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Differential linkages between soil respiration components and microbial community structures under long-term forest conversion

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Abstract

Purpose Soil respiration (Rs) can be significantly impacted by land-use change (LUC). This study aimed to determine the response of Rs components (i.e., heterotrophic respiration (Rh) and autotrophic respiration (Ra)) to long-term forest conversion and explore their associations with soil microbial community (SMC) structures.

Materials and methods Three plantations converted from natural forest 36 years ago were investigated: *Cryptomeria fortune* (CF), *Cunninghamia lanceolata* (CL), and *Metasequoia glyptostroboides* (MG), with the control of an adjacent natural forest (NF). In each forest site, Rh and Ra were measured using the root trenching method during the growing season. SMC structures in trenched and rhizosphere soils (0–10 cm depth) were analyzed.

Results We observed an evident differentiation between SMC structures in trenched and rhizosphere soils across forest types. SMC structural dynamic in trenched soil was primarily driven by the ratio of dissolved organic carbon © to dissolved organic nitrogen (DON) and bulk density, whereas that in rhizosphere soil was primarily driven by DON and pH. During the growing season, both Rh and Ra were greater in MG than in NF, but they showed non-significant differences among NF, CF, and CL. The Rh pattern was primarily modified by the SMC structure (e.g., arbuscular mycorrhizal fungi (AMF)) and soil temperature, whereas the Ra pattern was primarily modified by the SMC structure in rhizosphere soil (e.g., gram-positive bacteria (GP)) in addition to fine root quality and soil temperature.

Conclusions Rh and Ra patterns were jointly modified by SMC structure and microenvironment over long-term forest conversion, emphasizing the underlying roles of plant community attributes and forest management in soil C emission into the atmosphere.

Keywords Land-use change · Carbon cycling · PLFA · Heterotrophic respiration · Autotrophic respiration · Forest ecosystem

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Abbreviations

Methods
Rs	Soil respiration
Rh	Heterotrophic respiration
Ra	Autotrophic respiration
LUC	Land-use change
PLFA	Phospholipid fatty acid
PVC	Polyvinyl chloride
RDA	Redundancy analysis

Microbial groups
SMC	Soil microbial community
ACT	Actinomycetes
GP	Gram-positive bacteria
GN	Gram-negative bacteria
AMF	Arbuscular mycorrhizal fungi

F:B The ratio of fungi to bacteria
GP:GN The ratio of GP to GN

Forest types
NF Natural forest
CL *Cunninghamia lanceolata* Plantation
MG *Metasequoia glyptostroboides* Plantation
CF *Cryptomeria fortune* Plantation

Soil parameters
MMST Mean monthly soil temperature
SWC Soil water content
BD Bulk density
SOC Soil organic carbon
TN Total nitrogen
C:N The ratio of SOC to TN
DOC Dissolved organic carbon
DON Dissolved organic nitrogen
TDN Total dissolved N
DIN Dissolved inorganic nitrogen
MBC Microbial biomass carbon
AP Available phosphorus

Fine root parameters
Bfr Fine root biomass
Cfr Fine root carbon content
Nfr Fine root nitrogen content
C:Nfr The ratio of Cfr to Nfr

1 Introduction

Soil respiration (Rs), a crucial process of carbon (C) cycling, comprises autotrophic respiration (Ra), which represents the metabolic activities of plant roots and microbial processes in the rhizosphere, and heterotrophic respiration (Rh), representing organic matter decomposition by free-living microorganisms (Dong et al. 2020; Hanson et al. 2000; Whitaker et al. 2014). As the second largest source of greenhouse gas release, land-use change (LUC) can trigger drastic fluctuations in the soil C pool and soil microbial community (SMC) structure (Dixon et al. 1994; Hong et al. 2020; Lal 2008). Even a small fluctuation in soil C or SMC structure may cause tangible changes in Rs in forest due to its largest C pool in terrestrial ecosystems (Ji et al. 2020; Ren et al. 2018; Tischer et al. 2015). Although the Rs process under LUC has been well documented, few in situ studies have been performed regarding long-term forest conversion, particularly on how Rs components (i.e., Rh and Ra) link to SMC structures.

Rs is generally controlled by substrate availability, microbial characteristics, root dynamics, and microclimate, among which the SMC structure is the most pivotal driver (Mitra et al. 2019; Pajares et al. 2016; Ren et al. 2018). Different

microbial groups have specific roles in C and nutrient processes (Guo et al. 2016a; Liu et al. 2018b), and thus, SMC structure and Rs components are mediated via LUC-induced changes in C inputs, soil biogeochemical processes, and microclimate (Durrer et al. 2021; Fekete et al. 2016; Han et al. 2012). That is, SMC structures driving different Rs components would be differentiated following forest conversion. For example, Wu et al. (2020) reported that SMC structure changes from bacterial to fungal domination under LUC, and Rs is regulated by soil temperature associated with the C:nitrogen (N) ratio and fungi abundance. Compared to Ra, Rh is generally more sensitive to SMC structure variation under forest conversion (Zhao et al. 2016a). Over the long-term (e.g., 30–50 years) forest conversion, soil C processes tend to re-equilibrate with mature converted forests (Schipper and Smith 2018). In addition, the SMC structure may exhibit a resilient phenomenon (Jangid et al. 2011). Accordingly, Rs, particularly Rh, could weaken the response to long-term forest conversion. However, Wei et al. (2015) revealed that vegetation characteristics and soil C pool size are more crucial than SMC structure for determining Rh in subtropical forests. Thus, under long-term forest conversion, Rh could be regulated by multiple factors rather than a single SMC structure, depending on the colonization of tree species.

The SMC structure in rhizosphere soil is particularly sensitive to tree species because of species-specific substrate inputs (e.g., root exudates and fine roots) and soil properties in the rhizosphere area (Berendsen et al. 2012). This may be tightly linked to Ra. For example, Adamczyk et al. (2021) revealed that changes in root exudates can quickly alter the SMC structure in rhizosphere soil and increase Ra in forests. However, to date, the relationship between Ra and the SMC structure in rhizosphere soil has rarely been documented. Over a long-term forest conversion, the SMC structure in rhizosphere soil may not exhibit resilience as likely occurring in bulk soil, because its specific microbial groups will be continuously stimulated by the same kinds of root exudates that are continuously released into the soil by converted tree species (Emmett et al. 2017; Li et al. 2019). Thus, Ra in the converted forest would still be restricted by root characteristics and SMC structure in rhizosphere soil in the long term; this would be largely subject to tree species, presenting a different pattern from that of Rh. These possible differences in SMC structures driving Rh and Ra require clarification under a global change background.

Furthermore, Rs components have traditionally been considered a function of soil temperature and moisture because of their key roles in regulating soil biological processes and SMC structure, particularly under drastic environmental changes (Auffret et al. 2016; Mitra et al. 2019; Monson et al. 2006). However, emerging evidence indicates that Rs is sensitive to soil temperature but may not be affected by soil

moisture under afforestation (Chen et al. 2021). This would be more intensified in subtropical regions with abundant precipitation, which needs to be experimentally confirmed during long-term forest conversion.

By constructing a long-term forest conversion scenario in a subtropical region, we analyzed total Rs during examining C stock dynamics (Zhao et al. 2022), and compared SMC structures in bulk and rhizosphere soils (Zhao et al. 2021). However, how Rs components respond to the forest conversion and how they link to SMC structures need further clarification. In this study, we extended total Rs in the previous work to Rs components and assessed their associations with SMC structures in trenched and rhizosphere soils. We hypothesized that, over long-term forest conversion, (i) Rs components and the SMC structures in trenched and rhizosphere soils would be distinctly differentiated depending on tree species; (ii) Rh would be driven by multiple biotic/abiotic factors more than a single SMC structure, whereas Ra would be primarily driven by SMC structure in rhizosphere soils varying with tree species; and (iii) Rh and Ra would be sensitive to both soil temperature and moisture.

2 Materials and methods

2.1 Study area and investigation

The study area is located in Badagongshan National Nature Reserve (29° 39′ 18″–29° 49′ 48″ N, 109° 41′ 45″–110° 09′ 50″ E; mean annual temperature, 11.5 °C; mean annual precipitation, 2105 mm) in China. The soil is classified as Hapludalfs according to US Soil Taxonomy Series (1999). As described in our previous work (Zhao et al. 2022), a 36-year forest conversion from natural forest to plantations were investigated with a space-for-time substitution approach, including three plantations of *Cryptomeria fortunei* (CF), *Metasequoia glyptostroboides* (MG), and *Cunninghamia lanceolata* (CL) with natural forest (NF) as a control.

2.2 Experimental design and soil respiration measurement

The NF, CF, MG, and CL sites are adjacent to each other (separated by < 100 m) with each site of ca. 2 ha. Three plots of 30×30 m^2 were randomly established at each forest site. The root trenching method was used to estimate Rh (Ren et al. 2018), and Ra was estimated from the difference between the total Rs and Rh. In each plot, four pairs of trenched and untrenched quadrats (1×1 m^2) that were used for Rh and total Rs measurements, respectively, were randomly established in March 2017. The depths of the trenches were 0.8–1.0 m depending on the soil thickness and root distributions. For each trenched quadrat, a sheet of polyethylene

nets with a mesh size of 150 μm was placed along the sides of the quadrat to prevent root entry into the quadrat but allow others (e.g., water, microorganisms, organic matter). The soils were refiled in the trench according to their initial soil profile distributions, and the forest floor was undisturbed. Each pair of trenched and untrenched quadrats was directly adjacent to each other (approximately 1 m apart) to avoid environmental biases. Meanwhile, an extra quadrat (soil sampling quadrat) that was close to each trenched or untrenched quadrat was arranged for corresponding sample collections to avoid disturbing Rh or total Rs measurements. In each sampling quadrat, a button thermometer (iButton DS1923, Wdsen Electronic Technology, China) was buried in the soil at 5-cm depth for monitoring soil temperature enabling the calculation of the mean monthly soil temperature (MMST).

In March 2018, a polyvinyl chloride (PVC) collar with an internal diameter of 20 cm and height of 10 cm was inserted approximately 5 cm into the soil of each trenched or untrenched quadrat in advance and maintained during the entire experimental period. Living plants were removed but not litters. In May, August, and October, after the removal of visible living organisms, Rh and total Rs were measured in trenched and untrenched quadrats, respectively, between 9:00 am and 11:00 am on continuous 3–5 sunny days using a soil CO_2 flux system (Li-8100, Li-COR Biosciences, USA) on the PVC collar in situ. The average value of the 3–5 measurements was used to represent the Rh or total Rs value in each quadrat, and the four Rh or total Rs values (i.e., four quadrats) were then averaged in each plot. Simultaneously, soil temperature at 5-cm depth and moisture at 10-cm depth adjacent to each PVC collar were detected with thermocouple and moisture probes attached to the Li-8100 system.

2.3 Soil and fine root samplings

During Rh and total Rs measurements in August 2018, 1–2 soil points were sampled (0–10 cm depth) in each trenched or untrenched quadrat. These soil points from all sampling quadrats were mixed to a representative soil sample in each plot corresponding to Rh or total Rs, respectively. In each untrenched sampling quadrat, 1–2 soil cores were randomly sampled with a stainless-steel core (diameter 7.5 cm) at 0–10 cm depth, in which fine roots (diameter < 2 mm) were gently picked out based on their tensile strength and color (Beniston et al. 2014).

In each plot, four individual standard trees of each dominant species (for NF) or four individual standard trees (for the plantations) that were as close to each untrenched quadrat as possible were selected for rhizosphere soil sampling. At each sampling point, a profile of 0–10-cm depth was dug, and the soil adhered to the root surfaces was gently shaken and collected with a sterile paint brush (Cui et al. 2019). These soils were mixed as representative rhizosphere

soil samples for each plot. Some of these soil samples were immediately transported in an ice box (4 °C) for microbial property measurements within 72 h (freeze-dried at −80 °C for SMC structure measurement). The remaining soil samples were air-dried for physicochemical property measurements after the visible stones and roots were removed. Undisturbed soil samples were collected from three profiles in each plot with a cutting ring (100 cm^3) for soil bulk density (BD) measurements.

2.4 Measurements of chemical and microbial properties

Soil water content (SWC) and BD were detected via the oven-drying (105 °C, 48 h) method. The soil was extracted using ultrapure water (1:5, wt.:vol.) for 90 min (180 rpm) and filtered (0.45 μm), and dissolved organic C (DOC) and total dissolved N (TDN) in the extract were measured using a TOC/TN analyzer (Elementar Analysensysteme, Germany). Dissolved inorganic N (DIN) in the extract was measured using a flow injection analyzer (FIAStar 5000, Foss, Denmark), and dissolved organic N (DON) was obtained by subtracting DIN from TDN. Available phosphorus (AP) was detected using NH_4F-HCl extraction associated with photometric method (Lu 2000), and soil pH was measured using a digital pH meter (FE28-standard, Mettler-Toledo Inc., Switzerland). Based on our previous study (Zhao et al. 2015), microbial biomass C (MBC) was detected and calculated via the fumigation and 0.5 M K_2SO_4 extraction method. SMC structure was analyzed using the phospholipid fatty acid (PLFA) method, the details of which can be found in our previous work (Zhao et al. 2020). In short, actinomycetes (ACT), gram-positive bacteria (GP), gram-negative bacteria (GN), arbuscular mycorrhizal fungi (AMF), and fungi (except AMF) were identified. The sum of GP and GN was considered as the total bacteria. The fungi to bacteria ratio (F:B) and GP to GN ratio (GP:GN) were calculated.

2.5 Calculation and statistics

The relationships between Rs components and soil temperature and moisture were explored using Eqs. 1 and 2, respectively (Tong et al. 2020). The temperature sensitivity (expressed as Q10) was calculated using Eq. 3, and the combined effects of soil temperature and moisture on the Rs components were assessed using Eq. 4 (Han et al. 2012).

$$Rs = \alpha e^{\beta T} \tag{1}$$

$$Rs = a_0 W + b_0 \tag{2}$$

$$Q10 = e^{10\beta} \tag{3}$$

$$Rs = ae^{bT}W^c \tag{4}$$

where T (°C) is the soil temperature at 5-cm depth; W (%) is the soil moisture at 10-cm depth; and α, β, a_0, b_0, a, b, and c are fitted parameters.

One- and two-way ANOVA were used to test the differences in soil chemical and microbial properties across forest type (Tukey's test) and across trench treatment (trenched/untrenched, paired sample t-test). Repeated measure ANOVA was used to test the differences in Rs components across forests during the growing season. Spearman's rank correlation was used to assess the relationships between Rs components and influencing factors. All statistical analyses were conducted using SPSS v18.0 (SPSS Inc., USA). Rs component values in August were used to assess the relationships between Rs components and influential factors (e.g., soil properties, SMC structure and fine root traits). Correlation heatmaps of Rs components were plotted with R3.3.2 (*heatmap* package).

Redundancy analysis (RDA) was used to explore the relationships between the SMC structure and influencing factors on Canoco5 (Microcomputer Power, USA). The influencing factors with variance inflation factors > 20 were removed in the initial RDA. Monte Carlo permutation (standardized; 499 permutations), log-transformed and centered, was used to assess the RDA axis effect on the SMC structure, and a forward selection procedure was used to select influencing factors with significant ($P < 0.05$) and many contributions to SMC structure variances.

3 Results

3.1 Chemical properties of trenched and rhizosphere soils

In trenched soil, DOC and pH were higher ($P < 0.05$) in NF than in the plantations (Table 1). The lowest levels of DOC and DON and the highest MBC level were observed in MG; there was no significant difference in DOC:DON between NF and MG. In rhizosphere soil, most chemical properties (except DOC:DON) were higher in NF than in the plantations, with the lowest levels of DOC, DOC:DON, and MBC in MG. Other soil and microenvironment (e.g., MMST) characteristics are presented in Table S1, and fine root properties are presented in Table S2.

3.2 Rs component distributions across forests

During the growing season, the Rh and Ra were greater in MG than in other forests according to repeated measure ANOVA, particularly for Ra (Fig. 1a, b). There were no significant differences in Rh and Ra among NF, CF, and CL. MG had the highest Ra percentage among forests (Fig. S1a).

Table 1 Properties in trenched and rhizosphere soils

Forests	DOC (mg kg^{-1})	DON (mg kg^{-1})	DOC:DON	MBC (mg kg^{-1})	AP (mg kg^{-1})	pH
Trenched soil						
NF	89.18(4.42)c	22.08(1.97)b	4.06(0.40)b	71.26(2.80)b	2.64(0.38)b	4.68(0.02)c
CF	66.51(3.19)b	30.69(1.79)c	2.17(0.02)a	60.38(2.34)a	1.99(0.10)a	4.39(0.03)a
MG	44.44(2.33)a	10.58(0.99)a	4.21(0.21)b	78.82(1.63)c	2.20(0.10)ab	4.57(0.04)b
CL	58.68(2.54)b	30.77(1.83)c	1.91(0.13)a	55.22(3.85)a	2.72(0.20)b	4.44(0.01)a
Rhizosphere soil						
NF	121.47(11.08)c	60.56(5.79)b	2.02(0.23)ab	121.22(4.81)b	8.61(0.50)c	4.51(0.01)d
CF	97.90(2.88)b	39.26(2.93)a	2.50(0.23)b	97.33(3.08)a	4.35(0.28)a	4.15(0.02)a
MG	76.20(10.87)a	41.04(3.09)a	1.87(0.31)a	89.46(3.16)a	4.58(0.27)a	4.38(0.02)c
CL	89.52(1.04)ab	43.64(2.54)a	2.06(0.15)ab	94.93(2.68)a	6.11(0.25)b	4.24(0.02)b

Each value represents the mean with standard deviation in the bracket. The same lowercase letters across forest type (one-way ANOVA, Tukey's test) within trenched or rhizosphere soil indicate non-significant differences ($P > 0.05$)

NF natural forest, *CF C. fortune* plantation, *MG M. glyptostroboides* plantation, *CL C. lanceolata* plantation, *DOC* dissolved organic carbon, *DON* dissolved organic nitrogen, *DOC:DON* ratio of DOC to DON, *MBC* microbial biomass carbon, *AP* available phosphorus

3.3 SMC structures in trenched and rhizosphere soils

In trenched soil, NF had higher levels of AMF and GP than the plantations, but had a lower F:B level, significantly or non-significantly (Fig. 2a). Among the forests, NF had the lowest F:B level and the highest levels of AMF and GP, whereas MG had the lowest levels of AMF and GN and the highest GP:GN level. CL had the lowest GP:GN level among the forests in trenched soil. In rhizosphere soil, NF had the highest levels of GN and bacteria and the lowest F:B level among the forests, whereas MG had the highest levels of fungi and F:B (Fig. 2b). The plantations had higher levels of GP:GN and F:B than NF. The differences in AMF and GP between the MG and NF were non-significant.

RDA revealed that, NF, MG, and CL were clearly separated based on the SMC structure in trenched and rhizosphere soils (Fig. 3). GN, GP, and AMF dominated the variances of SMC structures in trenched soil; among them, DOC:DON and BD were the two largest contributors (Fig. 3a and Table S3). In rhizosphere soil, fungi, GN, and GP dominated the SMC structure variance, with DON and pH being the two largest contributors (Fig. 3b and Table S3).

3.4 Correlations of Rh and Ra with microbial parameters and other potential factors

Rh was negatively correlated with AMF, GN, bacteria, and AP (Fig. 4a); Ra was positively correlated with AMF and GP but negatively correlated with C:N in fine roots
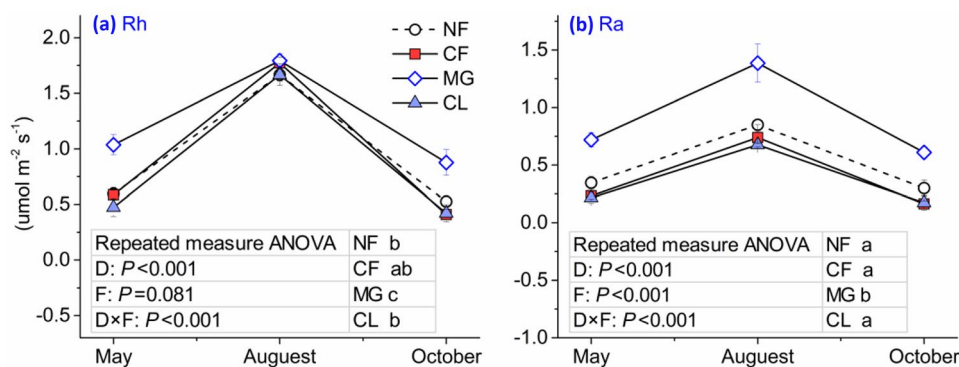
Fig. 1 Distributions of (**a**) Rh and (**b**) Ra across forests during growing season. NF, natural forest; CF, *C. fortune* plantation; MG, *M. glyptostroboides* plantation; CL, *C. lanceolata* plantation; D, measurement date; F, forest type; D×F, interaction between measurement date and forest type. Each value represents the mean with the vertical bar as the standard deviation. The same lowercase letters indicate non-significant differences ($P > 0.05$) based on repeated measure ANOVA
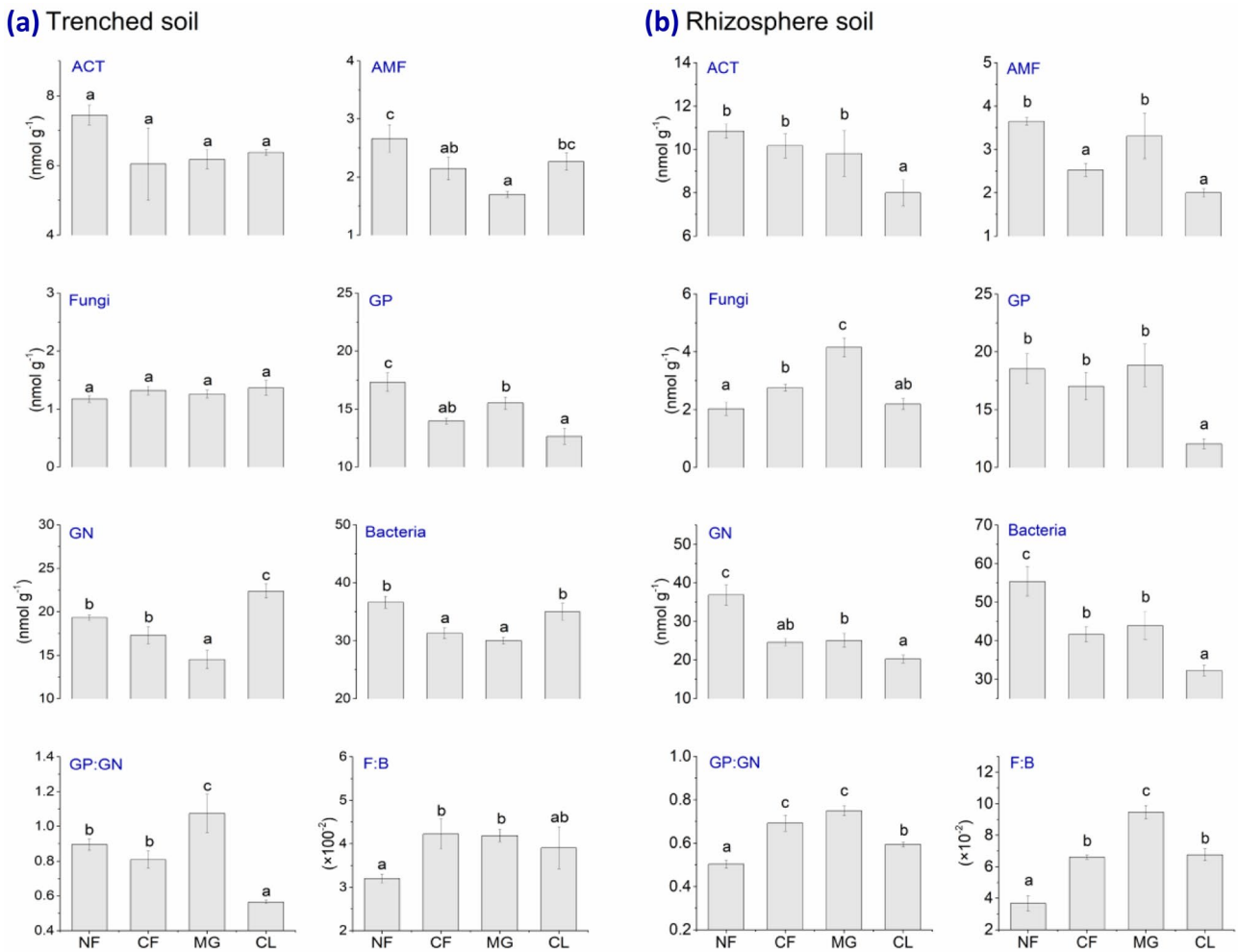
Fig. 2 Microbial groups in (**a**) trenched and (**b**) rhizosphere soils. ACT, actinomycetes; GN, gram-negative bacteria; GP, gram-positive bacteria; AMF, arbuscular mycorrhizal fungi; GP:GN, the ratio of GP to GN; F: B, the ratio of fungi to bacteria. Each value of a histogram is the mean with a vertical bar as the standard deviation. The same lowercase letters across forest types (one-way ANOVA, Tukey's test) within each trenched or rhizosphere soil indicate non-significant differences ($P > 0.05$)

(Fig. 4b). Model-fitted analysis revealed that Rh and Ra were highly significantly correlated with soil temperature but not with soil moisture in each forest (Table 2). Based

on the significant interactions between soil temperature and moisture, the soil temperature parameter b was greater than the moisture parameter c for both Rh and Ra in NF, CF, and

Fig. 3 RDA results of SMC structures in (**a**) trenched and (**b**) rhizosphere soils across forests. DOC, dissolved organic carbon; DON, dissolved organic nitrogen; DOC:DON, ratio of DOC to DON; AP, available phosphorus; C:N, ratio of soil organic carbon to total nitrogen; BD, bulk density; SWC, soil water content; MMST, mean monthly soil temperature in August
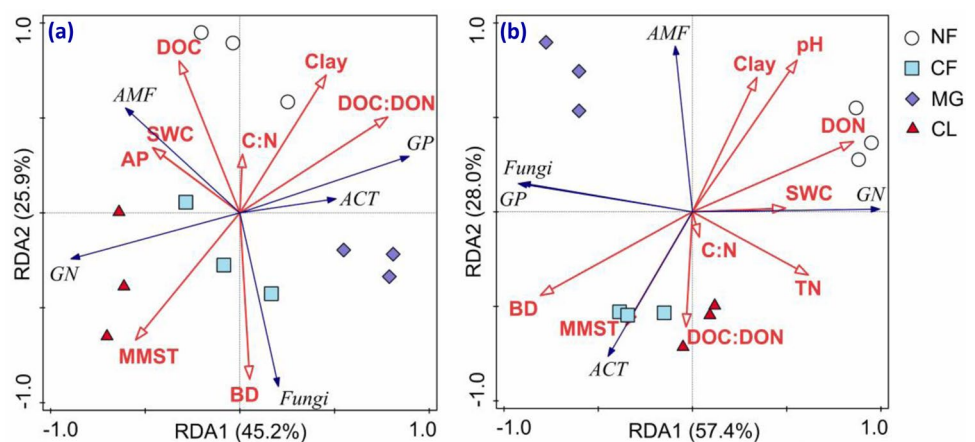
Fig. 4 Heat maps based on Spearman's rank correlation of (**a**) Rh and (**b**) Ra with influencing factors. SOC, soil organic carbon; TN, total nitrogen; MBC, microbial biomass carbon; Bfr, fine root biomass; Cfr, fine root carbon content; Nfr, fine root nitrogen content; C:Nfr, ratio of Cfr to Nfr. * and ** refer to significant levels at 0.05 and 0.01 levels, respectively
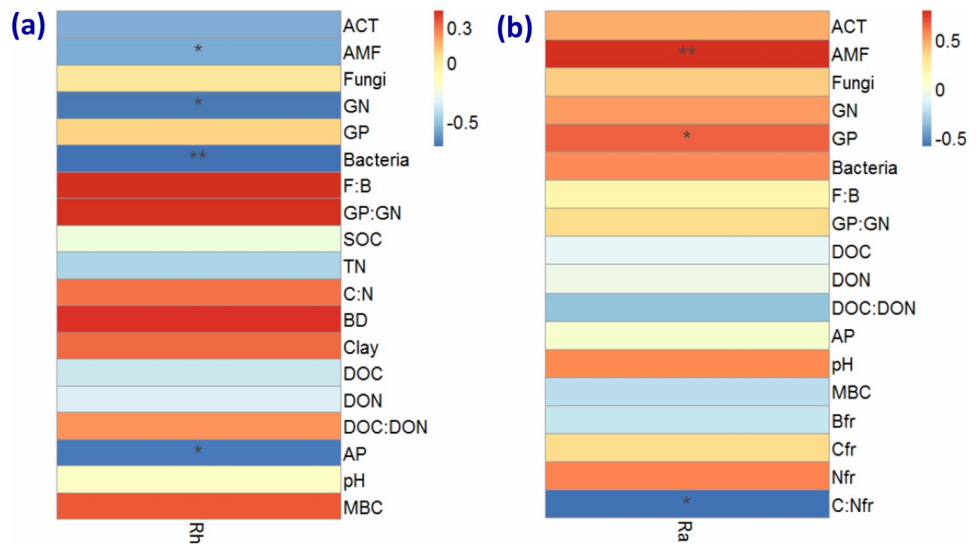
MG. Q10 was lower in MG than in other forests for both Rh and Ra.

4 Discussion

4.1 Differentiation of SMC structures mediating Rs components

SMC structures in trenched and rhizosphere soils were distinctly differentiated following forest conversion, corresponding with the hypothesis (i). The species dependence of the SMC structure is consistent with previous reports that SMC structure varies with vegetation characteristics under LUC

(Guo et al. 2016b; Wan and He 2020). In trenched soil, the decrease in AMF with forest conversion indicates that the SMC structure is nutrient sensitive, because AMF can relieve P deficiency by mineralizing and releasing P in organic matter (Herrera Paredes and Lebeis 2016). This phenomenon is more intense during NF-to-MG conversion with large declines in GN and AMF because GN is favored in nutrient-rich soils (Hammesfahr et al. 2008); this suggests that the soil in MG could exhibit a relatively *oligotrophic* status (Liu et al. 2018a), and is further reflected by the increase in GP:GN during NF-to-MG conversion. This is evidenced by the major role of DOC:DON in driving SMC structure dynamics, as dissolved organic resources are explicitly reactive to SMC structure dynamics via their direct and easy utilization by

Table 2 Model-fitted parameters of the relationships of Rh and Ra with soil temperature and moisture

		Rh				Ra			
		NF	CF	MG	CL	NF	CF	MG	CL
Temperature	α	0.196	0.123	0.518	0.119	0.128	0.046	0.326	0.056
	β	0.126	0.153	0.072	0.143	0.111	0.16	0.084	0.134
	R^2	0.980	0.983	0.963	0.976	0.965	0.976	0.923	0.962
	P	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Moisture	a_0	−0.072	0.354	0.185	0.143	−0.032	0.146	0.155	0.072
	b_0	3.552	−13.353	−5.835	−4.041	1.657	−5.500	−5.006	−2.103
	R^2	−0.136	−0.011	−0.063	−0.056	−0.137	−0.020	−0.069	−0.005
	P	-	-	-	-	-	-	-	-
The interaction	a	1.17E+06	6.04E+09	5.29E+04	0.009	1.04E+03	8.19E+09	5.27E+06	9.68E−05
	b	0.124	0.161	0.075	0.142	0.110	0.168	0.089	0.132
	c	−4.339	−6.686	−3.175	0.746	−2.503	−7.034	−4.57	1.807
	R^2	0.994	0.999	0.974	0.974	0.966	0.991	0.935	0.966
	P	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Q10		3.51	4.63	2.05	4.16	3.04	4.94	2.31	3.84

Rh soil heterotrophic respiration, *Ra* soil autotrophic respiration, *Q10* temperature sensitivity

microorganisms (Yuan et al. 2019). In addition, an increase in F:B with forest conversion implies an increase in C sequestration potential due to the low turnover rate and C-retaining ability of fungi (Clemmensen et al. 2015; Rousk et al. 2010), which is also an indication of nutrient constraints. An increase in BD with forest conversion also contributed to the F:B increase in trenched soil. In brief, the available nutrient quality is the primary driver of the SMC structure in trenched soil in response to forest conversion.

The SMC structure in rhizosphere soil is very species-specific due to its root exudate dependence (Thacker and Quideau 2021), exhibiting a high sensitivity to forest conversion (Fig. 3b). The major drivers of DON and pH support the close bonds among root exudates, microorganisms, and N availability and state the key impacts of organic acids in root exudates on the SMC structure in rhizosphere soil (Meier et al. 2017; Shi et al. 2011). Specifically, the decreases in DON and pH with the LUC increased fungi but decreased GN, also supported by the increases in F:B and GP:GN, particularly during NF-to-MG conversion. These shifts in the SMC structure imply a relative C-retaining potential and *oligotrophic* status in rhizosphere soil over LUC and may induce functional changes in ecological processes (Adamczyk et al. 2021). Thus, over long-term forest conversion, SMC structures in trenched and rhizosphere soils have been differentiated with different dominant groups, and those in rhizosphere soil are more species-specific. Whether in trenched or rhizosphere soil, available nutrients (quality or quantity) is a major constraint on SMC structure in response to long-term forest conversion.

4.2 Linkages of Rs components to SMC structures as well as other factors

Corresponding with the hypothesis (i), Rs components were differentiated by forest conversion, particularly by NF-to-MG conversion (Fig. 1). The LUC-induced changes in the SMC structure will trigger remarkable dynamics in Rs components, as different microbial groups have distinctive C-use efficiencies (CUEs) and preferences for substrates (Su et al. 2016). This is partly confirmed by the negative correlation between Rh and AMF and by the positive correlation between Ra and GP (Fig. 4a, b), since bacteria have a lower CUE than fungi and more CO_2 will be released from bacterium-dominated soil than from fungus-dominated soil (Keiblinger et al. 2010). Our observation is different from a previous report stating that vegetation attributes and soil organic C (SOC) stock other than the SMC structure preferentially drive Rh dynamics in subtropical forests (Wei et al. 2015). In contrast, the expected role of the SMC structure in rhizosphere soil for regulating Ra has been observed (Adamczyk et al. 2021). Root (particularly fine root) biomass generally plays a crucial role in driving Ra in terrestrial

ecosystems (Zhao et al. 2016b); however, we found that LUC-induced decrease in fine root quality (expressed as an increase in C:N) rather than biomass inhibited Ra (Fig. 4b and Table S2). This is also supported by the Ra increase only during NF-to-MG conversion, and the C:N ratio of fine roots did not have a similar trend (Fig. 1b and Table S2). These contributions of SMC structure and fine roots to Ra are different from a previous study reporting that SMC structure, but not litter or fine root quality, regulates the soil C process in subtropical forests (Wang et al. 2015).

During NF-to-MG conversion, the increase in Ra rather than Rh controls the total Rs enhancement (Figs. 1 and S1a), which is different from a previous report that Rh is more sensitive to global change scenarios than Ra (Zhao et al. 2016a). Specifically, the contributions of Ra to total Rs in NF, CF, and CL coincide with the average value of approximately 33% in the subtropical region of China (Zhang et al. 2017), but not in MG, implying a resilient status of soil C process during NF-to-CF and NF-to-CL conversions. This can be corroborated by the greater efficiencies of plant roots and SMC in C-resource utilization by CF and CL than by MG, indicated by the decreases in specific Ra and specific Rh with NF-to-CF and NF-to-CL conversions but not with NF-to-MG conversion (Figs. S1b, c) (Huang et al. 2016). Thus, a combination of reduced C loss (expressed as total Rs) and greater C-resource utilization efficiency indicates that more C has been retained as soil organic matter, plant, or microbial biomass in CF and CL than in MG (Ding et al. 1992). That is, because of the eco-physiological and biochemical dynamics in plant–soil–microbe interactions with forest conversion, MG still exhibits a relatively low energy efficiency even over more than three decades (Odum 1969), which may be attributed to its species or community attributes.

Not perfectly consistent with hypothesis (iii), soil temperature, but not soil moisture, significantly influenced Rh and Ra (Table 2), which does not agree with a previous report suggesting that both soil temperature and moisture are linked to Rs components (Zhou et al. 2021). LUC-induced changes in the microenvironment can improve the sensitivity of Rs components (Chen et al. 2021; Yao et al. 2019), corroborated by NF-to-CF and NF-to-CL conversions (Q10 in Table 2). However, both Rh and Ra had lower Q10 levels in MG than in other plantations, suggesting that soil C processes in MG could be less sensitive to LUC-induced microenvironments (Tong et al. 2020). The decrease in the Q10 of Ra during NF-to-MG conversion could be due to the higher fine root/substrate quality in MG than in other plantations (Zhang et al. 2014). The specific mechanisms governing Q10 regarding long-term LUC require further clarification.

The multifaceted factors involved in Rh and Ra modifications do not completely satisfy the hypothesis (ii). Our findings do not support Guo et al. (2016a) who found that, in a simlar scenario of 36-year natural forest-to-plantation

conversion, Rs decreases are primarily driven by SMC structure associated with SOC content and soil temperature, which could be due to the differences in tree species attributes, plant community characteristics, and management (e.g., tree density). However, in this study, the general roles of C and nutrient availability (e.g., DOC and DON) in regulating Rs components (Pajares et al. 2016; Wu et al. 2020) have not been observed, even for Ra with intense C and nutrient processes in rhizosphere soil (Thacker and Quideau 2021), which is different from the responses of the SMC structure to the LUC. These activating roles of SMC structure and soil temperature in Rs component modifications reflect ecological processes at the ecosystem level, which is particularly important for forest management and C maintenance in this region. This inference can be roughly reflected by the non-significant differences in SOC among the forests (Table S1), and has also been discussed in our previous work (Zhao et al. 2022).

5 Conclusions

We explored the Rs process by linking SMC structures in trenched and rhizosphere soils to Rh and Ra, respectively, providing a relatively new angle for assessing the underlying mechanism for Rs components under long-term forest conversion. These SMC structures were differentiated. The dynamic in the SMC structure in trenched soil is primarily driven by DOC:DON and BD with GN, GP, and AMF as dominant groups; however, the dynamic in the SMC structure in rhizosphere soil is primarily driven by DON and pH with GN, GP, and fungi as dominant groups. During the growing season, Rh and Ra were increased by NF-to-MG conversion but not by NF-to-CF and NF-to-CL conversions. The Rh dynamic is primarily driven by the SMC structure (e.g., AMF) and soil temperature, whereas the Ra dynamic is primarily driven by the SMC structure (e.g., GP), fine root quality, and soil temperature. Notably, even more than three decades after forest conversion, soil C loss as CO_2 will still be enhanced depending on the converted species (e.g., MG), which is predominately characterized by Ra dynamics.

These results suggest that microorganisms and the microenvironment (i.e., soil temperature) play crucial roles in modifying the belowground C process over long-term forest conversion. This study highlights the importance of plant community attributes and forest management (e.g., tree species and tree density) for soil C emission into the atmosphere, which should be considered when establishing long-term C assessments in subtropical regions.

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Declarations

Conflict of interest The authors declare no competing interests.

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