradient, supporting relatively high Q_{10} values in high-altitude regions. Our results provide new insights into the link between changes in major microbial assemblies with different trophic strategies and Q_{10} of soil microbial respiration along an altitudinal gradient, highlighting that warming could

have stronger effects on microbially-mediated soil organic matter decomposition in high-altitude regions than previously thought.

Keywords

Soil microbial respiration; temperature sensitivity; microbial community composition; ecological clusters; altitudinal gradient; Tibetan Plateau

1. Introduction

Soil contains about three times the carbon (C) stored in the atmosphere, and the release of C from soil through microbial respiration is a major component of global CO_2 fluxes (Guo et al., 2020; Raich and Potter, 1995; Raich and Schlesinger, 1992). Consequently, changes in soil microbial respiration could have profound effects on atmospheric CO_2 concentration, and thus affect future climate trajectories (Dacal et al., 2019; Wang et al., 2018). Soil microbial respiration is susceptible to temperature fluctuations (Bradford et al., 2019; Li et al., 2021b; Wang et al., 2016), with the respiration rates commonly increasing with rising temperature (Karhu et al., 2014). The response of soil microbial respiration to temperature changes is usually represented by the term temperature sensitivity or Q_{10}, quantified by the relative increase in respiration rate with each 10 °C rise in temperature (Davidson and Janssens, 2006; Xu et al., 2021; Yu et al., 2017). The Q_{10} value is a crucial parameter in benchmarking the magnitude and direction of terrestrial soil C-climate feedbacks (Davidson and Janssens, 2006; Li et al., 2020a). However, the magnitude of this feedback remains uncertain due to the different effects of biotic and abiotic factors (such as microbial activities, substrate quantity and quality) on soil respiration (Dacal et al., 2019; Wang et al., 2018). In particular, microbial communities are the fundamental drivers of soil microbial respiration (Bradford et al., 2019; Liu et al., 2018b; Wang et al., 2020b); however, the role of soil microbial communities in

68 regulating the response of soil microbial respiration to warming remains largely
69 unclear.

70 A growing body of literature has demonstrated that temperature sensitivity of soil
71 microbial respiration is significantly related to important microbial community-level
72 properties, including the biomass and physiology (Bradford et al., 2019; Wang et al.,
73 2018). For example, microbial biomass C (MBC) has been confirmed to have a
74 positive correlation with temperature sensitivity of soil microbial respiration (Čapek
75 et al., 2019). In addition, physiological features of microbial community, such as
76 extracellular enzymatic activities, have also been quantitatively linked to the response
77 of soil microbial respiration to temperature changes (Chen et al., 2018; Wang et al.,
78 2020a). Recent studies suggest that physiological activities at the community level
79 were dominantly determined by the composition of microbial communities (Monteux
80 et al., 2018; Wieder et al., 2014). Different microbial taxa decompose various organic
81 matter fractions at different rates and can fundamentally alter the response of soil
82 microbial respiration to warming (Bai et al., 2017; Luo et al., 2020; Wang et al., 2021).
83 For instance, some specific bacteria (e.g., Chlamydiae and Planctomycetia) and fungi
84 (e.g., Agaricomycetes and Mucoromycotina) are considered as main decomposers of
85 recalcitrant C, while other taxa such as Tremellomycetes and Pezizomycotina can
86 prefer utilizing labile C (Hale et al., 2019; Sun et al., 2020). Similarly, the specific
87 trophic patterns of soil microbes, such as r-strategists and K-strategists, can also affect
88 temperature sensitivity of soil microbial respiration due to differences in substrate

89 preference and C use efficiency (Bai et al., 2017; Li et al., 2021a; Luo et al., 2020).
90 However, soil respiration is generally considered as a “broad biological process”
91 involving a wide array of microbial taxa, metabolic reactions, and associated genes,
92 hence precluding targeting the taxa involved with classical molecular approaches
93 (Banerjee et al., 2016; Crowther et al., 2019). Therefore, detailed information on
94 specific microbial taxa that drive the responses of soil microbial respiration to
95 warming is still lacking. Unraveling the major microbial assemblies (groups)
96 associated with temperature sensitivity of soil microbial respiration is fundamental to
97 better forecasting the C-climate feedbacks in a warmer planet.

98 Here, we aimed to (1) investigate the associations between soil microbial
99 community composition and temperature sensitivity of soil microbial respiration, and
100 (2) identify major microbial assemblies associated with temperature sensitivity of soil
101 microbial respiration. We hypothesized that (1) shifts of soil microbial community
102 composition accounted for a large proportion of variations in temperature sensitivity
103 of soil microbial respiration; (2) particular ecological assemblies including co-
104 occurring microbial taxa had strong links with the temperature sensitivity of soil
105 microbial respiration. To test our hypotheses, we collected soil samples from 27 sites
106 along an altitudinal gradient on the Tibetan Plateau. This region is regarded as the
107 Earth’s largest and highest plateau with relatively pristine environment and high
108 sensitivity to climate change (Dong et al., 2020; Li et al., 2019). It has been reported
109 that the region is undergoing a more rapid warming than other parts of the world

(Zhao et al., 2017), thus the responses of multiple ecosystem process to warming in this region is currently receiving great attention (Ma et al., 2020a; Xu et al., 2021). There were drastic changes of climatic, biotic and abiotic environmental conditions over short vertical distances (Zeng et al., 2016). Moreover, soil microbial communities had been reported to vary significantly with abiotic factors (such as soil pH, moisture, and substrate availability etc.) along altitudinal gradient of the plateau (Li et al., 2019; Shen et al., 2019; Wang et al., 2017). Therefore, it provides an ideal natural platform for exploring the effect of soil microbial community on temperature sensitivity of soil microbial respiration. We evaluated the associations between soil microbial community-level properties (biomass, enzyme activities, bacterial and fungal diversity and community composition) and the temperature sensitivity of soil microbial respiration. Further, we identified the major microbial assemblies associated with the response of soil microbial respiration to temperature changes by constructing co-occurrence networks. The results of this study hold the potential in improving prediction of terrestrial C turnover in response to global climate changes.

2. Materials and Methods

2.1 Study area and field sampling

The study was conducted along an altitudinal gradient in Nyingchi Prefecture on the southeastern Tibetan Plateau (29°34′-29°37′ N, 94°19′-94°22′ E) (Fig. S1). The altitude ranges from 2974 to 3558 m, with mean annual temperature declining

significantly (R^2 = 0.86) from 8.6 to 4.7 °C along increasing altitude according to WorldClim (http://www.worldclim.org). The mean temperature in the growing season (between June and August) declined from approximately 19 to 6 °C with increasing altitude (Chen et al., 2014; Zhuo et al., 2010). Mean annual precipitation ranges from 680 to 1134 mm, with the most of precipitation occurring in July and August (Chen et al., 2014; Liang et al., 2009). The major ecosystem types changed from the temperate coniferous and broadleaved mixed forests (dominated by *Quercus aquifolioides* and *Populus simonii*) to frigid dark coniferous forests (dominated by *Pinus densata* and *Picea likiangensis* var. *linzhiensis*) with increasing altitude. Other coexisting plant species mainly included *Rhododendron triflorum* Hook., *Caragana franchetiana* Kom., *Iris latistyla* and *Anemone rivularis*. The dominant soil types belong to Luvisols and Cambisols based on World Reference Base for Soil Resources (IUSS Working Group WRB, 2007). Twenty-seven sites were selected in alpine forests along the altitudinal gradient in August 2018. At each site, a 50 m × 50 m plot was selected and then five 1 m × 1 m sub-plots were set up to represent five replicates. Composite soil samples (0-10 cm, from five soil cores) were collected from the understory or adjacent open grasslands of each sub-plots. Collected soil samples were immediately transported to the laboratory on ice. The stones and roots were carefully picked out, and then the soil samples were divided into two portions. One was stored at −20 °C for the analyses of microbial community (i.e., Miseq Illumina sequencing), and the other portion was stored at 4 °C for the analyses of enzyme activities and Q_{10} of soil

151 microbial respiration.

152 *2.2 Analyses of soil chemical and microbial properties*

153 Soil pH was determined at a ratio of soil to water ratio of 1: 2.5 (w/v) by a glass
154 electrode. Soil moisture was measured by oven-drying fresh soil for 24 h at 105 °C.
155 Soil organic carbon (SOC) content was determined by the K_2CrO_7 oxidation titration
156 method (Walkley, 1947). Soil total nitrogen (TN) was directly quantified by an
157 elemental analyzer (Vario PYRO Cube, Elementar, Germany). Dissolved organic
158 carbon (DOC) was extracted with deionized water at a ratio of 1:4 (w/v), and then
159 filtered through a 0.45 μM Millipore filter. The concentrations of DOC in the extracts
160 were analyzed using a TOC Analyzer (vario TOC, Elementar, Germany). Labile and
161 recalcitrant fractions of SOC were measured using a two-step acid hydrolysis method
162 (Rovira and Vallejo, 2008; Wu et al., 2018). Briefly, 0.5g of soil was hydrolyzed with
163 25 mL of 2.5 M H_2SO_4 at 105 °C for 30 min. The residue decanted by centrifuging
164 was washed twice with water and dried at 60 °C. The dried residue was re-hydrolyzed
165 with 2 mL of 13 M H_2SO_4 at 105 °C for 3 h, washed and then dried. The C content in
166 this fraction was measured using an elemental analyzer (Vario PYRO Cube,
167 Elementar, Germany) as recalcitrant C (ROC). The labile C (LOC) was calculated by
168 subtraction of ROC from total SOC.

169 Microbial biomass C was determined using the fumigation-extraction methods
170 (Vance et al., 1987). Soil enzyme activities involved in C cycling, including α-1,4-

glucosidase (AG), β-1,4-glucosidase (BG), cellobiohydrolase (CBH) and xylanase (XYL), were estimated by a fluorimetric microplate method (Marx et al., 2001). Briefly, 0.5 g of fresh soil was blended in 50 mL of deionized water for 15 min. Then each aliquot of soil homogenate was mixed with 100 μL of fluorometric substrate solution (200 μmol L^{-1}) and 50 μL of acetate buffer (0.2 mol L^{-1}, pH 5.5). Microplates were then incubated for 3 h at 30 °C (Feng et al., 2018). The released fluorescence was measured using a multifunctional fluorimetric plate reader (Tecan Spark™ 10M, Männedorf, Switzerland) with 360 nm excitation and 450 nm emission filters. The activities were expressed as nmol g^{-1} soil h^{-1}.

2.3 Measurements of temperature sensitivity of soil microbial respiration

Temperature sensitivity of soil microbial respiration was estimated using a short-term incubation method following many other studies (Liu et al., 2017; Wang et al., 2018). Specifically, all soil samples were incubated for 14 days at 10 °C and 20 °C, respectively, following the approximate air temperature ranges of growing season at our study sites (Li et al., 2021a; Zhang et al., 2020). We selected 14 days short-term aerobic incubation following previous studies to prevent significant changes in microbial community composition (Li et al., 2019; Zhang et al., 2020), as the legacy effects of environmental factors on soil microbial communities may last for years (Averill et al., 2016; Rousk et al., 2013). Our evaluation of Q_{10} can, at least potentially, reflect the responses of soil microbial respiration to temperature changes, as done in many previous studies (Guo et al., 2020; Johnston and Sibly, 2018; Xu et al., 2021).

The fresh soil sample (10 g, equivalent dry weight) was placed in a 250 mL incubation bottle (three replicates for each soil) and adjusted to 60% water holding capacity (WHC), which is well-suited for microbial respiration (Li et al., 2020b). The experimental bottles were sealed using parafilm with small holes for ventilation and to reduce water loss (Wang et al., 2018). In total, 162 incubations were performed, including 27 sites × 2 incubation temperatures × 3 replicates. During the incubation, soil WHC was maintained by adding deionized water based on the weighing method at intervals of 3-4 days (Liu et al., 2017). After 14-days incubation, we measured soil respiration rates of all incubation bottles. Before the incubation bottles were sealed, ambient air was continuously passed through the headspace of bottles for approximately 30 minutes by an air distribution system. After achieving the equilibrium stage, the incubation bottles were sealed, and 6 mL headspace samples were collected by plastic syringes. We additionally compared the CO_2 concentrations in the bottle headspace with the ambient air, and found no significant differences between them ($P > 0.05$). Moreover, the amounts of CO_2 in the headspace of different bottles at the time of sealing were comparable to those in the ambient air. We also conducted a pre-experiment to evaluate the effect of sampling time on the rates of soil respiration. We found that the concentration of CO_2 increased linearly over 0-5 h sampling period at both 10 °C and 20 °C incubation (Fig. S2; $R^2 = 0.83 \sim 0.99$), indicating that CO_2 was produced at a relatively constant rate during the sampling period. Therefore, we evaluated the soil microbial respiration rate based on the

measurement of CO_2 concentrations at 0 and 2 h, as done in previous studies (Chen et al., 2019; Li et al., 2020c). After 2 hours incubation, the headspace sample of each bottle was collected again. The concentrations of CO_2 were analyzed by gas chromatography (Agilent 7890A, Agilent Technologies, USA). The rate of soil microbial respiration was calculated using Eqs. (1) (Shaaban et al., 2016):

$$Rs = \rho \times V / W \times \Delta c / \Delta t \times 273 / (T + 273) \quad (1)$$

where Rs is the soil microbial respiration rate (mg kg^{-1} h^{-1}); ρ is CO_2 density at standard conditions (g L^{-1}); V is the volume of the incubation bottle (L), W is soil dry weight (g), Δc is the gas production during the sealed 2 h (mg kg^{-1}), Δt is the sealed time for gas production (h), and T is the incubation temperature (°C).

The Q_{10} of soil microbial respiration was calculated using Eqs. (2) (Hicks Pries et al., 2017):

$$Q_{10} = \left(\frac{R(T_2)}{R(T_1)}\right)^{\frac{10}{(T_2-T_1)}} \quad (2)$$

where $R(T_2)$ and $R(T_1)$ are the CO_2 production rates (mg kg^{-1} h^{-1}) in the two incubation temperatures T_1 and T_2 (°C), respectively.

2.4 Soil microbial community analysis

Soil DNA was extracted from 0.25 g of fresh soil stored at −20 °C using the MoBio Power Soil DNA Isolation Kit (MoBio Laboratories, Carlsbad, CA, USA) according to the manufacturer's instructions. The V3-V4 region of the bacterial 16S rRNA gene

and ITS of fungi were amplified using primers 338F/806R (ben Omar and Ampe, 2000; McBain et al., 2003) and ITS1F/ITS2R (Gardes and Bruns, 1993; White et al., 1990), respectively. The purified amplicons with different barcodes were equimolarly mixed, and 2 × 300 bp paired-end sequencing was carried out on an Illumina Miseq sequencer (Illumina, Inc., San Diego, CA, USA). The raw sequence data were processed using QIIME 1.7.0. The quality-filtered sequences were clustered and operational taxonomic units (OTUs) were generated according to the 97% sequence similarity (Metcalf et al., 2016). The diversity (Shannon index) and community composition of bacteria and fungi were calculated based on 97% OTUs similarity of obtained sequences.

2.5 Microbial co-occurrence network analysis

We constructed a co-occurrence network based on the relative abundances of bacterial and fungal OTUs, and then identified main ecological clusters (modules) of strongly associated OTUs as defined in Delgado-Baquerizo et al. (2020). To reduce rare OTUs in the data set, the OTUs with a relative abundance more than 0.01% were chosen (Ma et al., 2016), resulting in a dataset with 2340 taxa including 1433 bacterial and 907 fungal phylotypes (the operational taxonomic units or OTUs). We then calculated Spearman correlation coefficients between all the OTUs using the “WGCNA” package in R 4.0.2 (http://cran.r-project.org/) (Langfelder and Horvath, 2012). To reduce the chances of obtaining false positive results, the Benjamini and Hochberg FDR was used to adjust all *P*-values (Benjamini et al., 2006), as implemented in the

253 "multtest" R package (Pollard et al., 2005). Robust correlations with the Spearman
254 correlation coefficients > 0.60 and FDR adjusted *P*-value < 0.01 were used to
255 construct the network. The network was visualized by the interactive Gephi platform
256 (https://gephi.org/). The nodes in this network represent the OTUs and the edges
257 represent the significant correlations between different OTUs. We used default
258 parameters from Gephi to identify modules and the modularity reached 0.658 (values >
259 0.4 suggest that the network has a modular structure; Shi et al., 2016). The relative
260 abundance of each module was calculated by averaging the standardized relative
261 abundances (z-score) of the taxa that belong to each module (Liu et al., 2018a). We
262 also calculated the degree (i.e., the number of connections for each node) of each node
263 in the co-occurrence network by Gephi (Jiao et al., 2020). Nodes with high degree
264 values were considered as keystone taxa in the co-occurrence network (Zhang et al.,
265 2019).

266 *2.6 Statistical analysis*

267 The microbial community composition was determined by using the two axes of a
268 non-metric multidimensional scaling (NMDS) analysis based on the Bray-Curtis
269 dissimilarity matrix. Mantel test was used to test the statistical differences in
270 microbial community composition along the altitudinal gradient, using "vegan" R
271 package (Oksanen et al., 2016). We used correlation analysis to identify the
272 relationships between Q_{10} of soil microbial respiration, soil properties and microbial
273 community-level properties. We then conducted Random Forest machine learning

analysis to identify the significant environmental and microbial predictors of Q_{10} of soil microbial respiration using the "rfPermute" R package. We compared the percentage increases in the mean squared error (%IncMSE) of Q_{10} values to estimate the importance of different variables, with higher %IncMSE indicating more important variables. After that, we used regression analysis to further evaluate the relationships between Q_{10} of soil microbial respiration and main environmental and microbial factors.

Structural equation modeling (SEM) was conducted to evaluate the direct and indirect associations between altitude, soil and microbial properties and Q_{10} of soil microbial respiration. A prior model was established according to the known relationships between environmental variables and Q_{10} of soil microbial respiration (Banerjee et al., 2016; Dong et al., 2020; Feng et al., 2017) (Fig. S3). We considered that (1) altitude could drive Q_{10} of soil microbial respiration directly, and indirectly through impacting soil and microbial properties; (2) soil properties could indirectly drive Q_{10} of soil microbial respiration through microbial properties; (3) particular microbial assemblies (i.e., modules) including co-occurring microbial taxa could also directly affect Q_{10} of soil microbial respiration. Because the activities of four enzymes (AG, BG, CBH and XYL) were highly positively correlated (Table S1), we used a principal component analysis (PCA) to simplify the model and reduce the multicollinearity (Delgado-Baquerizo et al., 2016). The first component extracted from four enzymes (Enzyme) explained 81% of the total variance and was thus

295 considered as the representative of the overall variation in enzyme activities. The
296 maximum likelihood method was used for parameter estimations (Boldea and Magnus,
297 2009). There is no universally accepted single test of overall goodness of fit for SEM.
298 We used two goodness of fit measures of the model including (1) the chi-squared test
299 (χ^2; the model has a good fit when $0 \leq \chi^2/df \leq 2$ and $0.05 < P \leq 1.00$, and acceptable
300 fit when $2 < \chi^2/df \leq 3$ and $0.01 \leq P \leq 0.05$) and (2) the root mean square error of
301 approximation (RMSEA; the model has a good fit when $0 \leq RMSEA \leq 0.05$ and 0.10
302 $< P \leq 1.00$, and acceptable fit when $0.05 < RMSEA \leq 0.08$ and $0.05 \leq P \leq 0.10$)
303 (Delgado-Baquerizo et al., 2017). With a good model fit, we were free to interpret the
304 path coefficients of the model and their associated *P* values. Meanwhile, we also
305 calculated the standardized total effects of altitude, soil and microbial properties on
306 the Q_{10} values. All the SEM analyses were performed using AMOS 17.0 (SPSS Inc.,
307 Chicago, IL, USA).

308 **3. Results**

309 *3.1 Variations in temperature sensitivity of soil microbial respiration along the*
310 *altitudinal gradient*

311 The results of regression analysis showed that Q_{10} of soil microbial respiration
312 increased significantly along the altitudinal gradient ($P < 0.001$; Fig. 1). We found
313 significant variations in soil pH ($P = 0.003$), moisture ($P < 0.001$), and substrate
314 quantity (SOC, DOC, $P < 0.001$; TN, $P = 0.011$) and quality (C/N, $P = 0.009$;

LOC/ROC, P = 0.012; Fig. S4) along the altitudinal gradient, which were significantly correlated with Q_{10} of soil microbial respiration excluding pH and LOC/ROC (P < 0.05; Fig. 2b and S5). Specifically, Q_{10} of soil microbial respiration correlated positively with soil moisture (P = 0.004), carbon and nitrogen content (SOC, P = 0.026; TN, P = 0.023; DOC, P = 0.047) and C/N ratio (P = 0.041).

3.2 Relationships between temperature sensitivity of soil microbial respiration and microbial properties at the community level

The Q_{10} values of soil microbial respiration were generally correlated with microbial community-level properties (Fig. S6). Specifically, Q_{10} values were positively correlated with MBC and enzyme activities, including BG, CBH, and XYL (P < 0.05). More importantly, both Random Forest machine learning analyses and correlation analysis consistently indicated that bacterial community composition (Bacteria_NMDS2) and fungal diversity (Fungi_shannon) explained the highest proportion of variations in Q_{10} values (Fig. 2 and S6). However, the proportion of most dominant bacterial and fungal phyla, except for Mortierellomycota, had no significant associations with the Q_{10} values (P > 0.05; Table S2). Additionally, these microbial properties at the community level varied significantly along the altitudinal gradient (Fig. S7 and S8). In brief, microbial biomass (MBC, P = 0.02) and enzyme activities (AG, P = 0.041; XYL, P = 0.02) showed overall increasing trends as the altitude increased (Fig. S7), while bacterial and fungal diversity (Shannon) declined significantly with the increasing altitude (P < 0.05; Fig. S8). Mantel test and

correlation analysis consistently indicated that bacterial and fungal community composition also varied significantly along the altitude ($P < 0.05$; Fig. S6 and S9).

3.3 Microbial assemblies and their relationships with temperature sensitivity of soil microbial respiration

Soil bacterial and fungal taxa within the co-occurrence network could be grouped into eight major ecological modules (with nodes > 2, Fig. 3a). Among them, the relative abundances of module #1 and #8 decreased with the increasing altitude, while module #4 and #5 showed the opposite patterns (Fig. S10). Results of Random Forest machine learning analysis indicated that module #1 and #4 were significant predictors ($P < 0.05$) of the Q_{10} of soil microbial respiration, even considering other environmental factors (i.e., soil and microbial community-level properties; Fig. S11 and S12). Further regression analysis showed that the Q_{10} values were correlated negatively with the relative abundance of module #1 but positively with that of module #4 (Fig. 3b). The module #1 was dominated by Alphaproteobacteria (e.g., Sphingomonas, Methylobacterium and Nordella), Actinobacteria (e.g., Conexibacter and Arthrobacter), Ascomycota (e.g., Cladophialophora and Knufia). The dominant phylotypes within module #4 were Acidobacteria (e.g., RB41), Deltaproteobacteria (e.g., Haliangium), Basidiomycota (e.g., Clavaria). The keystone taxa in module #1 included Sphingomonas, Blastococcus and Skermanella etc., and those in module #4 included RB41, Xylophilus, Castanediella etc. (Fig. 3c, Table S3).

3.4 The role of soil microbial communities in driving temperature sensitivity of soil microbial respiration

Our SEM analysis provided further statistical evidence that Q_{10} of soil microbial respiration had a strong link with microbial properties when we concurrently considered microbial community-level properties and other environmental properties such as pH, moisture, SOC, TN, DOC, C/N and LOC/ROC in the model (Fig. 4). Importantly, ecological module abundances explained the highest proportion of variations in Q_{10} of soil microbial respiration, with module #1 showing the largest total standardized effect (sum of direct and indirect effects) on the Q_{10} values. Specifically, the relative abundance of module #1 was directly and negatively associated with the Q_{10} values, while module #4 had a direct and positive relationship with Q_{10} values. In contrast, soil properties were indirectly related to the Q_{10} of soil microbial respiration through ecological modules and microbial diversity. However, we did not observe significant associations of MBC and enzyme activities with Q_{10} of soil microbial respiration according to the model.

4. Discussion

Our study provided empirical evidence for the important associations between soil microbial community composition and the temperature sensitivity of soil microbial respiration in alpine forests along the altitudinal gradient from the climate-sensitive Tibetan Plateau. Particularly, shifts in microbial community composition were more

closely related to temperature sensitivity of soil microbial respiration than other environmental factors such as soil pH, moisture, and substrate quantity and quality. More importantly, we identified major microbial assemblies (ecological clusters or modules) with different trophic strategies that were significant predictors of the temperature sensitivity of soil microbial respiration, providing unique information on microbial taxa potentially associated with the response of soil microbial respiration to temperature changes. Further, progressive shifts of microbial assemblies dominated by the taxa preferentially utilizing labile C or recalcitrant C could be major regulators of variations in temperature sensitivity of soil microbial respiration along the altitudinal gradient. These findings advance our understanding of the feedbacks of terrestrial C cycles to global climate changes.

The increased Q_{10} values with the increasing altitude indicate that soil microbial respiration is more sensitive to temperature changes in cold high-altitude regions. This is in concordance with previous studies on different latitudinal and altitudinal gradients with distinct temperature patterns (Gutiérrez-Girón et al., 2015; Liu et al., 2017; Wang et al., 2018). Consistent with our first hypothesis, we observed that the variations in the Q_{10} values along the altitudinal gradient largely depend on soil microbial community-level properties according to our combined analyses of SEM and Random Forest machine learning. Particularly, our findings highlight the important role of microbial community composition in driving Q_{10} of soil microbial respiration. Recent studies demonstrated that harsh environments (such as low

substrate quality and temperature) at high-altitude areas could favor the prevalence of particular microbial taxa that adapted to cold and oligotrophic conditions (Feng et al., 2017; Karhu et al., 2014; Malik et al., 2020b), and further shift microbial community by deterministic processes (Xun et al., 2019). Similarly, our results showed that substrate quality decreased (i.e., increased C/N ratio and decreased LOC/ROC ratio) with increasing altitude, which supported unique microbial communities responsible for the decomposition of low-quality C (e.g., phenolic and aromatic compounds commonly with high C/N ratio) at the high-altitude areas (Ali et al., 2018; Liu et al., 2017). Apart from soil substrate quality status, the altitude-induced changes in temperature could also influence soil microbial communities. Previous studies have suggested that shifts of microbial community composition responding to altitude were often dependent on temperature variations (Frindte et al., 2019; Ren et al., 2021). For instance, decreased temperature along increasing altitude would favor the dominance of fungal communities that preferentially utilize recalcitrant C, as lower temperature was more optimal for fungal growth compared with bacteria (Cheng et al., 2021; Whitaker et al., 2014). According to the C quality temperature hypothesis, the decomposition of low-quality substrate (recalcitrant C) is more sensitive to temperature changes than the high-quality substrate (labile C) because of its higher activation energy (Lefevre et al., 2014; Wang et al., 2018). Thus, the increased Q_{10} of soil microbial respiration could be partly attributed to the shifts in microbial community composition that subjected to the decreased substrate quality and

418 temperature along the altitudinal gradient. This is evident by the strong associations
419 between altitude, soil C/N and LOC/ROC ratios and microbial community structure,
420 which is in accordance with previous studies (Ding et al., 2015; Fanin and Bertrand,
421 2016; Frindte et al., 2019). Our study also presents that the decreased fungal diversity
422 had a direct relationship with the increased Q_{10} values along increasing altitude,
423 further indicating that microbial communities shaped by environmental selection
424 contribute to temperature sensitivity of soil microbial respiration. Furthermore,
425 changes in other factors (such as SOC, TN, MBC, enzyme activities etc.) along the
426 altitudinal gradient may also affect Q_{10} (Čapek et al., 2019; Chen et al., 2018; Li et al.,
427 2020c). However, our SEM suggested no significant direct associations of these
428 factors with Q_{10} of soil microbial respiration, emphasizing the importance of
429 microbial community composition for predicting temperature sensitivity of soil
430 microbial respiration.

431 It is thus essential to unravel the taxonomic attributes of the microbes involved in
432 C metabolisms, although identifying the taxa responsible for the Q_{10} variations
433 remains challenging. Soil respiration is generally considered as a “broad biological
434 process” involving a wide array of microbial taxa in terrestrial ecosystems (Banerjee
435 et al., 2016; Crowther et al., 2019). Further, different microbial taxa may utilize
436 resources via distinct trophic strategies, contributing differently to Q_{10} of soil
437 microbial respiration at a community level. Our results indicated that the phylogenetic
438 groups based on high-level classification (e.g., class or phylum level) might be weak

predictors of changes in Q_{10} of soil microbial respiration along the altitudinal gradient, as most dominant bacterial and fungal taxa at the phylum level had no significant associations with Q_{10} values. This weak association could be due to taxa within each phylum that have enormous phylogenetic and physiological diversity and thus have distinct potential to metabolize C (Li et al., 2021a). Therefore, we identified particular ecological clusters associated with Q_{10} of soil microbial respiration based on the microbial co-occurrence network analysis, where the taxa that share similar niche and ecological functions could be grouped into the same ecological cluster (Liu et al., 2018a; Ma et al., 2020b). The identification of co-occurring microbial assemblies has implications for screening the microbial taxa associated with temperature sensitivity of soil microbial respiration, though their specific functions need to be validated in the future.

Our results are consistent with the second hypothesis that particular microbial ecological clusters are the most important predictors of the Q_{10} values. For example, keystone taxa within module #1 such as Skermanella and Blastococcus are known to preferentially utilize labile C (Wang et al., 2021). Moreover, the most genera of module #1 are essential members of Alphaproteobacteria and Actinobacteria (known as r-strategists), which are more adapted to warm and nutrient-rich conditions and efficient to mineralize labile C (Li et al., 2021a; Uksa et al., 2015; Yao et al., 2017). These r-strategists could also invest most energy and resources into reproduction and subsequently reduce the proportion of substrate allocated to respiration (Malik et al.,

2020a). Thus, the decreased module #1 may lead to the increased Q_{10} of soil microbial respiration with the increasing altitude. In contrast, our results imply that module #4 may have a positive effect on the Q_{10} of soil microbial respiration. This is because considerable members of module #4 belonged to Acidobacteria, Basidiomycota, and Deltaproteobacteria, which are commonly classified as K-strategists (Bledsoe et al., 2020; Yao et al., 2017). Previous studies indicated that Basidiomycota, and Deltaproteobacteria were generally found to be predominant in the Antarctic and Arctic samples and may thus represent typical colonizers of cold ecosystems (Duarte et al., 2018; Varin et al., 2012). These K-strategists in harsh environments (i.e., low substrate quality and temperature) commonly have slow growth rates and preferentially utilize recalcitrant C (Hale et al., 2019; Sun et al., 2020). The decomposition of recalcitrant C via enzymes is energy cost, and thus K-strategists are likely to invest a large proportion of energy and resources into the respiration rather than growth yield (Malik et al., 2020a). The positive relationship between module #4 and Q_{10} values further confirmed that the Q_{10} of soil microbial respiration would increase with the prevalence of microbial K-strategists along the altitudinal gradient. This finding was also supported by a recent measurement of the Q_{10} of soil microbial respiration along the latitudinal gradient in temperate mixed forest ecosystems (Li et al., 2021a). Therefore, these ecological clusters with different trophic strategies could help to explain the observed variations in Q_{10} of soil microbial respiration along the altitudinal gradient. However, we note that the trophic strategies of soil microbial

community require further validation using methods such as omics (i.e., genomics, transcriptomics, proteomics) and stable isotope tracing (Malik et al., 2020a). Future works on trophic strategies of microbial communities and their effects on temperature sensitivity of soil microbial respiration should consolidate our findings.

In addition, the Q_{10} of soil microbial respiration was also related to the fungal community, which has been reported to have predominant ability to decompose complex and recalcitrant C (Cheng et al., 2021; Wang et al., 2018). Thus, a large proportion of soil fungi in the module #4, which could be attributed to the low temperature and soil C quality conditions, may partially account for the relatively high Q_{10} values at high-altitude regions (Fig. S13). These observations agree with a previous study indicating significant associations between fungal abundance and Q_{10} of soil microbial respiration in high-altitude regions of the Western Carpathians (Klimek et al., 2016). In addition, some fungal genera within particular ecological cluster (i.e., module #4) such as Clavaria, Botryobasidium, Hypochnicium, and Pseudotricholoma may prefer degrading recalcitrant C, which likely stimulate the Q_{10} of soil microbial respiration. We subsequently provide a conceptual framework for the links between microbial community composition and Q_{10} of soil microbial respiration. The altitude-induced differences in temperature and soil substrate quantity and quality have significant effects on the shifts of microbial assemblies with different trophic strategies, and eventually influence the response of soil microbial respiration to temperature changes. In high-altitude regions with historically low temperature, the

large accumulation of recalcitrant C favors the growth of soil microbes such as bacterial Haliangium and fungal Clavaria, shaping microbial community dominated by taxa that prefer utilizing recalcitrant C. Our results advance the present knowledge by providing a list of candidate microbial taxa associated with temperature sensitivity of soil microbial respiration, though further work needs to be done to uncover the underlying mechanisms of how the specific taxa affect temperature sensitivity of soil microbial respiration.

Overall, our study determines the role of soil microbial communities in affecting Q_{10} of soil microbial respiration. We clearly showed that microbial community composition is responsible for the Q_{10} values along the altitudinal gradient. We have identified two major microbial assemblies associated with Q_{10} of soil microbial respiration. However, microbial assemblies are characterized by distinct altitudinal patterns that often covary with other abiotic factors such as soil pH and moisture (Delgado-Baquerizo et al., 2018; Wang et al., 2015). Therefore, the roles of these abiotic factors in regulating Q_{10} of soil microbial respiration cannot be ignored. In this study, Q_{10} values was well related to soil moisture, which is concordant with the previous studies showing that Q_{10} of soil respiration was positively correlated with soil moisture (Liu et al., 2016; Zhao et al., 2017). For instance, increased soil moisture could facilitate mobility of those microorganisms towards substrate (i.e., recalcitrant C) due to substrate diffusion (Abera et al., 2011; Liu et al., 2019). However, it should be noted that microbial properties, particularly microbial assemblies with different

trophic strategies, were important predictors of the response of soil microbial respiration even after considering these key abiotic factors. The effects of abiotic factors (e.g., soil pH and moisture) on Q_{10} values could be achieved partly through their effects on microbial community properties along the altitudinal gradient (Liu et al., 2017; Zhao et al., 2017). Therefore, our results highlighted the potential importance of shifts in microbial assemblies with different trophic strategies in affecting temperature sensitivity of soil microbial respiration.

5. Conclusions

Our results identify how shifts of microbial assemblies from labile to recalcitrant C utilization affect Q_{10} of soil microbial respiration in alpine forests along the altitudinal gradient on the Tibetan Plateau. Progressive shifts of microbial assemblies from labile to recalcitrant C consumption could contribute to the higher Q_{10} values in relatively higher altitude regions. These findings indicate that the historically accumulated huge amounts of C in high-altitude regions are more vulnerable to global warming. Our study offers new insights from specific shifts in microbial assemblies to understand Q_{10} of soil microbial respiration along the altitudinal gradient on the Tibetan Plateau. By exploring the potential links between specific microbial taxa and soil C dynamics and by incorporating those links into data-driven models, we could improve the understanding of microbially-mediated soil C dynamics under climate warming scenarios.

CRediT authorship contribution statement

Xiao-Min Zeng: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Writing – original draft, Visualization. **Jiao Feng**: Conceptualization, Writing – review & editing, Supervision, Funding acquisition. **Ji Chen**: Writing – review & editing. **Manuel Delgado-Baquerizo**: Writing – review & editing, Funding acquisition. **Qianggong Zhang**: Funding acquisition, Resources. **Xin-Quan Zhou**: Investigation, Data curation. **Yusen Yuan**: Methodology. **Songhui Feng**: Methodology. **Kexin Zhang**: Methodology. **Yu-Rong Liu**: Conceptualization, Resources, Writing – review & editing, Supervision, Project administration, Funding acquisition. **Qiaoyun Huang**: Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Figure Legends

Figure 1. The pattern of the temperature sensitivity (Q_{10}) of soil microbial respiration along the altitudinal gradient.

Figure 2. The potential predictors of Q_{10} of soil microbial respiration evaluated by Random Forest machine learning analysis **(a)**, and relationships between selected biotic and abiotic factors and Q_{10} of soil microbial respiration **(b)**. Significant predictors ($P < 0.05$) are plotted in orange or blue. The higher %IncMSE values represent the more important variables. SOC, soil organic carbon; TN, total nitrogen; DOC, dissolved organic carbon; LOC/ROC, percentage of labile and recalcitrant C; MBC, microbial biomass carbon; AG, α-1,4-glucosidase; BG, β-1,4-glucosidase; CBH, cellobiohydrolase; XYL, xylanase.

Figure 3. The network diagram with nodes colored by each of the eight ecological clusters (modules, Mod#1-8) **(a)**, relationships between relative abundance of the selected ecological clusters and Q_{10} of soil microbial respiration **(b)**, and operational taxonomic units (OTUs) number properties of the dominant bacterial and fungal genus in the main modules associated with Q_{10} of soil microbial respiration **(c)**. The outer ring and interior pie represent OTUs number properties of the dominant phylum (top 10) and genus (top 20%), respectively. The red triangle represents the keystone taxa in modules. Additional information on the OTUs in the modules is available in Supplementary Table S3.

Figure 4. The structural equation modeling (SEM) identifying the direct and indirect associations between altitude, soil and microbial properties and Q_{10} of soil microbial respiration **(a)**, and the standardized total effects (STE, direct plus indirect effects) derived from the SEM **(b)**. Numbers labeling the arrow lines are indicative of the effect size of the relationship. We only included those direct or indirect associations that could affect Q_{10} values for graphical simplicity. $*P < 0.05$ and $**P < 0.01$. The rest of associations between altitude and soil and microbial properties are available in Supplementary Figure S14. Information on the environmental factors included in our SEM can be found in Supplementary Figure S3.

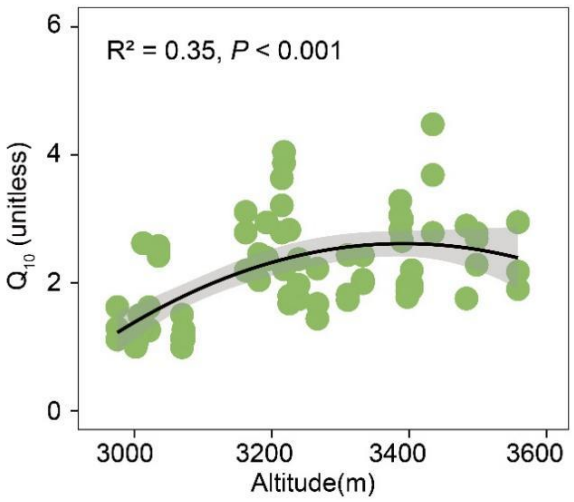
R² = 0.35, P < 0.001
Q10 (unitless)
0
2
4
6
3000
3200
3400
3600
Altitude(m)

Figure 1

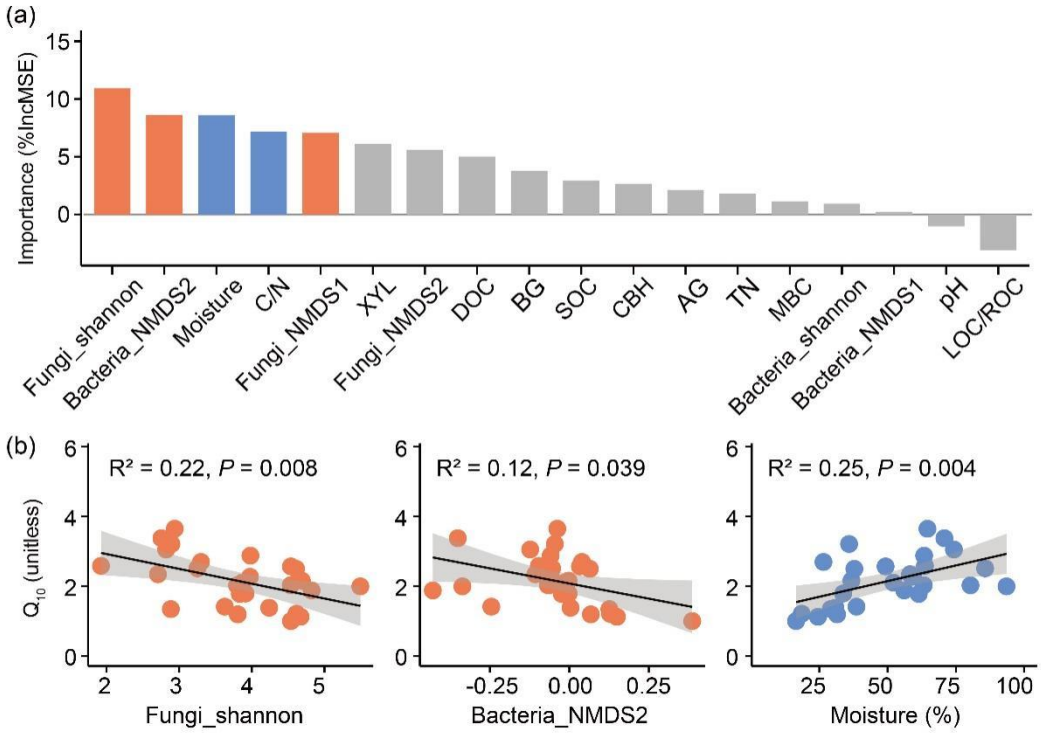
(a)
Importance (%IncMSE)
15
10
5
0
Fungi_shannon
Bacteria_NMDS2
Moisture
C/N
Fungi_NMDS1
XYL
Fungi_NMDS2
DOC
BG
SOC
CBH
AG
TN
MBC
Bacteria_shannon
Bacteria_NMDS1
pH
LOC/ROC
(b)
Q_{10} (unitless)
R² = 0.22, P = 0.008
R² = 0.12, P = 0.039
R² = 0.25, P = 0.004
Fungi_shannon
Bacteria_NMDS2
Moisture (%)

Figure 2

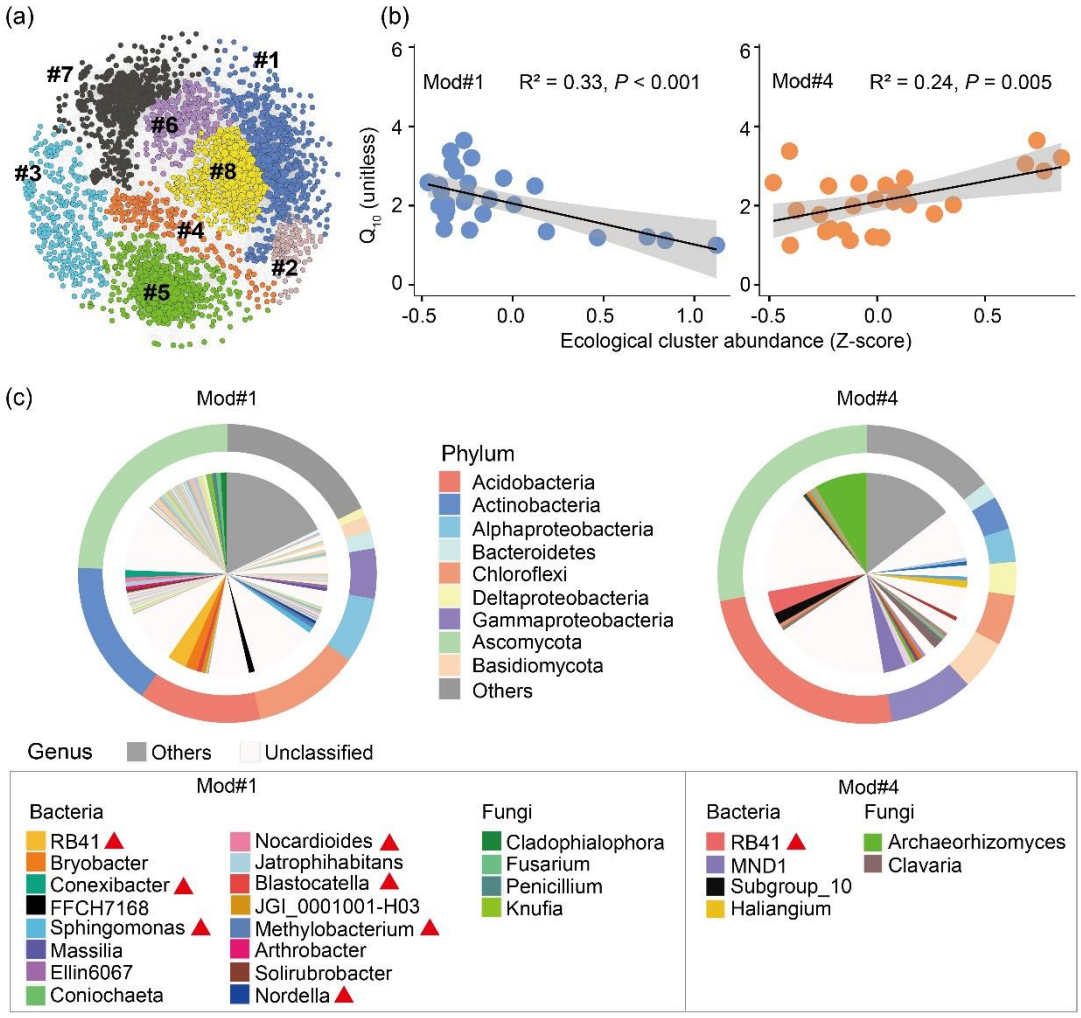
(a)
#1
#2
#3
#4
#5
#6
#7
#8
(b)
Mod#1 R² = 0.33, P < 0.001
Mod#4 R² = 0.24, P = 0.005
Q10 (unitless)
Ecological cluster abundance (Z-score)
(c)
Mod#1
Mod#4
Phylum
Acidobacteria
Actinobacteria
Alphaproteobacteria
Bacteroidetes
Chloroflexi
Deltaproteobacteria
Gammaproteobacteria
Ascomycota
Basidiomycota
Others
Genus
Others
Unclassified
Mod#1
Bacteria
RB41
Bryobacter
Conexibacter
FFCH7168
Sphingomonas
Massilia
Ellin6067
Coniochaeta
Nocardioides
Jatrophihabitans
Blastocatella
JGI_0001001-H03
Methylobacterium
Arthrobacter
Solirubrobacter
Nordella
Fungi
Cladophialophora
Fusarium
Penicillium
Knufia
Mod#4
Bacteria
RB41
MND1
Subgroup_10
Haliangium
Fungi
Archaeorhizomyces
Clavaria

Figure 3

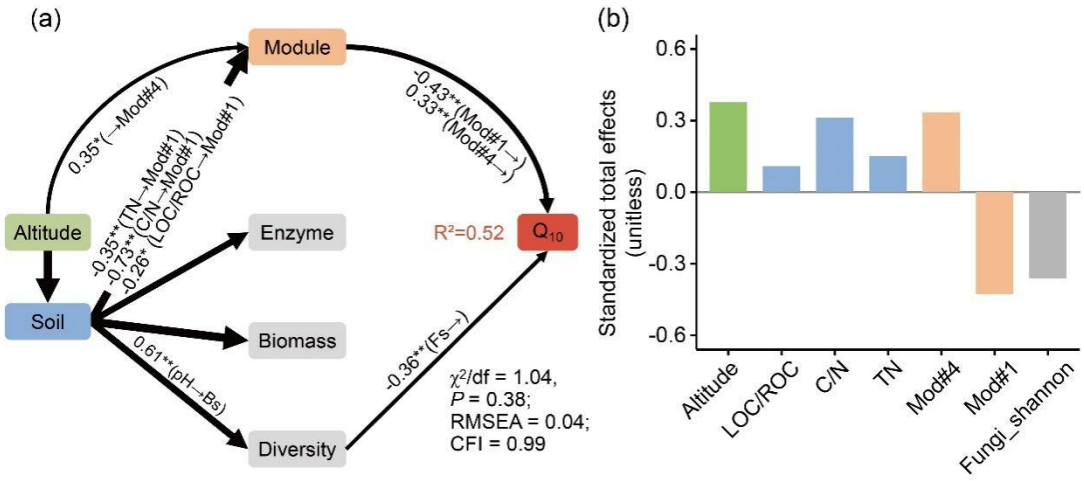
(a)
Module
Altitude
Enzyme
Soil
Biomass
Diversity
R²=0.52
Q10
0.35*(→Mod#4)
-0.35**(TN→Mod#1)
-0.73**(C/N→Mod#1)
-0.26* (LOC/ROC→Mod#1)
-0.43**(Mod#1→)
0.33**(Mod#4→)
0.61**(pH→Bs)
-0.36**(Fs→)
χ²/df = 1.04,
P = 0.38;
RMSEA = 0.04;
CFI = 0.99
(b)
Standardized total effects (unitless)
0.6
0.3
0.0
-0.3
-0.6
Altitude
LOC/ROC
C/N
TN
Mod#4
Mod#1
Fungi_shannon

Figure 4

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Supplementary Material

Supplementary_Table_S3.xlsx

Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Author Contribution Statement

Title: Microbial assemblies associated with temperature sensitivity of soil respiration along an altitudinal gradient

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Qianggong Zhang: Funding acquisition, Resources.

Xin-Quan Zhou: Investigation, Data curation.

Yusen Yuan: Methodology.

Songhui Feng: Methodology.

Kexin Zhang: Methodology.

Yu-Rong Liu: Conceptualization, Resources, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Qiaoyun Huang: Supervision.