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# Global patterns of soil microbial nitrogen and phosphorus stoichiometry in forest ecosystems

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## ABSTRACT

**Aim** To investigate broad-scale patterns of soil microbial nitrogen (N) and phosphorus (P) stoichiometry and their environmental drivers.

**Location** Global forests.

**Methods** By synthesizing 652 observations of soil microbial biomass N and P derived from the published literature, we investigated global patterns of soil microbial N, P and N:P ratios and their relationships with climate, soil and vegetation types.

**Results** Microbial N and P concentrations varied widely among forest types, with relatively low N and P concentrations but high N:P ratios in tropical forests. The N and P concentrations increased and the N:P ratio decreased with increasing latitude (or decreasing temperature). The N:P ratio showed a similar pattern along the precipitation gradient to that along the temperature gradient, whereas microbial N and P displayed weak trends along the precipitation gradient. Edaphic variables also regulated the patterns of microbial N and P stoichiometry: microbial N and P concentrations increased with soil N and P concentrations as well as with soil pH. Mixed-effects models revealed that edaphic factors explained the largest part of the variation in microbial N, P and the N:P ratio, suggesting their dominant role.

**Main conclusions** Our findings highlight that there are broad-scale patterns in microbial N, P and the N:P ratio along the gradients of latitude, temperature and precipitation, which are similar to those reported in plants and soils. The consistency of these patterns in plant–soil–microbe ecosystems supports the hypothesis that P is more often the major limiting element at low latitudes than at high latitudes.

## Keywords

**Climate, forests, microbial biomass, nitrogen and phosphorus stoichiometry, soil, soil pH, vegetation type.**

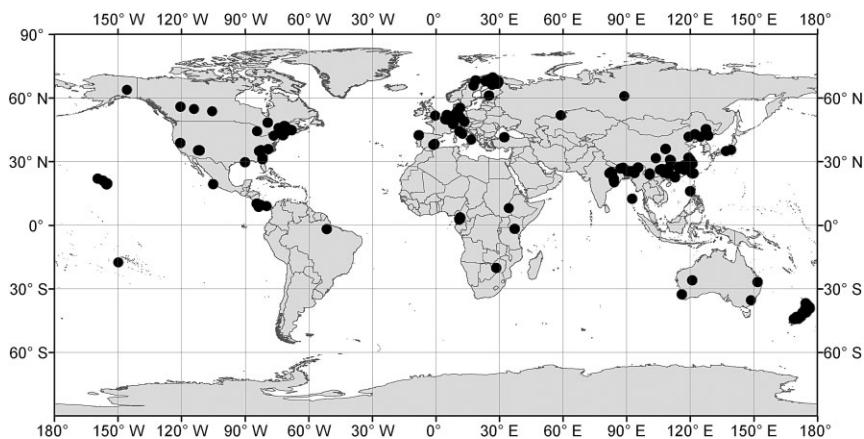
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## INTRODUCTION

Nitrogen (N) and phosphorus (P) are the two most important growth-limiting elements in terrestrial ecosystems (Chapin, 1980; Reich & Oleksyn, 2004). The stoichiometric ratio of N to P has been widely used as an indicator of nutrient limitation of terrestrial net primary production (Koerselman & Meuleman, 1996; Güsewell, 2004; Reich & Oleksyn, 2004). It has been suggested that vegetation growth is limited by N if the plant N:P ratio is less than 14, constrained by P if the ratio is greater than 16, and co-limited by N and P if the ratio is between 14 and 16 (Koerselman & Meuleman, 1996). Plant N:P stoichiometry has

been shown to be associated with many biotic and abiotic factors, including biomes (Yuan *et al.*, 2011), species composition (Han *et al.*, 2005, 2011), tissue types (Sturner & Elser, 2002), and environments (Reich & Oleksyn, 2004; Yuan & Chen, 2009; Han *et al.*, 2011; Chen *et al.*, 2013). The evaluation of N and P stoichiometry across a broad geographical scale could therefore enhance our understanding of nutrient cycling and nutrient limitation in terrestrial ecosystems (Cleveland & Liptzin, 2007; Elser *et al.*, 2010; Chen *et al.*, 2013).

During the past decade, many studies have focused on geographical variations in plant N and P stoichiometry and have consistently revealed that N and P concentrations increase, but



**Figure 1** Distribution of forest sites used in this synthesis. A total of 164 sites are obtained from 117 publications across the world.

the N:P ratios decreases, with increasing latitude (or decreasing temperature/precipitation) in green leaves (e.g. McGroddy *et al.*, 2004; Reich & Oleksyn, 2004; Han *et al.*, 2005, 2011; Elser *et al.*, 2010; Chen *et al.*, 2013), senesced-leaf litters (e.g. McGroddy *et al.*, 2004; Yuan & Chen, 2009; Tang *et al.*, 2013) and fine roots (e.g. Yuan *et al.*, 2011). Given that the stoichiometries of N and P are strongly coupled within plant–soil–microbe systems (McGroddy *et al.*, 2004), similar geographical and/or climatic patterns of N and P stoichiometry might also exist in microbial systems. Our understanding of N and P stoichiometry in microbial systems, especially at the global scale, is, however, limited.

Two data syntheses have been conducted to examine large-scale patterns of microbial C:N:P stoichiometry. First, Cleveland & Liptzin (2007) provided the first synthesis of the C:N:P stoichiometry of soil microbial biomass, and reported that microbial N:P ratios had no significant relationships with environmental variables (either latitude or soil N:P ratios). Second, Xu *et al.* (2013) suggested that microbial N and P concentrations and N:P ratios were significantly correlated with latitude. These two pioneering studies provided a basic understanding of large-scale patterns of N and P stoichiometry in microbial systems, but several points remain to be addressed. First, previous studies did not thoroughly evaluate the variations in microbial N and P stoichiometry along environmental gradients (e.g. temperature, precipitation and soil pH). Second, little is known about the integrated effects of environmental variables and vegetation types on microbial N and P stoichiometry. Third, it is still unclear whether the stoichiometric patterns of N and P that exist in microbial systems are similar to those observed in plant and soil systems.

In this study, we developed a global database from 117 published reports, including 652 observations of microbial biomass N and P and associated environmental factors (e.g. climate, soil and vegetation types) across 164 sites. Based on this global dataset, we investigated large-scale patterns of microbial N, P and N:P ratio in forest ecosystems. Specifically, we addressed the following two questions: (1) How do microbial N, P, and N:P ratio vary among vegetation groups and along geographical gradients? (2) Are the variations in microbial N, P and N:P ratio related to environmental variables (climate, soil and vegetation

types)? By addressing these questions, we aim to explore global patterns of microbial N and P stoichiometry along geographical, climatic and edaphic gradients.

## MATERIALS AND METHODS

### Literature synthesis

We collected data from 117 published reports on soil microbial biomass N and P in forest ecosystems, with 652 observations from 164 sites worldwide (Fig. 1). The data included by Cleveland & Liptzin (2007) and Xu *et al.* (2013) were also included in our synthesis. For each site, we collected information on its geographical location (latitude and longitude), forest type (boreal, temperate or tropical forest), soil N, soil P, soil pH and climatic variables (mean annual temperature, MAT; mean annual precipitation, MAP) (see Table S1 in Supporting Information). The sites spanned latitudes from 43.2° S to 63.9° N, and longitudes from 159.2° W to 176.2° E, with MAT varying from −3.8 °C to 30.1 °C and MAP from 238 mm to 5100 mm. We classified these sites into three biomes: boreal, temperate and tropical forests. The boreal forests included all forests situated between 46° N and 66° N; tropical forests included those situated between 23.5° S and 23.5° N; temperate forests included all those between the tropical and boreal latitudes (Yuan *et al.*, 2011). MAT and MAP data were estimated from a global climate dataset with a resolution of 0.0083° × 0.0083° (c. 1 km × 1 km; Hijmans *et al.*, 2005; available at: <http://www.worldclim.org/>), for those sites where MAT/MAP data had not been recorded.

To avoid bias in selecting publications, we adopted the following three criteria. First, microbial biomass must have been estimated using the chloroform fumigation–extraction (CFE) technique (Vance *et al.*, 1987), because this method is the most commonly used and provides an index of total microbial biomass in soil (including both bacteria and fungi) (Fierer *et al.*, 2009). Second, only data from the ‘control’ plots were used from papers that reported the results of manipulation experiments. Third, microbial data must have been obtained from surface soil horizons (depths of 0 to 30 cm).

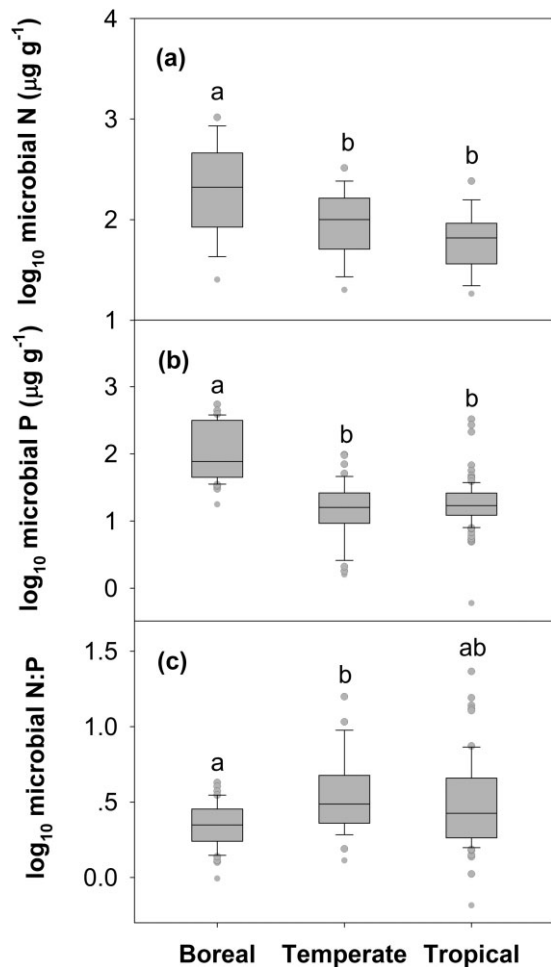


Figure 2 Box-and-whisker plots showing differences in microbial biomass N and P concentrations and N:P ratios in boreal, temperate and tropical forests worldwide. Statistical differences are denoted by different letters (*t*-test in mixed-effects model,  $P < 0.05$ ).

### Data analyses

N, P and N:P ratio were  $\log_{10}$ -transformed before analysis, because of their log-normal distributions in both microbial biomass and mineral soils (Kolmogorov–Smirnov test,  $P > 0.05$ ). Mixed-effects models were fitted in order to compare the microbial biomass N, P and N:P ratio among various vegetation types (i.e. boreal, temperate and tropical forests), treating the vegetation type as a fixed factor and the site as a random factor (see Table S2). Regressions were performed using maximum-likelihood estimation of microbial biomass N, P and N:P ratio against latitude and other environmental variables (MAT, MAP, soil N and P concentrations, and soil pH) in order to examine the individual effects of these factors.

Mixed-effects models were then applied to quantify the combined effects of climate, soil and vegetation type on soil microbial N, P and N:P ratio. Climate, soil type and vegetation type were treated as fixed factors, and site was treated as a random factor to account for the non-independence of microbial

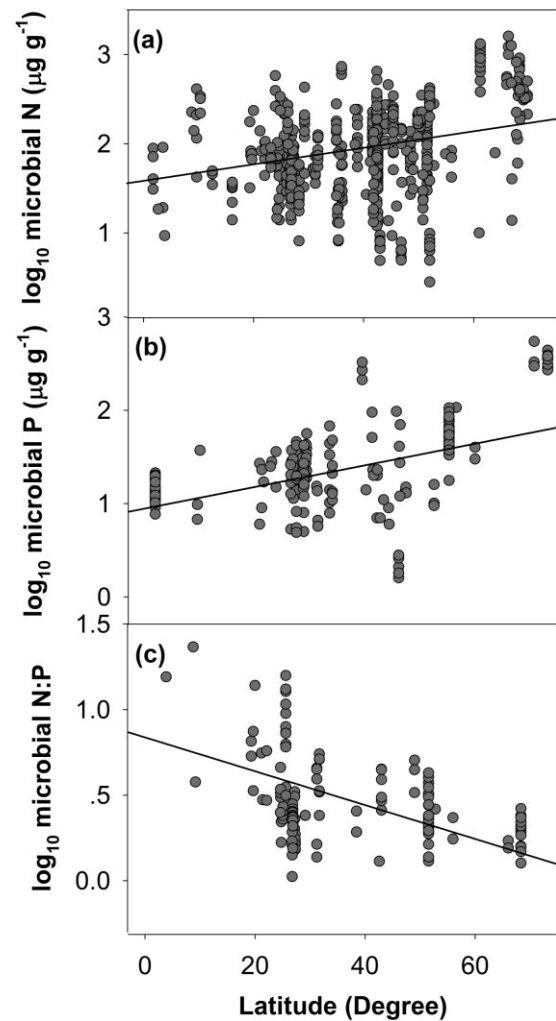


Figure 3 Latitudinal patterns of microbial biomass N and P concentrations and N:P ratios in forest ecosystems around the world.

biomass N and P within site. Given that some climatic (MAT and MAP) and edaphic (soil N and P concentrations and soil pH) variables are intercorrelated (Table S3), subsets of the climatic and edaphic variables were included in each model to avoid multiple collinearity (Table S4). The environmental variables that had significant effects on microbial N, P and the N:P ratio, and the interaction terms between vegetation type and the climatic and edaphic variables were included in the final model. The model with the lowest Akaike information criterion (AIC) value was chosen as the final model (Table S4). All statistical analyses were performed using the software package R 3.0.2 (R Development Core Team, 2013).

## RESULTS

### Patterns of microbial N, P and N:P across forest biomes

Microbial N and P varied widely between forest types (Fig. 2). Microbial N and P concentrations were higher in boreal forests

**Table 1** Summary of maximum-likelihood estimates of the parameters in the mixed-effects models of microbial nitrogen (N) and phosphorus (P) concentrations and N:P ratios in forests worldwide.

| Variable |               | d.f. | Slope    |            |         |         | Intercept |            |         |         | F     | P(> F)   |
|----------|---------------|------|----------|------------|---------|---------|-----------|------------|---------|---------|-------|----------|
| x        | y             |      | Estimate | Std. Error | t value | P(> t ) | Estimate  | Std. Error | t value | P(> t ) |       |          |
| Latitude | Microbial N   | 449  | 0.0092   | 0.0022     | 4.25    | 0.0000  | 1.5838    | 0.0870     | 18.20   | 0.0000  | 18.09 | < 0.0001 |
| Latitude | Microbial P   | 128  | 0.0124   | 0.0040     | 3.06    | 0.0027  | 0.9482    | 0.1435     | 6.61    | 0.0000  | 9.38  | 0.0027   |
| Latitude | Microbial N:P | 94   | -0.0099  | 0.0030     | -3.27   | 0.0015  | 0.8365    | 0.1025     | 8.16    | 0.0000  | 10.69 | 0.0015   |
| MAT      | Microbial N   | 449  | -0.0136  | 0.0039     | -3.53   | 0.0005  | 2.1052    | 0.0620     | 33.94   | 0.0000  | 12.48 | 0.0005   |
| MAT      | Microbial P   | 128  | -0.0155  | 0.0071     | -2.17   | 0.0337  | 1.6105    | 0.1266     | 12.72   | 0.0000  | 4.73  | 0.0337   |
| MAT      | Microbial N:P | 94   | 0.0089   | 0.0056     | 1.59    | 0.1197  | 0.3726    | 0.1095     | 3.40    | 0.0010  | 2.53  | 0.1197   |
| MAP      | Microbial N   | 449  | 0.00002  | 0.00004    | 0.43    | 0.6642  | 1.8994    | 0.0665     | 28.55   | 0.0000  | 0.19  | 0.6642   |
| MAP      | Microbial P   | 128  | -0.00005 | 0.00006    | -1.00   | 0.3189  | 1.4484    | 0.1041     | 13.92   | 0.0000  | 1.00  | 0.3189   |
| MAP      | Microbial N:P | 94   | 0.0002   | 0.00004    | 4.41    | 0.0000  | 0.2254    | 0.0800     | 2.82    | 0.0059  | 19.45 | < 0.0001 |
| Soil pH  | Microbial N   | 55   | 0.0545   | 0.0210     | 2.59    | 0.0123  | 1.5288    | 0.1303     | 11.74   | 0.0000  | 6.70  | 0.0123   |
| Soil pH  | Microbial P   | 54   | 0.0309   | 0.0180     | 1.72    | 0.0416  | 1.2304    | 0.1117     | 11.01   | 0.0000  | 2.95  | 0.0416   |
| Soil pH  | Microbial N:P | 55   | 0.0257   | 0.0115     | 2.22    | 0.0303  | 0.2489    | 0.0695     | 3.58    | 0.0007  | 4.95  | 0.0303   |
| Soil N   | Microbial N   | 53   | 0.7935   | 0.0863     | 9.19    | 0.0000  | 1.5520    | 0.0581     | 26.72   | 0.0000  | 84.52 | < 0.0001 |
| Soil P   | Microbial P   | 52   | 0.6341   | 0.0896     | 7.08    | 0.0000  | 1.6921    | 0.0535     | 31.62   | 0.0000  | 50.10 | < 0.0001 |
| Soil N   | Microbial N:P | 53   | 0.0548   | 0.0639     | 0.86    | 0.3950  | 0.3549    | 0.0333     | 10.66   | 0.0000  | 0.74  | 0.3950   |
| Soil P   | Microbial N:P | 53   | 0.0342   | 0.0722     | 0.47    | 0.6372  | 0.4002    | 0.0410     | 9.76    | 0.0000  | 0.22  | 0.6372   |
| Soil N:P | Microbial N:P | 50   | -0.0813  | 0.0620     | -1.31   | 0.1960  | 0.3882    | 0.0268     | 14.47   | 0.0000  | 1.72  | 0.1960   |

than in temperate forests, and the N:P ratio was lower. There were no significant differences in microbial N, P and N:P ratio between temperate and tropical forests.

### Changes in microbial N, P and N:P along environmental gradients

Microbial N and P were both significantly correlated with latitude and MAT (all  $P < 0.05$ ; Table 1), increasing with increasing latitude (Fig. 3a,b) and decreasing MAT (Fig. 4a,c). In contrast, the microbial N:P ratio declined with decreasing latitude (Fig. 3c) or exhibited slight increases along the temperature gradient (Fig. 4e). Microbial N and P were, however, only weakly correlated with MAP ( $P = 0.6642$  and  $0.3189$ , respectively; Table 1, Fig. 4b,d), whereas the microbial N:P ratio increased along the MAP gradient ( $P < 0.0001$ ; Table 1, Fig. 4f).

Microbial N concentration was associated with soil N concentration, microbial P with soil P, and both microbial N and microbial P with topsoil pH (Fig. 5a–d, Table 1), but the microbial N:P ratio was only correlated significantly with topsoil pH (Fig. 5h, Table 1). No significant relationships were detected between the microbial N:P ratio and other edaphic factors, such as soil N and P concentrations and soil N:P ratio (all  $P > 0.05$ ; Fig. 5e–g, Table 1).

### Effects of climate, soil and vegetation type on microbial N, P and N:P ratio

Mixed-effects models were used to explain the effects of environmental factors and vegetation on the microbial N, P and N:P ratio (Table 2). For microbial N, the best model included only

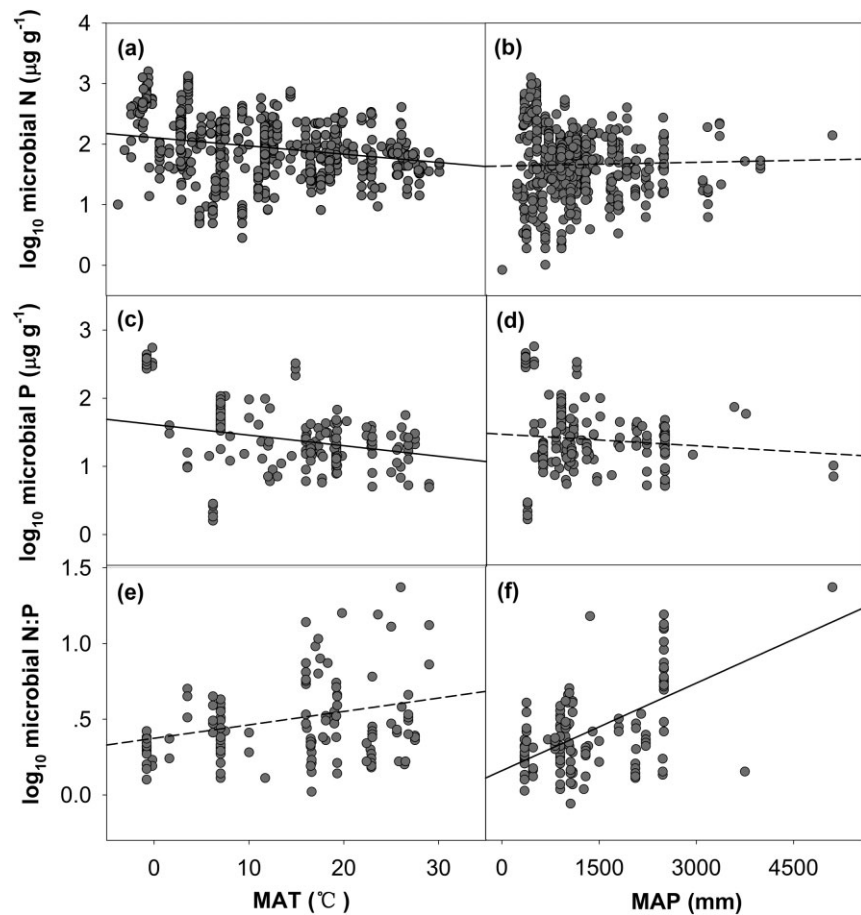
soil N, soil pH and their interaction as predictors. All of these variables had significant effects ( $P < 0.001$ ) except for the interaction term, together accounting for 51.5% of variance, with site explaining an additional 18.4%. For microbial P, the best model included only soil N and soil P. Edaphic factors explained 52.5% of the variance, and site accounted for an additional 15.5%. The best model of microbial N:P included only vegetation type and pH as predictors, which accounted for 10.7% of the variance, and site accounted for 14.9% of the variance.

## DISCUSSION

### Variations in microbial N and P stoichiometry and their climatic controls

Our results revealed a general trend of low microbial P concentrations but high microbial N:P ratios in relatively low-latitude forest biomes (Fig. 2); this trend matches those reported for plant leaves (McGroddy *et al.*, 2004; Reich & Oleksyn, 2004; Chen *et al.*, 2013; Tang *et al.*, 2013) and roots (Yuan *et al.*, 2011). Relatively low-latitude soils are geologically older than soils in other regions on average, are highly leached and are often P-limited (Walker & Syers, 1976; Crews *et al.*, 1995; Vitousek & Farrington, 1997; Chadwick *et al.*, 1999). Low P availability in tropic ecosystems could then strongly limit microbial biomass and activity (Gallardo & Schlesinger, 1994; Cleveland *et al.*, 2002; Cleveland & Townsend, 2006; Reed *et al.*, 2007). This leads to lower microbial P and higher microbial N:P ratios in low-latitude forest biomes than those in high-latitude forest biomes.

Microbial N and P concentrations increased but N:P ratios decreased along the latitudinal gradient (i.e. with decreasing



**Figure 4** Relationships between microbial biomass N and P concentrations and N:P ratio and mean annual temperature (MAT) and mean annual precipitation (MAP). (a) microbial N vs. MAT; (b) microbial N vs. MAP; (c) microbial P vs. MAT; (d) microbial P vs. MAP; (e) microbial N:P ratios vs. MAT; (f) microbial N:P ratios vs. MAP. Solid lines are fit by an equation with  $P < 0.05$ , and dashed lines denote the equation with  $P > 0.05$ .

**Table 2** Summary of mixed-effects models for the ecological effects on soil microbial N, P and N:P ratios in forests worldwide.

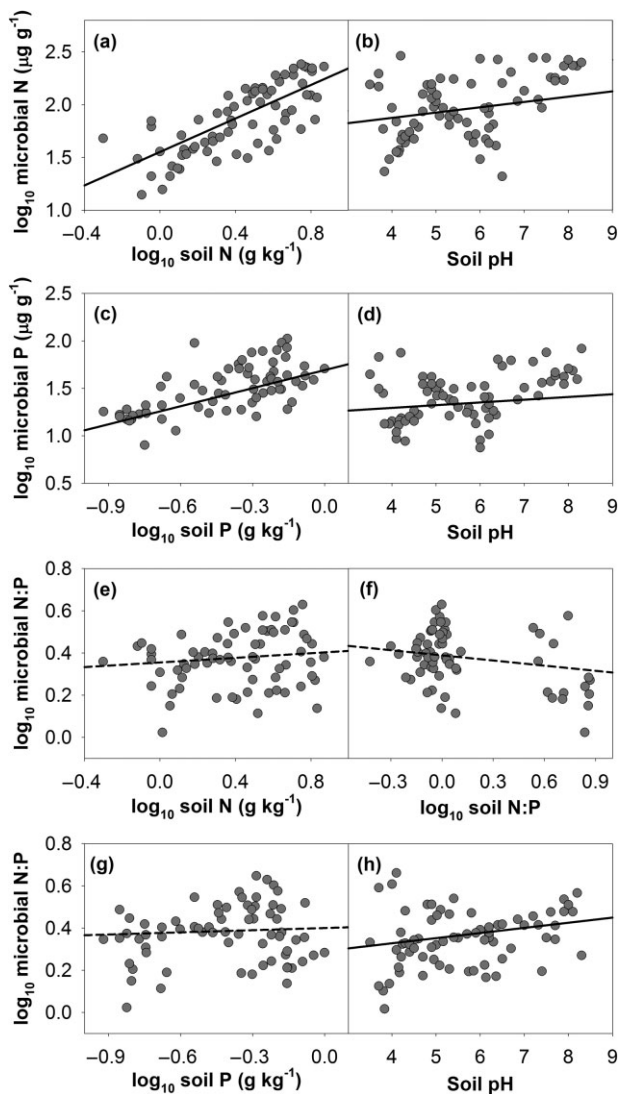
| Factor      | Log N |       |       |       |          | Log P |       |       |       |          | Log N:P |       |       |      |        |
|-------------|-------|-------|-------|-------|----------|-------|-------|-------|-------|----------|---------|-------|-------|------|--------|
|             | d.f.  | MS    | SS%   | F     | P        | d.f.  | MS    | SS%   | F     | P        | d.f.    | MS    | SS%   | F    | P      |
| VT          |       |       |       |       |          |       |       |       |       |          | 2       | 0.002 | 0.63% | 0.34 | 0.7193 |
| Soil N      | 1     | 0.916 | 40.0% | 62.55 | < 0.0001 | 1     | 0.254 | 18.3% | 27.20 | < 0.0001 |         |       |       |      |        |
| Soil P      |       |       |       |       |          | 1     | 0.475 | 34.2% | 51.43 | < 0.0001 |         |       |       |      |        |
| pH          | 1     | 0.264 | 9.7%  | 15.19 | < 0.001  |       |       |       |       |          | 1       | 0.067 | 10.1% | 6.85 | < 0.05 |
| pH × soil N | 1     | 0.038 | 1.8%  | 2.83  | 0.0991   |       |       |       |       |          |         |       |       |      |        |
| Site        | 13    | 0.027 | 18.4% |       |          | 13    | 0.016 | 15.5% |       |          | 13      | 0.008 | 14.9% |      |        |
| Residuals   | 47    | 0.013 | 30.0% |       |          | 48    | 0.009 | 32.0% |       |          | 47      | 0.010 | 74.4% |      |        |

Note: VT, vegetation type: tropical versus temperate versus boreal. Soil N, soil nitrogen concentration; Soil P, soil phosphorus concentration; pH, topsoil pH values. Soil N:P, the ratios of soil N and P concentration. d.f., degrees of freedom; MS, mean squares; SS, proportion of variances explained by the variable. Model with the lower Akaike information criterion (AIC) value was chosen as the model (Table S4).

temperature; Fig. 4a,c,e). These patterns accord well with the predictions of the temperature–biogeochemistry hypothesis and/or the latitudinal/temperature compensation hypothesis (Levinton, 1983; Reich & Oleksyn, 2004). According to these hypotheses, soil microbes at high latitudes may increase their N and P contents to compensate for their low activity in low-temperature environments. The latitudinal or climatic patterns of variation in the microbial N:P ratio is also consistent with

that of the litter N:P ratio (McGroddy *et al.*, 2004; Yuan & Chen, 2009; Tang *et al.*, 2013), reflecting the stoichiometric constraints of the microbial food supply (i.e. the litters consumed by heterotrophic microbes via the decomposition process).

The microbial N:P ratio was more variable than microbial N or P, and more closely associated with precipitation (Fig. 4b,d,f). Given that P is a more ‘rock-derived’ element, whereas N is mainly derived from biological materials (Walker & Syers, 1976;



**Figure 5** Relationships between microbial biomass N and P concentrations, and N:P ratios and soil N and P concentrations and soil N:P ratios. (a) microbial N vs. soil N; (b) microbial N vs. soil pH; (c) microbial P vs. soil P; (d) microbial P vs. soil pH; (e) microbial N:P ratios vs. soil N; (f) microbial N:P ratios vs. soil N:P ratios; (g) microbial N:P ratios vs. soil P; (h) microbial N:P ratios vs. soil pH. Solid lines denote equations with  $P < 0.05$ ; dashed lines denote equations with  $P > 0.05$ .

Chapin, 1980; Vitousek & Farrington, 1997), the highly variable N:P ratio in microbes may reflect the high variability in site-related P availability (Chen *et al.*, 2013; Tang *et al.*, 2013). P availability is closely related to soil development, driven by factors such as precipitation (leaching effect) (Crews *et al.*, 1995; Chadwick *et al.*, 1999). Precipitation can enhance leaching and deplete P (Walker & Syers, 1976; Vitousek & Farrington, 1997), resulting in low P availability and low soil fertility. In addition, these patterns in microbial N, P and N:P ratio (low variability in N and P but high variability in N:P ratio) support the idea that variation in P regulates large-scale patterns of microbial N and P

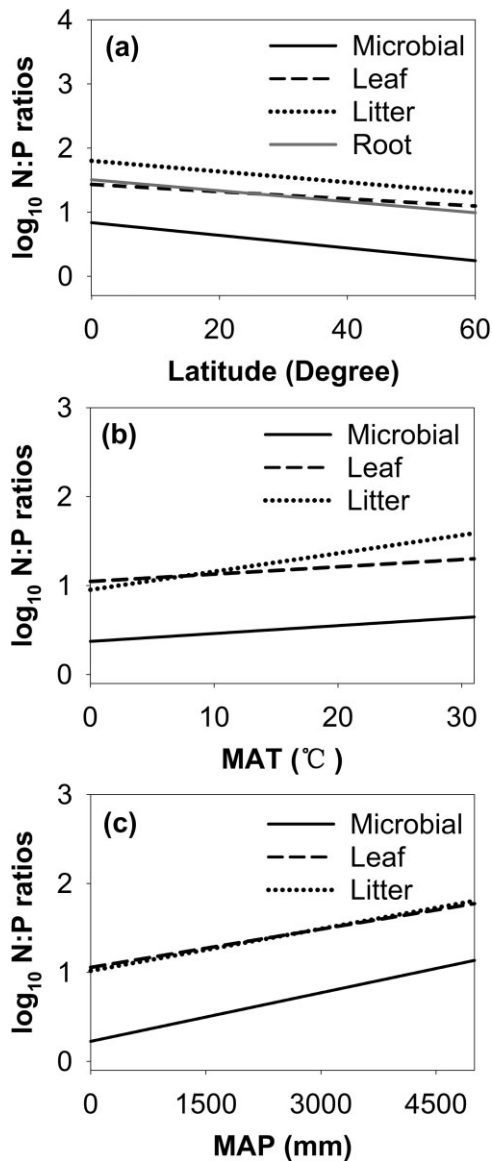
stoichiometry and nutrient-use strategies (Vitousek *et al.*, 2010).

### Microbial N and P stoichiometry in relation to edaphic factors

Our results show that the microbial N:P ratio and microbial N and P concentrations are correlated with soil pH (Fig. 5b,d,h), and analysis using mixed-effects models also showed that soil pH had significant effects on microbial N, P and N:P ratio. This finding is inconsistent with those reported by Cleveland & Liptzin (2007) and Xu *et al.* (2013). In those studies, there were no significant correlations between microbial biomass (or microbial N:P ratios) and soil pH. Soil pH is generally recognized as one of the most important abiotic factors that regulate microbial biomass and activity (Fierer & Jackson, 2006; Aciego Pietri & Brookes, 2009); it may strongly affect the metabolic condition of soil microbes (Sawada *et al.*, 2009), the quality and decomposition of litter and soil organic matter (Anderson & Joergensen, 1997; Pal *et al.*, 2007), and nutrient availability. Soil pH can, for example, alter the soil's capacity for ion exchange, the adsorption and solubility of mineral nutrients in soil, and the nutrient-uptake activities of soil microbes (Cheng *et al.*, 2010; Han *et al.*, 2012). In addition, soil microbes in acid soils divert energy from growth to cell maintenance (Anderson & Domsch, 1993). Thus, microbes in acid soils have much lower microbial N and P contents than those of their counterparts in high-pH soils. Given that soil organic N is more easily immobilized and assimilated than P by the microbial community, especially in relatively alkaline soils (Kooijman *et al.*, 2009), microbial growth tends to be P-limited (or microbial N:P ratios increase) with increasing of soil pH.

### Collective effects of environmental variables on microbial N/P stoichiometry

Climate, soil and vegetation type have complex effects on microbial N, P and N:P ratios, as is the case for plant green leaves (Reich & Oleksyn, 2004; Han *et al.*, 2011; Chen *et al.*, 2013) and senesced-leaf litters (Tang *et al.*, 2013). The analysis using mixed-effects models indicated that soil played a dominant role in determining microbial N and P, explaining more of the variance than climate and vegetation type (Table 2). In contrast, vegetation type showed the greatest effect in other reservoirs of N and P elements such as plant-leaf minerals (Han *et al.*, 2011; Chen *et al.*, 2013) and leaf nutrient resorption (Tang *et al.*, 2013). These differences suggest that the geographical patterns of microbial N and P are largely controlled by the soil. That is, microbial biomass N and P are mainly derived from total soil N and P, and when soil nutrients are insufficient to maintain microbial growth, microbes start to immobilize and use the available N and P. Broadly speaking, plant nutrients (including N and P) are mainly derived from the available forms of N and P in soil that are produced by microbial decomposition (Chapin *et al.*, 2003; McGroddy *et al.*, 2004). Therefore, the different responses of plants and microbes to environmental variables



**Figure 6** N:P ratios in relation to (a) latitude, (b) mean annual temperature (MAT) and (c) mean annual precipitation (MAP), compared to microbial (black solid line; data from this paper), leaf (black dashed line; data from McGroddy *et al.*, 2004; Reich & Oleksyn, 2004; Han *et al.*, 2005; and Chen *et al.*, 2013), litter (black dotted line; data from McGroddy *et al.*, 2004; and Yuan & Chen, 2009) and root (dark grey solid line; data from Yuan *et al.*, 2011) N:P ratios.

highlight the fact that soil microbes are more flexible and sensitive than plants in their responses to soil nutrient availability (Cleveland & Liptzin, 2007).

Site explained 18.4%, 15.5% and 14.9% of the variance in microbial N, P and N:P ratio, respectively (Table 2). These variance components represent the among-site variability that had not been captured by the climate and soil (Chen *et al.*, 2013). There are also considerable unexplained variances for microbial N, P and N:P ratio (30.0%, 32.0% and 74.4%, respectively), which may be explained by various sources, such as

unquantified microenvironments, many other soil properties (e.g. soil texture, soil type, soil chronosequences and soil health) and disturbance (Wardle, 1992, 1998; Walker *et al.*, 2010)

### Linking microbial N and P stoichiometry with ecosystem-scale nutrient cycling

According to our results, microbial N and P stoichiometry showed similar global patterns (Fig. 6) to those reported for green leaves (Reich & Oleksyn, 2004; Han *et al.*, 2005; Chen *et al.*, 2013), senesced-leaf litters (McGroddy *et al.*, 2004; Yuan & Chen, 2009; Tang *et al.*, 2013) and fine roots (Yuan *et al.*, 2011). The consistency of these patterns in plant–soil–microbe systems supports the idea that P is more often a major limiting nutrient in tropical ecosystems at low latitudes than it is in ecosystems at middle and high latitudes (Reich & Oleksyn, 2004; Vitousek *et al.*, 2010; Chen *et al.*, 2013). As major decomposers of organic matter (e.g. plant leaf and root litters), soil microbes drive N and P cycling via immobilization and mineralization in plant–microbe–soil systems, and link key nutrient processes between plants (litter) and soil (Chapin *et al.*, 2003; McGroddy *et al.*, 2004). Thus, the soil microbial N and P stoichiometry patterns revealed here, as well as their consistency with the stoichiometry patterns reported for plants and soil, suggest that soil microbes play a pivotal role in global nutrient cycling. Our results indicate that climate, ecological processes and N/P stoichiometric patterns can be coupled together via plant–soil–microbe feedbacks to the N and P cycles. Our findings also highlight the importance of including the roles of soil microbes in earth-system models when predicting the responses of ecosystem nutrient cycling to global environmental changes.

### ACKNOWLEDGEMENTS

We gratefully acknowledge all the scientists whose work was included in this synthesis. This study was supported by the National Basic Research Program of China on Global Change (2010CB950600 and 2014CB954001) and the National Natural Science Foundation of China (31321061, 31322011 and 41371213).

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

**Table S1** Published data of microbial N and P concentration and N:P ratios collected in this study.

**Table S2** Comparison of microbial biomass N and P concentrations and N:P ratios among various forest types, based on parameter estimates from the mixed-effects models.

**Table S3** Correlations among environmental variables involved in this study.

**Table S4** Mixed-effects models for soil microbial N, P and N:P ratios.

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Editor: Peter van Bodegom