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Temperature sensitivity of SOM decomposition is linked with a K-selected microbial community

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Abstract

Temperature sensitivity (Q_{10}) of soil organic matter (SOM) decomposition is a crucial parameter to predict the fate of soil carbon (C) under global warming. Nonetheless, the response pattern of Q_{10} to continuous warming and the underlying mechanisms are still under debate, especially considering the complex interactions between Q_{10}, SOM quality, and soil microorganisms. We examined the Q_{10} of SOM decomposition across a mean annual temperature (MAT) gradient from −1.9 to 5.1°C in temperate mixed forest ecosystems in parallel with SOM quality and bioavailability, microbial taxonomic composition, and functional genes responsible for organic carbon decomposition. Within this temperature gradient of 7.0°C, the Q_{10} values increased with MAT, but decreased with SOM bioavailability. The Q_{10} values increased with the prevalence of K-strategy of soil microbial community, which was characterized by: (i) high ratios of oligotrophic to copiotrophic taxa, (ii) ectomycorrhizal to saprotrophic fungi, (iii) functional genes responsible for degradation of recalcitrant to that of labile C, and (iv) low average 16S rRNA operon copy number. Because the recalcitrant organic matter was mainly utilized by the K-strategists, these findings independently support the carbon quality-temperature theory from the perspective of microbial taxonomic composition and functions. A year-long incubation experiment was performed to determine the response of labile and recalcitrant C pools to warming based on the two-pool model. The decomposition of recalcitrant SOM was more sensitive to increased temperature in southern warm regions, which might attribute to the dominance of K-selected microbial communities. It implies that climate warming would mobilize the larger recalcitrant pools in warm regions, exacerbating the positive feedback between increased MAT and CO_2 efflux. This is the first attempt to link temperature sensitivity of SOM decomposition with microbial eco-strategies by incorporating the genetic information and disentangling the complex relationship between Q_{10} and soil microorganisms.

KEYWORDS
carbon degradation genes, carbon quality and bioavailability, carbon quality-temperature hypothesis, microbial community composition, microbial respiration, microbial r-K selection theory, soil organic matter decomposition

Hui Li and Shan Yang contributed equally to this work.

1 | INTRODUCTION

Global warming will increase CO_2 release from soil by accelerating organic matter decomposition, triggering the positive carbon-climate feedback (Bond-Lamberty & Thomson, 2010; Crowther et al., 2016; Pries et al., 2017). The magnitude of this feedback is largely dependent on the temperature sensitivity (Q_{10}) of organic matter decomposition (usually measured by soil heterotrophic respiration, Rs; Davidson & Janssens, 2006; Heimann & Reichstein, 2008; Kirschbaum, 1995). Characterizing Q_{10} and its response to continuous warming is critical to a credible estimate of global carbon (C) balance under future climate change.

The temperature sensitivity of soil organic matter (SOM) decomposition is regulated by a complex set of physicochemical properties, microbial community composition, and environmental factors. It is widely accepted that the temperature response of Rs is influenced by SOM quality (Gershenson et al., 2009). Various studies have paradoxically concluded that the responses of the recalcitrant SOM components to warming could be greater than (Conant et al., 2008; Haddix et al., 2011; Knorr et al., 2005; Lefevre et al., 2014), equivalent to (Conen et al., 2006; Fang et al., 2005), or even less than (Bradford et al., 2008; Giardina & Ryan, 2000; Kurganova et al., 2012; Larionova et al., 2017; Liski et al., 1999) that of the labile organic matter. The picture is further complicated by uncertainty about the relationship between soil microbiota and SOM quality, and thus, the importance of microorganisms in regulating the temperature dependence of Rs. Despite increasing interest in understanding microbial mechanisms that control temperature sensitivity of Rs (Ding et al., 2016; Karhu et al., 2014; Thiessen et al., 2013), experimental evidences for the linkages between microbial communities and Q_{10} are scarce. The existing publications have primarily focused on the total microbial biomass, which was considered as the most important factor explaining the spatial variability of Rs (Colman & Schimel, 2013) and was positively correlated with its temperature response (Pang et al., 2015; Zhang et al., 2007). The simplification of microbial indicators to total biomass alone fails to capture population-specific parameters or changes in the dominance of specific microbial groups. This topic was moved a step forward through the use of phospholipid fatty acid analysis (PLFA) to elucidate microbial community composition. It was shown that the ratio of Actinomycetes to Bacteria (A/B; Liu et al., 2017) and fungal PLFAs (Qin et al., 2019) were positively correlated with Q_{10}, whereas the abundance of gram-negative bacteria decreased with the increasing Q_{10} (Wang et al., 2018). The development of new genomic approaches, such as next-generation sequencing (NGS), allows for the examination of the microbial community composition at a finer taxonomic resolution (Roesch et al., 2007). To our knowledge, however, the role of microorganisms in controlling temperature sensitivity of SOM decomposition has never been evaluated at fine taxonomic resolution (e.g., by the NGS methods). Still, we know little how to translate the genomic-based data into changes in ecological functions, such as Q_{10} (Fierer et al., 2007; Green et al., 2008).

Interpreting microbial phylogenetic composition under the ecological concept of r/K selection might hint at a way to elucidate the underlying microbial mechanisms for regulating Q_{10} in the context of massive sequencing data. In the broad ecological scheme, microbial taxa tended to be grouped into r- and K-strategists according to their growth, propagation, competition, and adaptation strategies (Fierer et al., 2007). The r-strategists (copiotrophic or opportunistic species) are defined as organisms having fast growth rates, flourishing in environments enriched with labile C and faster net C mineralization. In contrast, K-strategists (oligotrophic or equilibrium species) are slow-growing microorganisms that are more efficient on recalcitrant C with lower availability (Fierer et al., 2007; Trivedi et al., 2013). Based on 16S rDNA amplicon sequencing, members of the Proteobacteria and Acidobacteria have been classified as representatives of copiotrophic and oligotrophic bacteria (Fierer et al., 2007), respectively. The phyla of Ascomycota and Basidiomycota are representative of copiotrophic and oligotrophic fungi, respectively (Yao et al., 2017). With respect to the predicted functional guilds, ectomycorrhizal (ECM) fungi are primarily considered to be K-strategists, while saprotrophic fungi are generally considered r-strategists (Lindahl et al., 2007; Yao et al., 2017). Nevertheless, due to the enormous phylogenetic and physiological diversity within each phylum, it is unlikely that an entire phylum would share common ecological roles. For example, Actinobacteria may contain both copiotrophic and oligotrophic families (Morrissey et al., 2016). Consequently, the 16S rRNA (*rrn*) operon copy number has been suggested as a community-level microbial trait associated with r/K selection. In general, bacterial communities with fewer *rrn* operons tend to adopt K-strategy; whereas those with more *rrn* operons tend to adopt r-strategy (Klappenbach et al., 2000; Lee et al., 2009).

The r- and K-classification scheme might need to move beyond the restrictive focus on taxonomic genes, and we suggest expanding this theory to include datasets of functional genes. That is, the functional genes involved in degradation of the labile and recalcitrant C could be grouped into r- and K- categories, respectively. The carbon quality-temperature (CQT) hypothesis is a widely accepted theory to describe the relationship between SOM quality and Q_{10} which predicts that the decomposition rate of complex, low quality, and slowly decomposable compounds have greater temperature sensitivity than that of high quality, easily decomposable substrates (Bosatta & Agren, 1999; Craine et al., 2010; Davidson & Janssens, 2006). Based on this theory, we hypothesized that the phylogenetic traits representing the prevalence of K-strategy, such as the high proportions of oligotrophic members or recalcitrant C degradation genes, and low *rrn* operon copy number, would be positively linked with Q_{10}.

Latitudinal gradients are especially interesting to explore the effects of global warming on terrestrial ecosystems, because of the "natural" climate gradient. Latitudinal comparisons of the temperature sensitivity of Rs have been contradictory. The temperature sensitivity of Rs might increase with latitude (Enquist et al., 2003; Kirschbaum, 1995; Peng et al., 2009; Zheng et al., 2009), which could be explained by decreased litter/substrate quality with decreasing temperature (Leifeld & Fuhrer, 2005; Vanhala et al., 2008).

In contrast, it has been proposed that warmer regions would have higher Q_{10} of SOM decomposition because the labile compounds undergo faster mineralization, leaving behind a greater portion of biochemically unfavorable substrates with higher activation energies (Ea) of decomposition (Grisi et al., 1998). Previous publications have reported similar temperature sensitivities of SOM mineralization in the northern and southern regions, despite different bioavailability of SOM (Podrebarac et al., 2016; Vanhala et al., 2008). Whether the temperature sensitivity of SOM decomposition would increase or decrease with increasing latitude (decreasing temperature), and whether the change in Q_{10} is dependent on the latitudinal variations in SOM quality and microbial eco-function are still under debate.

To address these questions, we chose 13 sites of broadleaved Korean pine mixed forests distributed along a latitudinal transect ranging from 40°N to 49°N in northeastern China. The mean annual temperature (MAT) spanned a gradient of 7.0°C (from −1.9 to 5.1°C). The Q_{10} of SOM decomposition, main soil physicochemical characteristics, microbial community composition, and the abundance of eight organic C degradation genes were measured. We hypothesized two contrary relationships between Q_{10} and MAT, based on the CQT theory: (i) The soils from cold regions with a high conifer/broadleaf ratio would have lower substrate quality, and thus, correspond to the dominance of a K-selected microbial community (larger proportions of oligotrophic microbes, higher abundance of recalcitrant C degradation genes, and lower *rrn* copy number), upon which the higher temperature sensitivity of SOM decomposition would be based; (ii) The temperature sensitivity of SOM decomposition increases toward warmer sites, because cold regions have accumulated incompletely decomposed SOM and thus have a greater bioavailability in comparison with warm regions. In line with the second hypothesis, the southern soils would be associated with low soil C quality, and thereby the microbial community would shift toward K-strategy. Since the short-term incubations only determine the sensitivity of the relative labile fraction, we further conducted 365 days of lab-based incubation experiment combined with a two-pool model to determine the response of labile and recalcitrant C pools to temperature changes.

2 | MATERIALS AND METHODS

2.1 | Site description and soil collection

The broad-leaved Korean pine mixed forest distributed in northeast China is one of the three major temperate mixed forest types in the world, and represents the classical type of natural forest in Northeast Asia (Wang et al., 2010). The study transect was located between 40°54′51″–49°28′42″N and 124°47′18″–129°46′30″E (Figure 1a). Thirteen sampling sites along the latitudinal gradient were selected across three provinces (Figure 1a). We refer to the five sampling sites located in Heilongjiang province as the North region (N1–N5), among which the two northernmost sites, N1 and N2, were located in the Greater Xing'an Mountain Range; and the N3–N5 sites distributed in the Lesser Xing'an Mountain Range. The five sampling sites located in Jilin province are referred to as the Middle region (M1–M5), and the three sampling sites within Liaoning province as the South region (S1–S3). This transect has a typical temperate continental monsoon climate. The mean annual

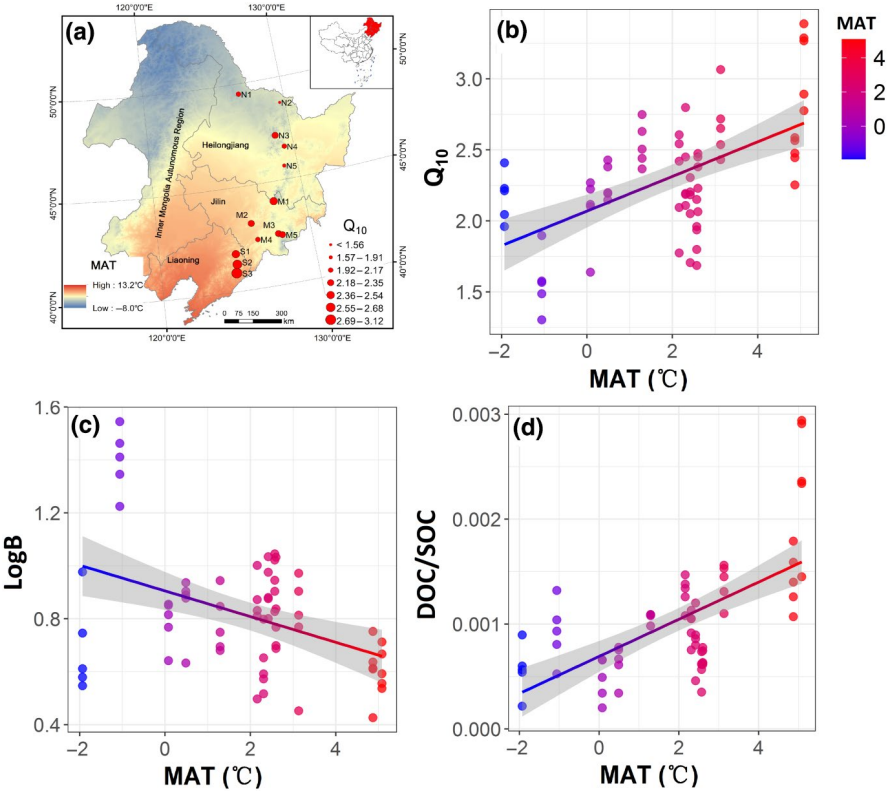

FIGURE 1 Temperature sensitivity of SOM decomposition, SOM quality, and bioavailability across the temperature gradient. (a) Locations of sampling sites (red circles) across the latitudinal gradient. The circle size represents the temperature sensitivity of SOM decomposition (Q_{10}). N, north region; M, middle region; S, south region. (b) Relationship between Q_{10} and mean annual temperature (MAT). (c) Organic carbon bioavailability (log transformation of the *B* value in Equation 1) against the MAT. (d) DOC/SOC ratio across the MAT gradient. The solid line denotes the linear regression and the shaded region denotes the 95% confidence intervals (n = 65). All regression lines are significant at $p < 0.05$

temperature (MAT) increases from −1.9 to 5.1°C, and the annual precipitation increases from 570 to 1100 mm, north to south. The altitudes range from 337 to 913 m above sea level. The soils from south to north are typical brown to dark brown forest soil, which correspond to Albi-Udic and Albi-Boric Argosols based on the Chinese Soil Taxonomy (CST) classification system (Table S1), or Leptic and Hortic Umbrisols according to World Reference Base for Soil Resources (WRB) classification.

This mixed forest ecosystem is generally dominated by Korean pine (*Pinus koraiensis*) and a variety of broad-leaved trees, including aspen (*Populus davidiana*, Dode), birch (*Betula platyphylla*, Suk), basswood (*Tilia amurensis*, Rupr), maple (*Acer mono*, Maxim), and elm (*Ulmus pumila*, L). The ratio of conifer to broadleaf trees (NRCB), as calculated by dividing the individual number of conifer trees by the individual number of broadleaf trees, decreased from north to south (Table S1).

Soil samples were collected in mid- to late-August 2015. During the fieldwork, we moved from north to south in order to obtain soil samples representing approximately similar ecological times of the growing season. At each site, we set up five 20 m × 20 m square plots as independent replicates. Ten soil cores were randomly selected from each plot and then mixed to form a composite sample. Only the Ah horizon (the thickness ranged from 7 to 15 cm) was cut and collected from each soil core. The field-moist samples were homogenized and divided into three subsamples after sieving with a mesh size of 2 mm. One subsample set was stored at 4°C for determining temperature sensitivity of respiration (Q_{10}), one was stored at −20°C for microbial DNA extraction, and the other set was air-dried to constant weight, and processed for measurements of physicochemical properties.

Representative sites from North (N3), Middle (M3), and South (S1) regions were selected for an additional 365 days of incubation experiment. At each sampling site, three 10 m × 10 m replicated plots were set up, and the entire Ah horizon of soil was collected from the center of the plot (approximately 25 kg of fresh weight). The collected soil samples were transported to the laboratory on ice. The homogenized and sieved (2 mm mesh) soil samples were stored at 4°C before the incubation experiment.

2.2 | Analysis of the general soil properties

The contents of soil organic carbon (SOC) and total nitrogen (TN) were measured with an elemental analyzer (Elementar Analysensysteme Vario MACRO cube), and the C/N ratio was calculated. Dissolved organic carbon (DOC) was extracted with 0.5 M potassium sulfate (K_2SO_4) and was analyzed using a TOC analyzer (High TOC, Elementar). NO_3^- and NH_4^+ were extracted in 2 M KCl and measured using a continuous flow on auto-analyzer (Scalar SANplus segmented flow analyzer, the Netherlands). Fresh soil was dried for 24 h at 105°C for the determination of soil moisture. Soil pH was determined using a suspension sample (1:2.5 w/v soil to water ratio) with a PHS-3G digital pH meter. Soil microbial biomass carbon (MBC) and nitrogen (MBN) were determined using the fumigation–extraction method (Brookes et al., 1985).

2.3 | SOM decomposition rate measurements and calculation of Q_{10} values

Before the SOM decomposition measurements, the samples were pre-incubated for 72 h at 25°C to stabilize the decomposition rate which had been affected by the sieving. To measure the temperature dependence of SOM decomposition, 20 g of soil from each of 65 samples (13 sampling sites × 5 replicates) was placed into 150 ml incubation flasks sealed with gas-tight rubber septa. The incubation temperatures were initially set at 25°C, then lowered to 5°C by a 10°C increments. The temperature limits of 5–25°C represent the temperature range experienced by surface soils at our study sites during the growing season. After 3 h of equilibration at the target temperature, headspace CO_2 concentrations were measured with an infrared gas analyzer Li-820 (Li-COR Biosciences). SOM decomposition rate was expressed as the rate of CO_2 release per unit of SOC; therefore, the effect of different SOC concentrations was effectively removed. A commonly used exponential function (Equation 1) was adopted to fit changes in soil CO_2 release rate with temperature. This exponential equation accurately described the data obtained for each sample ($R^2 > 0.95$ in all cases).

$$R = Be^{kT}, \tag{1}$$

$$Q_{10} = e^{10k}, \tag{2}$$

where R is the soil CO_2 release rate at a given temperature (mg C g^{-1} SOC h^{-1}); T is the incubation temperature (°C); and B and k are parameters. The parameter "B" represents the basal microbial respiration rate per unit organic C at 0°C, and it is an index of relative organic C quality (Ding et al., 2016; Fierer et al., 2006; Koch et al., 2007). Because the measurement of the respiration rate is a type of "biological" fractionation of SOM pools, here, we used the parameter B as an index of the substrate availability to microorganisms, referring to the decomposability and liability of SOM. Based on Equation (1), Q_{10} was then calculated from Equation (2) to describe the temperature sensitivity of SOM decomposition.

Temperature responses of labile and recalcitrant C pools were evaluated by 365 days of incubation experiment in combination with a first-order two-pool model. Three representative soils collected from northern (N3), middle (M3), and southern (S1) regions with MATs of 0.49, 2.31, and 4.87°C, respectively, were chosen. A total of 405 microcosms (3 latitudinal sites × 3 incubation temperatures × 15 sampling time × 3 replicates) were constructed. For each microcosm, 100 g of dry soil was placed into 450 ml glass jars and adjusted to 65% water holding capacity (WHC). Soil microcosms were pre-incubated for 48 h at 25°C in dark, and then 4 d at the respective incubation temperature before measurements to allow the soil to equilibrate after wetting up. All jars were incubated for further 365 days at 5, 15, and 25°C, respectively. During the incubation, jars were covered

with Parafilm M® (Bemis Co. Inc.) to allow gas movement into and out of the jars. The water loss from soil samples was regularly corrected by adding deionized water every 10 days. Three replicated microcosms were collected from each site and each incubation temperature after 1, 4, 7, 10, 15, 22, 29, 39, 51, 65, 95, 125, 185, 275, and 365 days of incubation. The rate of CO_2 release was determined on the basis of the changes in headspace CO_2 concentration. The cumulative proportion of soil C respired was calculated as the summed amounts of C respired before the given sampling time divided by SOC. The Q_{10} values at each sampling day were evaluated by fitting the respiration data to Equations (1) and (2).

The respiration data were then fitted to a first-order two-pool model (Equation 3) to determine the pool size and mineralization rate coefficient of labile and recalcitrant C (Andren & Paustian, 1987):

$$C_{cum}(t) = C_1\left(1 - e^{-k1t}\right) + C_2\left(1 - e^{-k2t}\right), \quad (3)$$

where $C_{cum}(t)$ is the cumulative CO_2 released (mg C g^{-1} initial C) until time t (days); C_1 and C_2 are the sizes of labile and recalcitrant C pools, respectively, and $k1$ and $k2$ are the decomposition rate coefficients for the labile and the recalcitrant compartments, respectively. It was assumed that (C_1 + C_2) = 1000 mg C g^{-1} initial C (i.e., the sum of the two pools is equal to the total amount of initial organic carbon in the sample).

The changes in decay rate coefficients ($k1$ or $k2$) with temperature were evaluated by an exponential function similar to Equation (1). In this case, R in Equation (1) was replaced by $k1$ or $k2$ (Lloyd & Taylor, 1994). Subsequently, the Q_{10} values of labile C ($Q_{10\text{-}L}$) and recalcitrant C ($Q_{10\text{-}R}$) were evaluated by using Equation (2) based on the temperature response of $k1$ and $k2$, respectively.

2.4 | Measurement of soil microbial community composition

Soil total genomic DNA was extracted from 0.25 g of fresh soil samples using a MoBio PowerSoil® DNA Isolation extraction kit (MoBio Laboratories Inc.) following the manufacturer's instructions. The DNA quality was preliminarily assessed on a spectrophotometer (NanoDrop Technology). The DNA concentration was determined with a Qubit™ dsDNA HS Assay kit on a Qubit™ 3.0 fluorometer (Thermo Fisher Scientific Inc.). The V_4–V_5 hypervariable regions of the bacterial 16S rRNA gene and fungal ITS2 region were amplified using the primers F515/R907 (Walters et al., 2016) and ITS1F/ITS2R (Ihrmark et al., 2012), respectively. Both forward and reverse primers were tagged with adapter, pad, linker, and 6 bp barcode sequences. PCR amplification of 16S rRNA genes was performed using a Gene Amp PCR-System 9700 (Applied Biosystems) in a total volume of 25 μl containing 2.5 μl 10× PCR buffer, 0.5 unit of TransStart Fastpfu DNA Polymerase (TransGen Biotech Co. Ltd.), 0.4 μl of 25 mM dNTP, 0.5 μl of 20 μM of each primer, 10 ng template DNA. The PCR program was as follows: 95°C for 3 min; 30 cycles of 95°C for 30 s, 50°C for 30 s, 72°C for 45 s, followed by a final extension at 72°C for 10 min. Amplification of fungal ITS region was performed in 20 μl mixtures which contained 4 μl of 5× FastPfu Buffer, 2 μl of 25 mM dNTPs, 0.8 μl of each primer (5 μM), 0.4 μl of FastPfu Polymerase, 0.2 μl of BSA, and 10 ng of template DNA. The thermocycler conditions were 35 cycles of 95°C for 30 s, 55°C for 30 s, and 72°C for 45 s, followed by a final extension at 72°C for 10 min. The triplicate PCR amplicons for each sample were combined and quantified using QuantiFluor™-ST (Promega). Finally, 200 ng of PCR product from each sample was pooled and purified through QIAquick Gel Extraction Kit (QIAGEN Sciences). The purified 16S rRNA gene and ITS region were sequenced using 300PE (paired-end) and 250 PE reads, respectively, on the Illumina Miseq platform (Illumina, USA) at Majorbio Bio-Pharm Technology Co.

Raw sequence files were demultiplexed, trimmed of reads containing ambiguous bases and long homopolymers, and merged using QIIME v 1.7.0 (Caporaso et al., 2012). Singletons were removed using USEARCH (http://drive5.com/usearch/manual/singletons.html). All quality-filtered sequences from 16S rRNA and ITS gene amplicons were clustered into OTUs (Operational Taxonomic Units) at 97% similarity cutoff using UPARSE (version 7.1, http://drive5.com/uparse/), followed by chimera filtering using the Ribosomal Database Project (RDP; Wang et al., 2007)and UCHIME (Edgar et al., 2011). To ensure an equal sampling depth, a subset of 15,470 sequences and 19,718 sequences per sample were randomly selected from bacterial 16S rRNA and fungal ITS datasets, respectively. Representative bacterial OTU sequences were classified taxonomically using the Ribosomal Database Project (RDP) classifier with a confidence cutoff of 50%, and the taxonomy of fungal OTU sequences was assigned against the UNITE database (Version 7.2; Nilsson et al., 2019). The raw sequence data have been deposited in NCBI under the BioProject ID of PRJNA615284.

2.5 | The averaged *rrn* operon copy number of bacterial community and prediction of functional guilds of fungal community

The rRNA operon copy number for each OTU was estimated through the *rrn*DB database, based on its closest relatives with known rRNA operon copy number (Stoddard et al., 2015). For each OTU, the mean operon copy number of the immediate child taxa was used. If the mean copy number is not available, the mean copy number of its parent was used. For each sample, the abundance-weighted average rRNA operon copy number was calculated by taking the product of the estimated operon copy number and the relative abundance for each OTU and summing this value across all OTUs in a sample.

The putative function of the fungal OTUs was predicted by FUNGuild (Nguyen et al., 2016), a database linking fungal community with function at the ecological guild level. Three main trophic types (Pathotroph, Saprotroph, and Symbiotroph), that included 62 functional guilds as classified by FUNGuild, were all detected in our samples.

2.6 | Measurement of functional gene abundances

Eight functional genes involved in the degradation of lignin (*lig*, *mnp*, *pox* coding for lignin peroxidase, manganese peroxidase, and phenol oxidase, respectively), Aromatic/Terpenes compounds (*glx* and *CDH* coding for glyoxal oxidase and cellobiose dehydrogenase, respectively), cellulose (*exg* coding for exoglucanase), hemicelluloses (*xylA* coding for xylanase), and starch (*amyA* coding for α-amylase) were measured by a high-throughput quantitative PCR-based method (HT-qPCR; SmartChip Real-time PCR system, WaferGen Biosystems). The primer information and the qPCR procedures are provided in B. Zheng et al. (2018). In brief, the qPCR reaction was an initial denaturation at 95°C for 10 min with 40 cycles of denaturation at 95°C for 30 s, annealing at 58°C for 30 s, and extension at 72°C for 30 s. The melting curve was automatically generated by the WaferGen software. Three technical replicates of each sample were amplified to ensure the reproducibility. To remove the influence of microbial biomass on gene abundance, the abundances of the genes were normalized by microbial biomass and were expressed as the copy number μg^{-1} MBC.

2.7 | Statistical analysis

Data normality was tested with a Shapiro–Wilk test. Variables that did not meet the normality and homoscedasticity of errors were log-transformed. All the data are presented as mean ± standard error. To evaluate the relationships between MAT and the temperature sensitivity of SOM decomposition (Q_{10}), the soil properties and microbial parameters, a linear mixed-effect model (lme) with the five replicates as random factor and the sampling site as fixed factor, were performed with package nlme in R. The relationships between Q_{10} and the soil variables and microbial properties were also evaluated by lme, with the five replicates as random factor and the MAT as fixed factor. Data fitting to the different equations were performed by using the SPSS 17.0 statistical package (SPSS Inc.).

Bray–Curtis distances of microbial community composition were computed using the vegan package in R (v 3.3.1) based on OTU tables, and were then visualized using nonmetric multidimensional scaling (NMDS) plots. To determine whether MAT significantly influenced microbial community composition, permutational multivariate analysis of variance (PERMANOVA) was performed using the ADONIS function, based on the Bray–Curtis dissimilarity matrix.

Structural equation modeling (SEM) was used to explore the direct and indirect factors regulating the Q_{10}, as well as to evaluate the contributions of these factors by assessing the degree of the standardized total effect (direct effect plus indirect effect). The bivariate relationships between all variables with simple linear regressions were checked before SEM analysis to ensure the appropriateness of the linear models. A conceptual model of hypothetical relationships was constructed (Figure S1) based on prior knowledge, assuming MAT would directly impact Q_{10}, or indirectly influence Q_{10} through changing SOM quality and liability, and/or altering soil microbial community r-K traits, including the oligotrophic/copiotrophic taxa ratio, averaged rRNA operon copy numbers of bacterial communities, ECM/saprotroph fungi ratio, and the recalcitrant/labile carbon degradation gene ratio. The adequacy of the model was accepted as no significant difference on the χ^2-test ($p > 0.05$), high GIF (>0.9), and low RMSEA (<0.05). The final model was improved by the stepwise removal of nonsignificant paths in the initial model, based on these criteria. SEM analysis was conducted in AMOS 18.0 software (IBM).

3 | RESULTS

3.1 | Temperature sensitivity of SOM decomposition

The temperature sensitivity of SOM decomposition (Q_{10}) in the warmer sites was larger than that in the colder sites (Figure 1a). The Q_{10} value increased with increasing MAT (linear mixed model $p < 0.001$; Figure 1b). We used parameter B in Equation 1 as an index of SOM bioavailability. The logB value decreased with increasing MAT ($p < 0.001$; Figure 1c), indicating that SOM in the warmer sites was less bioavailable. The DOC/SOC was higher in the warmer sites in comparison with the colder sites, and increased with increasing MAT ($p < 0.001$; Figure 1d). The other general soil properties along the MAT gradient are shown in Table S2.

3.2 | Dominance of specific microbial taxa and carbon degradation genes

NMDS plots of the overall microbial community composition showed that the soils were clearly differentiated by location (Figure S1), means by MAT. Both the bacterial and fungal taxonomic compositions were clearly different along the MAT gradient (PERMANOVA $p < 0.05$ for both groups). Alphaproteobacteria, Actinobacteria, Planctomycetes, and Chloroflexi were more predominant in the warm sites than in the cold sites (Figure S2a–d). The relative abundances of these bacterial taxa increased with increasing MAT (linear mixed model, $p < 0.01$). In contrast, the proportions of Betaproteobacteria, Firmicutes, Gemmatimonadetes, and Bacteroidetes declined with increasing MAT ($p < 0.01$; Figure S2e–h). The abundances of Acidobacteria, Gamma- and Deltaproteobacteria, and Armatimonadetes were independent of MAT ($p > 0.05$; Figure S2i–k). To calculate the ratio of oligotrophic to copiotrophic members, the likely oligotrophic (e.g., Acidobacteria, Actinobacteria, Planctomycetes, and Chloroflexi) and copiotrophic bacterial taxa (e.g., Betaproteobacteria, Firmicutes, Gemmatimonadetes, and Bacteroidetes) were summed up, respectively. Since Alphaproteobacteria have relative lower *rrn* copy number in comparison with Betaproteobacteria, here, we classified the Alpha subgroup of Proteobacteria into the oligotrophic group. The ratio of oligotrophic to copiotrophic bacteria increased with

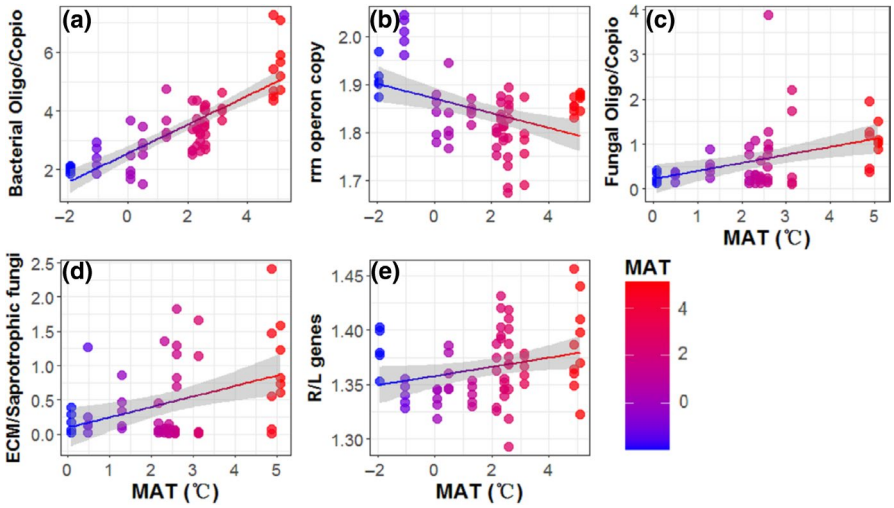

FIGURE 2 Microbial K-/r-strategy ratio along the mean annual temperature (MAT) gradient. (a) Bacterial oligotroph/copiotroph ratio. (b) The 16S rRNA operon copy number of the bacterial community. (c) Fungal oligotroph/copiotroph ratio. (d) Ectomycorrhizal (ECM)/saprotrophic fungi ratio. (e) Recalcitrant/labile organic C degradation gene abundance ratio (R/L genes). The solid line denotes the linear regression and the shaded region denotes the 95% confidence intervals (n = 65 for subfigures a, b, and e; *n* = 60 for c and d). All regression lines are significant at $p < 0.05$

increasing MAT ($p < 0.001$; Figure 2a). The latitudinal pattern of the rRNA operon copy number in the bacterial community still supported the prevalence of K-strategy in warmer sites, as evidenced by the declined community-level rRNA operon copy number with increasing MAT ($p < 0.001$; Figure 2b).

The relative abundances of all the dominant fungal phyla, including Ascomycota, Basidiomycota, and Zygomycota, were independent of MAT ($p > 0.05$). However, the relationships between the fungal taxa and MAT were improved when the two northernmost sites, which behave differently than the other soils, were removed. As a consequence, the relative abundances of Ascomycota and Zygomycota decreased ($p < 0.01$ for both cases; Figure S3a,c), and the relative abundance of Basidiomycota increased with increasing MAT ($p < 0.001$; Figure S3b). The ratio of oligotrophs (Basidiomycota) to copiotrophs (the sum of Ascomycota and Zygomycota) increased toward the warm regions ($p = 0.002$; Figure 2c). With respect to the functional guilds, the abundance of ectomycorrhizal (ECM) fungi was independent of MAT ($p > 0.05$; Figure S4a), whereas saprotrophic fungi were more predominant in the colder sites ($p < 0.001$; Figure S4b). The ratio of ECM to saprotrophic fungi increased with increasing MAT ($p = 0.004$; Figure 2d).

The copy number of the functional genes involved in degradation of a variety of C substrates varied from a magnitude of $\times 10^6$ to $\times 10^9$ μg^{-1} microbial biomass carbon (MBC). Overall, the gene abundances were stable with increasing MAT ($p > 0.05$; Figure S5a–e). We designated the sum of the genes involved in oxidation of lignin and aromatic/terpenes (*lig*, *mnp*, *pox*, *glx*, *CDH*) as the recalcitrant C degradation genes, while the sum of the genes involved in hydrolysis of cellulose (*exg*), hemicelluloses (*xyl*), and starch (*amyA*) as the labile C degradation genes. The ratio of recalcitrant to labile C degradation genes (referred as R/L genes) increased with increasing MAT ($p < 0.05$; Figure 2e), implying a high potential for recalcitrant C degradation in warm sites.

3.3 | Soil and microbial factors defining Q_{10} of organic matter decomposition

The temperature sensitivity of SOM decomposition (Q_{10}) in these temperate mixed forests increased with the increasing DOC/SOC ratio (linear mixed model $p < 0.001$; Figure 3a), but declined with the increasing SOM bioavailability to microorganisms (LogB; $p < 0.001$; Figure 3b).

In general, the Q_{10} value increased with the abundances of known or suspected oligotrophic taxa, such as the bacterial members of Acidobacteria, Planctomycetes, Alphaproteobacteria, and the Basidiomycota in fungal domain ($p < 0.05$ for all cases; Table S3). The Q_{10} value decreased with the abundances of copiotrophic taxa, including Betaproteobacteria, Firmicutes, Bacteroidetes in the bacterial domain and the fungal phyla of Ascomycota and Zygomycota ($p < 0.05$ for all cases; Table S3). The Q_{10} value increased with increasing oligotroph/copiotroph ratios of both the bacterial and fungal communities ($p < 0.05$ for both; Figure 3c,e), indicating the close associations between the dominance of K-strategists and the temperature sensitivity of SOM decomposition. The declined Q_{10} with concomitant increase in rRNA operon copy number ($p = 0.022$; Figure 2d) further implied that the prevalence of r-strategists might lower the temperature sensitivity. The Q_{10} value increased with the proportion of ECM fungi, but decreased with the proportion of saprotrophic fungi ($p < 0.05$; Table S3). As a consequence, the Q_{10} increased with the ECM/saprotrophic fungi ratio ($p < 0.001$; Figure 3f). Temperature sensitivity increased with the abundances of the measured C degradation genes ($p < 0.05$; Table S3). When the genes

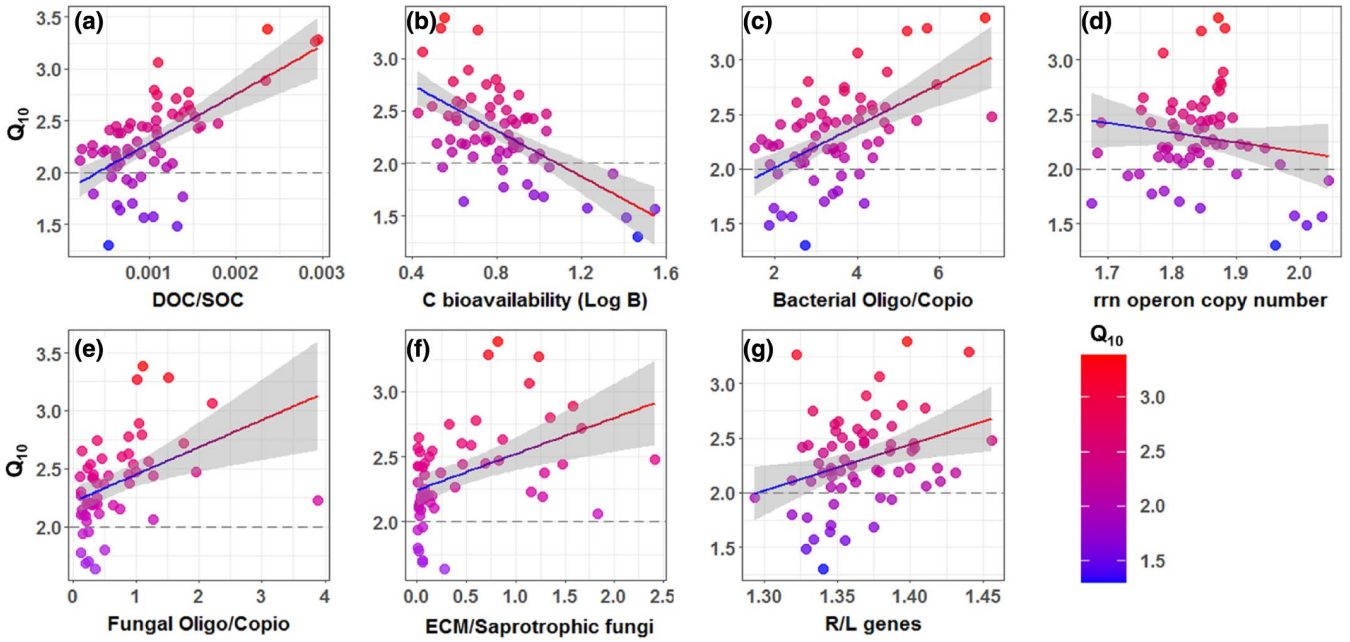

FIGURE 3 Organic C quality and the microbial K-/r-strategy ratio driving the temperature sensitivity of SOM decomposition (Q_{10}). (a) DOC/SOC ratio. (b) Bioavailability of organic C, as indicated by LogB value. (c) Bacterial oligotroph/copiotroph ratio. (d) The weighted average rRNA operon copy number of bacterial community. (e) Fungal oligotroph/copiotroph ratio. (f) Ectomycorrhizal (ECM)/saprotrophic fungi ratio. (g) Recalcitrant/labile organic C degradation gene abundance ratio. The solid line denotes the linear regression and the shaded region denotes the 95% confidence intervals (n = 65 for subfigures a, b, c, d, and g; n = 60 for e and f). All regression lines are significant at $p < 0.05$. The horizontal dashed lines indicate Q_{10} = 2.0, a constant value usually been set in most ecosystem models

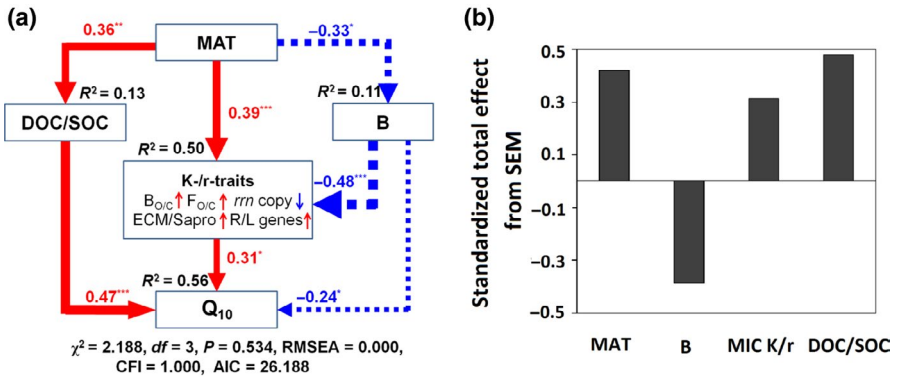

FIGURE 4 Direct and indirect effects of mean annual temperature (MAT), organic matter quality and bioavailability, and microbial ecological strategies on temperature sensitivity of SOM decomposition (Q_{10}), as evaluated by the structural equation model (SEM). (a) The final SEM model. (b) The total effects of the variables. We used principal component analysis (PCA) to create multivariate indexes for microbial K-/r-strategy ratio with variables of bacterial oligotroph/copiotroph ratio ($B_{O/C}$), fungal oligotroph/copiotroph ratio ($F_{O/C}$), the weighted average rRNA operon copy number of bacterial community (*rrn* copy), ECM/saprotrophic fungi ratio (ECM/Sapro), and recalcitrant/labile C degradation genes ratio (R/L genes). The first principal components (PC1) of site scores were used in the SEM analysis, and the symbols "↑"and "↓" in square boxes indicate positive and negative PC1 value of the variable, respectively. Arrow thickness represents the strength of the relationships. The blue dashed arrows indicated significant negative relationships and the red solid arrows indicated significant positive relationships ($p < 0.05$). The pathways without significant effects ($p > 0.05$) are removed in the final model. Numbers adjacent to the arrows represent standardized path coefficients. Percentages close to the variables indicate the variance explained by the model (R^2). *0.01 < p < 0.05, **0.001 < p < 0.01, ***p < 0.001

were classified into recalcitrant and labile C degradation categories, the Q_{10} value increased with the ratio of recalcitrant C to labile C degradation genes (R/L genes; $p < 0.01$; Figure 3g).

Structural equation model (SEM) analysis was used to further discriminate the direct and indirect effects of climate, organic C quality and bioavailability, and microbial r/K spectrum on temperature sensitivity of SOM decomposition (Figure 4). Q_{10} was indirectly influenced by MAT through changes in the extractable fraction of SOM (DOC/SOC), bioavailability (parameter B), and the K-/r-strategy ratio of the microbial community (including the ratio of oligotrophic

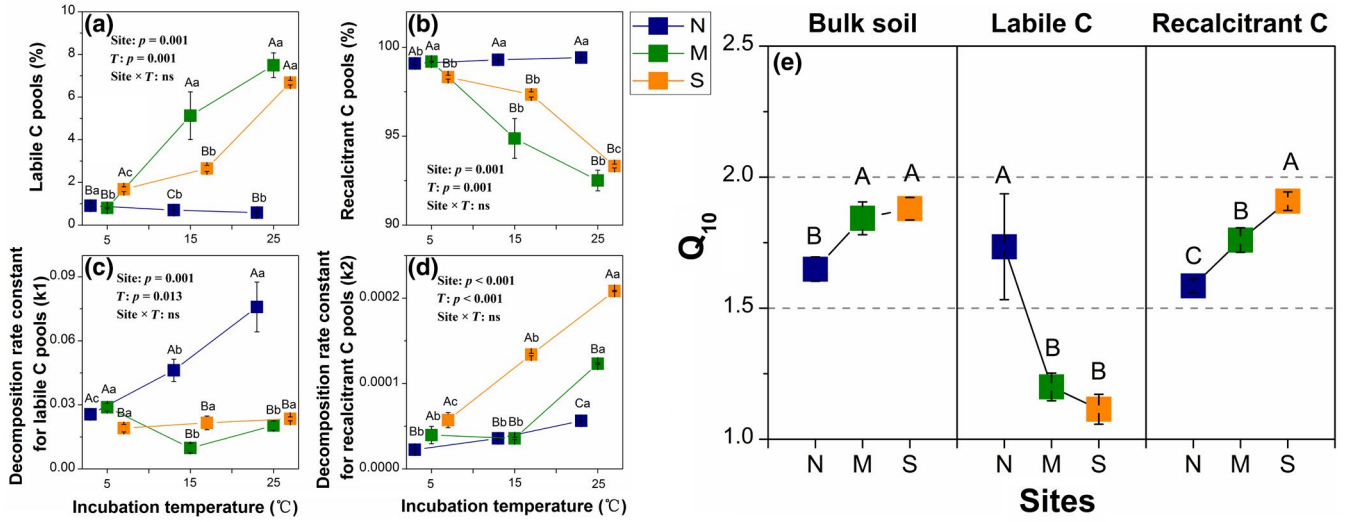

FIGURE 5 The pool sizes (a, b), decomposition rate coefficients (c, d), and the Q_{10} values of the labile and recalcitrant C (e) in the north (N), middle (M), and south (S) regions. The effects of incubation temperature (T) and sampling sites (Site) on the pool size and the decomposition rate coefficients were estimated by two-way ANOVAs. To determine the temperature effects within site or site effects within incubation temperature, one-way ANOVA and Duncan's multiple-range test were performed. Capital letters indicate significant differences among sites within incubation temperature, and lower letters indicate significant differences among incubation temperature within site ($p < 0.05$). In case of Q_{10}, the effects of sampling sites were determined (capital letters)

to copiotrophic members, the weighted average rRNA operon copy number of bacterial community, the ratio of ECM to saprotrophic fungi, and the ratio of recalcitrant to labile C degradation genes) (Figure 4a). The total effects of MAT on Q_{10} of SOM decomposition were positive, which is in line with the linear mixed model (Figure 1b). Soil DOC/SOC and the K-/r-strategy ratio of soil microbes had the positive prediction for variation in Q_{10}. In contrast, the C bioavailability (B) negatively affected Q_{10} along the MAT gradient. The C bioavailability can directly influence Q_{10}, or indirectly change Q_{10} through changing the K- and r-spectrum of the microbial community.

3.4 | Temperature sensitivity of labile and recalcitrant C pools

Three representative soils, one each collected from northern (N3), middle (M3), and southern (S1) regions, were chosen to estimate the MAT-associated variations in Q_{10} of labile and recalcitrant C pools. The two-pool model revealed that the middle site had the largest labile pool, while the northern site possessed the largest recalcitrant pool (Figure 5a,b). The decomposition rate constant of the labile pools (*k*1) from the northern site increased with incubation temperature, whereas the *k*1s of the middle and southern sites remained almost unchanged under warming conditions (Figure 5c). The decomposition rate constant of the recalcitrant pools (*k*2) only showed a slight increase in the northern site. The *k*2s of the middle and southern sites showed dramatic increases with incubation temperature. As a consequence, the Q_{10} value of the labile C ($Q_{10\text{-}L}$) was much higher in the northern site (the middle panel of Figure 5e), whereas the Q_{10} of the recalcitrant pool ($Q_{10\text{-}R}$) had greater value in the southern site (the right panel of Figure 5e). The total Q_{10} s of the southern and middle sites were higher than that of the northern site (the left panel of Figure 5e), consisting with the instantaneous Q_{10} as evaluated by short-term incubation.

4 | DISCUSSION

We started with two basic questions, (i) how would the temperature sensitivity (Q_{10}) of SOM decomposition respond to climate warming? and (ii) whether the response pattern of Q_{10} is dependent on the SOM quality and microbial eco-functions? The answer to the first question is temperature sensitivity of SOM decomposition will increase with increasing MAT in these temperate mixed forest ecosystems. The answer to the second question is the Q_{10} values will increase with the SOM recalcitrance and the prevalence of a K-selected microbial community.

4.1 | Temperature sensitivity of SOM decomposition increased toward the warm region

The response of Q_{10} to projected climate warming has long been a debated issue. We explored the relationship between Q_{10} and MAT along a forested latitudinal gradient (Figure 1). This climosequence provides a unique opportunity to determine the specific impact of climate on SOM cycling, given the similar vegetation composition and soil type (Argosols). This MAT gradient can serve to understand how the predicted temperature increase may impact soil C mineralization in temperate mixed forests. We observed a substantially higher Q_{10} for warm sites than cold sites, in terms of both short-term (Figure 1b) and long-term (Figure 5e) incubations. This pattern

was also supported by a recent measurement of the temperature sensitivity of soil microbial respiration in forest ecosystems at continental scale (Wang et al., 2018). In contrast, a number of previous case studies and meta-analyses documented that the SOM mineralization in cold, northern regions would be more sensitive to temperature than warm, southern regions (Enquist et al., 2003; Kirschbaum, 1995; Peng et al., 2009; Xu et al., 2015; Zheng et al., 2009). These inconsistent observations might be attributed to the conflicting latitudinal pattern of C quality, the uncertainty of estimation indexes, as well as the cancelling effect (Davidson et al., 2006; Razavi et al., 2015). In general, with increasing latitude (decreasing MAT), SOM becomes increasingly chemically recalcitrant due to the increased portion of coniferous trees (Fissore et al., 2008; Yang et al., 2019), and slower, incomplete decomposition. We indeed observed lower DOC/SOC and higher C/N values in the northern sites (Figure 1d; Table S2). According to the carbon quality-temperature (CQT) hypothesis (Bosatta & Agren, 1999), the temperature sensitivity of SOM decomposition would increase toward the cold regions. Nonetheless, our results did not support this prediction, and we even found a positive effect of DOC/SOC on Q_{10} (Figure 3a) and a negative effect of C/N on Q_{10} (Table S2). It indicates that indices other than chemical recalcitrance might be used to represent the SOM quality in temperate forest ecosystems. Previous studies have also proposed that the indices based on elemental ratios or chemical components, such as C/N ratio or DOC/SOC, are not very good predictors of organic C quality and availability for microorganisms (Fierer et al., 2006). The measurement of the specific rate of microbial respiration, as done here, is a type of "biological" fractionation of soil organic C pools and remains the most accurate method for estimating substrate availability to microorganisms (Kuzyakov, 2011). Thus, indicators representing the "biological" utilization have been recommended as the index for the decomposability and lability of SOC. For example, by defining C quality as the rate of microbial CO_2 production per unit organic C, there is a strong negative relationship between the relative quality of SOM and Q_{10} values across a wide range of soils (Ding et al., 2016; Fierer et al., 2005, 2006; Koch et al., 2007). Bosatta and Ågren (Bosatta & Agren, 1999) defined C quality biochemically, as the number of enzymatic steps required to mineralize organic matter to CO_2, and found that the lower substrate quality was more sensitive to temperature changes. We used the parameter B, which represents the basal microbial respiration rate per unit organic C at 0°C, as an index of the biochemical quality of SOM. The B values in warm sites are lower than the cold regions (Figure 1c), and the Q_{10} values decreased with increasing B value (Figure 3b). Our results are not contradictory to the classic CQT hypothesis. Instead, these findings provide extra support to this theory by using the "biological" parameters as the index of C quality or bioavailability (Kuzyakov, 2011).

The low SOM bioavailability in warm sites may depend on a set of complex factors. First, aboveground net primary production (NPP) and belowground C allocation both increase with MAT across biome types (Giardina et al., 2005); thus, soils at warm sites receive greater inputs of both labile (e.g., carbohydrates, proteins) and decay-resistant (e.g., lignin) compounds. The recalcitrant inputs were greater than the labile inputs in this broad-leaved Korean pine mixed temperate forest (Yang et al., 2019). Second, litter decomposition is fast under warming conditions. Initial rapid utilization of labile, high-quality litter leads to the relative accumulation of microbially derived stable compounds and production of a low biochemical quality SOM (Giardina et al., 2001; Liang et al., 2017). Third, stabilization of decomposition products proceeds more quickly at high temperatures (Dalias et al., 2001; Thornley & Cannell, 2001), resulting in a larger proportion of total SOM in stabilized, chemically protected forms. Last, in the long-term weathering processes, high temperatures tend to promote the loss of clay minerals, which have a high affinity to C (Birkeland, 1984).

4.2 | Temperature sensitivity of SOM decomposition increased with the prevalence of K-strategy of microbial community

Although the important role microbes play in regulating the temperature sensitivity of SOM decomposition has seen increased interest (Bai et al., 2017; Karhu et al., 2014), we are aware of no study that has examined the microbial mechanisms at the phylogenetic level. Here, we made the first attempt to link the temperature response of soil respiration with specific taxonomic groups (as measured by sequencing of 16S rRNA and ITS genes) and functional genes of the microbial community. The relationship between soil microbes and Q_{10} could be explained under the framework of r/K selection theory. It was clearly shown that the dominance of microbial K-spectrum is closely associated with the temperature sensitivity of Rs (Figure 3). Specifically, the Q_{10} increased with the bacterial and fungal oligotrophs/copiotrophs ratio, ECM/saprotrophic fungi ratio, and recalcitrant/labile C degradation genes ratio, and decreased with the averaged *rrn* operon copy number of bacterial communities. Previous PLFA-based measures of microbial community support the close associations between soil Q_{10} and microbial K-strategists. At continental scale, the Q_{10} value decreased with the abundance of gram-negative bacteria across forest ecosystems (Wang et al., 2018). Soil respiration Q_{10} in an alpine grassland increased with the relative abundance of fungal PLFAs (Qin et al., 2019). Across forests and grasslands, the Q_{10} value increased with the Actinomycetes/Bacteria ratio (Liu et al., 2017). Fungi are more likely to decompose recalcitrant SOM and, as such, are typically classified as K-strategists (Bahram et al., 2018; Fierer et al., 2009). Actinomycetes are slow-growing gram-positive bacteria and behave in a manner similar to fungi. Gram-negative bacteria prefer to utilize more labile organic C in comparison with gram-positive bacteria (Apostel et al., 2013; Biasi et al., 2005; Cui et al., 2020; Kramer & Gleixner, 2006), and thus, are classified as r-strategists. Since the K-strategists are more adapted to nutrient-poor niches and efficient to mineralize the recalcitrant C, the prevalence of K-strategy would be the underlying microbial mechanisms for the high Q_{10} in warm sites.

The nominated oligotrophic and copiotrophic bacterial taxa of this study are generally in line with previous publications. Comparable to the current study, the relative abundances of Alphaproteobacteria, Acidobacteria, and Actinobacteria have previously been shown to increase under soil warming conditions (DeAngelis et al., 2015; Jeewani et al., 2020). The Alpha- and Delta-Proteobacteria, Planctomycetes, and Acidobacteria can be qualified as relative K-strategists (oligotrophs) as they can grow on hemicellulose or cellulose and mineralize recalcitrant organic matter (Ali et al., 2018; Barret et al., 2011; Razanamalala et al., 2018). Chloroflexi have a very slow growth rate (Davis et al., 2011) and prevail in nutrient-poor soils (Fierer et al., 2012; Janssen, 2006; Will et al., 2010). Beta- and Gamma-Proteobacteria are fast-growing copiotrophic organisms feeding on labile organic substrates, and can be characterized as typical r-strategists (copiotrophs; Eilers et al., 2010; Fierer et al., 2007; Klappenbach et al., 2000). Bacteroidetes are also typical copiotrophs, dominating in upper humic horizons or in the rhizosphere, all are rich in labile organic C (Fierer et al., 2007) The Firmicutes are endowed with numerous enzymes for the depolymerization of fresh organic matter, and thus, are considered as copiotrophic members (Li et al., 2019).

The information gathered from full genome sequences provides the potential molecular mechanisms for explaining the ecological trophic cascades of soil bacterial taxa. The number of genes per genome involved in the decomposition of recalcitrant C is higher in bacteria belonging to Actinobacteria and Acidobacteria as compared to the majority of the Proteobacteria (Berlemont & Martiny, 2013). In addition, members of Actinobacteria and Acidobacteria possess well-equipped genetic machinery allowing breakdown, utilization, and biosynthesis of diverse structural and storage polysaccharides, which is important for increasing SOM stability (Trivedi et al., 2013). Genomic analysis has also shown that fast-growing bacteria (r-strategists), especially those of the phyla Proteobacteria and Firmicutes, have a higher number of total transporters including ATP-binding cassettes, phosphotransferase systems, and drug/metabolite transporters that could import or export a broad range of compounds (Barabote & Saier, 2005). The presence of low affinity transporters allows fast growth under high nutrient conditions, while slow growth under starvation conditions. Species belonging to the phyla Proteobacteria and Firmicutes also have higher numbers of flagellar motor/ExbBD outer membrane transport energizer (MotExb), a motility-relevant module, which can explain the dominance of these bacterial groups in nutrient-rich soil environments, such as the cold sites in the current study. However, slow-growing bacteria (K-strategists) in the Acidobacteria and Actinobacteria taxa possess a low number of total transporters that have high affinity to a specific substrate, allowing them to thrive when nutrient concentrations are low, but are replaced by fast growers in rich environments (Trivedi et al., 2013).

In addition to counting the proportion of likely oligotrophs or copiotrophs, the weighted averaged *rrn* operon copy number is a better indicator for the ecological strategy of a bacterial community (Shrestha et al., 2007; Wu et al., 2017). Organisms with many copies of the rRNA gene operon are broadly considered to be r-selected (Reznick et al., 2002), because the number of rRNA gene operon copies correlates with the maximum growth rate (Stevenson & Schmidt, 2004), the ability to change growth rates quickly (Klappenbach et al., 2000), and fewer types of more high-affinity transporters (Lauro et al., 2009). The rapid growth of copiotrophic bacteria requires a substantial increase in cellular ribosome content, which is achieved by an expansion of *rrn* copies in their genomes, particularly near the origin of replication which effectively amplifies rRNA gene (Roller et al., 2016). In contrast, bacteria with single or few copies are considered to be oligotrophs, adapted to extract maximum resources out of a limited supply (Klappenbach et al., 2000; Stevenson & Schmidt, 2004). The efficient growth of oligotrophs results in the production of more offspring per unit resource consumed, and drives gene loss and minimization of genome size and *rrn* copies (Roller et al., 2016). In terms of this classification framework, the Alphaproteobacteria should be classified as oligotrophs due to their lower *rrn* operon copy number (typically one or two) as compared with other proteobacterial subclasses. The Alphaproteobacteria indeed showed an oligotrophic tendency in our study, as evidenced by their declined abundances with increasing organic C bioavailability (Table S3). Within the Alphaproteobacteria, several species employ an oligotrophic strategy, for example, methanotrophs and methylotrophs are typical consumers of low-quality C substrates. At the community level, bacterial communities with high weighted *rrn* copy number should thus correspond to a dominance of r-organisms. The negative relationship between *rrn* copy number and Q_{10} further confirms the linkage between temperature sensitivity of SOM decomposition and the prevalence of microbial K-strategy (Figure 3d). In agreement with our study, soil warming decreased the average rRNA operon copy number, possibly reflecting shifts in C availability and thus microbial growth dynamics (DeAngelis et al., 2015).

Typically, saprotrophic fungi favor C and nutrient-rich niches, such as the forest floor, and are more efficient in utilizing fresh, energy-rich litter (Chen et al., 2019; Crowther et al., 2012). In contrast, ECM fungi typically have slow growth rates (Hibbett et al., 2000) and reside at deeper soil depths with fragmented litter and organic matter (Lindahl et al., 2007; McGuire et al., 2013). Thus, saprotrophic fungi and ECM fungi are ecologically recommended as r- and K-strategists, respectively. Genomic sequence analyses have shown that ECM fungi have a reduced complement of genes encoding plant cell wall-degrading enzymes compared to their saprotrophic precursors (Kohler et al., 2015). Because most ECM fungi are phylogenetically associated with Basidiomycota, while most saprotrophic fungi fall within the phyla of Ascomycota and Zygomycota, the phylum of Basidiomycota had been roughly categorized as to K-member, and the phyla of Ascomycota and Zygomycota were categorized as r-members (Yao et al., 2017). Supporting such classification, Basidiomycetes are typical decomposers of complex substrates such as lignin, whereas Zygomycetes, include fast-growing organisms, decompose labile C (Ali et al., 2018). The warm sites with low C bioavailability and high Q_{10} values had high Basidiomycota/(Ascomycota+Zygomycota) and ECM/

saprotrophic ratios (Figure 2c,d), implied that warming led to a shift in the structure and composition of the fungal community toward K-strategy. In line with our results, the abundances of Basidiomycota-affiliated members (Xiong et al., 2014) and ECM fungi (Solly et al., 2017) increased in responses to soil warming. Warming also increased the proportion of a oligotrophic fungal class (Dothideomycetes) and reduced the proportion of active saprotrophic fungi (Che et al., 2019).

Impacts of climate warming on the functions of soil microbial community have rarely been studied at the functional gene level. Here, the r/K selection concept was expanded to the functional gene data to explain the relationship between Q_{10} and C degradation genes. We define the prevalence of K-strategy as the decomposition of recalcitrant C, and the r-strategy as the mineralization of the relative labile fraction. The Q_{10} value increased with the ratio of recalcitrant C degradation genes to labile C degradation genes (R/L genes; Figure 3g), further supporting the close association between microbial K-strategy and the temperature sensitivity of SOM decomposition. Increased temperature might enhance the abundances of both labile and recalcitrant degradation genes in the first few years of warming (Xue et al., 2016). Soil microbes, however, consumed a greater amount of the labile fraction over the recalcitrant pool in response to sustained temperature increase, resulting in the accumulation of recalcitrant and complex C compounds in the long run. The depletion of labile C and the relative accumulation of recalcitrant C ultimately create a high R/L genes ratio and a high temperature sensitivity in soils of warm regions (Figure 1b). Twelve years of field warming experiment also revealed that warming accelerated the decomposition of recalcitrant C, and increased the signal intensities of microbial genes involved in degrading complex organic compounds (Feng et al., 2017). The functional capacities of microbial communities in an elevational gradient of the Tibetan grassland (Yang et al., 2014) and a naturally degrading permafrost region in Central Alaska (Yuan et al., 2018) both revealed that the starch degradation gene (*ipu*A, encoding isopullulanase) and cellulose degradation genes (*xyl*A, encoding exoglucanase) were more abundant in cold regions, whereas the lignin degradation gene (*glx*, encoding glyoxal oxidase) was more abundant in warm sites. In contrast, soil warming in a tall-grass prairie ecosystem stimulated the genes for degrading labile but not recalcitrant C (Zhou et al., 2012). Furthermore, a soil transplantation experiment conducted in alpine grasslands suggests a decline in the abundance of recalcitrant C degradation genes in response to simulated warming (Yue et al., 2015). These contradictory results are explained, at least partially, by the distinct experimental scheme and the duration at each independent study. The soil samples collected from the elevational gradient of the Tibetan grassland, from a naturally degrading permafrost region in Central Alaska, and from a latitudinal gradient of temperate mixed forests in this study (Figure 1) were all undisturbed for centuries. However, the short-term soil warming and transplantation experiments are strongly disturbed ecosystems, representing the effects only over short periods (Min et al., 2019). Thus, we must be cautious in drawing conclusions from disturbed experiments.

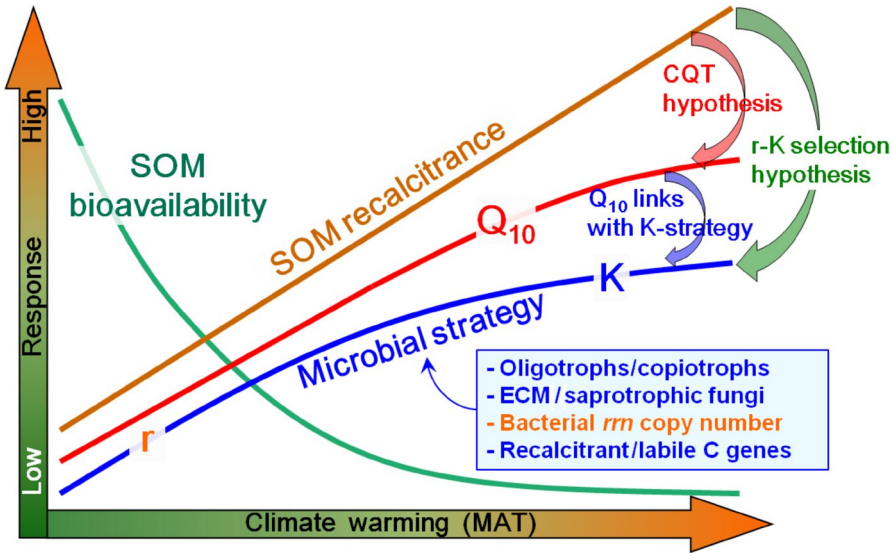

FIGURE 6 Conceptual framework on the response of temperature sensitivity (Q_{10}) of SOM decomposition to predicted climate warming, and the link of Q_{10} with SOM quality, bioavailability, and microbial ecological strategies. Q_{10} increases in response to warming, in parallel with the increasing dominance of microbial K-strategy and the declined SOM bioavailability (increasing recalcitrance). Box in light blue includes selected genomic attributes associated with the prevalence of microbial K-strategy. The texts in blue indicate the positive linkage with microbial K-strategy, while the text in orange means the positive linkage with r-strategy. The red arrow indicates that the decomposition rate of recalcitrant SOM would have greater temperature sensitivity than that of the labile SOM, as predicted by the carbon quality-temperature (CQT) hypothesis. The green arrow indicates the microbial r-K selection theory, which predicts that the K-strategist prefers to utilize the relative recalcitrant organic matter. The blue arrow indicates the links between Q_{10} and the prevalence of microbial K-strategy, the new concept raised by this study

4.3 | Climate warming will induce more recalcitrant C losses in warm region but more labile C losses in cold region

The two-pool model revealed a large fraction of labile SOC in warm regions; however, the response of decomposition of this labile fraction to increased temperature was absent. Instead, the decomposition of recalcitrant pool responded strongly to increased temperature in warm regions (Figure 5). The underlying microbial mechanisms are connected to the dominance of K-strategy in the southern warm regions, which are more associated with the mineralization of recalcitrant organic matter. For the same argument, though the northern cold regions possessed a large fraction of recalcitrant C, the mineralization of this fraction showed a weak response to increased temperature. Alternatively, the decomposition of labile C was more sensitive to increased temperature in cold regions (Figure 5), which might be attributed to the dominance of an r-selected microbial community. Consequently, we propose that the labile SOC decomposition makes a larger contribution to Q_{10} of soil CO_2 in the cold regions, whereas the mineralization of recalcitrant C contributes more to Q_{10} of soil CO_2 in the warm sites. These findings implied that all else being equal, if MAT increases, greater losses of active SOC will occur in cold ecosystems. In contrast, climate warming would mobilize more recalcitrant pool in warm region, exacerbating the positive feedback between increased MAT and CO_2 efflux.

We evaluated the response of temperature sensitivity of SOM decomposition to projected climate warming, by determining the Q_{10} changes across a temperate mixed forest distributed along a MAT gradient from −1.9 to 5.1°C. The temperature sensitivity of SOM decomposition increased with MAT, implying that the SOM decomposition in warmer regions would be more sensitive to projected climate warming compared to cold regions (Figure 6). The underlying microbial mechanism for regulating the temperature response of SOM decomposition was unraveled at the phylogenetic level. Overall, the Q_{10} values were closely associated with a K-selected microbial community, typically represented by the high ratios of oligotrophic/copiotrophic taxa. The K-spectrum is still parameterized as the high ECM/saprotroph fungi ratio, the low *rrn* operon copy number of the bacterial community, and the high recalcitrant/labile C degradation genes ratio. Since a K-selected microbial community is relevant to the decomposition of recalcitrant compounds, these findings independently confirm the carbon quality-temperature (CQT) theory, disentangling the complex Q_{10}-SOM quality–microbes relationship (Figure 6). The two-pool model suggested that the Q_{10} value of the recalcitrant pool in southern site was much higher than the value in northern site, which might be attributed to the dominance of K-strategy in the warmer region. Although the r/K selection theory is an oversimplified concept, it provides a fundamental scheme to link the response of soil microbial communities to environmental changes in an ecologically meaningful manner. To our knowledge, this study represents an important first step toward linking temperature sensitivity of SOM decomposition with the specific microbial community traits, by interpreting the phylogenetic data into ecological function.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in NCBI SRA at https://www.ncbi.nlm.nih.gov under the BioProject ID of PRJNA615284.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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