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Global synthesis for the scaling of soil microbial nitrogen to phosphorus in terrestrial ecosystems

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Abstract

Nitrogen (N) and phosphorus (P) are associated with the life history of all organisms. Soil microbes play essential roles in nutrient cycling and ecosystem dynamics. As compared to plants, however, our understanding of the soil microbial N versus P scaling relationship remains limited. In this study, we used a comprehensive dataset comprising 2210 observations from 422 sites worldwide to examine microbial C, N, and P concentrations and C:N:P ratios, and to determine the scaling of microbial N versus P in different ecosystems and spatial scales (i.e. soil depths, latitudinal zones, and local sites). The global mean values of microbial C, N, and P concentrations were 721.5 mg kg⁻¹, 84.7 mg kg⁻¹, 37.6 mg kg⁻¹, respectively, whereas C:N, C:P, and N:P ratios were 9.5, 30, and 3.4, respectively. Microbial C, N, and P concentrations varied within and across different ecosystems and spatial scales, but C:N:P ratios varied surprisingly little. The numerical value of the scaling exponent (i.e. the slope of the log-log linear relationship) of microbial N versus P was 0.89 across the entire dataset and for different ecosystems. However, the numerical value of the exponent varied significantly across different spatial scales. Soil total P was the largest contributor to the variation observed in the scaling of microbial N versus P at different local sites. These findings have important implications for predicting soil microbial growth rates and improving our understanding of nutrient cycling in plant-soil-microbe systems.

1. Introduction

Nitrogen (N) and phosphorus (P) are important growth-limiting elements in terrestrial ecosystems and regulate ecosystem functions and biogeochemical cycles (Chapin 1980, Güsewell 2004, Reich and Oleksyn 2004). It is critical for organisms to maintain

a balance of N and P for their basic metabolic requirements and to sustain the availability of N and P in the environment (Sterner and Elser 2002). Therefore, a quantitative evaluation of the N versus P scaling relationship across different organisms can improve our mechanistic understanding of nutrient cycling and ecosystem dynamics (Elser *et al*

2000, Hedin 2004, Kerkhoff *et al* 2006, Cleveland and Liptzin 2007, Reich *et al* 2010).

It is widely known that N and P concentrations in organisms are tightly correlated and can be quantified via a general log–log stoichiometric scaling relationship, taking the form $N = \beta P^\alpha$ (or, when log-transformed, $\log N = \log \beta + \alpha \log P$), where β and α are the scaling constant and scaling exponent (i.e. the *Y*-intercept and slope of the log–log linear relationship), respectively (Sternner and Elser 2002, Niklas *et al* 2005, Kerkhoff *et al* 2006). This simple N versus P scaling relationship provides a useful empirical model to predict the N and P limitation of organisms and ecosystem functioning (Elser *et al* 2000, Díaz *et al* 2004). For example, the empirical stoichiometric growth model (also known as the growth rate hypothesis, GRH) states that rapidly growing organisms require disproportionately more P than N to ensure rapid protein synthesis (Elser *et al* 2003), thereby resulting in a N versus P scaling exponent below unity ($\alpha < 1$) (Sternner and Elser 2002).

During the past several years, numerous studies have explored N versus P relationship in plant tissues, such as leaves (Wright *et al* 2004, Han *et al* 2005, Niklas *et al* 2005, Reich *et al* 2010), stems (Niklas and Cobb 2005, Wang *et al* 2018, Zhang *et al* 2018), roots (Yuan *et al* 2011, Wang *et al* 2019), and seeds (Wang *et al* 2020). These studies have revealed that the strategic allocation of N and P in plant tissues appears to follow fundamental stoichiometric rules (Niklas *et al* 2005, Niklas 2006, Ågren 2008) that regulate the stoichiometry of elements in plant tissues. Previous work has also shown that the scaling exponent for the N versus P relationship is apparently constant, as a result of environmental convergence and evolutionary history (McGroddy *et al* 2004, Wright *et al* 2004). For example, based on a large and comprehensive dataset, the exponent of the N versus P scaling relationship is reported to be 0.66 for leaves (Reich *et al* 2010) and 0.82 for fine roots (Wang *et al* 2019). Nevertheless, several studies have reported significant interspecific variation in the N versus P scaling exponent in leaves (Niklas and Cobb 2005, McGroddy *et al* 2004, Tian *et al* 2017), roots (Yuan *et al* 2011, Geng *et al* 2014, Zhao *et al* 2016), and among geographical locations due to environmental differences.

Despite extensive studies of plant organs, our quantitative understanding of the covariation of these two nutrients in soil microbes remains extremely limited in comparison (Cleveland and Liptzin 2007, Hartman and Richardson 2013). As an important indicator of soil fertility, soil microbes play fundamental roles in driving and regulating fundamental terrestrial ecosystem processes such as soil carbon (C) sequestration, organic matter decomposition, and nutrient recycling (Li *et al* 2012, Mooshammer *et al* 2014a, Heuck *et al* 2015, Chen *et al* 2016, Spohn 2016), and thus affect ecosystem productivity

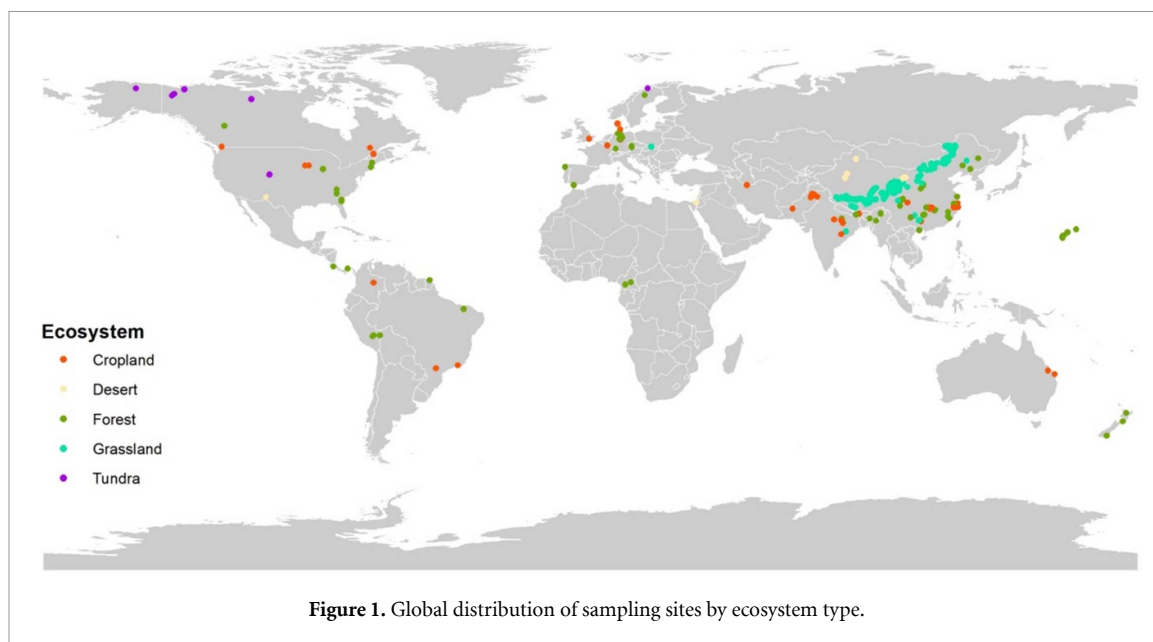
(Van Der Heijden *et al* 2008). For example, soil microbial biomass accounts for approximately 1%–5% of the soil organic C (Jenkinson *et al* 1990), and soil microbial dynamics largely determine the release of immobilized labile nutrients (Singh and Gupta 2018). Soil microbes also contribute to soil N mineralization and soil respiration by recycling C and N as carbon dioxide and ammonium (Moorhead *et al* 2012). Equally important, soil microbes can transform soil N and P into a labile pool of plant-available nutrients. In turn, important resources are supplied to soil microbes through the input of plant necromass, root exudation, and other soil organic matter (Mooshammer *et al* 2014b). Given that the stoichiometry of N and P is tightly coupled within plant–soil–microbe systems (McGroddy *et al* 2004), a scaling relationship of N versus P might also exist in soil microbial systems in a manner similar to that of plants.

In this study, we compiled a comprehensive global dataset of paired soil microbial biomass C, N, and P to explore whether a general N versus P scaling relationship exists. Specifically, we (a) estimated microbial C, N, and P concentrations and C:N:P ratios across different ecosystems, soil depths, and latitudinal zones; (b) quantified the microbial N versus P scaling exponent across ecosystems, soil depths, latitudinal zones, and local sites; and (c) explored the relationships among environmental factors and the scaling exponent across sites.

2. Materials and methods

2.1. Data sources

We compiled a dataset of soil microbial biomass carbon (MBC), microbial biomass nitrogen (MBN), and microbial biomass phosphorus (MBP) from the primary published literature using the phrase ‘soil microbial biomass’ in Google Scholar, Web of Science (<http://apps.webofknowledge.com>), and the China National Knowledge Infrastructure Database (<http://cnki.net>) from 1980 to 2019. Four criteria were used to avoid bias in selecting publications. First, microbial C, N, and P had to be reported simultaneously for the same samples. Based on this criterion, we excluded some publications used in previous studies (Cleveland and Liptzin 2007, Xu *et al* 2013, Li *et al* 2014). Second, microbial C, N, and P data had to be for mineral soil depths between 0 and 30 cm. Third, only data from control plots that reported the results of manipulation experiments were used. Finally, fourth, to avoid variation among methods, soil microbial biomass had to be evaluated using the chloroform fumigation-extraction (CFE) method (Vance *et al* 1987). CFE is the most commonly used method and provides an index of total soil microbial biomass, including both bacteria and fungi (Fierer *et al* 2009).



We recorded additional site-specific data from the original publications, including geographic location (i.e. latitude and longitude), climatic variables (i.e. mean annual temperature MAT, and mean annual precipitation, MAP), and soil physical and chemical properties (i.e. soil pH, soil organic C, and total N and P). When data were presented graphically, they were extracted from figures, tables, and appendices of the original publications using GetData Graph Digitizer (version 2.22). When the geographical coordinates and climatic factors were not specified in the original articles, they were obtained from the Global Gazetteer Version 2.2 (www.fallingrain.com/world/index.html) and the WorldClim global climatic database (<http://worldclim.org/>) with a grid precision of $0.5^\circ \times 0.5^\circ$ according to geographical coordinates, respectively. To standardize the data, all microbial biomass N and P values were converted into units of mg kg^{-1} dry soil. The final dataset consisted of 2210 observations from 422 sites worldwide, reported in 131 published studies (figure 1; a list of the data sources is provided in the supplementary materials). The dataset encompassed five types of terrestrial ecosystems, including croplands (1030 observations), forests (657 observations), grasslands (366 observations), deserts (81 observations), and tundra (76 observations).

2.2. Data analysis

One-way ANOVA was used to evaluate possible differences in microbial C, N, P concentrations, and C:N, C:P, and N:P ratios among ecosystems, latitudinal zones, and soil depths, followed by Tukey's *post-hoc* comparisons when effects were significant ($P < 0.05$). All of the data were log-transformed to achieve a normal distribution for robust statistical analysis (figure S1 (available online at stacks.iop.org/ERL/16/044034/mmedia)). Standard

major axis regression (SMA, a form of model II regression) was used to determine the microbial N versus P scaling relationship for ecosystems, soil depths, latitudinal zones, and the sites using log-transformed values of microbial N and P. Each site was sorted into one of five ecosystems (croplands, forests, grasslands, deserts, or tundra). Given the influence of climate and soil properties on soil microbial biomass (Li *et al* 2012, Xu *et al* 2013, Tischer *et al* 2014, Liu *et al* 2020), sites were also sorted into one of three latitudinal zones (tropical $0\text{--}25^\circ$, temperate $25\text{--}50^\circ$, and boreal $>50^\circ$) and into one of three soil depths (0–10 cm, 10–20 cm, and 20–30 cm). Data for other depth thresholds (e.g. 0–15 cm, 0–20 cm or 15–30 cm) were excluded from soil depth analyses. Finally, we examined the microbial N versus P scaling relationships for each of the 26 sites with 10 or more records. These 26 sites included croplands (6 sites), forests (8 sites), grasslands (2 sites), deserts (2 sites), tundra (3 sites), and croplands + forests (5 sites). Heterogeneity of the numerical values of scaling exponents within the different categories of ecosystems, soil depths, and latitudinal zones was tested using likelihood ratio tests (Warton *et al* 2006). ‘Funnel’ graph analyses were used to evaluate whether scaling exponents varied with sample size for the 26 sites with 10 or more samples (Wright *et al* 2005, Reich *et al* 2010).

We further analyzed the influence of environmental factors on variation in the numerical values of the microbial N versus P scaling exponents for the 26 sites with 10 or more samples. Stepwise multiple regression (SMR) was used to identify the contributions of six environmental factors (i.e. MAT, MAP, soil organic C, total N and P, and pH). Environmental factors that did not significantly contribute to the variation in scaling exponent were excluded from subsequent analyses. Redundancy analysis (RDA)

was used to determine the proportion of variation in scaling exponents explained by each significant environmental factor. All statistical analyses were performed using R 3.4.0 (R Core Team 2017).

3. Results

3.1. C, N, and P concentrations and C:N:P stoichiometry in soil microbial biomass

The overall mean values of microbial C, N, and P concentrations were 721.5 mg kg⁻¹, 84.7 mg kg⁻¹, and 37.6 mg kg⁻¹, respectively. The overall mean values of C:N, C:P, and N:P ratios were 9.5, 30, and 3.4, respectively (table 1). Microbial C, N, and P concentrations varied among ecosystems, soil depths, and latitudinal zones. Across ecosystems, tundra had the highest concentrations of microbial C, N, and P. In contrast, the microbial C was lowest in deserts, whereas the microbial N and P were lowest in grasslands. Across soil depths, microbial C, N, and P concentrations were largest in the 0–10 cm soil layer, and microbial C and P were lower in the 20–30 cm layer, whereas microbial N was lowest in the 10–20 cm soil layer. Across latitudinal zones, the boreal and temperate zones had the highest and lowest concentrations of microbial C, N, and P, respectively. The global averaged microbial C:N:P ratio was 32:3:1. Compared to microbial C, N, and P concentrations, microbial C:N:P ratios were confined to a relatively modest range in different ecosystems, soil depths, and latitudinal zones (table 1). For example, microbial C:N ratios ranged from 5.0 for deserts to 10.9 for croplands. Microbial C:P ratios ranged from 24.8 in forests to 42.6 in grasslands, whereas microbial N:P ratios only ranged from 2.1 for deserts to 4.3 for grasslands.

3.2. Microbial N versus P scaling exponents across ecosystems, soil depths, and latitudinal zones

Across the entire dataset, the numerical value of the microbial N versus P scaling exponent was 0.89 ($P < 0.001$, $r^2 = 0.62$; figure 2(a), table 2). The numerical values of the scaling exponent showed no significant differences among ecosystems, with all ecosystems having values close to 0.89 (figures 2(b)–(f), table 2). In contrast, the numerical values of the scaling exponent differed significantly among soil depths, ranging from 0.89 in the 0–10 cm soil layer to 0.63 in the 20–30 cm soil layer (figure 3(a), table 2). The numerical values of the scaling exponent also differed significantly among latitudinal zones, with larger values in the tropical (0.96) and boreal (0.98) zones than in the temperate (0.85) zone (figure 3(b), table 2).

3.3. Microbial N versus P scaling exponents across local sites

The numerical values of the scaling exponent of the microbial N versus P scaling relationship varied

significantly among sites with 10 or more values (figure 4(a)). A funnel-plot assessment of the scaling exponent in relation to the sample size for the 26 sites showed that the numerical values of the scaling exponent ranged from 0.45 to 1.41 with a mean value of 0.92. The numerical values converged around the mean value with increasing sample size (approx. equal to 0.89) (figure 4(b)).

Preliminary SMR analysis demonstrated that MAT, soil organic C, and total N did not significantly affect the numerical values of the microbial N versus P scaling exponent. The SMR analysis showed that MAP, soil pH, and soil total P explained 74% of the variation in the numerical values of the scaling exponents across sites ($r^2 = 0.74$, $P < 0.001$). The values of scaling exponents were positively correlated with MAP (a standardized coefficient = 0.30, $P < 0.05$), and negatively correlated with soil pH (a standardized coefficient of = -0.30 , $P < 0.05$) and soil total P (a standardized coefficient of = -0.69 , $P < 0.001$) (figure S2). RDA analyses demonstrated that MAP, soil pH, total P, and their interactions collectively explained 80.2% of the observed variation in the numerical values of the microbial N versus P scaling exponents (figure 5). When these factors were decomposed, soil total P was the largest contributor (49.1%) to the numerical values of the scaling exponent.

4. Discussion

4.1. Variation in microbial C, N, and P concentrations and C:N:P ratios across ecosystems, soil depths, and latitudinal zones

The results reported here indicate that global mean microbial C, N, and P concentrations are 721.5 mg kg⁻¹, 84.7 mg kg⁻¹, and 37.6 mg kg⁻¹, respectively, which are lower than those global means reported by Xu *et al* (2013) (748.4 mg kg⁻¹, 131.4 mg kg⁻¹, and 67.5 mg kg⁻¹, respectively). The discrepancy between our study and that of Xu *et al* (2013) can be attributed to using different datasets to calculate mean values. For example, the global average of microbial C, N, and P concentrations reported here are based on paired microbial C, N, and P values, whereas comparatively few paired microbial C, N, and P values were used in the study of Xu *et al* (2013). Moreover, the dataset used by Xu *et al* (2013) included a significant proportion of data drawn from manipulated plots (e.g. fertilizer and temperature treatments), organic layers or unspecified soil depths. However, our data were obtained from control plots and from specific surface soil horizons (depths of 0–30 cm). These differences probably also contribute to the lower microbial C, N, and P concentrations reported in our study. In addition, it is important to point out that the majority of microbial C, N, and P in our dataset were obtained from croplands and forest ecosystems. This inequality

Table 1. MBC, MBN and MBP concentrations and their ratios for different ecosystems, soil depths, and latitudinal zones.

Group	<i>n</i>	MBC (mg kg ⁻¹)	MBN (mg kg ⁻¹)	MBP (mg kg ⁻¹)	MBC:MBN	MBC:MBP	MBN:MBP
All	2210	721.5 (678.9–764)	84.7 (79.9–89.5)	37.6 (34.9–40.4)	9.5 (9.3–9.8)	30 (27.9–32.1)	3.4 (3.2–3.6)
Ecosystem							
Cropland	1030	897.8 ^b (846.8–948.8)	75.8 ^b (72.8–78.8)	30.9 ^c (29.3–32.4)	10.9 ^a (10.5–11.2)	30.3 ^b (29.3–31.4)	3.1 ^b (3.0–3.3)
Forest	657	491.9 ^c (455.8–528.1)	78.9 ^b (72.4–85.5)	33.0 ^c (29.4–36.7)	7.5 ^b (7.1–8)	24.8 ^b (22.1–27.4)	3.7 ^a (3.4–4)
Grassland	366	301.8 ^c (274.6–329.0)	39.0 ^c (35.3–42.6)	16.1 ^d (14–18.2)	9.8 ^a (9.0–10.6)	42.6 ^a (31.5–53.7)	4.3 ^a (3.5–5)
Desert	81	193.3 ^d (142.4–244.2)	69.5 ^b (56.6–82.4)	58.8 ^b (48.8–68.7)	5 ^b (2.1–8)	25.6 ^b (13.6–37.6)	2.1 ^b (1.4–2.7)
Tundra	76	4158.9 ^a (3067.2–5250.7)	492.1 ^a (481.7–500)	248.6 ^a (199.2–298)	10.6 ^a (9.3–11.8)	38.8 ^a (25.4–52.2)	3.1 ^b (2.4–3.8)
Soil depth							
0–10 cm	697	762.8 ^a (653.7–872.0)	114.3 ^a (101.3–127.4)	54.2 ^a (46.4–61.9)	9.4 ^a (8.7–10.1)	32.3 ^a (28.0–36.6)	4.0 ^a (3.6–4.4)
10–20 cm	124	204.8 ^b (177.2–232.4)	41.2 ^b (34.7–47.7)	20.5 ^c (15.8–25.3)	6.5 ^b (5.6–7.4)	32.5 ^a (14.7–50.3)	4.0 ^a (2.8–5.1)
20–30 cm	48	114.8 ^b (80.8–148.8)	35 ^b (24.2–45.7)	30.9 ^b (21.3–40.4)	5.6 ^b (3.4–7.9)	52.5 ^a (5.7–110)	4.1 ^a (0.9–7.2)
Latitudinal zone							
Tropical (0–25°)	660	1030.6 ^b (954.0–1107.2)	89.6 ^b (84.5–94.7)	33.2 ^b (30.4–35.9)	10.8 ^a (10.3–11.3)	32.6 ^a (30.7–34.5)	3.4 ^a (3.2–3.7)
Temperate (25–50°)	1418	466.9 ^c (446.2–487.5)	60.2 ^c (57.0–63.3)	27.1 ^c (25.5–28.6)	9.0 ^b (8.7–9.4)	29.3 ^a (26.2–32.4)	3.5 ^a (3.2–3.7)
Boreal (>50°)	132	2273.6 ^a (1678.2–2869.1)	323.6 ^a (270.8–376.5)	173.4 ^a (140.1–206.8)	8.8 ^b (8.1–9.6)	23.4 ^a (17.0–29.8)	2.5 ^b (2.1–2.9)

Values are means with 95% confidence intervals in parentheses. *n* is the number of samples. Different letters mean significant differences at the 0.05 level.

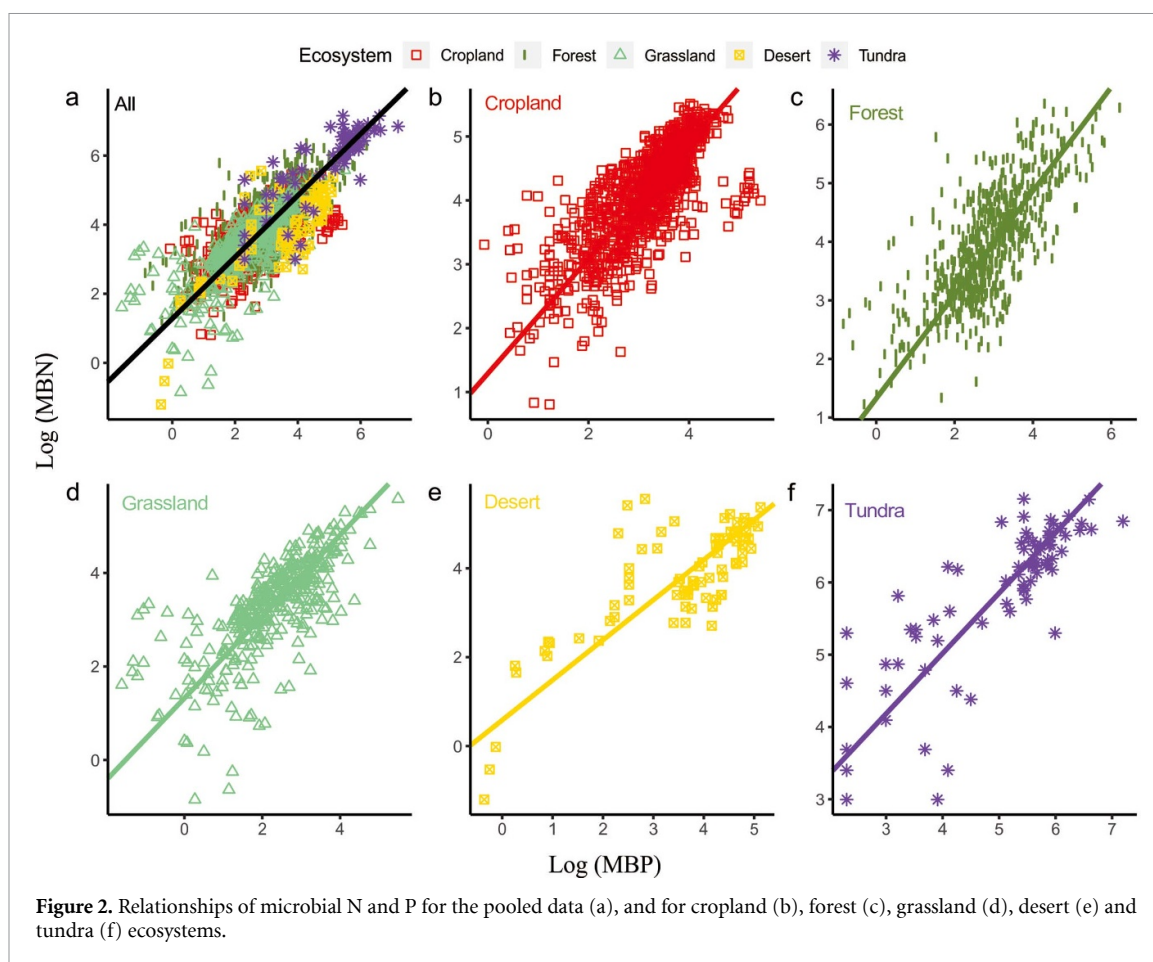


Table 2. Summary of standard major axis (SMA) regression analyses for the relationship between microbial N versus P for different ecosystems, soil depths and latitudinal zones.

Group	<i>n</i>	Intercept	Exponent	Low CI	High CI	<i>r</i> ²
All	2210	1.28	0.89	0.87	0.91	0.62
Ecosystem						
Cropland	1030	1.29	0.90 ^a	0.86	0.93	0.55
Forest	657	1.32	0.89 ^a	0.84	0.93	0.54
Grassland	366	1.32	0.87 ^a	0.81	0.94	0.51
Desert	81	0.57	0.90 ^a	0.79	1.04	0.62
Tundra	76	1.68	0.83 ^a	0.73	0.95	0.66
Soil depth						
0–10 cm	697	1.29	0.89 ^a	0.85	0.93	0.66
10–20 cm	124	1.73	0.70 ^b	0.62	0.79	0.54
20–30 cm	48	1.43	0.63 ^c	0.52	0.76	0.59
Latitudinal zone						
Tropical (0–25°)	660	1.20	0.96 ^a	0.92	1.00	0.68
Temperate (25–50°)	1418	1.33	0.85 ^b	0.82	0.88	0.52
Boreal (>50°)	132	0.77	0.98 ^a	0.90	1.07	0.74

Different letters denote significant differences in exponents based on a likelihood ratio test. Each regression relationship is statistically significant at $P < 0.001$ (all data were log₁₀-transformed before analysis).

in the data drawn from different ecosystems could lead to the differences in the global values reported here and elsewhere. Clearly, there is a need for more data on microbial C, N, and P from other

ecosystems before any canonical conclusions can be drawn.

Indeed, large differences in microbial C, N, and P concentrations across different ecosystems, soil

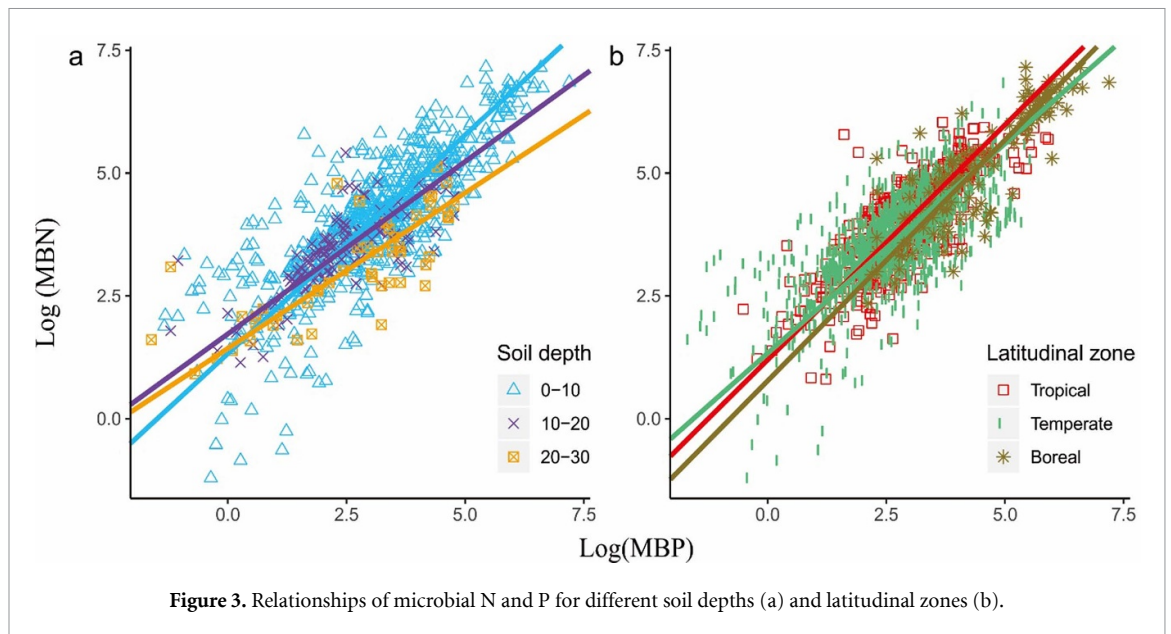


Figure 3. Relationships of microbial N and P for different soil depths (a) and latitudinal zones (b).

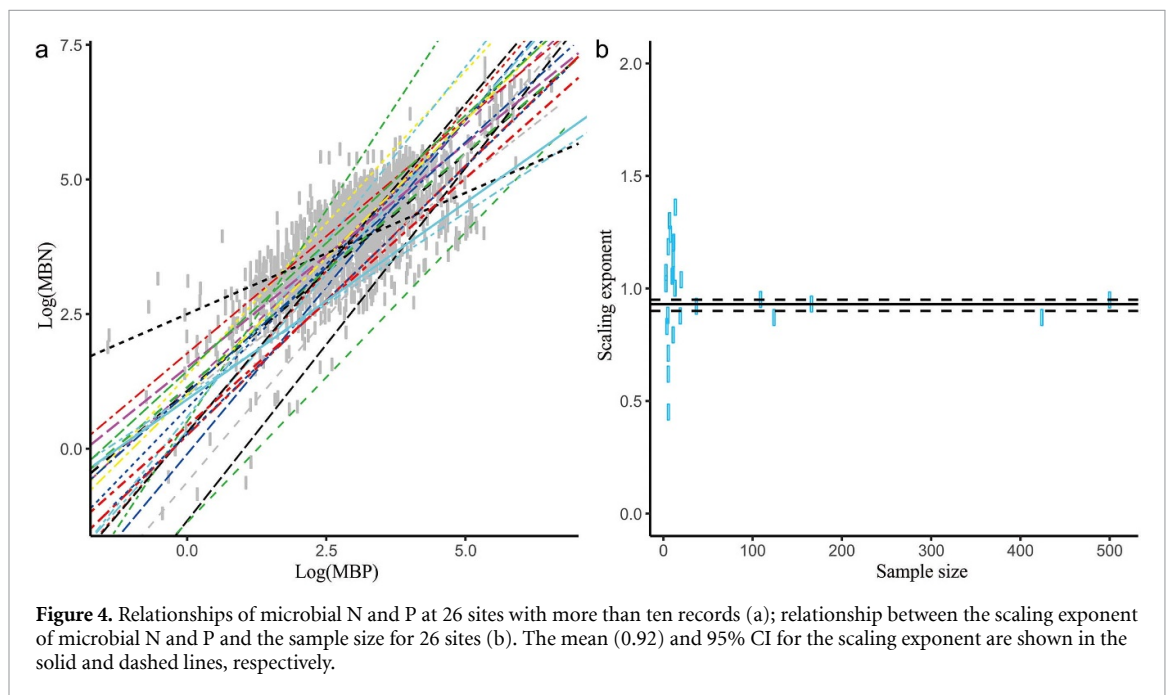


Figure 4. Relationships of microbial N and P at 26 sites with more than ten records (a); relationship between the scaling exponent of microbial N and P and the sample size for 26 sites (b). The mean (0.92) and 95% CI for the scaling exponent are shown in the solid and dashed lines, respectively.

depths, and latitudinal zones are evident in our global dataset (table 1). The microbial C, N, and P concentrations in the tundra sites in our dataset are significantly higher than in other ecosystems, which is consistent with the results reported previously by Xu *et al* (2013). We found that the microbial C, N, and P concentrations are significantly higher in the 0–10 cm soil layer than in deeper soil layers. This finding probably reflects surface C, N, and P inputs from plant residues, including litterfall and necromass (Sistla and Schimel 2012). We also observed significantly higher microbial C, N, and P concentrations in the boreal zone compared to the other latitudinal zones. This finding is consistent with the hypothesis that soil microbes at high latitudes with low temperatures tend to have higher C, N, and P concentrations, most probably in

order to compensate for their lower metabolic activity (Li *et al* 2014).

The global average microbial C:N:P ratio (i.e. 32:3:1) in our study is considerably lower than that reported by Xu *et al* (2013) (42:6:1). This difference is likely attributable to the factors previously discussed, e.g. a large proportion of microbial C, N, and P data (30%) used by Xu *et al* (2013) was drawn from manipulated plots, which can result in differences in microbial C, N, and P concentrations and thus their ratios. In addition, all of the microbial C, N, and P data used in our study are based on the FE determination method, whereas the microbial C, N, and P data used in previous datasets are based on only 55% of studies using this protocol. Thus, a ‘method discrepancy’ may also lead to higher C:N:P ratios in previous

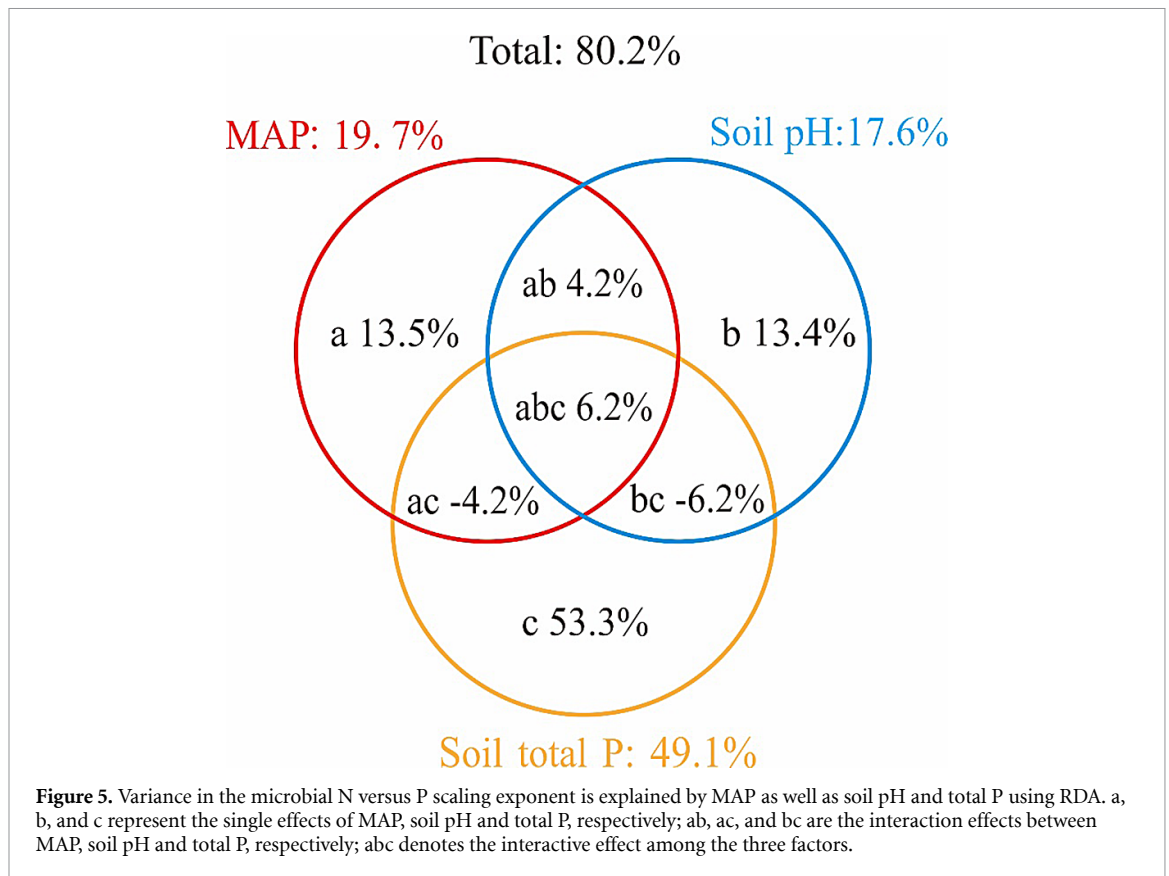


Figure 5. Variance in the microbial N versus P scaling exponent is explained by MAP as well as soil pH and total P using RDA. a, b, and c represent the single effects of MAP, soil pH and total P, respectively; ab, ac, and bc are the interaction effects between MAP, soil pH and total P, respectively; abc denotes the interactive effect among the three factors.

studies (e.g. Jenkinson *et al* 2004) compared to ours. Microbial C, N, and P concentrations tend to covary across ecosystems, soil depths, and latitudinal zones so that C:N:P ratios vary less than do C, N, and P concentrations (table 1). This result supports the existence of ‘Redfield-like’ ratios in soil microbes (Redfield 1958, Cleveland and Liptzin 2007). In addition, our results further support the contention that the growth of soil microbes is limited by C, rather than by N or P, indicating the soil microbial biomass N:P ratios should not be used as an indicator of ecosystem limitation (Allison *et al* 2010, Xu *et al* 2013).

4.2. The numerical values of microbial N versus P scaling exponents across different ecosystems, soil depths and latitudinal zones

The numerical value of the scaling exponent governing the microbial N versus P scaling relationship is approximately 0.89 across the different ecosystems (figure 2, table 2). This value is slightly lower than that reported by Hartman and Richardson (2013) at the global scale, i.e. 1.04. This difference is likely a result of the different communities sampled. For example, a large proportion of data (34%) used in the Hartman and Richardson (2013) study comes from land-use regimes (e.g. pastures and grazed lands). The 0.89 scaling exponent for the microbial N versus P scaling relationship reported here indicates that microbial P concentrations increase faster than microbial N concentrations (i.e. the microbial N versus P scaling

exponent is below unity), which supports the growth rate hypothesis of Sterner and Elser (2002).

The numerical value of the microbial N versus P scaling exponent declines from the 0–10 cm to the 20–30 cm soil layer (figure 3(a)), which may reflect an adaptive response to changes in the availability of soil resources. In deeper soil layers, studies have shown that microbial metabolic processes are limited by C availability as a reflection of denitrification and P mineralization processes (Fierer *et al* 2003, Camenzind *et al* 2018). Like other organisms, soil microbes must optimize their resource allocation in response to nutrient limitation, which can lead to lower scaling exponent values. Moreover, soil microbes can regulate their nutrient-use efficiencies within different soil depths to adjust N and P investments in growth (Manzoni *et al* 2012, Mooshammer *et al* 2014b). Thus, soil microbes are flexible and very efficient in acquiring nutrients from different soil depths to maintain their metabolic functions (Bardgett *et al* 2003).

We found that the numerical values of the microbial N versus P scaling exponents in boreal and tropical latitudes are similar and close to 1.0. Due to the N and P limitations in boreal and tropical ecosystems, microbial communities can also mobilize N and P elements to meet their demands by producing specific extracellular enzymes to alleviate limitations (Zechmeister-Boltenstern *et al* 2015). Moreover, in boreal areas, low temperatures may strongly restrain microbial growth by reducing metabolic activity. Our

SMR analysis shows that the numerical value of the microbial N versus P scaling exponent is negatively correlated with soil pH, such that the scaling exponent in acid soils is numerically greater than in alkaline soils, perhaps greater N and P use efficiency in more acidic soils with less diversity (Fierer and Jackson 2006). This result supports the notion that in tropical areas, soil microbes in acid soils redirect their metabolic energy from growth to cell maintenance (Anderson and Domsch 1993). Therefore, it is not particularly surprising that the numerical value of the microbial N versus P scaling exponent is close to 1.0 in boreal and tropical areas compared to temperate areas with more equitable climates.

4.3. Variant numerical values of microbial N versus P scaling exponents across local sites

Large differences in the numerical values of microbial N versus P scaling exponents are observed across local sites (figure 4). MAP, soil pH, and soil total P play key roles in determining these numerical values across local sites, indicating the observation that soil microbial growth is influenced significantly by climate and soil conditions (Maria *et al* 2014). RDA indicates that soil total P is an important driver in determining the numerical value of microbial N versus P scaling exponents compared to MAP and soil pH (figure 5). This result supports the idea that soil P regulates microbial N and P stoichiometry and nutrient use strategies (Vitousek *et al* 2010, Camenzind *et al* 2018). In addition, our analyses provide empirical evidence that soils with high P concentrations (which support a high microbial composition and diversity) may favor fast growing microorganisms such as bacteria (Delgado-Baquerizo *et al* 2016). However, our understanding of the N versus P scaling relationship in bacteria and fungi is still very limited. Hence, future studies on bacterial and fungal N and P stoichiometry are clearly required.

5. Conclusions

To the best of our knowledge, this study is the first to comprehensively document pairwise soil MBC, MBN, and MBP concentrations and to provide detailed information on microbial N versus P scaling relationships for different ecosystems, soil depths, latitude zones, and local sites at the global scale. Based on the pooled data, the numerical value of the microbial N versus P scaling exponent is 0.89 as well as for different ecosystems, supporting the growth rate hypothesis. However, the data also indicate that the numerical value of the N versus P scaling exponent differs as a function of soil depth, latitudinal zones, and across local sites. Soil total P appears to be the most important factor explaining differences in the numerical values of the microbial N versus P scaling exponent. These findings highlight

the importance of climate and soil factors in shaping soil microbial investment strategies and improve our understanding of nutrient cycling in plant–soil–microbe networks. However, it is clear that additional research is required to understand the influence of climate and soil conditions on microbial N versus P scaling relationships, especially from low- and high-latitude ecosystems. This need is particularly important in the context of temperature-controlled studies to address how global climate change may affect soil temperatures and microbial metabolic and growth rates.

Data availability statement

All data that support the findings of this study are included within the article (and any supplementary files).

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Conflict of interest

The authors declare no competing financial interests.

Author contributions

Z Wang, H Huang and B Yao conceived the study with M Wang and J Wright wrote the first draft of the paper. All authors contributed to the writing of the paper.

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