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Soil microbial community composition does not predominantly determine the variance of heterotrophic soil respiration across four subtropical forests

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To explore the importance of soil microbial community composition on explaining the difference in heterotrophic soil respiration (R_h) across forests, a field investigation was conducted on R_h and soil physiochemical and microbial properties in four subtropical forests in southern China. We observed that R_h differed significantly among forests, being 2.48 ± 0.23, 2.31 ± 0.21, 1.83 ± 0.08 and 1.56 ± 0.15 μmol m^{-2} s^{-1} in the climax evergreen broadleaf forest (BF), the mixed conifer and broadleaf forest (CF), the conifer plantation (CP), and the native broadleaved species plantation (BP), respectively. Both linear mixed effect model and variance decomposition analysis indicated that soil microbial community composition derived from phospholipid fatty acids (PLFAs) was not the first-order explanatory variable for the R_h variance across the forests, with the explanatory power being 15.7%. Contrastingly, vegetational attributes such as root biomass (22.6%) and soil substrate availability (18.6%) were more important for explaining the observed R_h variance. Our results therefore suggest that vegetation attributes and soil carbon pool size, rather than soil microbial community composition, should be preferentially considered to understand the spatial R_h variance across the subtropical forests in southern China.

Heterotrophic soil respiration (R_h), often used to approximate the rate of soil organic matter (SOM) decomposition, is regulated by numerous factors such as climate and chemical recalcitrance of its components to decay[1–3]. Although having been acknowledged to play a critical role in the process of SOM decomposition[4–6], the importance of soil microorganisms as a determinant of R_h variances across study sites has rarely been carefully examined[3,5,7], probably because of the huge diversity and functional redundancy of microbial communities and the metabolic flexibility of individual microbial species[4]. Due to the lack of empirical evidence, soil microorganisms have been included only in exceptionally few ecosystem or soil process models, and even then treated merely as a "black box"[5,8,9], although the existing models involving SOM mineralization are highly diverse with very different complexity levels[10]. Explicit representation of microorganisms was recommended as a future component of models, but the optimal level of detail remains to be defined[3].

Also in southern China, few studies have explored whether the spatial variations of soil microbial community composition affected the R_h variances across Chinese subtropical forests, despite that this region has been identified as a substantial carbon sink[11,12]. The mechanisms controlling CO_2 fluxes are not deeply understood. In particular, the roles of soil microorganisms on spatial dynamics of heterotrophic soil respiration remain unclear in this area, raising extra uncertainty to estimate the change of carbon source-sink relationship for these subtropical forests under the future environmental changes.

Furthermore, carbon fractions of surface soil in these subtropical forests could change in response to environmental changes[13]. To better understand the soil carbon cycle in this area, it is urgent to determine if soil microbial community composition is one of the main factors controlling the R_h variances across these forests, due to the potential shifts of soil microbial community as a result of changed environmental conditions and substrate supply[14–16]. In this study, we conducted field measurements on heterotrophic soil respiration and soil physico-

chemical and microbial properties across four forests in southern China to explore whether soil microbial community composition was relevant to varied R_h across forests. Such observations were expected to provide empirical supports for predicting the future forest carbon cycling more exactly in this region.

Results

Heterotrophic soil respiration and vegetational and soil properties across the four forests. Heterotrophic soil respiration rate was significantly higher in the two natural forests compared to the two plantations (P=0.002, Fig. 1a), being 2.48 ± 0.23, 2.31 ± 0.21, 1.83 ± 0.08 and 1.56 ± 0.15 μmol m^{-2} s^{-1} in BF, CF, CP, and BP, respectively. No statistically significant difference existed between the two young plantations (P=0.14) or between the two natural forests (P=0.51). Because soil carbon stock was significantly higher in the climax forest than in the other three sites (Table 1), we also tested the differences in heterotrophic respiration rate per unit of total organic carbon (R_h/TOC) or readily oxidizable organic carbon (R_h/ROC). These two indexes of relative decomposition capacity tended to be higher in the mixed forest than in the other three forests studied (Fig. 1b). We therefore assessed whether the higher respiration rates in climax forest or the higher relative decomposition capacity in mixed forest could be attributed to compositional differences of soil microbial community. Moreover, much higher litterfall production and root biomass were observed in the two natural forests than in the two plantations (Table 1).

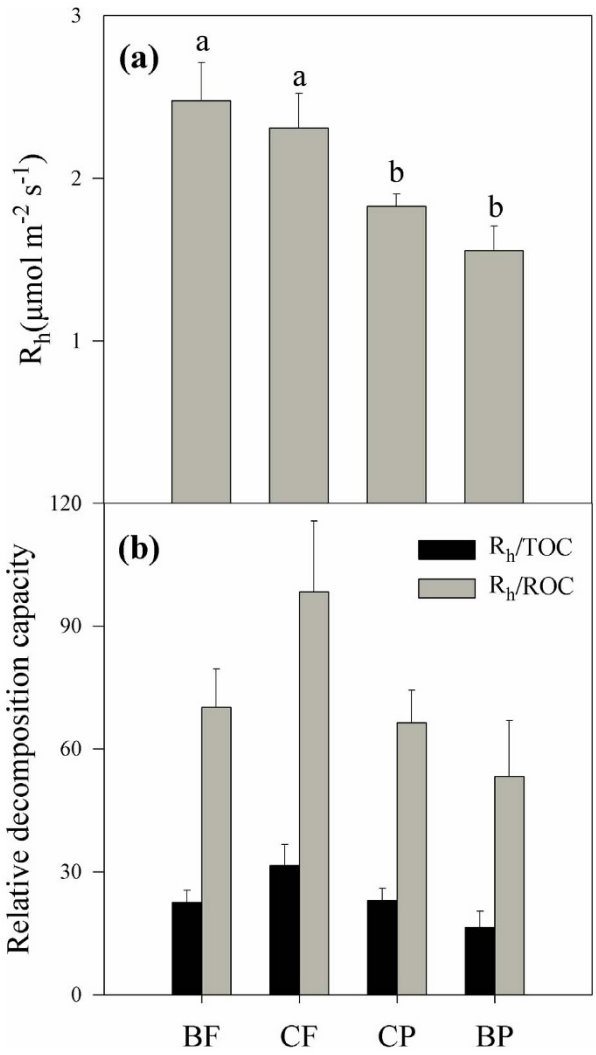

Figure 1 | Heterotrophic soil respiration rate (a) and relative decomposition capacity (b) in the four forests. Columns represent average values and error bars represent standard errors (n=3). Different letters above bars indicate significant differences at P<0.05 level. The BF stands for climax evergreen broadleaf forest, CF for mixed conifer and broadleaf forest, CP for conifer plantation, and BP for native broadleaved species plantation. Relative decomposition capacity was defined as the ratio of the heterotrophic respiration rate over total organic carbon (R_h/TOC), and as the ratio of the heterotrophic respiration rate over readily-oxidizable organic carbon (R_h/ROC).

Microbial biomass carbon (MBC) was the highest at the climax forest (P=0.011) whereas it was not significantly different among the other three sites (P>0.05). The PCA on phospholipid fatty acids (PLFAs) showed that, for our single sampling event, only the soil microbial structure in the climax forest was isolated from the others (Fig. 2a). When pooling the fatty acids into different microbial functional groups, we further observed that BF contained significantly higher contents of Gram-positive bacterial PLFAs than CP, and also significantly higher actinomycetal PLFAs content than CP and BP (P<0.05, Fig. 2b). When looking at the ratios of PLFAs for different microbial functional groups, however, we did not observe significant variation among the four forests (P>0.05, Fig. 2c).

Explanatory variables for the R_h variances across forests. For differences in heterotrophic respiration rate and the relative decomposition capacities across the forests, neither of them was attributed to the variation of soil microbial community composition (P>0.05, Table 2). However, soil carbon stocks (TOC) or decomposability (ROC/TOC) induced significant or marginally significant effects on heterotrophic respiration rate (Table 2). Moreover, the results of variance decomposition (Table 3) showed that root biomass explained the most of the R_h variance among forests (22.6%), followed by SAP_PC2 (18.6%; the second principal component of the dataset including soil abiotic properties), PLFA_PC2 (15.7%), and litterfall production (12.6%). As well, SAP_PC2, a principal component closely related to soil carbon pool size indexes including TOC, ROC, and NROC (non-readily oxidizable organic carbon), explained the most of the total variances of the two relative decomposition capacity indexes R_h/TOC (35.1%) and R_h/ROC (30.5%).

Discussion

In the present study, R_h was significantly higher in the two older natural forests than in the two younger plantations. This could be attributed to different age-related stand and soil properties across the four forests, e.g., litterfall inputs and soil substrate supply. Likewise, Saiz et al.[17] observed that soil CO_2 efflux rate at trenched plots across a Sitka spruce chronosequence was the highest in the forest with the largest annual litter inputs and pool of easily decomposable organic matter. The substrate-mediated heterotrophic respiration has been recorded in previous studies[18–20]. Consistently, much higher litterfall production and root biomass mean more supplies of nutrients from both litterfall decomposition and root excretions in the two natural forests, comparing with the two plantations in this study. Therefore, forest type and soil substrate supply seem to be of major importance to explain the R_h differences across forests, by controlling organic matter inputs and recalcitrance to decay. This is supported by both results of linear mixed effect model and variance decomposition analysis, which presented that vegetational attributes and soil substrate supplies together explained most of the cross-site R_h variance in this study.

Soil microbial biomass and community composition were also significantly different across the studied forests, indicated by fumigation-extracted MBC and the result of PCA on the profile of PLFA biomarkers. However, our results of linear mixed effect model suggested that neither of soil microbial biomass and community structure was the first-order variable to explain the R_h pattern across

Table 1 | Vegetation and soil properties in the four subtropical forests. Numbers are average values with standard errors in the parenthesis (n=3). The BF stands for climax evergreen broadleaf forest, CF for mixed conifer and broadleaf forest, CP for conifer plantation, and BP for native broadleaved species plantation. ST_5 is soil temperature at 5 cm depth, SM_5 soil moisture at 5 cm depth, DOC dissolved organic carbon, MBC microbial biomass carbon, ROC readily-oxidizable organic carbon, TOC total organic carbon, and TN total nitrogen. Soil samples were collected at 0–20 cm depth. In BF and CF, litterfall production was cited from ref. 36, root biomass from ref. 37, and clay content from ref. 38. In CP and BP, litterfall production, root biomass and clay content were cited from ref. 39. Two measured MBC in CF were negative and therefore not used for statistical analysis

Vegetation type	BF	CF	CP	BP
Dominant species	*Castanopsis chinensis, Schima superba, Cryptocarya chinensis, Machilus chinensis, Syzygium rehderianum*	*Pinus massioniana, Schima superba*	*Pinus massoniana, Cunninghamia lanceolata*	*Schima superba, Schima wallichii*
Litterfall (kg m^{-2} yr^{-1})	0.8	0.9	0.3	0.6
Root biomass (kg m^{-2})	9.6	8.8	3.7	3.8
ST_5 (°C)	26.2(0.2)^{c}	26.1 (0.1)^{c}	28.9(0.2)^{b}	26.7(0.0)^{a}
SM_5 (v,v)	0.29(0.01)	0.29(0.01)	0.28(0.00)	0.33(0.02)
pH (KCl)	3.1(0.0)^{d}	3.2(0.0)^{c}	3.6(0.1)^{b}	3.4(0.0)^{a}
Clay (%)	40.5	33.8	21.7	16.1
DOC (g m^{-2})	35.1(2.9)	37.0(4.0)	44.5(6.1)	43.3(6.4)
MBC (g m^{-2})	53.6(4.5)^{a}	24.6	19.3(4.4)^{b}	24.8(10.6)^{b}
ROC (kg m^{-2})	1.6(0.1)	1.1(0.1)	1.2(0.1)	1.4(0.2)
TOC (kg m^{-2})	4.9(0.3)^{b}	3.3(0.3)^{a}	3.6(0.3)^{a}	4.4(0.6)^{ab}
TN (kg m^{-2})	0.45(0.03)^{b}	0.30(0.02)^{a}	0.31(0.03)^{a}	0.36(0.02)^{ab}

^{a,b,c,d} indicate significant differences at $P<0.05$ among forests.

the forest sites. The absence of soil microbial communities controlling on R_h implies a subordinate effect of PLFA-derived soil microbial communities on the R_h variance across forests. This is verified by the insignificantly different ratios of PFLA biomarkers for different microbial groups among the four forests, in spite of the significantly different R_h. The observation was also confirmed by results of variance decomposition that vegetational and soil properties explained greater proportions of the R_h variance across forests than soil microbial communities. Moreover, soil microbial biomass and community structure are greatly affected by substrate supply[5,21], and the latter is mainly determined by standing vegetation by means of litter input and root excretions. In consideration of complex interactions among environmental variables in natural ecosystems, modifications of changed microbial community composition on R_h could have confounded with that of changes in other preferable variables[22], e.g., forest type and soil substrate supply[21]. Likewise, Wang and colleagues observed that R_h was determined to a greater extent by substrate supply than by microbial biomass carbon across thirty soils, which were collected from three states of Australia[23]. The R_h variance may be mainly determined by soil microbial communities only when substrate supply is sufficient and soil microorganisms in different soils have similar decomposability to substrate[23].

An alternative, but not mutually exclusive, explanation is that PLFAs are not sufficiently discriminative to detect the differences in microbial community structure that may control the decomposition pattern across the study sites. By short term laboratory incubation, for example, Cleveland et al.[5] found that increased R_h induced by the additions of dissolved organic matter (DOM) coincided with a profound raise in the abundances of some opportunistic soil bacterial groups. Fierer et al.[24] also observed that SOC mineralization rate was significantly correlated with the abundances of several dominant bacterial groups across ecosystems in North America. Comparing with the present study, the two aforementioned studies employed molecular biology techniques with higher identifying capacity, i.e., 16S ribosomal DNA analysis, to further identify bacterial phylogenetic groups and observed synchronous changes in R_h and soil bacterial community composition. Moreover, soil microbial communities among the studied forests may not vary enough to explore the relationship with the R_h variance. In the present study, the PLFA ratios of different microbial functional groups, indicating soil microbial community structure to some extent, did not show significant differences among these forests, although BF was isolated from the other three by PCA on PLFAs profile. Obviously, further studies using advanced molecular analyses (e.g., quantitative polymerase chain reaction [qPCR] and 16S ribosomal DNA) and including more forest types might help confirming the role of soil microbial community composition in the heterotrophic soil respiration process in the forests of southern China.

Nevertheless, it must be noted that we conducted this study aiming to test the explanatory capacity of soil microbial communities for the spatial variations in R_h across forests and used only a single sampling event when R_h was at its maximum, since we assumed microorganisms at this period were the most active and therefore the most representative to study the role of activated community structure within a year. Hence, we cannot rule out the potential importance of soil microbial communities in heterotrophic soil respiration processes, as soil microbial community composition may play a crucial role in the temporal variation of R_h[25,26], as well as in the R_h responses to environmental changes[27]. Moreover, microbial extracellular enzyme activities, representing soil microbial community functions to a great extent, are frequently observed to influence SOM decomposition[28,29], but changes in soil microbial enzyme activities are not always accompanied with variations in soil microbial community composition, and vice versa[30,31]. Further studies remain needed to test whether microbial community composition and enzyme activities play a dominant role in explaining the temporal variation of heterotrophic decomposition processes.

In summary, vegetational attributes such as root biomass and litter production and soil carbon pool size such as TOC and ROC played the dominant role in determining the variance of R_h across the four forests. Soil microbial community composition identified by PLFAs was not a major determinant of the R_h differences across the forests included in our study. These results suggest that a good representation of vegetational attributes and soil carbon pool size appears to be

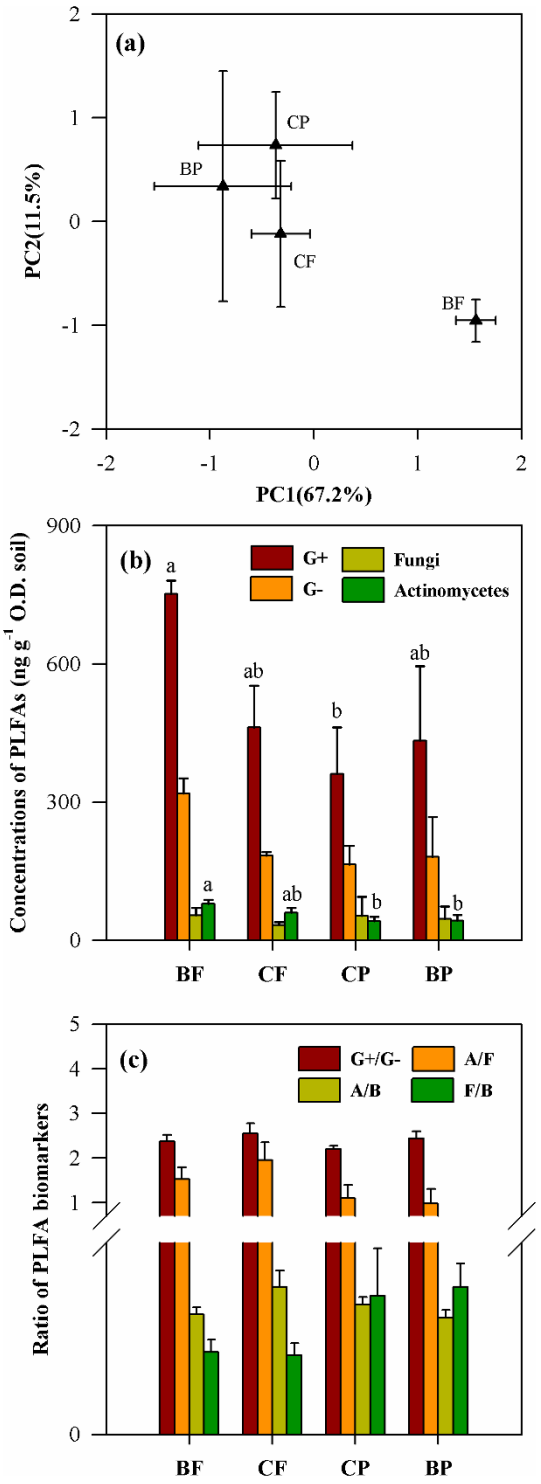

Figure 2 | Scores of the first two principal components of PLFA profile (a), contents of PLFA biomarkers for different microbial groups (b) and ratios of PLFA content between different microbial groups (c) in the four forests. Columns and triangles represent average values and error bars give standard errors (n=3). For each microbial group, different letters above bars indicate significant differences at P<0.05 level among forests. In the figure, G+ stands for Gram-positive bacterial PLFAs, G- for Gram-negative bacterial PLFAs, B for total bacterial PLFAs, A for actinomycetal PLFA, and F for fungal PLFA. The abbreviations for the four forests are the same with that in Fig. 1.

Table 2 | Potential variables explaining variances of heterotrophic soil respiration rate or that of relative decomposition capacity in the linear mixed effect model using sites as the random effect factor across the four studied forests. R_h is heterotrophic soil respiration, TOC total organic carbon, ROC readily-oxidizable organic carbon, DOC dissolved organic carbon, MBC microbial biomass carbon, PLFAs phospholipid fatty acids, G+ Gram-positive bacteria, and G- Gram-negative bacteria. Relative decomposition capacity was defined as the ratio of the heterotrophic respiration rate over total organic carbon (R_h/TOC), and as the ratio of the heterotrophic respiration rate over readily-oxidizable organic carbon (R_h/ROC)

	R_h		R_h/TOC		R_h/ROC	
Variables	*t*	*P*-value	*t*	*P*-value	*t*	*P*-value
DOC	−1.13	0.38	−3.48	0.07	−1.46	0.28
TOC	−3.19	0.09	−4.93	0.04	−2.34	0.14
ROC/TOC	−4.08	0.06	−3.15	0.09	−4.33	0.05
MBC	−1.52	0.37	−1.99	0.30	−2.37	0.25
Total PLFAs	−1.17	0.45	−0.48	0.71	−0.83	0.56
G+ PLFAs	1.20	0.44	1.52	0.37	0.95	0.52
G- PLFAs	0.50	0.70	−0.26	0.83	0.72	0.60
Fungal PLFAs	0.06	0.96	−0.42	0.75	−1.12	0.46
Actinomycetal PLFAs	1.78	0.33	2.26	0.27	1.74	0.33
Actinomycetal/ Bacterial PLFAs	1.07	0.36	0.95	0.39	1.26	0.28
Actinomycetal/ Fungal PLFAs	−0.15	0.89	0.26	0.81	−0.53	0.63
Fungal/Bacterial PLFAs	−0.11	0.92	0.18	0.86	−0.77	0.48
G+/G− PLFAs	−0.75	0.51	0.10	0.92	0.43	0.69

more important to reproduce the observed spatial pattern of heterotrophic soil respiration with a model, whereas an explicit representation of soil microbial community composition might be only alternative.

Table 3 | The explanation proportions of vegetational and soil abiotic properties, and microbial community composition for the R_h variances or changes in the relative decomposition capacity indexes across the four studied forests. Numbers in cells are R^2 by the calc.relimp function with lmg method of ''relaimpo'' package in R software. The abbreviation R_h stands for heterotrophic soil respiration, TOC for total organic carbon, ROC for readily oxidizable organic carbon, SAP for soil abiotic properties, PLFA for phospholipid fatty acids, and PC1 - 4 for the first to forth principal component, respectively. Relative decomposition capacity was defined as the ratio of the heterotrophic respiration rate over total organic carbon (R_h/TOC), and as the ratio of the heterotrophic respiration rate over readily-oxidizable organic carbon (R_h/ROC)

	R_h	R_h/TOC	R_h/ROC
Root biomass	22.6%	12.2%	11.7%
Litterfall	12.6%	8.4%	9.5%
SAP_PC1	7.7%	9.1%	7.6%
SAP_PC2	18.6%	35.1%	30.5%
SAP_PC3	3.5%	2.3%	4.6%
SAP_PC4	2.5%	1.2%	3.4%
PLFA_PC1	6.5%	8.7%	7.4%
PLFA_PC2	15.7%	13.4%	14.0%
PLFA_PC3	1.8%	3.3%	4.5%
PLFA_PC4	2.0%	3.7%	3.0%

Methods

Site description. This study was conducted in four subtropical forests in southern China, including two natural forests: one climax evergreen broadleaf forest (BF, more than 400 years old) and one mixed conifer and broadleaf forest (CF, about 110 years old), and two plantation forests: one conifer plantation (CP, 26 years old) and one native broadleaved species plantation (BP, 26 years old; see details in Table 1). Three 10×10 m^2 replicate quadrats were established in each forest in November 2009 and each quadrat included three trenched plots with a size of 1×1 m^2. In the trenches, double nylon net (100 meshes) was used to prevent roots from penetrating in, and meanwhile get allow lateral transfers of water and solutes. A polyvinyl chloride collar of 20 cm in diameter was installed in each plot, with the upper 2 cm letting above ground for R_h measurements.

Field measurements. In July 2011 when soil microorganisms were the most active, heterotrophic soil respiration rate, together with soil temperature (ST_5) and moisture (SM_5) at 5 cm depth, was recorded in the field by a Li-cor 8100 Auto Soil CO_2 Flux System connecting with temperature and moisture sensors (Li-Cor Biosciences, NE, USA). Before recording, litterfall within the measurement collars was removed by hands carefully. Surface soil at 0–20 cm depth was then collected once per plot by an auger with 4 cm of inner diameter and samples in the same quadrat were mixed completely to form a composite sample for further analysis. Finally, twelve soil samples were analyzed for soil microbial community composition (via phospholipid fatty acids analysis; PLFAs) and soil physicochemical properties.

Laboratory analyses. Microbial biomass carbon was analyzed with the fumigation extraction method[32], in which carbon content of unfumigated soil samples was considered as an estimate for dissolved organic carbon (DOC). ROC was determined using wet oxidization with 333 *mM* $KMnO_4$[33]. TOC was analyzed by the Walkley-Black method and total nitrogen concentration (TN) by the micro-Kjeldahl method[34]. The PLFAs analysis was conducted following Bossio & Scow[35], in which lipids 15:0, a15:0, i15:0, i16:0, a17:0, i17:0 were considered as Gram-positive bacterial biomarkers (G+), cy17:0 and cy19:0 as Gram-negative bacterial biomarkers (G-), 18:2ω6,9c as fungal biomarker (F) and 10ME18:0 as actinomycetal biomarker (A). The ratios of G+ to G- PLFAs, fungal to bacterial PLFAs (G+ plus G-), actinomycetal to fungal PLFA and actinomycetal to bacterial PLFAs were also used to indicate soil microbial community structure.

Statistical analyses. One-way analysis of variance (ANOVA) with Student-Newman-Keuls post-hoc multiple comparisons was used to test significant differences in heterotrophic soil respiration rate and other soil and microbial properties among forests, and principal components analysis (PCA) was conducted on microbial community composition based on PLFA biomarker contents of the entire microbial fatty acids profile. A linear mixed effect model using the sites as random effect to take into account the non-independency of the replicates was employed to determine the significant explanatory variables for different R_h. Considering the limitation of number of sample in our case, all the soil indexes were separated into five groups when tested in the linear mixed effect model, including environmental variables (ST_5, SM_5 and pH), soil nutrients (DOC, ROC, TOC, TN, ROC/TOC, and TOC/TN), PLFA contents of microbial groups (MBC, total PLFAs, G+, G-, bacteria, fungi and actinomycetes), ratios of the PLFA biomarker for different microbial groups to the total PLFA content (G+ PLFAs ratio, G- PLFAs ratio, bacterial PLFAs ratio, fungal PLFAs ratio and actinomycetal PLFAs ratio) and soil microbial community structure (G+/G-, F/B, A/F and A/B). We also employed variance decomposition analysis to explore the explanation capacity of vegetational attributes and soil physiochemical and microbial properties on the total variance of R_h across forests, by using calc.relimp function in the "relaimpo" package in R. The PCA was first conducted on soil abiotic properties (SAP) for extracting principal components (PCs). The first four PCs of SAP and PLFA profiles, explaining more than 90% of the total variances of the SAP and PLFA datasets accordingly, were used in further analysis. Because of non-normality and heteroscedasticity, the data were rank transformed before analyses if necessary. Significant level was set at $P<0.05$. The PCA and linear mixed effect model analyses were also conducted in R software (version 2.15.2) and ANOVA in SPSS 16.0 for windows (SPSS Inc., Chicago, US).

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Author contributions

H. W. and G. X. contributed equally to this study. W. S. conceived the study. H. W. and G. X. carried out the field measurements and laboratory analyses. H. W. and B. G. conducted statistical analyses. H.W., G. X., B. G., I. J., and W. S. contributed to manuscript writing and revisions.

Additional information

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