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RESEARCH ARTICLE

Temperature legacies predict microbial metabolic quotient across forest biomes

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Abstract

Aim: Palaeoclimate legacies have been reported to influence microbial communities and carbon (C) stocks even after thousands of years. However, the direct and indirect influences of climate legacies on microbial C processes remain poorly understood and thus limit our capacity to predict how climate legacies regulate C cycling. Here, we conducted microbial, soil and vegetation surveys along a continental latitudinal transect of 4200 km covering a wide range of forest biomes. With these data, we evaluated the potential capacity of climate legacies to predict direct and indirect variations in microbial metabolic quotient (MMQ) across and within three main forest biomes: tropical, subtropical and temperate forests.

Location: North–south transect (4200 km), China.

Time period: 2019.

Major taxa studied: Soil microbes.

Methods: We used molecular ecology technology to determine microbial biomass and diversity, in addition to a soil incubation experiment to measure MMQ.

Results: Palaeoclimate explained a unique portion of the variation in the continental distribution of MMQ, which showed a hump-shaped pattern with latitude. Locations with increased isothermality (an index of temperature) over the last 20,000 years also showed the highest MMQ in the present day. Moreover, we found multiple indirect effects of climate legacies on MMQ caused either by changes in key soil properties, such as soil organic carbon and ammonium (NH_4^+), in lower latitudinal regions or by

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plant traits in higher latitudinal regions. Furthermore, MMQ was positively related to bacterial richness but negatively to fungal richness across forest biomes.

Main conclusions: Climate legacies associated with continuous changes in temperature over the last 20,000 years influenced MMQ across forest biomes. Our findings demonstrate that including climate legacies in climate carbon models is essential for better prediction of the microbe-driven ecosystem processes under global environmental change.

KEYWORDS
carbon cycling, climate legacy, forest ecosystem, microbial diversity, microbial metabolic quotient, plant attribute

1 | INTRODUCTION

Globally, soils in terrestrial ecosystems contain much more carbon (C) than the atmosphere, supporting key ecosystem services such as climate regulation (e.g., CO_2), soil fertility and plant production (Delgado-Baquerizo, Karunaratne, et al., 2018; García-Palacios et al., 2021). The amount of organic C stored in the soil is regulated by soil microbes, which are in control of the formation and decomposition of soil organic C (SOC) (Chen et al., 2019; Crowther et al., 2019; Rillig et al., 2019). Microbial respiration, which is a key process of SOC decomposition, depends on microbial biomass, activity and community composition (Crowther et al., 2019; Wang et al., 2018). To gain a better understanding of the role of the microbial community in biogeochemical processes, the microbial metabolic quotient (MMQ) was established (Anderson & Domsch, 1993) as an important quantitative surrogate describing net organic carbon oxidation per unit microbial biomass. Owing to an increasing loss of the carbon storage capacity of soils in recent decades, accurate MMQ modelling associated with SOC depletion and C fluxes is crucial for predicting rapid changes in SOC stocks on a global scale (Davidson & Janssens, 2006; Heimann & Reichstein, 2008; Johnston & Sibly, 2018). Although some of the locally important drivers of MMQ have been identified in temperate forests (e.g., Spohn & Chodak, 2015) and other ecosystems (e.g., Francaviglia et al., 2017; Xu et al., 2017), there are still some major gaps in our knowledge about the factors regulating MMQ at the continental scale, which imposes a critical uncertainty when predicting the changes in soil C cycling at a large spatial scale (Hartman & Richardson, 2013).

Temperature is one of the most important drivers of MMQ (Hagerty et al., 2014; Li et al., 2019; Xu et al., 2017), and soil microbes are known to adapt rapidly to changing temperatures (Dacal et al., 2019; Zhou et al., 2012). Warming can cause an increase in microbial activity and turnover rate (Guo et al., 2018; Hagerty et al., 2014), which can result in more C being respired as CO_2 and less C being incorporated into microbial biomass. The soil microbial community composition can also shift towards dominance of microbial species with faster turnover under high temperatures, thus affecting MMQ (Xu et al., 2017). Besides this, some previous studies showed that microbial communities in warming soil could retard soil carbon losses, which was supported by the theory of thermal adaptation (Bradford et al., 2019; Dacal et al., 2019). Therefore, we hypothesized that microbial communities originating from soils with long-term exposure to high temperatures (tropical or subtropical forests) might have lower MMQ at constant temperatures (Dacal et al., 2019; Johnston & Sibly, 2018), whereas communities originating from soils exposed to lower temperatures (e.g., temperate forest) and those with increasing temperature variability might have higher MMQ.

Long-term climate legacies representing continuous changes in temperature and precipitation over millennia were good at predicting global variations in soil microbial diversity and carbon stocks across terrestrial ecosystems (Delgado-Baquerizo, Bissett, et al., 2017; Delgado-Baquerizo, Eldridge, et al., 2017; Ding et al., 2019; Ye et al., 2019; Zhou et al., 2022). However, much less is known about the underlying causes and processes whereby soils with contrasting temperature legacies differ in MMQ in the context of global warming. It has been shown that climate legacies are still influencing the distribution of soil carbon and microbial communities (Delgado-Baquerizo, Bissett, et al., 2017; Ding et al., 2019), with strong effects on plant community assembly and productivity (Delgado-Baquerizo, Karunaratne, et al., 2018; Lyons et al., 2015; Svenning et al., 2015). Thus, climate legacies can affect MMQ directly and/or indirectly by changing plant traits [e.g., root C and nitrogen (N) contents] and/or soil chemical properties (e.g., SOC and ammonium N contents) (Delgado-Baquerizo, Eldridge, et al., 2017; Monger et al., 2015). Also, climate legacies play important roles in regulating current soil microbial distributions (Delgado-Baquerizo, Bissett, et al., 2017) whereby microbial ecological clusters are similar to those of the plant community (Delgado-Baquerizo, Eldridge, et al., 2018). As such, climate legacies can also regulate MMQ indirectly by shaping the soil microbial community. Furthermore, current SOC accumulation in soils is one function of ecosystem development with a long-term climate history (Delgado-Baquerizo, Eldridge, et al., 2017; Delgado-Baquerizo, Karunaratne, et al., 2018; Schlesinger, 1990). In this respect, we expect that climate legacies could be related indirectly to current MMQ by shaping the rates of SOC accumulation during millennial pedogenesis. Deciphering how long-term temperature legacies influence soil microbes and their capacity to regulate the SOC cycle through MMQ is fundamental to prediction and assessment of the

impacts of the ongoing global environmental change on terrestrial ecosystems.

To test these hypotheses, we measured variables related to the microbial communities (bacterial and fungal biomass, diversity and potential functions), plant communities (species identity, community biomass production and fine root traits) and soil properties (multiple chemical variables) along a continental latitudinal transect of 4200 km covering a wide range of forest biomes. By doing this, we were able to evaluate the potential capacity of climate legacies to predict the variations in MMQ across and within three main forest biomes: tropical, subtropical and temperate forests. Specifically, we compared direct and indirect driving mechanisms of climate legacies influencing MMQ in warmer ecosystems (tropical and subtropical forests) and in colder ecosystems (temperate forests).

2 | MATERIALS AND METHODS

2.1 | Site description and sampling

We conducted soil and vegetation surveys at 26 sites belonging to long-term ecological research stations across Eastern China (Supporting Information Figure S1). The selected sites cover a broad spectrum of latitudinal forest biomes including temperate, subtropical and tropical forests. Mean annual temperature (MAT) ranged from −5.8 to 22.4°C (Supporting Information Figure S1). At each site, one or two native forest types were selected. In each forest type, we established five or six plots (15 m × 15 m). A minimum distance of 10 km was kept between two plots. Latitude, longitude and elevation for each plot were recorded. In each plot, 20 soil cores from the top 10 cm of soil were collected within a 50 cm radius of individual dominant trees and after removal of the litter layer, then pooled per plot. The dominance of tree species was determined by using abundance and basal area data from the database of the National Ecosystem Research Network of China (http://www.cnern.org.cn/index.jsp). Root samples were taken from these dominant tree species per plot and site. In planted forests, we sampled the three most abundant species. In naturally regenerated forests, we sampled the top eight species with the highest abundances. Finally, we collected 13 soil samples from tree plantations, which were monocultures of *Cunninghamia lanceolate* and *Pinus massoniana* in tropical or subtropical regions. Given that the age at maturity for *C. lanceolate* and *P. massoniana* is 25–30 and 40 years, respectively, we selected plantations with an age >50 years to decrease the anthropogenic effect on soil microbial processes for soil sampling. In total, 85 dominant tree species were recorded and sampled along this latitudinal transect. Living fine roots from each soil core were collected. To ensure the accuracy of fine root sampling from the chosen trees, we initially sampled thick roots and traced the root branches to the focal tree, then separated fine roots from thick roots. The collected soil samples were stored in a cooling box in the field, then frozen at −80°C in the laboratory for later DNA extraction and phospholipid fatty acid measurements. For physical and chemical analyses, soils were sieved to 2 mm and stored at 4°C. To avoid the effect of low sequencing efforts on our results, a total of 141 soil samples were considered for final statistical analysis.

2.2 | Climatic data

A total of 19 standardized climate variables (Supporting Information Table S1) were obtained from the Worldclim database (www.worldclim.org) for every site. In the case of mid-Holocene and Last Glacial Maximum climates, we used estimates provided by the community climate system model (Bystriakova et al., 2014). We used data at a spatial resolution of 2.5′, because this is the highest resolution available for the Last Glacial Maximum period. Bioclimatic data are also available at this resolution for current and mid-Holocene climates, allowing direct comparison among bioclimatic data at different periods. In all cases, climatic data were at a spatial resolution of 30″ for the present and mid-Holocene, which allowed us to compare data at resolutions of 2.5′ and 30″ for these two periods. We calculated the climate legacy as the mathematical difference between the present climate and Last Glacial Maximum, for each climate variable and site as follows:

$$\text{Climate legacy} = (P_i - P_j), \quad (1)$$

where P_i is the predictor of the current climate and P_j of the Last Glacial Maximum.

2.3 | Vegetation measurements

The normalized difference vegetation index (NDVI) was used as a proxy for net plant primary productivity as done by Delgado-Baquerizo, Karunaratne, et al. (2018). The NDVI data were obtained from the Moderate Resolution Imaging Spectroradiometer aboard NASA's Terra satellites (http://neo.sci.gsfc.nasa.gov/).

2.4 | Soil and fine root chemical analysis

A total of 16 soil chemical properties were measured, namely soil pH, soil moisture, SOC, total N, ammonium (NH_4^+) and nitrate (NO_3^-), total phosphorus (P), plant-available P, exchangeable K^+, Na^+, Ca^{2+}, K^+ and Mg^{2+} contents, and ratios of C:N, C:P and N:P. Soil pH was measured using a ratio of 1:2.5 (weight:volume) of soil and 1 mol L^{-1} KCl solution. Soil organic C and total N content were measured using a C/N analyser (Elementar, Germany). The NH_4^+ and NO_3^- of soil samples were extracted using 2 mol L^{-1} KCl solution, then determined by colorimetry. Soil total P was measured directly through colorimetry. Plant-available P in soils was analysed colorimetrically with a Molybdate Blue method after soils were extracted with 1 mol L^{-1} NH_4F solution. Contents of exchangeable Na^+, Ca^{2+}, K^+ and Mg^{2+} and other variables were analysed with standard

protocols and reported by Wang et al. (2018). Fine roots (Supporting Information Figure S2) for each dominant tree species were dried after the removal of rhizosphere soil, and their C and N contents were measured using standard protocols (Cornelissen et al., 2003). The fine root samples were dried for 72 h at 60°C for measurement of the fine root C and N concentration with a C/N analyser (Elementar, Germany).

2.5 | Measurement of soil MMQ

The soil MMQ (in milligrams of C per gram of MBC per hour) was calculated as the ratio of the microbial respiration to microbial biomass (Anderson & Domsch, 1993). For measurement of microbial respiration, *c*. 20 g (dry weight) of fresh soil for each soil sample (with 60% water-holding capacity) was placed into 100 ml rectangular glass containers, then incubated for 7 days at the MAT of the corresponding site. When differences in the MAT between sites were <1°C, the soils collected from these sites were incubated at the average temperature of their MAT. Using a constant incubation temperature (e.g., 25°C) can result in inaccurate simulations of common scenarios of periodic and continuous temperature changes (Conant et al., 2008; Karhu et al., 2014; Zhu & Cheng, 2011); therefore, we used incubation with diurnally varying temperature, which better reflects field conditions and thus the microbial respiration in the field. To measure microbial respiration, we connected each 100 ml rectangular soil container to an infrared gas analyser (Li-Cor 820) in a closed-loop configuration. The CO_2 production rate by microbial respiration was measured by the Li-Cor 820. Microbial biomass C was determined by the fumigation extraction method (Vance et al., 1987). Subsamples of sieved soil were fumigated with ethanol-free $CHCl_3$ for 24 h, then extracted with 0.5 M K_2SO_4 solution. MBC was calculated as the difference in extractable dissolved organic carbon between fumigated and unfumigated soils using a correction factor of 0.45.

$$\text{MMQ} = \text{net organic carbon oxidation} / \text{microbial biomass C}. \quad (2)$$

2.6 | Microbial biomass and enzyme activity analyses

Microbial biomass was determined through phospholipid fatty acid (PLFA) analysis as described by Bardgett et al. (1996). Phospholipids were extracted from 1.5 g of fresh soil and analysed using an Agilent 6890 Gas Chromatograph. Gram-positive bacteria were identified by the terminal and mid-chain branched fatty acids (i15:0, a15:0, i16:0, i17:0 and a17:0), and Gram-negative bacteria by cyclopropyl saturated and monosaturated fatty acids (16:1ω7c, cy-17:0, 18:1ω7c and 8cy-19:0) (Rinnan & Baath, 2009). The fatty acids 18:2ω6,9 and 18:1ω9 were considered to represent saprotrophic and ectomycorrhizal fungi (Kaiser et al., 2010). The total PLFA concentration was calculated from the identified PLFAs (15:0, 14:0, 16:1, 16:1ω5, 16:0, 17:1ω8, 7Me-17:0, br17:0, br18:0, 18:1ω5, 18:0 and 19:1; and those listed above). The ratios of fungal to bacterial (F:B) PLFA and Gram-positive to Gram-negative (GP:GN) PLFA were taken to represent the relative abundance metrics of these groups. The biomarker of 16:1w5c was used to indicate arbuscular mycorrhizal fungi (Olsson, 1999).

Furthermore, enzyme activity was determined by detecting invertase, β-glucosidase, urease and calatase activities. Invertase activity was determined with 35.06 mM of saccharose in 2 M of acetate buffer. β-Glucosidase activity was determined by measuring the rate of p-nitrophenol formation during soil incubation with *p*-nitrophenyl-β-D-glucopyranoside. Urease activity was determined through the colorimetric determination of ammonium. Catalase activity was determined as the capacity to decompose H_2O_2 at 20°C after 10 min of soil incubation with 30% H_2O_2 and subsequent titration with 0.05 N of $KMnO_4$. More detailed information about these measurements can be found in the paper by Wang et al. (2018).

2.7 | Microbial DNA extraction and amplicon sequencing

Total genomic DNA from soil samples weighing 0.5 g was extracted using a PowerSoil DNA Isolation Kit (MoBio Laboratories, USA) following the manufacturer's instructions. Triplicate extractions were implemented for each soil sample. The DNA concentration and the degree of purity were checked on 1% agarose gels, then DNA was diluted to 1 ng μl^{-1} with sterile water. The DNA samples were sent to Novogene (Beijing, China) for analysis using the MiSeq sequencing platform. For bacteria, the V4 region of 16S ribosomal RNA genes was amplified using the primer pair 515F (5′-GTGCCAGCMGCCGCGGTAA-3′) and 806R (5′-GGACTACHVGGGTWTCTAAT-3′) (Delgado-Baquerizo, Eldridge, et al., 2018). For fungi, the ITS2 region was amplified using the primer pair gITS7F (5′-GTGARTCATCGARTCTTTG-3′) and ITS4R (5′-TCCTCCGCTTATTGATATGC-3′) (Ihrmark et al., 2012). More detailed information about amplicon sequencing and bioinformatic analyses can be found in the paper by Liu et al. (2020). Three samples were removed owing to low sequencing yields, and the other samples were subsampled to 25,000 and 6000 sequences per sample for 16S and ITS, respectively. To identify potential microbial ecological functions across forest biomes, the operational taxonomic units obtained were compared against the FAPROTAX 1.1 database to predict potential metabolic functions of the bacterial community (Louca et al., 2016). The functional groups of soil fungi were identified using FUNGuild (Nguyen et al., 2016) and FungalTraits (Põlme et al., 2020).

2.8 | Statistical analysis

The pairwise distance matrix was calculated using the Euclidean metric in the "vegan" R package (Oksanen, 2013). Tree species identity was transformed to dummy variables in principal components analysis (PCA), also using the "vegan" package. The microbial

operational taxonomic unit table was Hellinger-transformed to perform further multivariate analyses. The Kruskal–Wallis test was performed to test the significant difference in MMQ among vegetation types (tropical, subtropical and temperate forests) and functional types (broadleaved, coniferous and a mix of broadleaved and coniferous trees).

To represent vegetation identity, we used the most important components (total explanations >85%), which were calculated from PCA. The PCA was performed using the "vegan" package, and the selected important components were included in further analysis. To test and quantify the relative importance of environmental predictors for MMQ, all determined predictors were classified into five categories, namely "current climate"; "palaeoclimate"; "vegetation attributes" [plant identity, net primary production (NPP), fine root N and C content]; "soil properties" (SOC, total N, total P, plant-available P, pH, moisture, exchangeable K^+, Na^+, Ca^{2+}, Mg^{2+}, NH_4^+, NO_3^-, C:N, C:P and N:P); and "microbial attributes" (microbial PLFAs, invertase, β-glucosidase, urease, microbial richness, microbial community composition and microbial functional potentials). The importance of each category for MMQ was evaluated through variance partitioning using the "varpart" function of the "vegan" R package. The "forward.sel" function was used to avoid redundancy and resulting multicollinearity in variation partitioning analysis. The classification random forest analysis was performed to identify the important predictors of microbial diversity as applied by Delgado-Baquerizo, Bissett, et al. (2017). These analyses were conducted using the "rfPermute" R package (Archer, 2013).

Structural equation modelling was used to determine the underlying pathways of the observed effects of environmental predictors on MMQ. Structural equation modelling is widely used in large-scale studies, because it allows the partitioning of causal relationships among multiple variables and the separation of direct and indirect effects of model predictors (Delgado-Baquerizo, Bissett, et al., 2017). Owing to the large number of predictors used, we conducted a classification random forest analysis to preselect the most important variables for each category for the structural equation model (SEM). The measured variables for climate, soil properties, microbial properties and vegetation traits included in this model were initially divided into "composite variables", then included in the SEM (Tian et al., 2021). The SEM was conducted using the R packages "piecewiseSEM" (Lefcheck, 2016), "nlme" and "lme4" (Bates et al., 2017). The piecewiseSEM could also account for random effects of sampling sites by providing "marginal" and "conditional" contributions of environmental predictors in driving MMQ. Fisher's C test (when $0 \le$ Fisher's C/d.f. ≤ 2 and $.05 < p \le 1.00$) was used to confirm the goodness of the modelling results. The prior model was constructed as in the study by Delgado-Baquerizo, Bissett, et al. (2017). We then modified our models according to the significance ($p < .05$) and the goodness-of-fit of the model.

In order to identify the most important biomarkers of MMQ, the random forests model was used to identify the most important biomarkers for the bacterial and fungal communities, separately. The importance of features was determined over 100 iterations. The number of marker taxa was determined using 10-fold cross-validation implemented with the "rfcv" function of the R package "randomForest" with five repeats (Breiman, 2001).

3 | RESULTS

The MMQs showed a hump-shaped pattern with latitude (Figure 1a). Temperate and subtropical forest soils had higher MMQs than tropical forest soils (Figure 1b). Coniferous forest soils with relatively low SOC content (Supporting Information Figure S2b) had higher MMQs than broadleaved forest and broadleaved-coniferous forest soils with relatively high SOC quality (Figure 1b).

Initially, we used variation partitioning to identify the predictors of MMQ at the continental scale. Most variations in MMQ [adjusted R^2 (R^2_{adjust}) = 59.6–86.9%] were attributed to the unique and shared effects of palaeoclimate, current climate, environmental variables (including geography, plant attributes and soil properties) and microbial attributes across all biomes (Figure 2). In particular, palaeoclimate predicted more unique and shared variations in MMQ than did current climate (Figure 2), with the maximum temperature of the warmest month (MTWM) being the most useful predictor of past or current climates in explaining MMQ across all biomes (Table 1; Supporting Information Table S2), tropical and subtropical forests (Supporting Information Table S3) and temperate forests (Supporting Information Table S4).

Among environmental drivers, vegetation attributes had the potential to predict unique variations in MMQ across all biomes (Table 1; Supporting Information Table S2), and this potential tended to be more important in temperate forests (Supporting Information Table S4) than in tropical and subtropical forests (Supporting Information Table S3). Fine root C and N contents were more predictive of MMQ in tropical or subtropical forests (R^2_{adjust} = 41%; Supporting Information Table S3) than in temperate forests (R^2_{adjust} = 3%; Supporting Information Table S4), whereas plant identity was more important for explaining MMQ in temperate forests (R^2_{adjust} = 40%; Supporting Information Table S4) than in tropical or subtropical forests (R^2_{adjust} = 9%; Supporting Information Table S3). These results suggest that the importance of different plant attributes in regulating variations in MMQ varied among the biomes. Moreover, we also detected biome-dependent associations between MMQ and soil properties. Although soil C:N could predict variations in MMQ well across all biomes, particularly in temperate forests (R^2_{adjust} = 25%; Supporting Information Table S4), the primary predictor for MMQ was NH_4^+ across all biomes (R^2_{adjust} = 31%; Supporting Information Table S2) and in tropical or subtropical forests (R^2_{adjust} = 53%; Supporting Information Table S3).

Among microbial attributes, Gram-negative bacterial biomass (GN) and the microbes with the potential function of driving soil N cycles (Supporting Information Table S5; nitrite respiration; e.g., *Rhodoplanes*, *Pseudomonas* and *Clostridium*) or recalcitrant C decomposition (chitinolysis; e.g., *Lysobacter*) were found to be good predictors of MMQ across all biomes and for subtropical forests

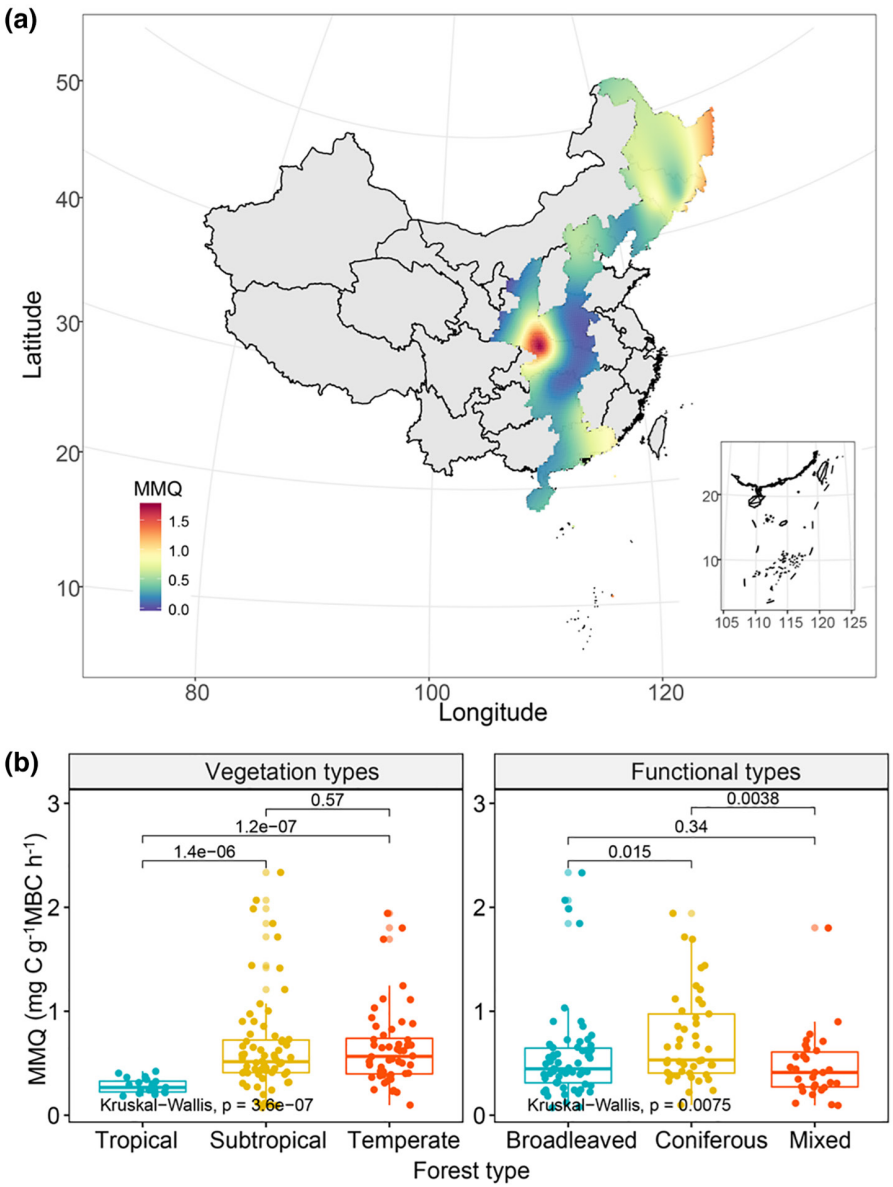

FIGURE 1 Soil microbial metabolic quotient (MMQ) varies with latitudinal gradient and forest types. (a) Spatial mapping of MMQ across sampling regions using ordinary kriging interpolation. (b) The significant difference in MMQ among three forest types. Kruskal–Wallis tests were performed to test the significant difference in MMQ among three forest types. The significance level was regarded as $p < .05$.

(Figure 3; Supporting Information Tables S2 and S3; Figure S2). Ascomycota richness was found to be more important in temperate forests (R^2_{adjust} = 22%; Supporting Information Tables S4 and S6–S8) than in others. Thus, soil microbial properties played different roles in shaping the variation in MMQ in different forest biomes. Specifically, MMQ showed positive relationships with the richness of bacteria and some associated phyla (Figure 3a–c), but negative links with the richness of fungi and their associated phyla (Figure 3e–g). Furthermore, we detected an important role of fungal community composition in shaping the variations of MMQ across and within all biomes (Figure 3j), and Gram-negative bacteria were found to be important across all biomes and in subtropical forests (Figure 3k). From the above results, we conclude that the underlying mechanisms of climate legacies influencing MMQ differ among diverse forest biomes.

We performed piecewiseSEM to determine how long-term climate legacies drove the variation in MMQ at the continental and regional scales. Initially, the random forest model was used to select the best predictors across all biomes (Supporting Information Table S6) and in subtropical (Supporting Information Table S7) and temperate forests (Supporting Information Table S8) separately. Our models provided solid evidence that climate legacies consistently had larger positive effects on MMQ than the current climate across all biomes (Figure 4; Supporting Information Figures S3–S5) and within tropical and subtropical forests (Supporting Information Figure S4a). Among climate legacies, isothermality (ISO) and mean diurnal ranges (MDR), which are indices of temperature, were the best predictors of the variations in MMQ (Figures 4 and 5; Supporting Information Table S6). Specifically, climate legacies had both direct and indirect effects on MMQ, showing larger indirect effects by regulating soil properties (e.g., SOC and NH_4^+) across all biomes (Figure 4) and in tropical and subtropical forests (Figure S4a), whereas in temperate forests MMQ was regulated by vegetation attributes (Figure S4b).

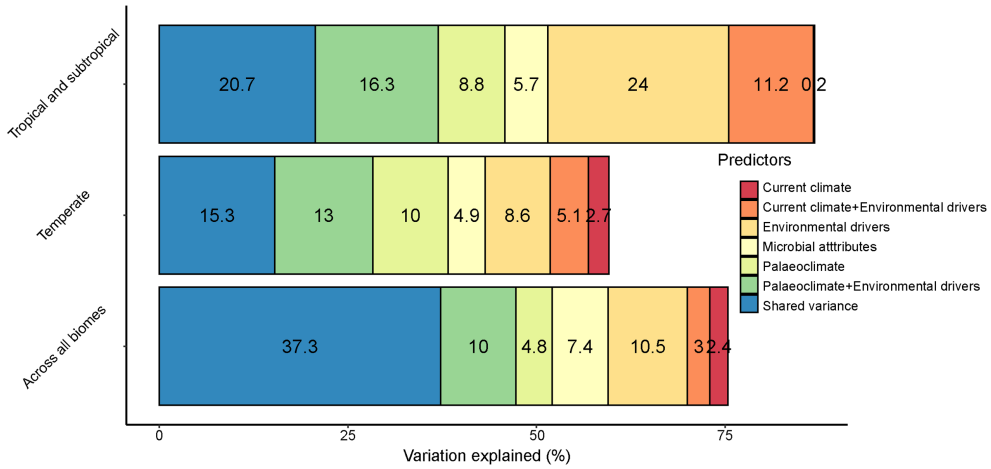

FIGURE 2 Relative contribution of the different predictors used to model microbial metabolic quotient (MMQ). The bars represent results from variation partitioning modelling aiming to identify the percentage variance of the MMQ explained by palaeoclimate and current climate variables across or within biomes. Environmental drivers included soil properties, plant attributes and geographical location. Significant predictors were selected at the level of $p < .05$. The *p*-values associated with the most important predictors can be found in the Supporting Information (Tables S2–S4).

TABLE 1 The best predictors selected from variation partitioning modelling for soil microbial metabolic quotient across all forest biomes or within each forest biome

Biomes	Variable	Adjusted R^2	*F*	*p*-value
Across all biomes	Plant principle component 1	.12	19.48	.001
	Fine root carbon	.09	15.42	.001
	NH_4^+-N	.31	63.46	.001
	Soil total phosphorus	.14	34.85	.001
	Gram-negative bacteria biomass	.42	102.62	.001
	MTWM-current	.28	52.91	.001
	MTWM-mid	.22	39.43	.001
	PS_last	.11	23.54	.001
Tropical + subtropical	Fine root nitrogen	.26	23.72	.001
	NH_4^+-N	.54	81.1	.001
	Soil total phosphorus	.22	59.96	.001
	Gram-negative bacteria biomass	.66	136.79	.001
	MTWarmQ-current	.4	45.27	.001
	MTWM-last	.39	44.18	.001
Temperate	Plant principle component 1	.18	14.9	.002
	Plant principle component 2	.12	11.32	.002
	soil C:N ratio	.26	24.25	.001
	Ascomycota richness	.23	20.54	.001
	MTWM-current	.13	10.3	.002
	MTWM-mid	.18	15.21	.001

Note: The significance level was regarded as $p < .05$ (for other significant predictors see Tables S2–S4). MTWM-current, max temperature of warmest month for current climate; MTWM-mid, max temperature of warmest month for mid-Holocene climate; MTWarmQ-current, Mean temperature of warmest quarter for current climate; MTWM-last, max temperature of warmest month for Last Glacial Maximum climate; PS-last, precipitation seasonality for Last Glacial Maximum climate.

We also used a random forest machine-learning method to determine accurately the biomarkers of soil microbes involved regulating the spatial variations in MMQ. The cross-validation error curve stabilized when the 30 and 46 most relevant families of bacteria and fungi, respectively, were tested (Supporting Information Figure S6). Among them, the biomarkers closely linked to rhizosphere conditions

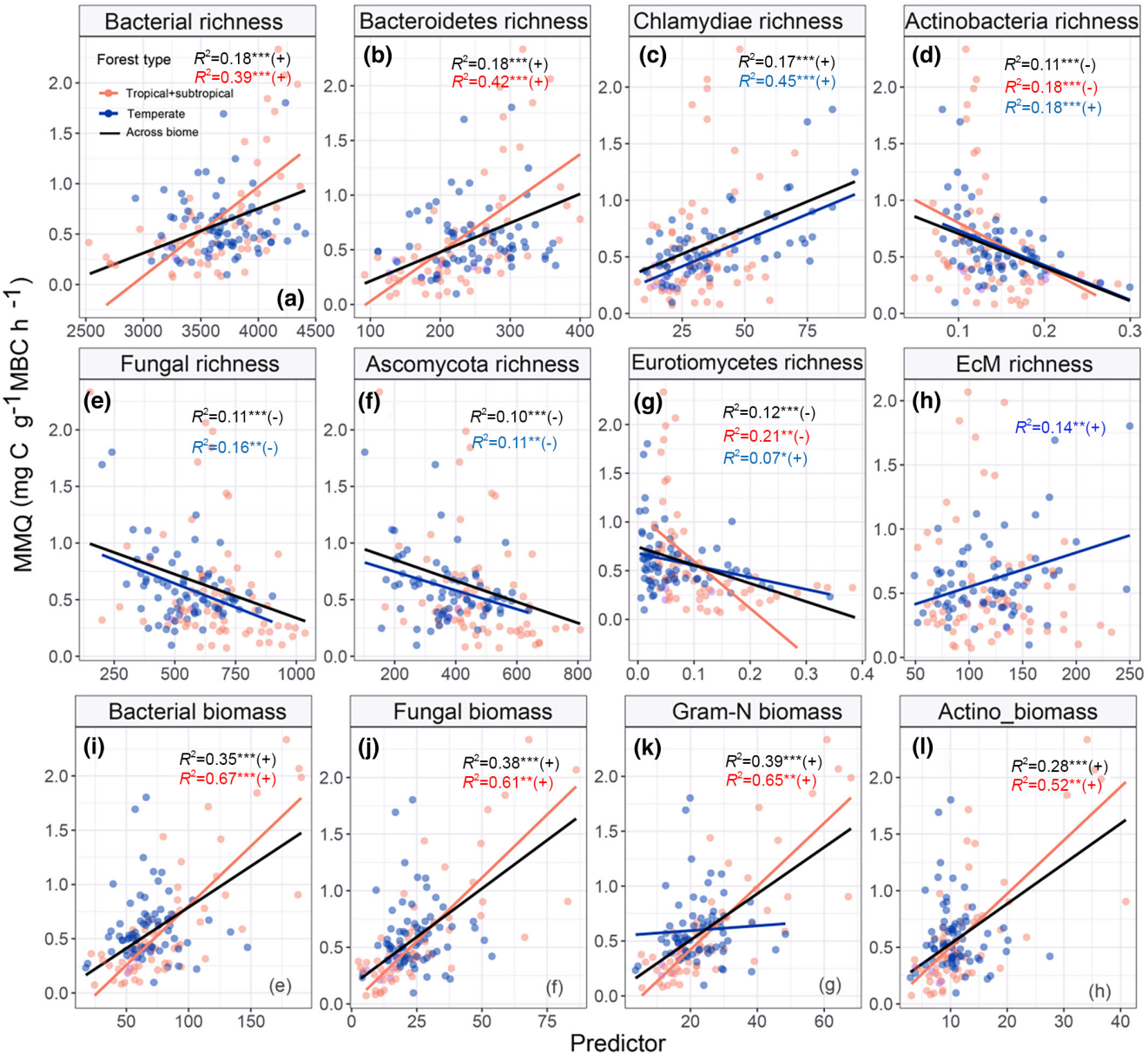

FIGURE 3 Soil microbial biomass and diversity predict microbial metabolic quotient (MMQ) in different forest biomes. Random forest modelling was performed to select the best microbial predictors. Forest biomes are indicated by different colours. Significant associations between MMQ and microbial diversity (operational taxonomic unit richness) and functional potentials are reported within each panel. The characters "+" and "−" represent positive and negative relationships between microbial properties and MMQ. The significance level was regarded as $p < .05$.

(Bacteroidetes and Actinobacteria) or that prefer a high-N niche (Actinobacteria and Proteobacteria) (Supporting Information Figure S6a) and the biomarkers of fungi (Tremellales and Eurotiales) depending on woody debris (Supporting Information Figure S6b) were identified as the most important predictors of MMQ.

4 | DISCUSSION

In the present study, we measured MMQ based on the MAT of the sites where the soil was collected rather than using the same temperate for all soils. Therefore, we believe that our experiment provides more realistic and close-to-nature results than those of some previous studies (e.g., Spohn & Chodak, 2015). We found that: (1) MMQ changed in a nonlinear manner along the latitudinal transect, with higher MMQ in temperate and subtropical forests than in tropical forests; and (2) the underlying mechanisms of variation in MMQ were related mainly to climate legacies, either by biome-specific direct effects or indirectly, via changes in vegetation attributes, soil chemical or microbial properties. Previous studies, such as the study by Xu et al. (2017), demonstrated that the variation in MMQ is determined by multiple factors by synthesizing the published data

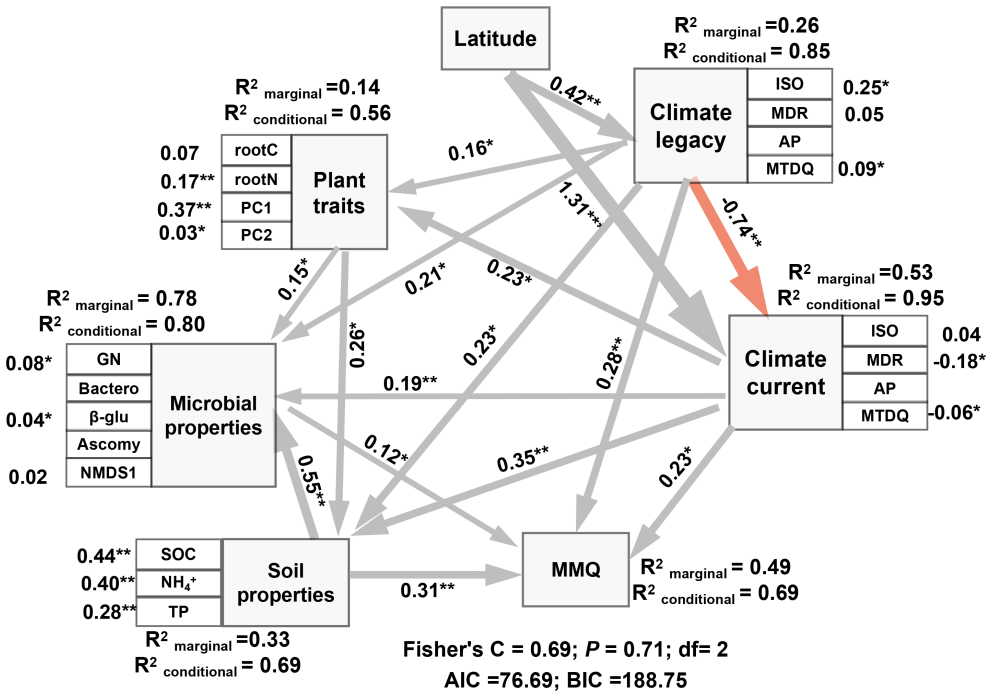

FIGURE 4 PiecewiseSEM accounting for the direct and indirect (plant traits, soil properties and microbial properties) effects of climate legacies on microbial metabolic quotient (MMQ) across all biomes. Plant traits, soil properties, microbial properties, current climate and climate legacy are composite variables. Numbers adjacent to the measured variables are their coefficients with composite variables. Numbers adjacent to arrows are path coefficients and are the directly standardized effect size of the relationship. The thickness of the arrow represents the strength of the relationship. Acronyms for climate are shown in the Supporting Information (Table S1). The conditional and marginal R^2 represent the proportion of variance explained by all predictors without and with accounting for random effects of "sampling site". Relationships between residual variables of measured predictors are not shown. Significance levels of each predictor are $^{*}p < .05$, $^{**}p < .01$ and $^{***}p < .001$. The variables rootC and rootN are carbon and nitrogen contents in fine roots, while PC1 and PC2 are the two most significant principal components of plant identity. Abbreviations: Ascomy, Ascomycota richness; Bactero, *Bacteroides* richness; β-glu, β-glucosidase; GN, biomass of Gram-negative bacteria; NMDS-1, fungal community composition. For results for tropical and subtropical forests and for temperate forests separately, see the Supporting Information (Figure S4a,b).

across different ecosystems (e.g., deserts, forests, croplands and grasslands), but they did not consider the role of climate legacy in regulating MMQ. Thus, our findings advance our understanding of the relative importance of microbial processes and functions in the global soil C cycle and their dependence on the palaeoclimate.

Our first hypothesis, that forest soils with lower temperature variability (e.g., mean diurnal ranges or isothermality) and those with decreasing temperature variability over millennia have a higher MMQ than others, was confirmed, in part. We were able to show that MMQ was higher in subtropical and temperate forest soils than in tropical forest soils, but we found no difference in MMQ between subtropical and temperate forests. Thus, our results confirm, in part, the compensation hypothesis, which states that spatial variation in MMQ across biomes decreases with increasing MAT (Bradford et al., 2019), showing a negative response of microbial respiration rates to warming. The difference in MMQ across different forest biomes was probably attributable to the differences in soil microbial community composition and activity, which is supported by the positive correlations between MMQ and microbial biomass found in our study (Supporting Information Figure S2e–h). Differences in soil microbial community composition across forest biomes might result in different MMQs because fungi have higher C use efficiency (CUE) than bacteria (Sinsabaugh et al., 2013; Takriti et al., 2018). Given that MMQ is the ratio of microbial respiration to microbial biomass, a higher MMQ can be indicative of more C being respired and released to the atmosphere as CO_2 and less C being incorporated into microbial biomass for growth (i.e., a higher MMQ represents lower a CUE for microbes). Moreover, communities with higher MMQ can have either a high metabolic rate per unit biomass or high biomass production, indicating a trade-off between maintenance of their metabolism and growth (Xu et al., 2017). Therefore, our results suggest that in tropical forests with lower MMQ, soil microbes might have a higher CUE than in subtropical and temperate forests, which might favour SOC sequestration in tropical forests because of a higher MMQ accompanied by more rapid SOC decomposition and C loss.

In line with our expectations, climate legacies, especially temperature legacies, directly affected MMQ across all forest biomes (Figure 3) and in tropical and subtropical forests (Supporting Information Figure S4a) but did not in temperate forests (Supporting Information Figure S4b). These results indicate that the effects of climate legacies on MMQ were biome dependent, supporting close linkages between climate legacies

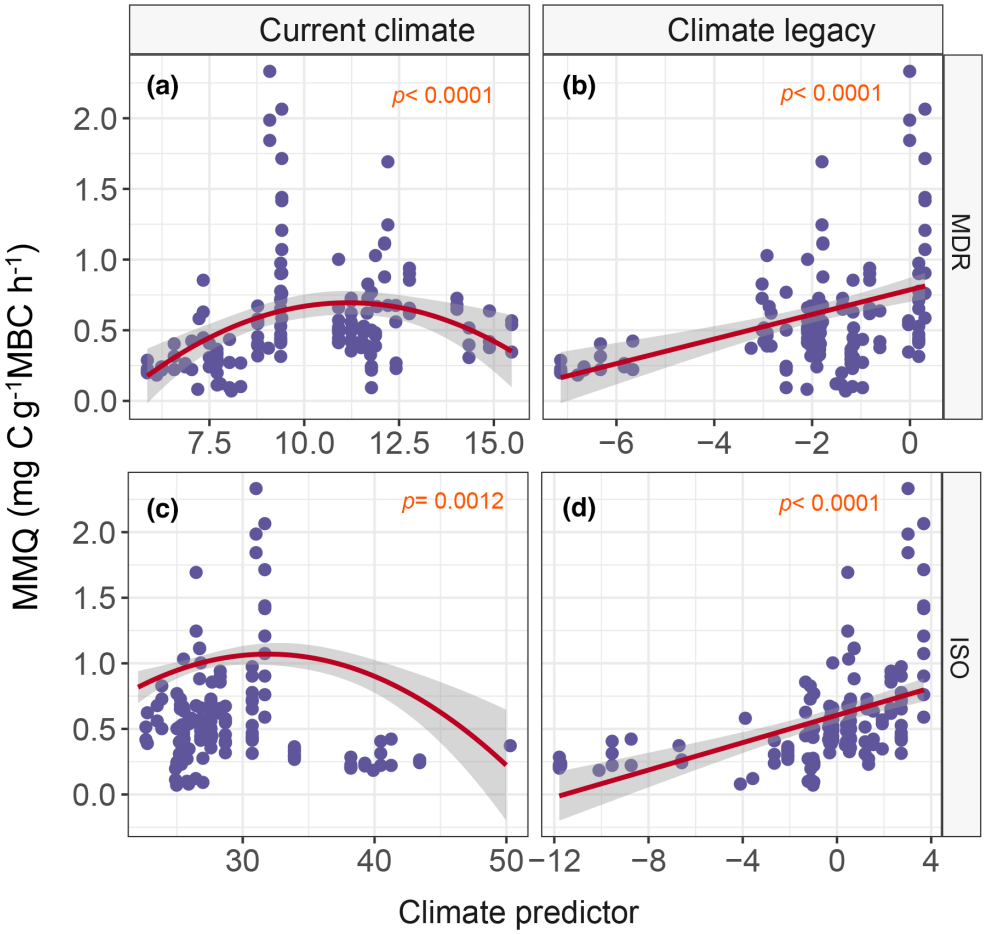

FIGURE 5 Relationships between current climate (a,c), climate legacies (b,d) and microbial metabolic quotient (MMQ). The Akaike information criterion was used to select the best model.

and MMQ. Previous studies have shown that climate legacies can have a strong impact on plant communities and productivity, SOC stocks and microbial community composition (Delgado-Baquerizo, Bissett, et al., 2017; Delgado-Baquerizo, Karunaratne, et al., 2018; Liu et al., 2022; Lyons et al., 2015; Svenning et al., 2015), which is in line with our findings. Thus, we assume that the climate legacies on MMQ in different forest biomes were probably caused by differences in plant traits, soil properties and microbial characteristics in our study. Therefore, further research is needed to test whether climate legacies can also have direct effects on microbial processes, such as MMQ.

Temperature legacies had substantially indirect effects on MMQ, primarily by changing key soil properties across all forest biomes (Figure 3) and in tropical and subtropical forests (Supporting Information Figure S4a) and by changing plant community composition in temperate forests (Supporting Information Figure S4b). These results suggest that the underlying mechanisms of indirect effects of climate legacies on MMQ varied in different forest biomes. Forest ecosystems are composed of unique geographical units with various climate, plant, edaphic and microbial traits (Anderson, 1992), meaning that different factors influence MMQ. Although limited studies have shown the effects of climate legacies on soil properties (Delgado-Baquerizo, Eldridge, et al., 2017; Ding et al., 2019), less is known about how climate legacies affect MMQ indirectly. We found that climate legacies had strong positive and indirect effects on MMQ, mainly by changing SOC and NH_4^+ contents across all forest biomes (Figure 3) and in tropical and subtropical forests (Supporting Information Figure S4a). Soil NH_4^+, SOC and pH showed strong positive correlations with MMQ during millennial climate changes (Supporting Information Figure S3b–d) in subtropical forests with high ecosystem productivity because of optimized temperate and precipitation. This is mainly because resource quality (i.e., SOC and NH_4^+) is commonly considered to be a limiting factor for microbial diversity and metabolic processes during long-term climate changes (e.g., Vitousek, 2004).

Climate legacies also affected MMQ indirectly by altering plant traits (e.g., plant identity and fine root N content) in temperate forests, but not in other forest biomes. A possible explanation could be that spatial variations in plant cover were more associated with increases in soil microbial diversity in higher latitudinal regions as a function of millennial climate changes (Delgado-Baquerizo, Karunaratne, et al., 2018). Of course, plants not only provide C sources for soil microbes via litter and root exudates but also affect microenvironmental conditions (Gessner et al., 2010;

Tedersoo & Bahram, 2019), especially in low-productivity ecosystems, where temperatures are often low (Delgado-Baquerizo, Eldridge, et al., 2018).

Vegetation attributes regulated the spatial variation in MMQ indirectly, by modifying soil chemical properties and microbial community composition and diversity (Figure 4; Supporting Information Figure S4), which is in line with previous studies showing that vegetation attributes altered organic matter through litter or root input, edaphic properties and soil microbial characteristics (e.g., Bardgett & van der Putten, 2014; Gessner et al., 2010). Strong correlations between microbes with functions of chemoheterotrophy and hydrocarbon degradation and fine root N content across forest biomes or within specific biomes (Supporting Information Figure S3) might explain, in part, why bacterial and fungal biomasses regulated MMQ positively. Our findings are supported by previous laboratory incubation studies showing that the SOC decomposition rate was closely linked to the size of microbial biomass C pools (Hartman & Richardson, 2013).

Soil microbial community composition and activity controlled MMQ directly, owing to the fact that bacteria and fungi have different CUE (Sinsabaugh et al., 2013; Takriti et al., 2018). As stated above, the effects of plant traits on MMQ were caused by changing soil microbial characteristics. Our piecewiseSEM results (Figure 3; Supporting Information Figures S4 and S5) and previous evidence showed that climate legacy can leave a strong signature in the contemporary distribution of microbial communities indirectly, through its influence on plant diversity and soil properties (Delgado-Baquerizo, Eldridge, et al., 2017). Thus, variations in soil properties such as SOC and nutrient availability can have strong effects on microbial community distributions (Fierer, 2017; Tedersoo et al., 2014) and change slowly during ecosystem development (Wardle et al., 2004), which can explain the effects of climate legacy on the spatial variations in microbial metabolic processes (e.g., MMQ) nowadays.

In conclusion, using a natural forest platform with a large range of forest biomes, we have explored the variations in MMQ at regional and continental scales and revealed that their underlying mechanisms are forest biome dependent. Our findings provide the first continental-scale evidence that the palaeoclimate legacy, particularly temperature, influences MMQ directly. Furthermore, our study highlights the importance of indirect effects of climate legacy on MMQ through shaping plant traits, soil properties and microbial community composition and activity. Furthermore, our findings provide important insights into the fundamental role of microbial processes in driving soil organic C stocks across diverse forest biomes. Our results also suggest that considering climate legacies in contemporary climate models will improve our ability to predict soil C cycles and dynamics under the ongoing global environmental change.

AUTHOR CONTRIBUTIONS

Q.W. and M.D.-B. designed the research; S.L., Z.S., P.T. and X.Z. performed the research; S.L. analysed the data; S.L., M.D.-B. and Q.W. wrote the first draft, and the rest of the co-authors helped to improve the final draft.

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CONFLICT OF INTEREST

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The database of microbial communities used for this paper has been deposited on figshare (https://doi.org/10.6084/m9.figshare.11317175; and https://doi.org/10.6084/m9.figshare.11317094).

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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