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 (Rθ) across forests, a field investigation was conducted on Rθ and soil physiochemical and microbial properties in four subtropical forests in southern China. We observed that Rθ 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 Rθ 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 Rθ 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 Rθ variance across the subtropical forests in southern China.

Heterotrophic soil respiration (Rθ), 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. Although having been acknowledged to play a critical role in the process of SOM decomposition, the importance of soil microorganisms as a determinant of Rθ variances across study sites has rarely been carefully examined, probably because of the huge diversity and functional redundancy of microbial communities and the metabolic flexibility of individual microbial species. 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”, although the existing models involving SOM mineralization are highly diverse with very different complexity levels. Explicit representation of microorganisms was recommended as a future component of models, but the optimal level of detail remains to be defined.

Also in southern China, few studies have explored whether the spatial variations of soil microbial community composition affected the Rθ variances across Chinese subtropical forests, despite that this region has been identified as a substantial carbon sink. The mechanisms controlling CO₂ 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. 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 Rθ variances across these forests, due to the potential shifts of soil microbial community as a result of changed environmental conditions and substrate supply. In this study, we conducted field measurements on heterotrophic soil respiration and soil physico-
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 \((P=0.002, \text{Fig. 1a})\), being \(2.48 \pm 0.23\), \(2.31 \pm 0.21\), \(1.85 \pm 0.08\) and \(1.56 \pm 0.15\) \(\mu\)mol 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 \((R_h/\text{TOC})\) or readily oxidizable organic carbon \((R_h/\text{ROC})\). 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).

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 \((P<0.05, \text{Fig. 2b})\). When looking at the ratios of PLFAs for different microbial functional groups, however, we did not observe significant variation among the four forests \((P>0.05, \text{Fig. 2c})\).

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 \((P>0.05, \text{Table 2})\). 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 \(R_h/\text{TOC}\) (35.1%) and \(R_h/\text{ROC}\) (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\(^{18-21}\). 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...
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 PLFA 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 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, e.g., forest type and soil substrate supply. 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. 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. 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. 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. 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 $R_h$ 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 $R_h$, as well as in the $R_h$ responses to environmental changes. Moreover, microbial extracellular enzyme activities, representing soil microbial community functions to a great extent, are frequently observed to influence SOM decomposition, but changes in soil microbial enzyme activities are not always accompanied with variations in soil microbial community composition, and vice versa. 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

| Vegetation type | BF | CF | CP | BP |
|-----------------|----|----|----|----|
| Dominant species| Castanopsis chinensis, Schima superba, Cryptocarya chinensis, Schima wallichii | Pinus massoniana, Machilus chinensis, Syzygium rehderianum | Pinus massoniana, Schima superba | 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)$^c$ | 37.0(4.0)$^b$ | 35.1(4.5)$^a$ | 3.4(0.1)$^d$ |
| $SM_5$ (v,v) | 0.29(0.01)$^a$ | 0.29(0.01)$^b$ | 0.28(0.00)$^c$ | 0.33(0.02)$^d$ |
| pH (KCl) | 3.1(0.0)$^d$ | 3.2(0.1)$^b$ | 3.6(0.1)$^d$ | 3.4(0.0)$^c$ |
| Clay (%) | 40.5 | 33.8 | 21.7 | 16.1 |
| DOC (g m$^{-2}$) | 35.1(2.9)$^c$ | 44.5(6.1)$^c$ | 43.6(6.4)$^c$ | 43.3(6.4)$^c$ |
| MBC (g m$^{-2}$) | 3.5(6.4)$^a$ | 24.6 | 19.3(4.4)$^b$ | 24.8(10.6)$^b$ |
| ROC (kg m$^{-2}$) | 1.6(0.1)$^a$ | 1.1(0.1)$^a$ | 1.2(0.1)$^a$ | 1.4(0.2)$^a$ |
| TOC (kg m$^{-2}$) | 4.9(0.3)$^b$ | 3.3(0.3)$^a$ | 3.6(0.3)$^b$ | 4.4(0.6)$^b$ |
| TN (kg m$^{-2}$) | 0.45(0.03)$^b$ | 0.30(0.02)$^b$ | 0.31(0.03)$^b$ | 0.36(0.02)$^b$ |

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

| Variables                  | $R_h$  | $R_h$/TOC | $R_h$/ROC |
|----------------------------|--------|-----------|-----------|
| tP-value                   |        | tP-value  | tP-value  |
| DOC                        | -1.13  | 0.38      | -3.48     |
| TOC                        | -3.19  | 0.09      | -4.93     |
| ROC/TOC                    | -4.08  | 0.06      | -3.15     |
| MBC                        | -1.52  | 0.37      | -1.99     |
| Total PLFAs                | -1.17  | 0.45      | -0.48     |
| $G^+$ PLFAs                | 1.20   | 0.44      | 1.52      |
| $G^-$ PLFAs                | 0.50   | 0.70      | -0.26     |
| Fungal PLFAs               | 0.06   | 0.96      | -0.42     |
| Actinomycetals             | 1.78   | 0.33      | 2.26      |
| PLFAs                      |        |           |           |
| Actinomycetals/Bacterial PLFAs | 1.07 | 0.36      | 0.95      |
| Actinomycetals/Fungal PLFAs | -0.15 | 0.89      | 0.26      |
| Fungal/Bacterial PLFAs     | -0.11  | 0.92      | 0.18      |
| $G^+$/G$-$ PLFAs           | -0.75  | 0.51      | 0.10      |

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).

| Variables                  | $R_h$  | $R_h$/TOC | $R_h$/ROC |
|----------------------------|--------|-----------|-----------|
| $R_h$                      |        |           |           |
| tP-value                   |        | tP-value  | tP-value  |
| 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                    | 6.5%   | 8.7%      | 7.4%      |
| PLFA_PC1                   | 15.7%  | 13.4%     | 14.0%     |
| PLFA_PC2                   | 1.8%   | 3.3%      | 4.5%      |
| PLFA_PC3                   | 2.0%   | 3.7%      | 3.0%      |
| PLFA_PC4                   |        |           |           |
5. Cleveland, C. C., Nemergut, D. R., Schmidt, S. K. & Townsend, A. R. Increases in native broadleaved species plantation (BP, 26 years old; see details in Table 1). Three than 400 years old) and one mixed conifer and broadleaf forest (CF, about 110 years 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 Rg measurements.

Field measurements. In July 2011 when soil microorganisms were the most active, heterotrophic soil respiration rate, together with soil temperature (ST) and moisture (SM), at 5 cm depth, was recorded in the field by a Li-cor 8100 Auto Soil CO2 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 quadrate 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, in which carbon content of unfumigated soil samples was considered as an estimate for dissolved organic carbon (DOC). ROC was determined using with 32, in which carbon content of unfumigated soil samples was 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-, bacteria to 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+ to G- F:B, A:B) were also employed. We also employed variance decomposition analysis to explore the explanation capacity of vegetational attributes and soil physicochemical and microbial properties on the total variance of Rg 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 models analyses were also conducted in R software (version 2.15.2) and ANOVA in SPSS 16.0 for windows (SPSS Inc., Chicago, US).

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 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 Rc. 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, SM, 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), substrate availability and clay content. Significant level was set at P<0.05. The PCA and linear mixed effect model

7. Waldrop, M. P., Balser, T. C. & Firestone, M. K. Linking microbial community composition to function in a tropical soil. Soil Biol. Biochem. 32, 1837–1846 (2000).
8. Friedlingstein, P. et al. Climate-carbon cycle feedback analysis: Results from the C4MIP model intercomparison. J. Climate 19, 3337–3353 (2006).
9. Manzoni, S., Taylor, P., Richter, A., Porporato, A. & Ågren, G. I. Environmental and stoichiometric controls on microbial carbon-use efficiency in soils. New Phytol. 196, 79–91 (2012).
10. Manzoni, S. & Porporato, A. Soil carbon and nitrogen mineralization: theory and models across scales. Soil Biol. Biochem. 41, 1355–1379 (2009).
11. Zhou, G. et al. Old-growth forests can accumulate carbon in soils. Science 314, 1417–1417 (2006).
12. Piao, S. et al. The carbon balance of terrestrial ecosystems in China. Nature 458, 1009–1013 (2009).
13. Chen, X. M., Liu, J. X., Deng, Q., Yan, J. H. & Zhang, D. Q. Effects of elevated CO2 and nitrogen addition on soil organic carbon fractions in a subtropical forest. Plant Soil 357, 35–34 (2012).
14. Jaffrézic, F. et al. Reduction of forest soil respiration in response to nitrogen deposition. Nature Geoscience 3, 315–322 (2010).
15. Guentert, B. et al. The impact of long-term CO2 enrichment and moisture levels on soil microbial community structure and enzyme activities. Geoderma 170, 331–336 (2012).
16. Liu, L., Onderksen, P., Zhang, T. & Mo, J. M. Effects of phosphorus addition on soil microbial biomass and community composition in three forest types in tropical China. Soil Biol. Biochem. 44, 31–38 (2012).
17. Saiz, G. et al. Stand age-related effects on soil respiration in a first rotation Sitka spruce chronosequence in central Ireland. Global Change Biol. 12, 1007–1020 (2006).
18. Kord Yuste, J. et al. Microbial soil respiration and its dependency on carbon inputs, soil temperature and moisture. Global Change Biol. 13, 2018–2035 (2007).
19. Fanin, N., Hattenschwiler, S., Barantal, S., Schimann, H. & Fromin, N. Does variability in litter quality determine soil microbial respiration in an Amazonian rainforest? Soil Biol. Biochem. 43, 1014–1022 (2011).
20. Luan, J., Liu, S., Wang, J., Zhu, X. & Shi, Z. Rhizospheric and heterotrophic respiration of a warm-temperate oak chronosequence in China. Soil Biol. Biochem. 43, 503–512 (2011).
21. Fierer, N., Strickland, M. S., Liptzin, D., Bradford, M. A. & Cleveland, C. C. Global patterns in belowground communities. Ecology Letters 12, 1238–1249 (2009).
22. Degens, B. P. Decreases in microbial functional diversity do not result in corresponding changes in decomposition under different moisture conditions. Soil Biol. Biochem. 30, 1989–2000 (1998).
23. Wang, W. J., Dalal, R. C., Moody, P. W. & Smith, C. J. Relationships of soil respiration to microbial biomass, substrate availability and clay content. Soil Biol. Biochem. 35, 273–284 (2003).
24. Fierer, N., Bradford, M. A. & Jackson, R. B. Toward an ecological classification of soil bacteria. Ecology 88, 1354–1364 (2007).
25. Treseder, K. K. et al. Interacting microbial ecology into ecosystem models: challenges and priorities. Biogeochemistry 109, 7–18 (2012).
26. Wieden, W. R., Bonan, G. B. & Allison, S. D. Global soil carbon projections are improved by modelling microbial processes. Nature Clim. Change 3, 909–912 (2013).
27. Wei, H. et al. Thermal acclimation of organic matter decomposition in an artificial forest soil is related to shifts in microbial community structure. Soil Biol. Biochem. 71, 1–12 (2014).
28. Sinsabaugh, R. L., Gallo, M. E., Lauher, C., Waldrop, M. P. & Zak, D. R. Extracellular enzyme activities and soil organic matter dynamics for northern hardwood forests receiving simulated nitrogen deposition. Biogeochemistry 75, 201–215 (2005).
29. Bell, C., Stromberger, M. & Wallenstein, M. New insights into enzymes in the environment. Biogeochemistry 117, 1–4 (2014).
30. Allison, S. D. & Martiny, B. H. Resistance, resilience, and redundancy in microbial communities. Proc. Natl. Acad. Sci. USA 105, 11512–11519 (2008).
31. Puralong, W. et al. Uncoupling of microbial community structure and function in decomposing litter across beech forest ecosystems in Central Europe. Sci. Rep. 4, 7014; DOI:10.1038/srep07014 (2014).
32. Vance, E. D., Brookes, P. C. & Jenkinson, D. An extraction method for measuring soil microbial biomass. C. Soil Sci. 190, 703–707 (1987).
33. Blair, G. J., Lefroy, R. D. & Lisle, L. Soil carbon fractions on their basis of oxidation, and the development of a carbon management index for agricultural systems. Aust. J. Agr. Res. 46, 1459–1466 (1995).
34. Liu, G. S. Soil physicochemical analysis and description of soil profiles. China Normative Publishing House, Beijing, 1996 (in Chinese).
35. Bossio, D. A. & Scow, K. M. Impacts of carbon and flooding on soil microbial communities: phospholipid fatty acid profiles and substrate utilization patterns. Microbial Ecol. 35, 265–278 (1998).
36. Huang, W., Liu, J., Zhou, G., Zhang, D. & Deng, Q. Effects of precipitation on soil acid phosphatase activity linked to rapid shifts in soil microbial community composition. Biogeosciences 8, 1901–1910 (2011).
37. Zhou, C., Zhou, G., Zhang, D., Wang, Y. & Liu, S. CO2 efflux from different forest soils and impact factors in Dinghu Mountain, China. Sci. China Ser. D, 198–206 (2005).
38. Fang, H. et al. $^{13}$C abundance, water-soluble and microbial biomass carbon as potential indicators of soil organic carbon dynamics in subtropical forests at different successional stages and subject to different nitrogen loads. *Plant Soil* **320**, 243–254 (2009).

39. Fu, S., Lin, Y., Rao, X. & Liu, S. Investigation and research dataset of stand properties in Chinese forest ecosystems - Heshan National Field Research station of Forest Ecosystem (1998-2008). *China Agriculture Press, Beijing, 2011 (in Chinese).*

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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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