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RESEARCH ARTICLE

Mycorrhiza-dependent drivers of the positive rhizosphere effects on the temperature sensitivity of soil microbial respiration in subtropical forests

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Abstract

1. Tree roots and their fungal symbionts mediate the response of rhizosphere soil organic carbon (SOC) decomposition to climate warming, specifically the temperature sensitivity of soil microbial respiration (Q_{10}), which is a critical parameter for projecting the magnitude of terrestrial soil C-climate feedbacks. However, the intensity of the rhizosphere effects (RE; rhizosphere soils vs. bulk soils) on Q_{10} in forest soils associated with different mycorrhizal groups and their seasonal dynamics are poorly understood.
2. Here, we selected nine tree species associated with either arbuscular mycorrhizal (AM) or ectomycorrhizal (EM) fungi in subtropical forests of China and collected bulk soil and rhizosphere soil in both the warm and cold seasons to explore the RE on Q_{10}, respectively.
3. Our results showed a positive RE on Q_{10} (ranging from 20.1% to 87.5%) for all tree species, independent of the season. For EM tree species, the RE on Q_{10} was 64.5% higher in the warm season and 44.4% higher in the cold season, compared with AM tree species. The RE on Q_{10} of AM and EM tree species was 44.8% and 65.0% larger in the warm season than that in the cold season, respectively. Fine root traits (including biomass, the carbon-to-nitrogen ratio, and soluble sugar content) predominantly controlled the RE on Q_{10} in AM-dominated forests, whereas the RE on soil properties (such as NH_{4+} and C availability) dominantly governed the RE on Q_{10} in EM-dominated forests. Furthermore, the RE on Q_{10} was also positively correlated with the RE on soil microbial phospholipid fatty acids in both AM- and EM-dominated forests.

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4. These findings suggest that rhizosphere soils in EM-dominated forests are more susceptible to C losses under climate warming than those in AM-dominated forests, compared with their respective bulk soils, potentially limiting rhizosphere SOC sequestration. The greater vulnerability of EM-dominated forests underscores the importance of accounting for root–soil interactions, mycorrhizal associations, and seasonal dynamics in C-climate models to improve predictions of SOC cycling and its feedback to global warming.

KEYWORDS
rhizosphere effect, soil microbial respiration, temperature sensitivity, mycorrhizal types, seasonal variations

1 | INTRODUCTION

Soil microbial respiration (Rm) represents the second-largest carbon (C) release from soil to the atmosphere (60 Pg C $year^{-1}$) (Karhu et al., 2014), which is increasingly recognized as an important positive feedback to global warming (Song et al., 2019). The magnitude of this positive feedback can be expressed as the temperature sensitivity (Q_{10}), which is the factor by which Rm increases with a 10°C rise in temperature (Davidson & Janssens, 2006). Previous studies have shown that Q_{10} of Rm is affected by soil nutrient availability, the quality and quantity of soil organic carbon (SOC), and soil microbial properties (Davidson & Janssens, 2006; Karhu et al., 2014; Wang et al., 2018). These factors differ significantly between rhizosphere soil and bulk soil (Finzi et al., 2015). As a key root–soil–microbe resource exchange microdomain, rhizosphere soil only occupies a relatively small percentage of total soil volume but may contribute nearly 50% of the total CO_2 fluxes released from the terrestrial surface (Hopkins et al., 2013). Generally, rhizosphere soils have higher C content, nutrient concentrations, and microbial activity than bulk soils (i.e., root-free soils), and the differences between rhizosphere soil and bulk soil are usually referred to as rhizosphere effects (RE (%) = (rhizosphere soil − bulk soil) / bulk soil × 100%) (Finzi et al., 2015; Phillips & Fahey, 2006). It is important to note that most Q_{10} studies have focused on bulk soils, with rhizosphere soils receiving less attention (Wang et al., 2018, 2019). Only a limited number of studies have reported either negative (Bader & Cheng, 2007) or positive (Zhao, Tian, Liu, et al., 2022; Zhu & Cheng, 2011) results regarding RE on Q_{10}. This knowledge gap is critical as most C-climate models usually apply Q_{10} values of bulk soil to represent the whole soil that includes bulk soil and rhizosphere soil, assuming similar Q_{10} values between rhizosphere soil and bulk soil or disregarding rhizosphere soil altogether. Thus, if warming differentially affects microbial processes in bulk soil compared with rhizosphere soil, it could introduce significant uncertainties in SOC cycling estimates. A better understanding of root–soil interactions in forest ecosystems under climate warming could enhance our ability to assess and predict rhizosphere SOC cycling and nutrient dynamics.

Arbuscular mycorrhizal (AM) and ectomycorrhizal fungi (EM) form symbioses with most tree species (Genre et al., 2020; Tedersoo & Bahram, 2019). AM and EM fungi differ in their nutrient acquisition strategies, physiology, and morphology (Phillips et al., 2013; Zheng et al., 2023), leading to varied effects on rhizosphere SOC cycling (Han et al., 2020; Phillips & Fahey, 2006; Yin et al., 2014). AM fungi have limited saprotrophic capacities to mineralize complex organic matter and primarily acquire nutrients from inorganic sources (Duan et al., 2024; Genre et al., 2020). Consequently, AM tree species rely more on fine roots for nutrient acquisition, investing more C into developing and maintaining fine roots compared with EM tree species (Jevon & Lang, 2022; Tedersoo & Bahram, 2019). EM fungi are considered more efficient at decomposing organic matter through the production of extracellular hydrolytic and oxidative enzymes (Akroume et al., 2019; Lindahl et al., 2021; Maillard et al., 2023). This has been well demonstrated for organic nitrogen (N), which EM fungi acquire by degrading organic matter, suggesting that C may remain in the soil as EM fungi obtain C from their host trees (Lindahl & Tunlid, 2015). As a result of C liberation facilitated by the organic nutrient mining activities of EM fungi, rhizosphere soils of EM tree species may exhibit higher C availability. Empirical studies have shown that EM tree species exhibit greater root exudation than AM tree species (Yin et al., 2014), which enhances substrate availability and microbial activity, directly stimulating SOC decomposition and the RE on Q_{10} in EM-dominated forests. To date, these differences in the RE on Q_{10} between AM and EM tree species have not been experimentally verified, limiting our comprehensive understanding of the tight linkage between mycorrhizal types and the positive feedback of rhizosphere SOC decomposition to climate warming.

Seasonal variations affect plant photosynthesis rates, root exudates, and rhizosphere microbial activities, which in return regulate RE on Q_{10}. Compared with the cold season, the warm season exhibits greater root-derived C inputs to rhizosphere soil (Li, Shi, et al., 2021; Xiong et al., 2020), eventually stimulating microbial activity and enhancing Rm (Finzi et al., 2015; Xu et al., 2023). Therefore, we expect that the RE on Q_{10} should be higher in the warm season than that in the cold season, given the increased substrate availability and microbial activity (Cheng & Kuzyakov, 2005; Davidson et al., 2006). Moreover, AM and EM fungi respond differently to seasonal variations in temperature and humidity

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(Fei et al., 2022), further influencing the seasonal variations in RE on Q_{10} between mycorrhizal types. Compared with AM tree species, EM tree species may release more C belowground to rhizosphere soils through photosynthetic C fixation and root exudates during the warm season. This could promote microbial metabolic activity and SOC decomposition (Tedersoo & Bahram, 2019; Yin et al., 2014), potentially leading to greater seasonal variations in RE on Q_{10} for EM tree species than that for AM tree species. However, there remains insufficient evidence to confirm the differences in seasonal variations of RE on Q_{10} between EM and AM tree species. Thus, clarifying the seasonal variations of RE on Q_{10} in AM- and EM-dominated forests is essential for understanding and modelling SOC cycling under climate warming, ultimately increasing confidence in climate-C feedback projections.

To address this knowledge gap and to identify the differences in seasonal variations of RE on Q_{10} between AM and EM tree species, we selected five AM tree species and four EM tree species in subtropical China and collected rhizosphere soil and bulk soil in both the warm and cold seasons. Our primary objectives were: (i) to assess whether the magnitudes of the RE on Q_{10} differ between mycorrhizal types in the warm and cold seasons; (ii) to examine the seasonal variations (including warm and cold seasons) in the RE on Q_{10} between mycorrhizal types; and (iii) to identify the main determinants of the RE on Q_{10} for each mycorrhizal type. To achieve these goals, we quantified the RE on Q_{10} and its potential predictor variables including soil chemical properties, microbial properties, enzyme activities, and fine root traits. We hypothesized that (H1) the RE on Q_{10} is larger in EM-dominated forests than in AM-dominated forests; (H2) the primary drivers of the RE on Q_{10} differ between EM- and AM-dominated forests; and (H3) the RE on Q_{10} is greater in the warm season than in the cold season.

2 | MATERIALS AND METHODS

2.1 | Site information and field sampling

This study was conducted at the Huitong Experimental Station of Forest Ecology, Chinese Academy of Sciences (26°50′ N, 109°36′ E) in Hunan Province, China. The experimental site is characterized by a subtropical monsoon climate with a mean annual temperature (MAT) of 16.5°C. A mean minimum temperature of 1.9°C is recorded in January and a mean maximum temperature of 29.0°C appears in July. The mean annual precipitation (MAP) is 1200 mm, and precipitation events occur between April and August. The soils are approximately 80 cm deep and classified as Ultisol according to the US Soil Taxonomy System (Wang et al., 2013). The site is characterized by a subtropical evergreen forest, mainly composed of native broadleaved trees and *Cunninghamia lanceolata* plantations.

In July 2019 and January 2020, we selected five AM tree species and four EM tree species from subtropical Chinese forests and collected rhizosphere soil and bulk soil. The AM tree species included *C. lanceolata*, *Liquidambar formosana*, *Machilus pauhoi*, *Podocarpus macrophyllus*, and *Schima superba* (Soudzilovskaia et al., 2020; Steidinger et al., 2019). The EM tree species were *Castanopsis fargesii*, *Cyclobalanopsis glauca*, *Lithocarpus glaber*, and *Quercus fabri* (Koele et al., 2012). We established replicate plots (100–150 m^2) in four pure forests dominated by each target tree species, resulting in 36 study plots. We used the 'root tracing from trunk' method to identify fine roots (diameter < 2 mm) of the selected species (Liu et al., 2015). Subsequently, the fine roots attached to the trees were dug out and then gently shaken, and soils still adhering to the fine roots were carefully sampled and considered as rhizosphere soils (Phillips & Fahey, 2006). Further, soils that did not adhere to the roots were also collected and treated as bulk soils. The fine roots of the selected tree species were collected simultaneously. Rhizosphere soil samples were collected from five randomly selected individuals of each target tree species in July 2019 (warm season) and January 2020 (cold season) and combined to form a composite sample for each forest plot. Correspondingly, root-free soils (i.e., bulk soils) were also sampled and combined into a composite sample for each forest plot. A total of 72 bulk soil samples (36 per season) and 72 rhizosphere soil samples (36 per season) were used for laboratory analysis. The samples were stored at cold temperature until transported to the laboratory. After removing root debris and gravel, soil samples were passed through 2 mm sieves, and subsequently divided into two halves. One part was stored at 4°C for measuring microbial properties and soil mineral N content and for incubation within 48 h. The other part was air-dried for soil chemical property analysis.

2.2 | Determination of soil chemical properties

Soil mineral N (NO_{3-} and NH_{4+}) was extracted with 2 M KCl and analysed using a continuous flow analyser (AA3, Seal Analytical, Germany). Available phosphorus (AP) was extracted with hydrochloric acid and ammonium fluoride and measured using the molybdenum blue method (Lu, 2000). The concentrations of total phosphorus (TP) and total potassium (TK) were determined using the procedures described by Lu (2000). For soil total nitrogen (TN) and SOC measurements, soil samples were passed through 0.2 mm sieve and measured by combustion using an elemental analyser (Elementar, Germany). Soil exchangeable cations (e.g., Na^+, Mg^{2+}, K^+, and Ca^{2+}) were extracted with ammonium acetate solution (pH = 7) and quantified using an atomic absorption spectrometer (Varian AA240, USA). The pH value was determined using a pH meter with a 1:2.5 soil/water suspension. The labile organic C (LOC) content was quantified using the method described by Blair et al. (1995), and the amount of recalcitrant organic C (ROC) was calculated based on the differences between SOC and LOC. We measured the water-extractable organic C (WEOC) concentration using a C analyser (Vario TOC cube; Elementar, Germany) according to De Feudis et al. (2017).

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2.3 | Measurements of soil microbial properties

We measured the activities of seven soil extracellular enzymes using a microplate spectrophotometer, including β-glucosidase (βGC), cellulase (CL), polyphenol oxidase (PPO), urease (UE), N-acetylglucosaminidase (NAG), leucine aminopeptidase (LAP), and acid phosphatase (ACP). We quantified the microbial community composition using phospholipid fatty acid (PLFA) analysis (Buyer & Sasser, 2012). Then, PLFAs were analysed using an Agilent 6890 Gas Chromatograph fitted with a microbial identification system (MIDI Inc., DE, USA). The PLFA biomarkers were assigned to specific microbial groups according to Fan et al. (2020) and Xu et al. (2020), such as gram-positive bacteria (GP), gram-negative bacteria (GN), actinomycete (Actin), saprotrophic fungi (SF), and arbuscular mycorrhizal fungi (AMF). High-throughput sequencing was used to evaluate microbial taxonomic composition. The V3-V4 targeting region of the bacterial 16S rRNA gene was amplified using the 338F/806R primer pair (Caporaso et al., 2012; Dennis et al., 2013), and the ITS-1 region of the fungal rDNA gene was amplified using ITS1-F and ITS2 primer pair (Wang et al., 2017). The PCR products were sequenced using an Illumina's MiSeq platform at Allwegene Technologies (Beijing, China). Sequencing reads were analysed using QIIME (Caporaso et al., 2012). Operational taxonomic units (OTUs) were clustered using the algorithm UParse at the 97% similarity threshold (Edgar, 2013). The Unite and Silva databases were assigned as references for fungi and bacteria, respectively (Kõljalg et al., 2013; Quast et al., 2013). The predominant bacterial and fungal taxa were categorized into two ecological guilds, r- and K-strategists, based on sequencing data (Fierer et al., 2007; Li, Yang, et al., 2021; Yao et al., 2017). We used the FUNGuid algorithm to predict fungal function guilds, including pathogenic, symbiotic (e.g., EM fungi), and saprotrophic groups (Nguyen et al., 2016). Detailed information about microbial r- and K-strategists is provided in Table S1.

2.4 | Analyses of fine root properties

In each plot, 10 randomly selected soil cores (5 cm diameter, 10 cm depth) were sampled from around each target tree to estimate the fine root biomass. The fine roots were carefully separated from soil cores, cleaned, and oven-dried at 65°C until reaching a constant mass. Element concentrations of C and N were determined by an elemental analyser (Elementar, Germany). The concentrations of soluble sugars and starch were determined using the anthrone colorimetric method described by Piper et al. (2022). The concentrations of total P, condensed tannin, soluble phenolics, and total phenolics were analysed with colorimetric methods (Chao et al., 2019; Lu, 2000). The lignin concentration was measured spectrophotometrically as described by Chao et al. (2019).

2.5 | Quantification of soil microbial respiration

Rhizosphere soils and bulk soils were adjusted gravimetrically to 60% of their water-holding capacity (WHC). Four replicates of fresh soil samples (40 g dry weight each) were placed in 500 mL jars with sealed lids. All soils were equilibrated for 3 days at 20°C to eliminate pulses in microbial metabolisms caused by the disturbances of sieving and moisture modifications. Subsequently, soil samples were incubated at 16.5°C (i.e., MAT) and 21.5°C (i.e., MAT + 5°C) for 12 days, respectively. Short-term incubation can maintain soil conditions (e.g., soil microbial community and labile nutrients) in a relatively stable state (Zhang et al., 2020). According to Wang et al. (2018), we conducted a sequential incubation procedure. Take 16.5°C incubation temperature as an example, the temperature was gradually increased from 11.5 to 21.5°C and subsequently decreased from 21.5 to 11.5°C within 24 h to simulate the diurnal temperature changes in the field. The temperature range of 16.5–26.5°C represents the 21.5°C incubation temperature. The time-weighted average temperature was equal to the setting incubation temperature for 12 days. Small vials (80 mL) containing 20 mL of 1 M NaOH solution were periodically placed in each jar to trap the released CO_2 for one temperature cycle (i.e., 24 h). The Rm rates were measured three times by titrating the NaOH with 0.5 M HCl to pH 8.3 using an automatic titrator (Mettler Toledo G20, Switzerland). During incubation, deionized water was added to maintain the soil moisture content at 60% WHC.

2.6 | Calculations and statistical analyses

The following formula was used to calculate Q_{10} of Rm: $Q_{10} = (R_{Th} / R_{Tl})^{10 / (Th - Tl)}$,

$$Q_{10} = \left(R_{Th}/R_{Tl}\right)^{10/(Th-Tl)},$$

where R_{Th} and R_{Tl} represent the mean Rm rates (μg C g^{-1} SOC day^{-1}) at T_h (21.5°C) and T_l (16.5°C), respectively.

The following equation was used to calculate the RE (the percentage differences in ecosystem function variables between paired rhizosphere soil and bulk soil): RE (%) = $(V_R - V_B) / V_B \times 100\%$,

$$\mathrm{RE}\,(\%) = \left(V_R - V_B\right) / V_B \times 100\%,$$

where V_R and V_B represent the measured variables of rhizosphere soils and bulk soils, respectively.

Data were checked for normality of residuals (Shapiro–Wilk test) and homogeneity of variances (Levene's test). The differences between rhizosphere soils and bulk soils for each measured variable were compared using paired-sample *t*-tests, but the Wilcoxon signed-rank test was applied to compare paired nonnormally distributed data. A repeated-measures ANOVA was employed to evaluate the effects of mycorrhizal types, seasons, and their interactive effects on the fine root properties and the RE on measured variables, and a post hoc test with the least significant difference was subsequently performed for pairwise comparisons. In cases when the normality test or homogeneity was not respected, variables were tested using nonparametric test (e.g., Mann–Whitney *U* test). Linear mixed-effect model analysis was conducted to assess the single variable relationships between the RE on measured variables and fine root properties

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with the RE on Q_{10}. The model included the above-mentioned predictors as fixed effects and tree species as a random effect using the 'nlme' and 'lme4' packages (Bates et al., 2015; Pinheiro et al., 2019). If frequentist models were found as singular, we instead used an identically structured Bayesian linear mixed-effect model with the default prior as implemented in 'blme' package (Chung et al., 2013; Smith & Peay, 2021). We performed a multiple linear regression model (MLR) to quantify the effects of the potential predictors on the RE on Q_{10}. Before conducting regression analysis, all response variables and predictors were standardized using the *Z*-scores, and the 'forward.sel' procedure was used to avoid redundancy and multicollinearity (Oksanen et al., 2020). The relative importance of each explanatory predictor was determined in this model using the method of relative weights (Kabacoff, 2011). The following five identifiable importance fractions were calculated: fine root properties (including fine root biomass, C:N ratio, total P, soluble sugars, soluble phenolics, and total phenolics), the RE on soil properties (including WEOC, LOC, C:N ratio, pH, and NH_{4+}), the RE on enzyme activities (including CL, βGC, and PPO), the RE on microbial richness (including bacterial and fungal richness), and the RE on K-/r- traits (including saprotrophic fungi PLFA, GN PLFA, the relative abundances of EM fungi and r-strategy bacteria). These analyses were conducted using the 'car' and 'MASS' packages. We constructed a piecewise structural equation model (piecewiseSEM) to further disentangle the regulatory mechanisms of explanatory factors on the RE on Q_{10} for AM tree species and EM tree species. The above-mentioned factor categories, which were constructed as composite variables, were incorporated into the piecewise SEM as fixed effects (Liu et al., 2022). Seasons, treated as ordinal categorical variables, were encoded as 1 for warm season and 2 for cold season. Within the model, we considered 'tree species' as a random effect. Subsequently, we reported marginal R^2 (R^2_M) which represents the proportion of variance elucidated by fixed effects, and conditional R^2 (R^2_C) indicative of the proportion of variance explained by both fixed and random effects, for each response variable. The analysis was performed using the R 'piecewiseSEM' (Lefcheck, 2016) and 'nlme' (Pinheiro et al., 2019) packages. The goodness-of-fit for piecewiseSEM was evaluated using the Fisher's C statistic with $p > 0.05$, low Akaike information criterion, and Bayesian information criterion values. All analyses were conducted in R 3.5.2.

3 | RESULTS

3.1 | Variations in the fine root properties

Fine root traits showed significant variation across the nine tree species (Table S2). In the warm season, the concentrations of N and condensed tannins were larger in AM tree species than those in EM tree species, whereas C:N ratio, soluble sugars, and total and soluble phenolic concentrations were higher in EM tree species ($p < 0.05$; Table S2). In the cold season, the fine roots of AM tree species had higher lignin and total P concentrations, and lower soluble phenolic concentration compared with EM tree species ($p < 0.05$; Table S2).

3.2 | Variations in the REs on soil chemical and microbial properties

We observed positive RE on soil properties for all nine tree species, except for pH, AP, and NO_{3-} (Tables S3–S5). The RE on soil properties (including TN, SOC, C:N ratio, WEOC, LOC, and ROC) and RE on microbial traits (including PPO, βGC, CL, GP, SF, and fungal PLFAs) were strongly influenced by mycorrhizal types and seasons ($p < 0.05$). Compared with AM tree species, EM tree species had significantly higher RE on TN, SOC, WEOC, LOC, ROC, βGC, CL, GP, GN, Actin, SF, bacterial and fungal PLFAs in the warm season, and displayed significantly greater RE on LOC, AP, and NO_{3-} in the cold season ($p < 0.05$; Tables S3–S5). The RE on PPO and RE on UE for EM tree species were significantly greater than those of AM tree species in both the warm and cold seasons ($p < 0.05$; Table S5).

3.3 | Variations in the RE on Q_{10}

Overall, rhizosphere soils had significantly greater Q_{10} values of Rm than bulk soils across nine tree species in both the warm and cold seasons ($p < 0.05$; Figure 1), indicating a positive RE (ranging from 20.1% to 87.5%). Mycorrhizal types and seasons significantly affected the RE on Q_{10} ($p < 0.01$), with a marginally significant interactive effect of mycorrhizal types and seasons ($p = 0.062$; Figure 1). Compared with AM tree species, the RE on Q_{10} of EM tree species was 64.5% higher in the warm season and 44.4% higher in the cold season ($p < 0.01$; Figure 1). In the warm season, the RE on Q_{10} of AM and EM tree species was 44.8% and 65.0% greater than that in the cold season, respectively ($p < 0.05$; Figure 1).

3.4 | Relationships between the RE on Q_{10} and predictors

The RE on Q_{10} was strongly associated with fine root properties, the RE on soil properties, and RE on microbial properties (Figures S1–S3). Specifically, the RE on Q_{10} of both AM and EM tree species significantly increased with the RE on soil properties, such as TN, SOC, WEOC, and ROC ($p < 0.05$; Figure S1a,b,d,f). The RE on C:N ratio, LOC, NH_{4+}, and pH showed positive associations with the RE on Q_{10} in EM tree species ($p < 0.05$; Figure S1c,e,g,h). Furthermore, in both AM and EM tree species, the RE on Q_{10} exhibited positive relationships with fine root biomass, the concentrations of condensed tannins, and soluble sugars ($p < 0.05$; Figure S1k,n,o). The RE on Q_{10} was positively correlated with fine root N concentration but negatively associated with fine root C:N ratio and lignin content in AM tree species ($p < 0.05$; Figure S1i,j,l), and the RE on Q_{10} of EM tree species was negatively related to total phenolic content of fine roots ($p < 0.05$; Figure S1p). The RE on Q_{10} was positively related with the RE on PPO, βGC, and CL activities in both AM and EM tree species ($p < 0.05$; Figure S2a,c,d), was positively associated with the RE on UE, ACP, and NAG activities in EM tree species ($p < 0.05$;

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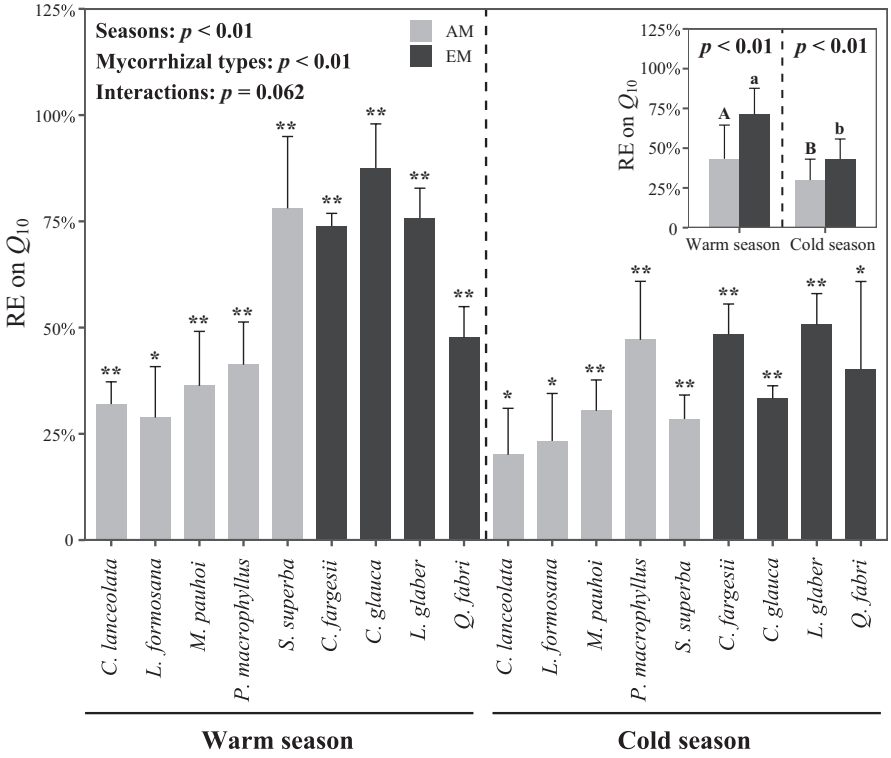

FIGURE 1 The rhizosphere effect (RE) on the temperature sensitivity of soil microbial respiration (Q_{10}) among nine tree species in the warm and cold seasons. Bars represent the means of each tree species and error bars represent the standard deviation of four replicates. * and ** indicate significant differences of each tree species between rhizosphere soils and corresponding bulk soils at the $p < 0.05$ and $p < 0.01$ level based on paired *t*-tests, respectively. Inset shows arbuscular mycorrhizal (AM) versus ectomycorrhizal (EM) cross-species means, with $p < 0.01$ indicating significant differences between mycorrhizal types in the warm and cold seasons, respectively. Lowercase letters represent significant differences between seasons in AM tree species ($p < 0.05$), and uppercase letters denote significant differences between seasons in EM tree species ($p < 0.05$).

Figure S2b,e,f). The RE on Q_{10} of both AM and EM tree species was significantly associated with the increased RE on microbial PLFAs ($p < 0.05$; Figure S2g–m), but had no significant correlations with the RE on K-strategist bacteria and K-strategist fungi (Table S6).

3.5 | Dominant drivers of the RE on Q_{10} in different mycorrhizal tree species

The results of MLR and piecewiseSEM collectively demonstrated that the dominant determinants of the RE on Q_{10} differed between mycorrhizal types (Figures 2 and 3). For AM tree species, the MLR result showed that fine root properties and the RE on K-/r- traits together explained 67.3% of the total explained variation in the RE on Q_{10} ($R^2 = 0.83$), with the unique effects being 42.0% and 25.3%, respectively (Figure 2a). PiecewiseSEM analysis also revealed that the RE on Q_{10} was primarily and directly influenced by fine root properties and the RE on K-/r- traits, with the standardized direct effect of 0.66 and 0.19, respectively (Figure 3a). In addition, fine root properties indirectly affected the RE on Q_{10} by regulating the RE on soil properties, RE on enzyme activities, and RE on K-/r- traits (Figure 3a,c). For EM tree species, MLR result showed that the unique effects of fine root properties, the RE on soil properties, RE on K-/r- traits, and RE on enzyme activities were 18.8%, 35.2%, 20.5%, and 17.3% of the total explained variation in the RE on Q_{10} ($R^2 = 0.81$), respectively (Figure 2b). PiecewiseSEM analysis confirmed that the RE on soil properties exhibited the highest direct effect on the RE on Q_{10}, and also exerted indirect effects via affecting the RE on K-/r- traits and RE on microbial richness (Figure 3b,d). Fine root properties directly affected the RE on Q_{10} in EM-dominated forests (Figure 3b,d). Irrespective of the mycorrhizal types, seasons had an insignificant direct effect on the RE on Q_{10}, and indirectly affected it by altering other environmental variables (Figure 3a,b).

4 | DISCUSSION

4.1 | Differences in the RE on Q_{10} between mycorrhizal types

We observed a positive RE on Q_{10} across diverse tree species in both the warm and cold seasons (Figure 1), indicating that SOC decomposition rates in rhizosphere soils are more responsive to climate warming compared with bulk soils. Our results align with previous studies that rhizosphere soil exhibited more active SOC decomposition processes than bulk soil (Finzi et al., 2015;

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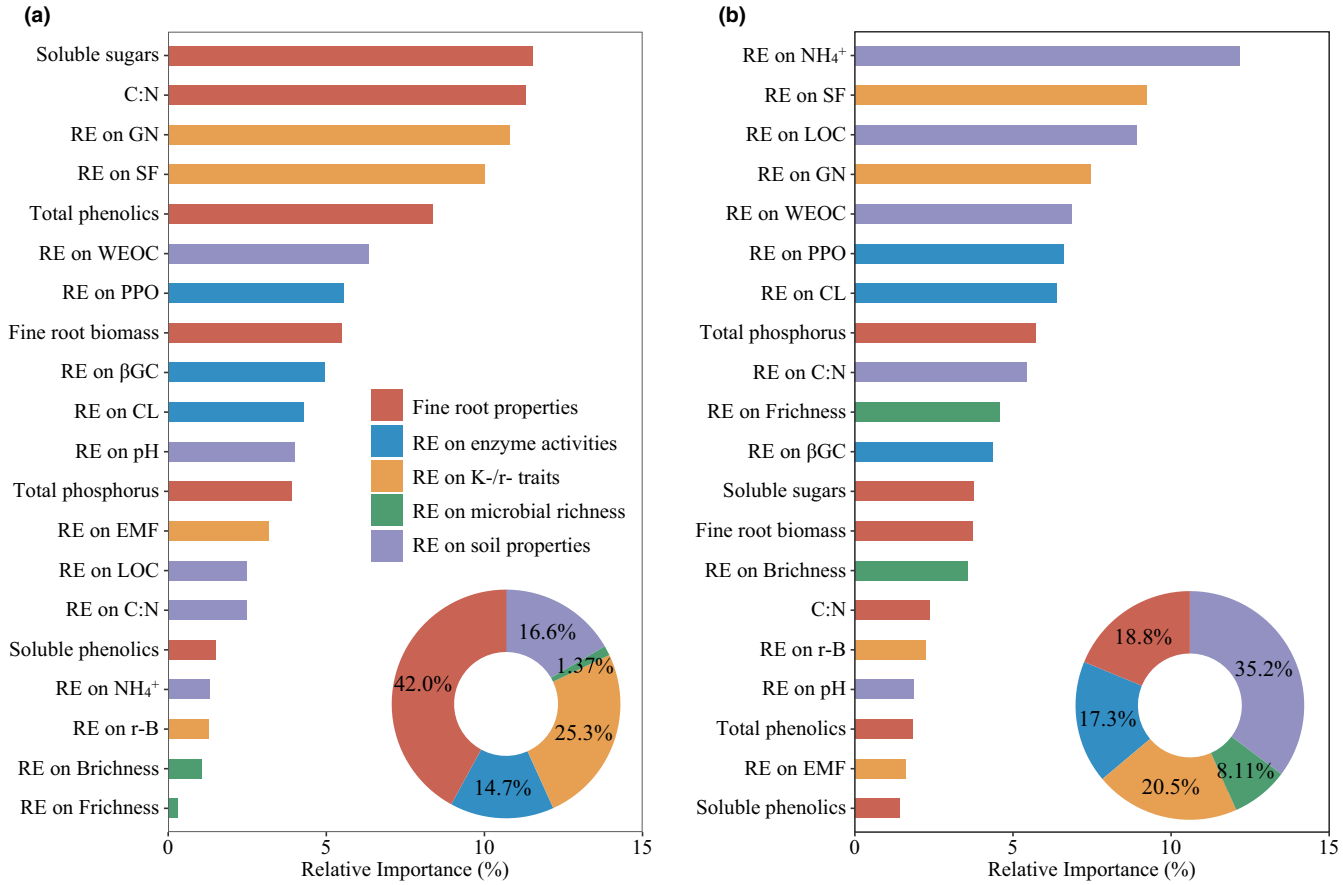

FIGURE 2 Relative importance of the different predictors on the rhizosphere effect (RE) on temperature sensitivity of soil microbial respiration (Q_{10}) for arbuscular mycorrhizal (AM, a) and ectomycorrhizal (EM, b) tree species based on multiple linear regression model using the method of relative weights. Donut charts represent the sum of the relative importance of each group of predictors, expressed as the percentage of explained variance. Brichness, bacterial richness; C:N, the carbon-to-nitrogen ratio; CL, cellulase; EMF, the relative abundance of EM fungi; Frichness, fungal richness; GN, gram-negative bacteria phospholipid fatty acid (PLFA); LOC, labile organic C; PPO, polyphenol oxidase; r-B, the relative abundance of r-strategy bacteria; SF, saprotrophic fungi PLFA; WEOC, water-extractable organic C; βGC, β-glucosidase.

Zhao, Tian, Liu, et al., 2022), due to higher microbial activity and greater C availability in rhizosphere hotspots that can stimulate microbial decomposition (Tables S3–S5). This is supported by significantly positive relationships between RE on Q_{10} and RE on C availability (Figure S1b,d–f), RE on C-acquiring enzyme activities (Figure S2a,c,d), and RE on microbial PLFAs (Figure S2g–m) across all tree species, consistent with the Michaelis–Menten kinetics and microbial activation hypothesis (Cheng & Kuzyakov, 2005; Davidson et al., 2006). Therefore, we evidenced that SOC decomposition rates in rhizosphere soil are more sensitive to climate warming than in bulk soil, which should be incorporated into C-climate models.

Consistent with our first hypothesis (H1), we found that EM tree species induced a higher RE on Q_{10} compared with AM tree species (Figure 1), which was attributed to the higher C availability, greater microbial biomass, and elevated enzyme activities in rhizosphere soil of EM tree species (Figure 4; Tables S3–S5). EM tree roots can exude more C than AM tree roots (Yin et al., 2014), increasing substrate availability and leading to higher Q_{10} in rhizosphere soil of EM tree species, consistent with Michaelis–Menten kinetics (Davidson et al., 2006; Zhu & Cheng, 2011). This aligns with our data as we also found that EM tree species had greater RE on C availability than AM tree species (Figure 4; Tables S3–S5), and the RE on C availability positively influenced RE on Q_{10} (Figure S1b,d,f; Figure 4). Moreover, the organic nutrient mining activities of EM fungi, which selectively target N and P over C, may explain the higher C availability in rhizosphere soil of EM tree species (Figure 4; Table S3; Lindahl & Tunlid, 2015). This interpretation is further supported by the overall higher RE on extracellular enzyme activities in EM tree species compared with AM tree species (Table S5; Lindahl et al., 2021; Maillard et al., 2023). This explanation is strengthened by the significant positive relationships between RE on Q_{10} and RE on UE, NAG, and ACP in EM-dominated forests, but not in AM-dominated forests (Figure S2b,e,f). Thus, the higher substrate availability in rhizosphere soils of EM-dominated forests may stimulate microbial activities that further accelerate SOC decomposition (Moore et al., 2020; Wang et al., 2016), supporting the microbial activation hypothesis (Cheng & Kuzyakov, 2005), and ultimately generating higher RE on Q_{10} in EM-dominated forests (Figure 4). The positive relationships between the RE on microbial PLFAs and RE on C-acquiring enzyme activities (PPO, βGC, and CL) with the RE on Q_{10} further support

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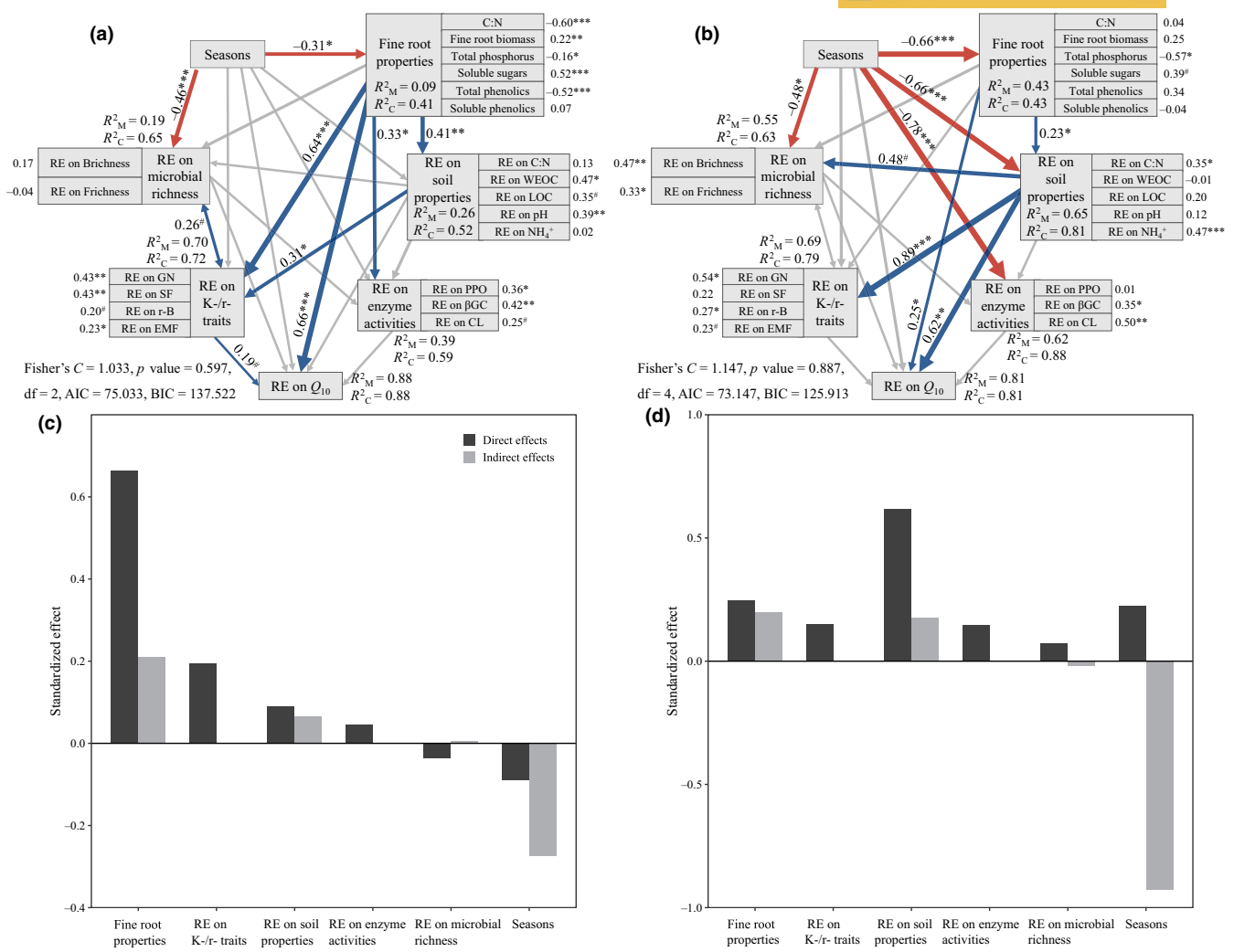

FIGURE 3 Piecewise structural equation models (piecewiseSEM) revealing the direct and indirect effects of predictors on the rhizosphere effect (RE) on temperature sensitivity of soil microbial respiration (Q_{10}) in arbuscular mycorrhizal (AM, a) and ectomycorrhizal (EM, b) tree species. We grouped the different categories of predictors (fine root properties, the RE on soil properties, RE on enzyme activities, RE on microbial richness, and RE on K-/r- traits) in the same box to denote composite variables. Single-headed and double-headed arrows indicate causal links and covariations, respectively. Red and blue arrows represent significantly negative and positive relationships, respectively. Grey arrows represent non-significant relationships ($p > 0.1$). The numbers adjoining the arrows are standardized path coefficients. The arrow thickness is proportional to the strength of the relationship. R^2_C (conditional R^2) indicates the proportion of variance explained by the fixed and random effects, and R^2_M (marginal R^2) indicates the proportion of variance explained by the fixed effects. Standardized effects (direct and indirect standardized effects) of predictive variables on the RE on Q_{10} in AM (c) and EM (d) tree species were displayed, respectively. AIC, Akaike information criterion; BIC, Bayesian information criterion; df, degree of freedom. $^{\#}0.05 < p < 0.1$ (marginally significant), $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$. The abbreviation of measured variables could be found in Figure 2.

this suggestion (Figure S2). This explanation is reinforced by the results showing that the RE on soil properties (e.g., WEOC, LOC, and NH_{4+}) exhibited greater direct effects on the RE on K-/r- traits and microbial richness in EM-dominated forests compared with AM-dominated forests (Figure 3).

4.2 | Factors controlling mycorrhizal association effects on the RE on Q_{10}

Our findings supported our second hypothesis (H2), showing that the primary determinants of the RE on Q_{10} differed between mycorrhizal types. Although RE on Q_{10} was significantly related to various predictors, fine root properties predominantly governed the RE on Q_{10} in AM-dominated forests (Figures 3 and 4). In contrast, the RE on soil properties dominated the RE on Q_{10} in EM-dominated forests. AM plants typically exhibit an inorganic nutrient economy, relying primarily on root pathways for nutrient acquisition due to the limited saprotrophic capacity of AM fungi (Chen et al., 2016; Phillips et al., 2013; Yan et al., 2022). Compared with EM tree species, AM tree species invest relatively more energy into the development and maintenance of fine roots (Jevon & Lang, 2022; Tedersoo & Bahram, 2019), reinforcing the significant role of fine root properties in regulating the RE on Q_{10} in AM-dominated forests (Figures 2a, 3a

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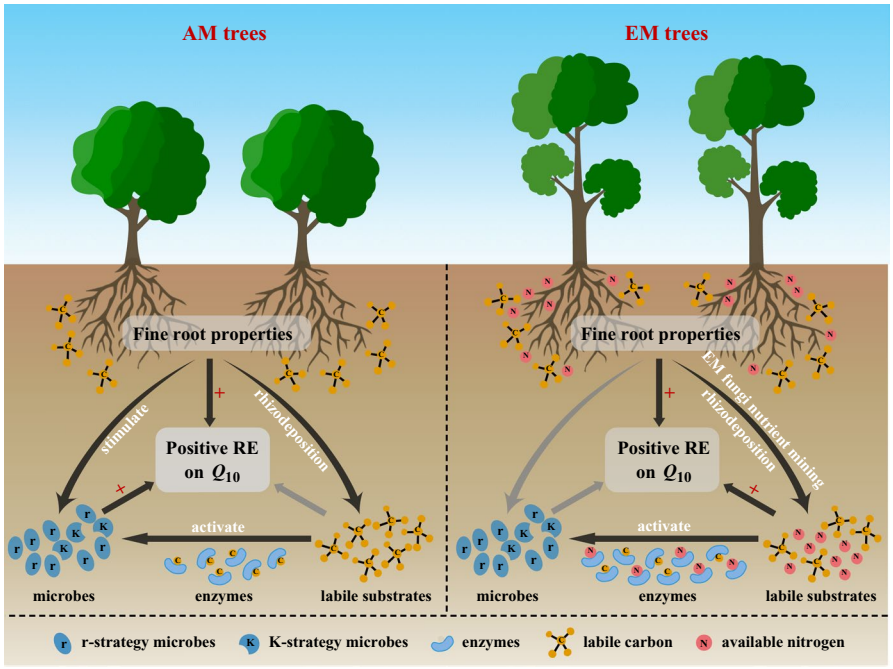

FIGURE 4 A conceptual diagram showing the potential regulation mechanism of the rhizosphere effect (RE) on the temperature sensitivity of soil microbial respiration (Q_{10}) in arbuscular mycorrhizal- (AM) and ectomycorrhizal- (EM) dominated forests. AM tree species invest relatively more into development and maintenance of fine roots and largely depend on fine roots to acquire nutrients. In AM-dominated forests, the input of root-derived components can directly stimulate rhizospheric microbial activity (especially r-strategy microbes) and enzyme production to compensate for the limited saprotrophic capacities of AM fungi. Hence, fine root properties dominantly regulated the RE on Q_{10} in AM-dominated forests. In contrast, EM fungi can produce a wide range of extracellular enzymes to attack substrates, resulting in the higher nutrient availabilities and microbial activities in rhizosphere soils of EM tree species. Therefore, the RE on soil properties (particularly labile C and N) predominantly governed the RE on Q_{10} in EM-dominated forests. The symbol '+' represents the positive effect.

and 4). We found that fine root biomass and soluble sugar content were positively associated with the RE on Q_{10} in AM-dominated forests (Figure 3a; Figure S1k,o). This suggests that root exudates and detritus directly stimulate microbial turnover and exoenzyme production, accelerating SOC decomposition and enhancing the RE on Q_{10} in AM-dominated forests (Figure 4). This is supported by positive relationships between the RE on microbial PLFAs and RE on C-acquiring enzyme activities with the RE on Q_{10} in AM-dominated forests (Figure S2a,c,d,g–m). These findings are in line with a recent study conducted in a *C. lanceolata* forest (Zhao, Tian, Liu, et al., 2022). Additionally, the negative relationship between the RE on Q_{10} and fine root C:N ratios in AM-dominated forests (Figure 3a; Figure S1j) can be explained by two factors. First, fine roots with high C:N ratios may reduce exudation rates or intensify N competition between plants and microorganisms (Akatsuki & Makita, 2020; Dijkstra et al., 2021), partially limiting the microbial activity and SOC decomposition. A recent study also depicted that the RE on SOC decomposition was negatively correlated with root C:N ratios across 14 tree species (Han et al., 2020). Second, fine roots with low C:N ratios may induce microbial N limitations, hindering substrate decomposition as predicted by stoichiometric decomposition theory (Bonanomi et al., 2021; Sinsabaugh & Follstad Shah, 2012). The positive effects of fine root N concentration on the RE on Q_{10} (Figure S1i) and rhizosphere priming effect supported this explanation (Vargas et al., 2020). Recalcitrant compounds in fine roots, such as lignin and phenolics, have antagonistic effects on RE on Q_{10} in AM-dominated forests (Figure 3a; Figure S1l), as these compounds resist enzymatic attack and inhibit decomposition processes (Jiang et al., 2021). These findings provide crucial insights into understanding how fine root traits affect rhizosphere SOC cycling in AM-dominated forests under global warming (Figure 4).

In contrast, the RE on soil properties played a dominant role in modulating RE on Q_{10} in EM-dominated forests (Figures 2b, 3b and 4). EM plants have an organic nutrient economy and generally depend on their fungal symbionts producing hyphae for nutrient acquisition (Phillips et al., 2013; Tedersoo & Bahram, 2019). EM fungi outperform AM fungi in secreting a wide range of extracellular enzymes that oxidize substrates and release nutrients needed for metabolic functions (Kyaschenko et al., 2017; Phillips et al., 2013; Tedersoo & Bahram, 2019), leading to higher nutrient availabilities and microbial activities in rhizosphere soils of EM tree species (Tables S3–S5; Figure 4). The high availabilities of labile C and N in rhizosphere soils stimulate rhizospheric microbial metabolic processes (Karhu et al., 2022; Zhang et al., 2021; Zhao, Tian, Sun, et al., 2022), increasing SOC decomposition and inducing a positive RE on Q_{10} in EM-dominated forests (Figures 3b and 4). Ammonium nitrogen is the preferred N source for most microbes (Geisseler & Scow, 2014), and NH_4^+ enrichment positively affects microbial biomass and is a key

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determinant of EM fungal community (Liu et al., 2020; Pellitier & Zak, 2021). Consistent with this deduction, the RE on NH_4^+, RE on C availability (LOC and WEOC), and RE on enzyme activities positively affect RE on Q_{10} in EM-dominated forests (Figure 3b; Figures S1 and S2), likely due to EM fungi organic nutrient mining activities, as stated above. The above-mentioned positive effects may trigger a feedback loop that accelerates SOC decomposition and improves soil nutrients and microbial properties, resulting in positive RE on Q_{10} in EM-dominated forests (Figure 4; Tables S3–S5). As such, our findings link the RE on soil nutrient availabilities to C emissions in EM-dominated forests, suggesting that EM tree species may impede rhizospheric SOC accumulation under climate warming due to two potential independent and mutually non-exclusive mechanisms—a higher rhizodeposition for EM tree species than AM tree species and the organic nutrient acquisition activities of EM fungi (Figure 4).

As expected, the RE on Q_{10} was positively associated with the RE on GN PLFA and RE on SF PLFA in both AM- and EM-dominated forests (Figure 3; Figure S2h,j). Gram-negative bacteria and saprotrophic fungi were classified as r-strategists, which preferentially utilize labile C and exhibit a fast growth rate and high metabolic activity in a high-resource environment (Fierer et al., 2007; Shao et al., 2021; Yao et al., 2017). High substrate availabilities in rhizosphere micro-ecosystems favour r-strategists and stimulate enzyme synthesis, which could enhance SOC mineralization and generate higher RE on Q_{10}, supporting the 'microbial activation hypothesis' (Cheng & Kuzyakov, 2005; Koranda et al., 2011; Ling et al., 2022). This point was supported by the significantly positive relationships between the RE on Q_{10} and RE on C-acquiring enzyme activities in this work (Figure S2a,c,d). Previous studies also reported that r-strategists were positively associated with Q_{10} values in bulk soils (Li et al., 2024; Yang et al., 2022), indirectly supporting our findings. Our results highlight that the temperature responses of rhizospheric microbial groups might cause pronounced feedbacks between SOC dynamics and global warming, providing a more nuanced insight of the complexity of climate–plant–microbe interactions in forest ecosystems.

4.3 | Significant role of seasons in regulating the RE on Q_{10}

Supporting our third hypothesis (H3), our results showed that the RE on Q_{10} was higher in the warm season than that in the cold season (Figure 1), indicating that rhizospheric SOC decomposition is more responsive to temperature fluctuations during the tree-growing season than in bulk soils. During the warm season, trees have higher productivity, leading to increased allocation of belowground photosynthates and fine root production, which increases root-derived C inputs to rhizosphere soils (Li, Shi, et al., 2021; Xiong et al., 2020). Thus, increased substrate availability in the warm season can promote SOC decomposition, leading to higher RE on Q_{10}, consistent with Michaelis–Menten kinetics (Davidson et al., 2006; Zhu & Cheng, 2011). Supporting this explanation, we observed higher fine root biomass and RE on C availability (SOC, LOC, WEOC, and ROC) in the warm season compared with the cold season (Tables S2 and S3). Moreover, increased C inputs may stimulate rhizosphere microbes to produce more enzymes for SOC decomposition, thereby generating higher RE on Q_{10} in the warm season, supporting the microbial activation hypothesis (Cheng & Kuzyakov, 2005). This is consistent with the higher RE on C-acquiring enzyme activities (PPO, βGC, and CL) observed in the warm season compared with the cold season (Table S5). In addition, AM and EM tree species showed similar seasonal variations in the RE on Q_{10}, and the RE on Q_{10} of EM tree species was higher than AM tree species in both the warm and cold seasons (Figure 1). This may be because EM tree species displayed higher RE on C availability (SOC, LOC, and ROC) and microbial properties (PPO, CL, GP, GN, and SF PLFAs) in both the warm and cold seasons than AM tree species (Tables S3–S5), as stated above. Interestingly, the effect of mycorrhizal types on RE on Q_{10} was less pronounced in the cold season compared with the warm season. Just like trees, EM fungi might be less active during the cold season, when C fluxes from the trees are scarcer, and thus have limited organic nutrient mining activities, limiting the formation of labile organic C in rhizosphere soils outside of the tree-growing season.

4.4 | Limitations and future research

There are several limitations that should be addressed in future research. First, the relatively limited number of tree species included in this study, due to logistical constraints and permissions, may prevent us from fully capturing the effects of mycorrhizal types on root–soil–microorganism interactions under climate warming. The findings should be cautiously generalized to other forest ecosystems with different tree species and climate conditions. Second, tree species of the same mycorrhizal type but from different families may exhibit variations in plant traits (e.g., leaf habits, root lifespans, and root activities). These species-specific traits may obscure the effects of mycorrhizal types on rhizosphere processes, due to large intraspecific and interspecific variations within each mycorrhizal association. Despite these limitations, clarifying the specific correlations between mycorrhizal associations with rhizospheric biochemical processes is helpful to develop better representations of root–soil–microorganism interactions in this study. Future studies should consider incorporating a larger number of tree species from each mycorrhizal association to enable more precise evaluations of the pivotal role of tree-associated mycorrhizal types in regulating rhizosphere SOC cycling under climate warming.

5 | CONCLUSIONS

Our study shows that microbial respiration rates in rhizosphere soil are more temperature-responsive than those in bulk soils in both AM- and EM-dominated forests. Treating soil as a homogeneous unit in ecological research and modelling can significantly

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underestimate the impact of climate–carbon feedback by overlooking the distinct biochemical properties of rhizosphere soils. Compared with their respective bulk soils, rhizosphere SOC losses in EM-dominated forests exhibit greater susceptibility to temperature increases than those in AM-dominated forests, indicating a heightened vulnerability of soil ecosystem processes in EM-dominated forests to climate warming. Additionally, the RE on Q_{10} was more pronounced in the warm season than that in the cold season, underscoring the importance of seasonal variations in refining our understanding of SOC dynamics and plant–soil feedback under climate warming. We also detected that the dominant drivers regulating the RE on Q_{10} were mycorrhiza-dependent: fine root traits predominantly governed the RE on Q_{10} in AM-dominated forests, while the RE on soil properties dominated the RE on Q_{10} in EM-dominated forests. Overall, our findings emphasize the crucial roles of rhizosphere processes for accurate predictions in forest SOC cycles, and highlight the necessity to evaluate the direction of mycorrhizal links to rhizosphere C trajectories under changing climate conditions.

AUTHOR CONTRIBUTIONS

Qingkui Wang and Xuechao Zhao conceived the ideas; Xuechao Zhao collected soil samples, conducted the laboratory analysis and analysed the data; Xuechao Zhao and Qingkui Wang wrote the manuscript with assistance from Peng Tian, François Maillard, Shengen Liu, Zhaolin Sun, and Nadejda A. Soudzilovskaia. All authors contributed to subsequent revisions and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.h9w0vt4t3 (Zhao et al., 2024).

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SUPPORTING INFORMATION

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

Figure S1. Relationships between the rhizosphere effect (RE) on temperature sensitivity of soil microbial respiration (Q_{10}) with the RE on soil properties (a–h) and fine root properties (i–p) for arbuscular mycorrhizal (AM, blue lines and points) and ectomycorrhizal (EM, red lines and points) tree species based on the linear mixed-effect model.

Figure S2. Relationships between the rhizosphere effect (RE) on temperature sensitivity of soil microbial respiration (Q_{10}) with the RE on enzyme activities (a–f) and microbial properties (g–o) for arbuscular mycorrhizal (AM, blue lines and points) and ectomycorrhizal (EM, red lines and points) tree species based on the linear mixed-effect model.

Figure S3. Relationships between the rhizosphere effect (RE) on temperature sensitivity of soil microbial respiration (Q_{10}) with the RE on r-strategy bacteria (a) and ectomycorrhizal fungi (b) abundances for arbuscular mycorrhizal (AM, blue lines and points) and ectomycorrhizal (EM, red lines and points) tree species based on the linear mixed-effect model.

Table S1. Assignment of different main microbial functional groups.

Table S2. Fine root properties for nine tree species.

Table S3. Rhizosphere effects on soil chemical properties for nine tree species.

Table S4. Rhizosphere effects on soil microbial properties for nine tree species.

Table S5. Rhizosphere effects on soil enzyme activities for nine tree species.

Table S6. Relationships between the rhizosphere effect (RE) on temperature sensitivity of soil microbial respiration (Q_{10}) with the RE on K-strategist bacteria, r-strategist fungi, and K-strategist fungi for arbuscular mycorrhizal (AM) and ectomycorrhizal (EM) tree species based on the linear mixed-effect model.

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