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Soil resources and climate jointly drive variations in microbial biomass carbon and nitrogen in China's forest ecosystems

Z. H. Zhou[1,*] **and C. K. Wang**[1,*]

[1]Center for Ecological Research, Northeast Forestry University, 26 Hexing Road, Harbin 150040, China
[*]These authors contributed equally to this work.

Correspondence to: C. K. Wang (wangck-cf@nefu.edu.cn)

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Abstract

Microbial metabolism plays a key role in regulating the biogeochemical cycle of forest ecosystems, but the mechanisms driving microbial growth are not well understood. Here, we synthesized 689 measurements on soil microbial biomass carbon (C_{mic}) and nitrogen (N_{mic}) and related parameters from 207 independent studies published during the past 15 years across China's forest ecosystems. Our objectives were to (1) examine patterns in C_{mic}, N_{mic}, and microbial quotient (i.e., C_{mic}/C_{soil} and N_{mic}/N_{soil} rates) by climate zones and management regimes for these forests; and (2) identify the factors driving the variability in the C_{mic}, N_{mic}, and microbial quotient. There was a large variability in C_{mic} (390.2 mg kg^{-1}), N_{mic} (60.1 mg kg^{-1}), $C_{mic}:N_{mic}$ ratio (8.25), C_{mic}/C_{soil} rate (1.92 %), and N_{mic}/N_{soil} rate (3.43 %) across China's forests, with coefficients of variation varying from 61.2 to 95.6 %. The natural forests had significantly greater C_{mic} and N_{mic} than the planted forests, but had less $C_{mic}:N_{mic}$ ratio and C_{mic}/C_{soil} rate. Soil resources and climate together explained 24.4–40.7 % of these variations. The $C_{mic}:N_{mic}$ ratio declined slightly with the $C_{soil}:N_{soil}$ ratio, and changed with latitude, mean annual temperature and precipitation, suggesting a plastic homeostasis of microbial carbon-nitrogen stoichiometry. The C_{mic}/C_{soil} and N_{mic}/N_{soil} rates were responsive to soil resources and climate differently, suggesting that soil microbial assimilation of carbon and nitrogen be regulated by different mechanisms. We conclude that soil resources and climate jointly drive microbial growth and metabolism, and also emphasize the necessity of appropriate procedures for data compilation and standardization in cross-study syntheses.

1 Introduction

Microbial metabolism is closely coupled with ecological processes such as decomposition, nutrient cycling, and rhizosphere symbiosis, and hence plays a key role in regulating the biogeochemical cycle of terrestrial ecosystems (Chapin III et al., 2011).

Microbial communities convert soil organic carbon (C_{soil}) and nitrogen (N_{soil}) into microbial biomass and release CO_2 to the atmosphere, mineralize soil organic matter (SOM) and nutrients, and thus control energy and material flows between trophic levels (Miltner et al., 2012; Sinsabaugh et al., 2013). Although soil microbial biomass carbon

5 (C_{mic}) and nitrogen (N_{mic}) only account for 0.9–6.5 % of C_{soil} and 1.7–8.1 % of N_{soil}, respectively (Xu et al., 2013), microbial decomposition of SOM releases about half of the total soil CO_2 efflux (Wang and Yang, 2007). Microbes also provide supplementary nutrients for the plants especially in nutrient-limited ecosystems (Singh et al., 1989) because of the dichotomous seasonality between microbial biomass and soil nutrient

10 availability (Kaiser et al., 2011). Therefore, understanding soil microbial metabolism and its feedback to climate change is critical in carbon cycling studies (Davidson and Janssens, 2006; Singh et al., 2010) especially in forest ecosystems that contain more than 70 % of the global storage of C_{soil} (Jandl et al., 2007).

Recently, Xu et al. (2013) synthesized the global microbial biomass data of terres-

15 trial ecosystems, of which only about 24 % were of forest ecosystems mainly from North America and Europe. China has diverse geographic and environmental conditions, including a latitudinal gradient from boreal to tropical climate zones, a longitudinal gradient from arid desert to humid forest areas, and an altitudinal ladder-like topography from the east to the west, which allow various forests to exist (Fang et al., 2012;

20 Yang et al., 2014). Research on the forest soil microbes in China had lagged behind many regions in the world, but has been catching up rapidly since 2000. During the past 15 years, large amounts of data on microbial biomass have been produced but not synthesized to date. Synthetic analyses of these data are likely to shed light on the mechanism regulating soil microbial metabolism.

25 Soil resources saliently influence microbial growth (He et al., 2014; Jagadamma et al., 2014; Kaiser et al., 2014), because C_{soil} and N_{soil} are the fundamental sources of energy and nutrients for microbial metabolism (Wardle, 1992; Xu et al., 2014; Spohn, 2015). Soil microbial quotient (i.e., C_{mic}/C_{soil} and N_{mic}/N_{soil} rates) is an important index of carbon assimilation of microorganisms (Xu et al., 2014), and also a sensitive indi-

cator of soil biological responses to environmental changes (Sparling, 1992). To date, however, it is not conclusive how soil resources control microbial metabolic processes. For example, Xu et al. (2014), using field data and modeling simulation, indicated that soil microbial quotient decreased exponentially with the $C_{soil} : N_{soil}$ ratio at a biome-level. On the other hand, Spohn (2015), based on laboratory incubation data, reported microbial metabolic quotient (i.e., respiration rate per unit microbial biomass) linearly increased with the litter C : N ratio but decreased with the litter nitrogen concentration. Such diverse relationships between soil resources and microbial metabolism may be associated with environmantal conditions and research scales, because the transloca-tion of soil resources involves a series of biological activities and physical diffusion that are constrained by soil temperature and moisture regimes especially in frozen or arid harsh environment or seasons (Jefferies et al., 2010; Edwards and Jefferies, 2013).

At a large scale, geographic climate is the primary driver of vegetation communities (Drenovsky et al., 2010). Vegetation controls C_{soil} inputs, alters soil habitats by modi-fying rhizospheric activities and elemental stoichiometry, and eventually influences mi-crobial composition and metabolism (Paterson et al., 2007; Bell et al., 2014). Addition-ally, forest disturbances change soil and vegetation characteristics, which in turn alter microbial biochemical processes (Holden and Treseder, 2013). Of the diverse influenc-ing factors, it is not clear which are the major drivers of the variability in soil microbial biomass (Wardle, 1998; Xu et al., 2013).

In this study, we retrieved peer-reviewed papers on microbial biomass in China's for-est ecosystems published during the past 15 years. The database included 689 mea-surements from 207 independent studies (Table S1, Supplement S1) that covered all the climate zones (frigid highland, cool temperate, warm temperate, subtropical/tropical zones) and management regimes (natural vs. planted forests; Fig. 1). The objectives of this synthesis were to (1) examine patterns in C_{mic}, N_{mic}, and microbial quotient by climate zones and management regimes for China's forest ecosystems; and (2) identify the factors driving the variability in the C_{mic}, N_{mic}, and microbial quotient. We hypothe-sized that (1) C_{mic}, N_{mic}, and microbial quotient vary with climate zones and manage-

ment regimes because of different quality and quantity of soil resources and environmental conditions involved, and (2) the variability in C_{mic} and N_{mic} are jointly driven by soil resources and climate (a proxy of soil temperature and moisture regimes).

2 Methods

2.1 Data collection

We collected the data on soil microbial biomass of China's forest ecosystems published from January 2000 to November 2014. The literature retrieval was conducted through the China National Knowledge Infrastructure (CNKI, http://www.cnki.net) and the Web of Science (http://apps.webofknowledge.com) online databases using "soil microbial" and "forest" as key words. To enhance the cross-study comparability, the original papers were further screened by the following criteria: (1) The studies must contain corresponding C_{soil} or SOM and N_{soil} data. The SOM values were converted into C_{soil} values using the Bemmelen index (0.58, Mann, 1986). (2) There were no anthropogenic disturbances or management activities in recent years (> 7 years). (3) We only included the measurements from the control or untreated plots if a manipulated experiment was employed. And (4) we only adopted the data on C_{mic} and N_{mic} determined with the chloroform fumigation-extraction method, but ignored the conversion factors due to lacking detailed description in the original literature. Eventually, 689 measurements from 207 peer-reviewed papers met the criteria above and were included in this synthesis (Table S1, Supplement S1). The dataset covered the forest regions across China, divergent in climate zones and management regimes (Fig. 1).

We also obtained corresponding data on the geographic locations (latitude, longitude), climate conditions (mean annual temperature (MAT), mean annual precipitation (MAP)), soil properties (bulk density), and vegetation characteristics (forest type, management regime). Unlike previous syntheses (e.g., Tian et al., 2010) that averaged the climate data across the whole climate zones for many years, the MAT and MAP in this

study were calculated from the original literature and weighted by the numbers of measurements. This algorithm may more realistically reflect the environmental conditions driving the microbial metabolism, because microbial communities are more directly responsive to the local habitat, rather than the large-scaled environment. All data collected in this study were numerical data from the tables, text, or extracted from the figures in the original papers with the Origin 7.0 digital plugin (Digitize) (OriginLab Ltd., China).

2.2 Data standardization and analyses

Considering the effects of climate, parent materials and vegetation, we standardized the dataset by implementing the following procedures. First, we, based on the 1 : 1 000 000 land-use map of China (Wu, 1988), categorized the dataset into five climate zones, i.e., frigid highland (FH), cool temperate (CT), warm temperate (WT), temperate desert (TD), and subtropical/tropical (ST) zones. Since forests are rarely distributed in the TD zone, we excluded it in this synthesis (Fig. 1). Second, we further divided the forests within each climate zone into natural and planted forests by management regimes. Third, the soil data were all standardized to the top 20 cm depth in order to maximize the cross-study comparison. The rationales for doing this are: (1) C_{mic} and N_{mic} are concentrated on the top soil layers (0–20 cm) (Cleveland and Liptzin, 2007); and (2) direct comparisons with the raw data are problematic, because the individual studies included in the current dataset applied different soil sampling methods (e.g., by soil profile horizons or fixed-depth layers) and sampling depths. About 75 % of the studies were implicated in the top 20 cm of the soil (Fig. 1 Ins. 2). Therefore, we conducted the following procedures for the topsoil standardization: (1) In the cases that the 0–20 cm topsoil was divided into more than one sublayers, we obtained the bulk density (BD) weighted means of C_{soil}, N_{soil}, C_{mic}, and N_{mic} across the 0–20 cm depth. The BD, if missing in the original papers, was derived from an empirical relationship between SOM and BD (i.e., BD = 0.29 + 1.2033 × exp (−0.0775 × SOM); Wu et al., 2003; Yang et al., 2007). (2) In the cases that the maximum sampling depth was less than

20 cm, we estimated the C_{soil}, N_{soil}, C_{mic}, and N_{mic} across the 0–20 cm depth with the empirical equations (C_{soil}: $y = 1 - 0.878^x$, $R^2 = 0.95$, $P < 0.001$; N_{soil}: $y = 1 - 0.893^x$, $R^2 = 0.95$, $P < 0.001$; C_{mic}: $y = 1 - 0.889^x$, $R^2 = 0.97$, $P < 0.001$; N_{mic}: $y = 1 - 0.869^x$, $R^2 = 0.97$, $P < 0.001$, where x is the soil depth (cm), and y is the cumulative fraction of the dependent variable. See details in Fig. S1). (3) In the cases that the seasonal dynamics in microbial biomass were reported, we calculated the arithmetic means of the data.

An ANOVA procedure was performed to test the differences in all variables among climate zones and between management regimes. A multiple regression procedure was employed to examine the effects of soil resources and climate on C_{mic}, N_{mic}, C_{mic} : N_{mic} ratio, and microbial quotient. A full model (including the independent variables of both soil resources and climate and possible interactions) and a reduced model (only including the independent variables of soil resources and possible interactions) for each dependent variable were developed to examine partial contributions of soil resources or climate to the variability. A backward elimination procedure was conducted to remove insignificant terms ($\alpha = 0.05$) in the models. The variables, if needed, were transformed with a 10-based logarithm to meet the assumptions of normality and homoscedasticity for the regressions.

To examine the effect of soil quality on C_{mic}, we subjectively divided the original dataset into two groups by the median of the C_{soil} : N_{soil} ratio, and defined as high-quality group (C_{soil} : N_{soil} ratio ≤ the median, $n = 251$) and low-quality group (C_{soil} : N_{soil} ratio > the median, $n = 250$). Then we applied the standardized major axis (SMA) procedure to compare the C_{mic}–C_{soil} or C_{mic}–N_{soil} relationship between the two groups. The SMA procedure was also used to compare the C_{mic} : N_{mic}–C_{soil} : N_{soil} relationship between this study and the one derived from the global dataset (Cleveland and Liptzin, 2007). All statistical analyses were performed with SPSS 19.0 for Windows, and the map (Fig. 1) was generated with ArcGIS 10.

3   Results

3.1   Concentrations of soil microbial biomass carbon and nitrogen

The C_{mic} in the topsoil (0–20 cm) varied by 142 folds (mean ± SD: $390.2 \pm 312.9\,g\,kg^{-1}$) with a coefficient of variation (CV) of 80.2 % across China's forest ecosystems; and the N_{mic} varied by 289 folds ($60.1 \pm 57.4\,g\,kg^{-1}$) with a CV of 95.6 %. The C_{soil} varied by 72 folds ($26.2 \pm 21.9\,g\,kg^{-1}$) with a CV of 83.8 %; the N_{soil} varied by 62 folds ($2.06 \pm 1.65\,g\,kg^{-1}$) with a CV of 80.1 %.

C_{mic} and N_{mic} differed significantly between management regimes and among climate zones (Fig. 2). In the natural forests, the C_{mic} and N_{mic} displayed similar patterns across the climate zones: ST > FH > CT > WT (Fig. 2e and g). The ST zone had the greatest C_{mic} and N_{mic} with the greatest MAT and MAP (Fig. 1 Ins. 1) in spite of the least C_{soil} and N_{soil} among the climate zones (Fig. 2a and b). The C_{soil} significantly ($P < 0.05$) decreased from cold humid FH zone to warm humid ST zone, the former was one fold greater than the latter (Fig. 2a). This pattern was largely opposite to that of MAT (Fig. 1 Ins. 1). There was no significant difference in N_{soil} ($P = 0.673$) among the climate zones ($2.83 \pm 1.85\,g\,kg^{-1}$; Fig. 2b).

The planted forests had significantly lower concentrations of C_{soil}, N_{soil}, C_{mic}, and N_{mic} than the natural forests ($P < 0.05$); the latter had 2.2, 2.0, 1.8, and 2.1 times as much as the former, respectively (Fig. 2 Ins.). Unlike the natural forests, the planted forests exhibited relatively consistent patterns of C_{soil}, N_{soil}, C_{mic}, and N_{mic} across the climate zones: FH > CT > WT or ST (Fig. 2b, d, f, and h).

C_{soil}, N_{soil}, and their interactions explained 36.6 % of the variability in C_{mic}, and 28.7 % in N_{mic}; MAT and MAP explained additional 2.6 and 12.0 %, respectively (Table 1). Both C_{mic} and N_{mic} were increasing in a power function with C_{soil} or N_{soil} (Fig. 3). Further SMA analysis showed that the high-quality (i.e., low $C_{soil} : N_{soil}$ ratio) and low-quality (i.e., high $C_{soil} : N_{soil}$ ratio) soil groups had a common slope ($P > 0.05$) of the $\log(C_{soil})$–$\log(C_{mic})$ or $\log(N_{soil})$–$\log(C_{mic})$ relationship (Fig. 4). However, the

high-quality group had a significantly greater intercept ($P < 0.001$) than the low-quality group for the $\log(C_{soil})$–$\log(C_{mic})$ relationship (Fig. 4a), while the former had a significantly less intercept ($P < 0.001$) than the latter for the $\log(N_{soil})$–$\log(C_{mic})$ relationship (Fig. 4b).

3.2 Stoichiometry of soil microbial biomass carbon and nitrogen

The $C_{soil} : N_{soil}$ and $C_{mic} : N_{mic}$ ratios varied by 15 folds (13.7 ± 6.63, CV = 48.4 %) and 41 folds (8.25 ± 6.20, CV = 75.1 %) across the country, respectively. Management regime and climate zone significantly affected the $C_{mic} : N_{mic}$ ratio (Fig. 5). The $C_{mic} : N_{mic}$ ratio in the natural forests was significantly less ($P < 0.05$) than that in the planted forests (Fig. 5d Ins.), while the $C_{soil} : N_{soil}$ ratio in the former was significantly greater ($P < 0.05$) than that in the latter (Fig. 5b Ins.). The $C_{mic} : N_{mic}$ ratio showed a similar pattern across the climate zones for both natural and planted forests, with the greatest ratio occurring in the CT zone and the least ratio in the FH zone (Fig. 5c and d).

Pooling the data across the climate zones and management regimes, we found a significant power relationship, rather than a linear, between C_{soil} and N_{soil} or between C_{mic} and N_{mic} ($P < 0.001$; Fig. S2). The C_{soil} and N_{soil} together explained 10.8 % of the variability in the $C_{mic} : N_{mic}$ ratio, and climate explained another 13.6 % (Table 1). There was a weak negative correlation between $C_{mic} : N_{mic}$ ratio and $C_{soil} : N_{soil}$ ratio ($n = 335$, $P = 0.002$, $R^2 = 0.04$; Fig. 6a), which was consistent with the relationship derived from the global dataset (Cleveland and Liptzin, 2007). The slope of the relationship was -0.13 [-0.21, -0.05] (mean [95 % confidence interval]) from this study and -0.12 [-0.23, -0.01] from the global dataset, while the intercept was 9.73 [8.45, 11.06] and 9.34 [7.86, 10.82], respectively. The $C_{mic} : N_{mic}$ ratio increased with latitude (Fig. 6b), decreased with MAT (Fig. 6c), and was correlated with MAP in a quadratic polynomial function (Fig. 6d).

3.3 Soil microbial quotient

The C_{mic}/C_{soil} rate varied by 91 folds (1.92 ± 1.17 %, CV = 61.2 %), while the N_{mic}/N_{soil} rate varied by 480 folds (3.43 ± 2.49 %, CV = 72.5 %). They differed significantly between management regimes and among climate zones (Fig. 5). The C_{mic}/C_{soil} rate in the natural forests was significantly ($P < 0.05$) less than that in the planted forests (Fig. 5f Ins.), while the N_{mic}/N_{soil} rate did not differ ($P > 0.05$; Fig. 5h Ins.). The C_{mic}/C_{soil} and N_{mic}/N_{soil} rates showed different patterns across the climate zones between the natural and planted forests (Fig. 5e–h). In the natural forests, the FH zone had the least C_{mic}/C_{soil} rate but the greatest N_{mic}/N_{soil} rate among the climate zones; the ST zone had greater C_{mic}/C_{soil} and N_{mic}/N_{soil} rates (Fig. 5e and g). In the planted forests, the C_{mic}/C_{soil} and N_{mic}/N_{soil} rates showed similar patterns across the climate zones: WT > ST > FH > CT (Fig. 5f and h).

C_{soil}, N_{soil}, and their combinations explained 36.7 % of the variability in the C_{mic}/C_{soil} rate, and 17.3 % in the N_{mic}/N_{soil} rate; MAT, MAP, and their interactions explained another 2.4 and 13.3 %, respectively (Table 1). The C_{mic}/C_{soil} rate decreased in a power function with the $C_{soil} : N_{soil}$ ratio (Fig. 7a), but the N_{mic}/N_{soil} rate increased linearly with the $C_{soil} : N_{soil}$ ratio (Fig. 7b). Both C_{mic}/C_{soil} and N_{mic}/N_{soil} rates increased with MAT (Fig. 7c and d). There was a quadratic polynomial function between the C_{mic}/C_{soil} rate and MAP (Fig. 7e), but there was no significant relationship ($P > 0.05$) between the N_{mic}/N_{soil} rate and MAP (Fig. 7f).

4 Discussion

4.1 Variability in forest soil microbial biomass carbon and nitrogen

The C_{mic} and N_{mic} in China's forest ecosystems varied substantially with climate zones and management regimes (CV up to 80–96 %), but the variability is less than previous large-scale synthesis (e.g., Xu et al., 2013), partly because of the difference in data se-

lection and standardization procedures (see Methods). In this study, for example, the data with maximum sampling depth less than 15 and 20 cm accounted for 30 and 75 % of the whole dataset, respectively (Fig. 1 Ins. 2). If we had applied the same procedure as Cleveland and Liptzin (2007) or Xu et al. (2013) without the soil-depth standard-ization (see Methods), then we would overestimate the $C_{soil} : N_{soil}$ ratio by 2.8 % and underestimate the $C_{mic} : N_{mic}$ ratio by 5.2 %. These pieces of evidence underpin the necessity of appropriate procedures for data compilation and standardization in such cross-study syntheses that should take soil depth, forest characteristics, and distur-bance regimes into account.

Forest disturbances contain various regimes and histories, and thus increase the complexity of the microbial biomass pattern associated with climate (Holden and Treseder, 2013). In this synthesis, the natural forests in the subtropical/tropical zones with the greatest MAT and MAP (Fig. 1 Ins. 1) had the greatest C_{mic} and N_{mic} among the climate zones (Fig. 2), while the planted counterparts had the least C_{mic} and N_{mic} (Fig. 2f and h). Similarly, the planted forests in both warm and cool temperate zones had lower C_{mic} and N_{mic} than those in the frigid highland zone. The reason for these different patterns between the natural and planted forests is probably associated with more afforestation and younger plantations in regions other than the frigid highland zone in China (Fang et al., 2012; Yang et al., 2014).

In this study, soil resources and climate together explained about 40 % of the vari-ability in microbial biomass, to which C_{soil} and N_{soil} contributed 71–93 % (Table 1). All power functions of microbial biomass against soil resources had exponents of less than one (Fig. 3), indicating that microbes grow rapidly with soil resource availability increas-ing when the C_{soil} or N_{soil} is low, but the acceleration decreases as the C_{soil} or N_{soil} in-creases. This implies a shift in constraints of microbial growth from resource availability to other abiotic and/or biotic factors, such as soil moisture, temperature, pH, etc. Fur-thermore, the high-quality (i.e., low $C_{soil} : N_{soil}$ ratio) soils had a greater intercept of the log(C_{soil})–log(C_{mic}) relationship (Fig. 4a) but a less intercept of the log(N_{soil})–log(C_{mic}) relationship (Fig. 4b) than the low-quality soils. This result indicates that the microbes

grow faster in the soils with a lower $C_{soil} : N_{soil}$ ratio at a specific C_{soil} level or in the carbon-richer soils at a specific N_{soil} level. These findings illustrate that effects of soil resources on C_{mic} and N_{mic} change with the availability and stoichiometry of C_{soil} and N_{soil}.

4.2 Stoichiometry of forest soil microbial biomass carbon and nitrogen

The $C_{mic} : N_{mic}$ ratio in the topsoil for the natural forests in this study (7.3) is slightly greater than the global mean (6.9; Cleveland and Liptzin, 2007; Xu et al., 2013). It varied substantially less than C_{mic} (41 folds vs. 142 folds) or N_{mic} (289 folds) (Fig. 5). The relatively little variability in the $C_{mic} : N_{mic}$ ratio, together with its slight decline with the $C_{soil} : N_{soil}$ ratio (Fig. 6a), illustrates that soil microbes alleviate soil resource stoichiometry (Kaiser et al., 2014), rather than "you are what you eat" (Sterner and Elser, 2002).

Nevertheless, the $C_{mic} : N_{mic}$ ratio decreased by 13 % as the $C_{soil} : N_{soil}$ ratio increased (Fig. 6a), consistent with other terrestrial ecosystems studies (e.g., Cleveland and Liptzin, 2007; Fanin et al., 2013). And it also changed with latitude (Fig. 6b) and climate (Fig. 6c and d). These results indicate that the microbial carbon-nitrogen stoichiometry is plastic homeostatic and regulated by soil resources and environmental conditions (Fig. 6; Sterner and Elser, 2002; Li et al., 2012). It also raises caution regarding taking the $C_{soil} : N_{soil}$ ratio as a proxy of resource quality in exploring the effect of soil resource availability on microbial assimilation of carbon.

Our data also showed that the $C_{mic} : N_{mic}$ ratio was predictable to some degree (Table 1). The multiple regression model that included soil resources and climate did explain 24.4 % of the variability in the $C_{mic} : N_{mic}$ ratio. This might be useful for modeling the biogeochemical cycle of forest ecosystems, but no conclusive notion has been reached on the underlying mechanisms of such environmental plasticity of microbial stoichiometry. We speculate that the greater $C_{mic} : N_{mic}$ ratio in cold temperate zone (Figs. 1 Ins., 5c and d), perhaps similar to that in the plant leaves (He et al., 2006; Asner et al., 2014), might reflect an increased carbon investment on structural material (e.g.,

cell wall) as a defensive strategy in harsh environments. Additionally, environmental changes may shift microbial community composition, and thus change the $C_{mic} : N_{mic}$ ratio (Drenovsky et al., 2010; Tischer et al., 2014) because fungi have higher C : N ratio than bacteria (Keiblinger et al., 2010). Clearly, disclosing the underlying mechanisms of microbial metabolism is challenging but critically needed.

4.3 Forest soil microbial quotient

Soil microbial quotient is largely determined by microbial assimilation and respiration that are mainly affected by soil substrates and environment (Manzoni et al., 2012). In this study, we found that C_{mic}/C_{soil} and N_{mic}/N_{soil} rates responded to soil resources differently or even oppositely. First, soil resources explained 36.7 % of the variability in the C_{mic}/C_{soil} but only 17.3 % in the N_{mic}/N_{soil} (Table 1), indicating that the C_{mic}/C_{soil} rate was more controlled by soil resources. Second, the C_{mic}/C_{soil} and N_{mic}/N_{soil} rates responded oppositely to the $C_{soil} : N_{soil}$ ratio, i.e., decreasing in a power function (Fig. 7a) vs. increasing linearly (Fig. 7b). Third, much stronger interactions between MAT and MAP exerted on the N_{mic}/N_{soil} rate than the C_{mic}/C_{soil} rate (Table 1), because weak or no correlations between the N_{mic}/N_{soil} rate and MAT (Fig. 7d) or MAP (Fig. 7f) despite that climate factors explained 4.5 times more variability in the N_{mic}/N_{soil} rate than in the C_{mic}/C_{soil} rate (13.3 % vs. 2.4 %; Table 1). These results, together with Fig. 4 (See the discussion above), suggests that soil microbial assimilation of carbon and nitrogen are responsive to soil resources and climate differently, and might be regulated by different mechanisms.

Vegetation and disturbances modify soil resources, interact with climate, and eventually affect microbial growth and metabolism (Figs. 5 and 7). The rapid decrease in C_{mic}/C_{soil} rate with $C_{soil} : N_{soil}$ increasing (Fig. 7a) suggests that soil microbes produce less biomass and respire more carbon in N-limited soils (Xu et al., 2014). The underlying mechanisms, however, are not clear. Spohn (2015) summarized three potential explanations, i.e., microbial nitrogen mining, overflow respiration, and enzyme inhibition at high nitrogen concentrations. Additionally, microbial communities, in responses

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5   Conclusions

By synthesizing 689 measurements from 207 independent studies across China's forest ecosystems, we find large variations in soil microbial biomass carbon and nitrogen and microbial quotient that are subjected to changes in soil resources and climate.
10   Soil microbial assimilation of carbon and nitrogen are responsive to soil resources and climate differently, and might be regulated by different mechanisms. Identifying these interacting factors improves our understanding of the underlying mechanisms of microbial metabolism, and is useful for modeling the biogeochemical cycle of forest ecosystems.

15   **The Supplement related to this article is available online at doi:10.5194/bgd-12-11191-2015-supplement.**

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Table 1. Multiple regression models of microbial biomass carbon (C_{mic}), microbial biomass nitrogen (N_{mic}), $C_{mic} : N_{mic}$ ratio, and microbial quotients (i.e., C_{mic}/C_{soil} and N_{mic}/N_{soil} rates) against soil resources and climate. C_{soil} and N_{soil} stand for soil organic carbon and soil total nitrogen, respectively. Y, X_1, X_2, X_3, X_4, and X_5 in the models stand for the dependent variable, C_{soil}, N_{soil}, mean annual temperature, mean annual precipitation, and $C_{soil} : N_{soil}$ ratio, respectively. Y, X_1 and X_2 are 10-based log transformed. N, R^2, and P stand for sample size, determination coefficient, and probability, respectively. All the terms in the regression models are significant at $\alpha = 0.05$.

Dependent variable	Reduced model				Full model			
	Independent variables of soil resources	N	R^2	P	Independent variables of soil resources and climate	N	R^2	P
C_{mic}	$Y = 1.19 + 2.02X_1 - 0.850X_1^2 - 1.31X_2 - 1.08X_2^2 + 1.67X_1 \times X_2$	501	0.366	< 0.001	$Y = 2.27 + 0.206X_1 - 0.706X_2^2 + 0.493X_1 \times X_2 + 1.75 \times 10^{-2}X_3 - 5.40 \times 10^{-4}X_4 + 1.67 \times 10^{-7}X_4^2$	501	0.392	< 0.001
N_{mic}	$Y = 1.51 - 1.14X_2^2 + 0.752X_1 \times X_2$	338	0.287	< 0.001	$Y = 0.643 + 0.421X_1 - 0.626X_2 - 1.19X_2^2 + 0.984X_1 \times X_2 + 6.72 \times 10^{-2}X_3 + 1.29 \times 10^{-7}X_4^2 - 3.89 \times 10^{-5}X_3 \times X_4$	338	0.407	< 0.001
$C_{mic} : N_{mic}$	$Y = 0.956 + 0.578X_2 + 0.528X_2^2 - 0.640X_1 \times X_2 - 7.53 \times 10^{-3}X_5$	335	0.108	< 0.001	$Y = 1.24 + 0.759X_2 + 0.659X_2^2 - 0.843X_1 \times X_2 - 4.72 \times 10^{-2}X_3 + 1.06 \times 10^{-3}X_3^2 + 1.01 \times 10^{-5}X_3 \times X_4 - 1.25 \times 10^{-2}X_5$	335	0.244	< 0.001
C_{mic}/C_{soil}	$Y = 4.13 - 0.982X_1^2 - 1.22X_2 - 1.99X_2^2 + 2.39X_1 \times X_2$	501	0.367	< 0.001	$Y = 4.12 - 0.858X_1^2 - 1.38X_2 - 2.01X_2^2 + 2.38X_1 \times X_2 - 5.06 \times 10^{-4}X_4 + 2.46 \times 10^{-5}X_3 \times X_4$	501	0.391	< 0.001
N_{mic}/N_{soil}	$Y = -3.68 + 14.3X_1 - 9.17X_1^2 - 15.2X_2 - 10.3X_2^2 + 18.8X_1 \times X_2 + 0.205X_5$	338	0.173	< 0.001	$Y = -4.02 + 13.1X_1 - 8.73X_1^2 - 15.3X_2 - 10.9X_2^2 + 19.2X_1 \times X_2 + 0.141X_3 - 2.55 \times 10^{-3}X_3^2 - 2.80 \times 10^{-5}X_3 \times X_4 + 0.223X_5$	338	0.306	< 0.001
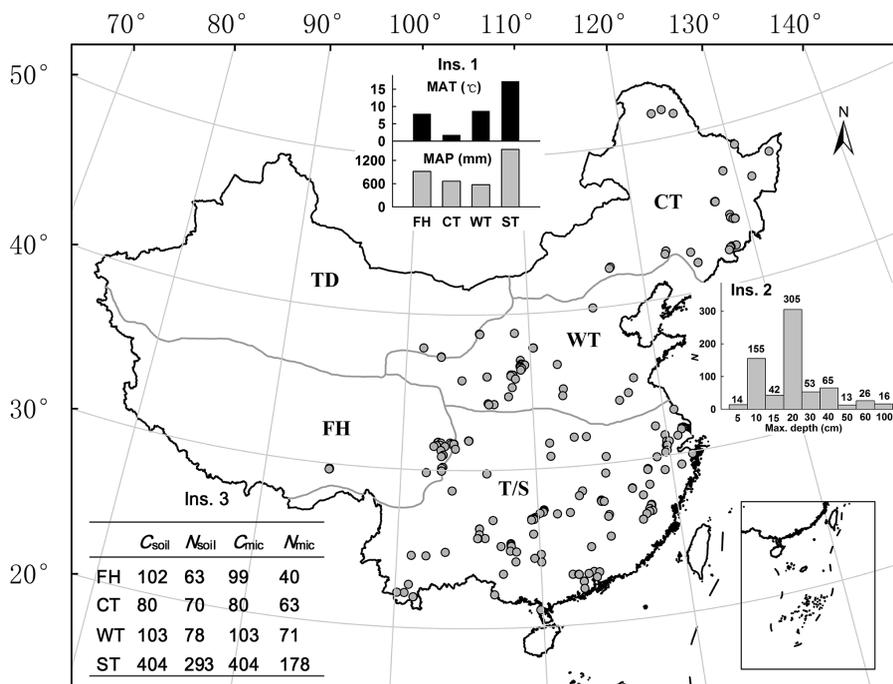
Figure 1. A map of China showing the distribution of sampling sites and data summary for this synthesis. The climate zones are categorized followed Wu (1988) into frigid highland (FH), cool temperate (CT), warm temperate (WT), subtropical/tropical (ST), and temperate desert (TD) zones. The TD is excluded in the synthesis because forests are rarely distributed in the zone. **Ins. 1:** Mean annual temperature (MAT) and mean annual precipitation (MAP) by climate zones. **Ins. 2:** Number of studies (N) of the maximum depth of soil sampling. **Ins. 3:** The number of measurements of soil organic carbon (C_{soil}), soil total nitrogen (N_{soil}), microbial biomass carbon (C_{mic}), and microbial biomass nitrogen (N_{mic}) by climate zones.
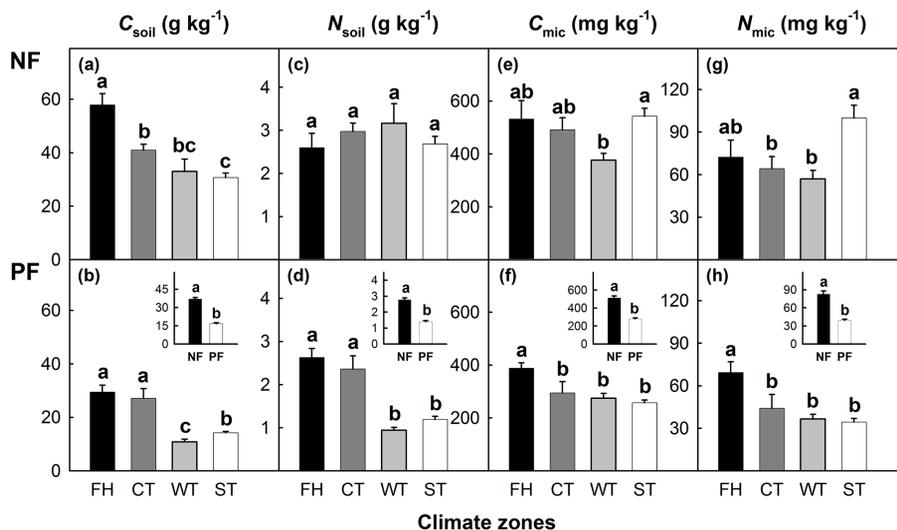
Figure 2. Comparison of C_{soil} (**a** and **b**), N_{soil} (**c** and **d**), C_{mic} (**e** and **f**), and N_{mic} (**g** and **h**) among climate zones and between management regimes. Inserted figures are the overall comparisons between the natural (NF) and planted forests (PF). C_{soil}, N_{soil}, C_{mic}, and N_{mic} stand for soil organic carbon, soil total nitrogen, microbial biomass carbon, and microbial biomass nitrogen, respectively. FH, CT, WT, and ST stand for frigid highland zone, cool temperate zone, warm temperate zone, and subtropical/tropical zone, respectively. Different lowercase letters denote significant differences among the climate zones or between the management regimes (mean ± SE, $\alpha = 0.05$).

Figure 3. Relationships between soil resources and microbial biomass. C_{soil}, N_{soil}, C_{mic}, and N_{mic} stand for soil organic carbon, soil total nitrogen, microbial biomass carbon, and microbial biomass nitrogen, respectively. The regression models are given.

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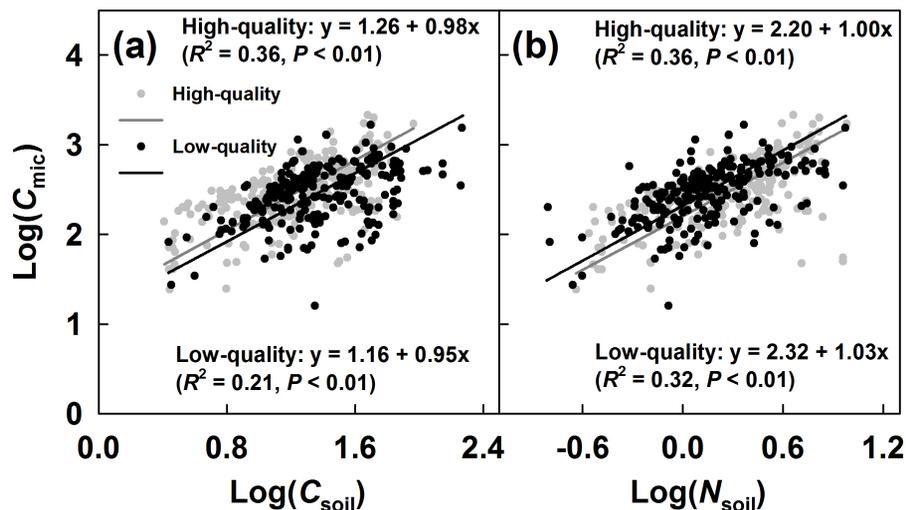
Figure 4. Relationships between microbial biomass carbon (C_{mic}) and soil organic carbon (C_{soil}, **a**), and soil total nitrogen (N_{soil}, **b**) by two soil quality groups: High-quality group ($C_{soil} : N_{soil}$ ratio $\leq$ the median of the whole dataset, $n = 251$) vs. Low-quality group ($C_{soil} : N_{soil}$ ratio > the median, $n = 250$) (See details in the Methods). Log stands for 10-based logarithm. The standardized major axis (SMA) models are given for each group.
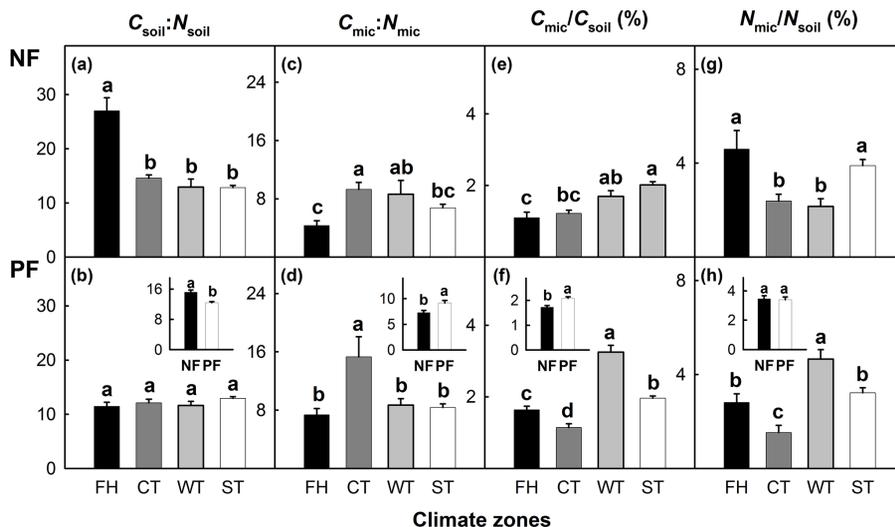
Figure 5. Comparison of $C_{soil} : N_{soil}$ ratio (**a** and **b**), $C_{mic} : N_{mic}$ ratio (**c** and **d**), C_{mic}/C_{soil} rate (**e** and **f**), and N_{mic}/N_{soil} rate (**g** and **h**) among climate zones and between management regimes. Inserted figures are overall comparisons between the natural (NF) and planted forests (PF). C_{soil}, N_{soil}, C_{mic}, and N_{mic} stand for soil organic carbon, soil total nitrogen, microbial biomass carbon, and microbial biomass nitrogen, respectively. FH, CT, WT, and ST stand for frigid highland zone, cool temperate zone, warm temperate zone, and subtropical/tropical zone, respectively. Different lowercase letters denote significant differences among climate zones or between management regimes (mean ± SE, $\alpha = 0.05$).

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Figure 6. Relationships between $C_{mic} : N_{mic}$ and $C_{soil} : N_{soil}$ ratios (China: from this study vs. Globe: from Cleveland and Liptzin, 2007) (**a**), latitude (**b**), MAT (**c**), and MAP (**d**), respectively. C_{soil}, N_{soil}, C_{mic}, N_{mic}, MAT, and MAP stand for soil organic carbon, soil total nitrogen, microbial biomass carbon, microbial biomass nitrogen, mean annual temperature, and mean annual precipitation, respectively. The regression models are given.
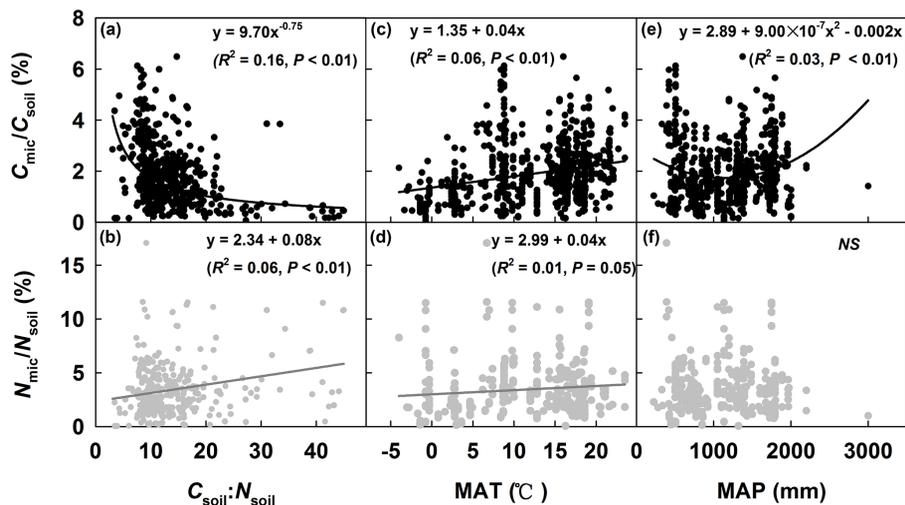
Figure 7. Relationships between C_{mic}/C_{soil} or N_{mic}/N_{soil} rate and $C_{soil} : N_{soil}$ ratio (**a** and **b**), MAT (**c** and **d**), and MAP (**e** and **f**), respectively. C_{soil}, N_{soil}, C_{mic}, N_{mic}, MAT, and MAP stand for soil organic carbon, soil total nitrogen, microbial biomass carbon, microbial biomass nitrogen, mean annual temperature, and mean annual precipitation, respectively. The regression models are given. *NS* stands for non-significant.