

# Three-dimensional mapping of carbon, nitrogen, and phosphorus in soil microbial biomass and their stoichiometry at the global scale

**Running title:** Three-dimensional maps of microbial biomass

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## Abstract

Soil microbial biomass and microbial stoichiometric ratios are important for understanding carbon and nutrient cycling in terrestrial ecosystems. Here, we compiled data from 8862 observations of soil microbial biomass from 1626 published studies to map global patterns of microbial biomass carbon (MBC), microbial biomass nitrogen (MBN), microbial biomass phosphorus (MBP), and their stoichiometry using a random forest model. Concentrations of MBC, MBN, and MBP were most closely linked to soil organic carbon (SOC), while climatic factors were most important for stoichiometry in microbial biomass ratios. Modeled seasonal MBC concentrations peaked in summer in tundra and in boreal forests, but in autumn in subtropical and in tropical biomes. The global mean MBC/MBN, MBC/MBP, and MBN/MBP ratios were estimated to be 10, 48, and 6.7, respectively, at 0–30 cm soil depth. The highest concentrations, stocks, and microbial C/N/P ratios were found at high latitudes in tundra and boreal forests, probably due to the higher soil organic matter content, greater fungal abundance, and lower nutrient availability in colder than in warmer biomes. At 30–100 cm soil depth, concentrations of MBC, MBN, and MBP were highest in temperate forests. The MBC/MBP ratio showed greater flexibility at the global scale than did the MBC/MBN ratio, possibly reflecting physiological adaptations and microbial community shifts with latitude. The results of this study are important for understanding C, N, and P cycling at the global scale, as well as for developing soil C-cycling models including soil microbial C, N, and P as important parameters.

**Keywords:** microbial biomass carbon, microbial biomass nitrogen, microbial biomass phosphorus, stoichiometry, terrestrial ecosystem, random forest

## 1 Introduction

Soil microorganisms play crucial roles in terrestrial ecosystem processes, such as carbon (C), nitrogen (N), and phosphorus (P) cycling (Martiny et al., 2006), soil organic matter (SOM) formation (Liang et al., 2019; Rillig and Mummey, 2006), and ecosystem productivity (Van Der Heijden et al., 2008). The stoichiometric ratios of C, N, and P in soil microbes are regarded as indicators of nutrient limitations of organisms and communities (Cleveland and Liptzin, 2007; Manzoni et al., 2010; McGroddy et al., 2004), although global patterns in nutrient availability (Augusto et al., 2017) may differ from patterns in the stoichiometry of microbial biomass (Xu et al., 2013). Recently, it has been proposed that soil microbial biomass should be included as a separate C pool in Earth System Models (ESMs) to improve predictions of global climate change (Fan et al., 2021; Wieder et al., 2013).

Soil microbial biomass has been shown to be associated with a multitude of factors, encompassing edaphic properties such as: SOM content, nutrient stoichiometry and availability, soil texture, structure, moisture, and aeration and climate, e.g., mean annual temperature and precipitation (Chen et al., 2016; de Vries et al., 2012; Li et al., 2014; Xu et al., 2013). These factors affect microbial biomass, either directly by influencing turnover rates and community structures or indirectly by modifying the habitat and resources of microbial communities (Manzoni et al., 2021; Zechmeister-Boltenstern et al., 2015). In addition, biotic factors are important drivers of variation in of soil microbial biomass (de Vries et al., 2012). For example, plants supply rhizosphere-associated microorganisms with C (Fan et al., 2022; Jackson et al., 2019) and provide nutrients through above- and below-ground litter input (Meier and Bowman, 2008). As a consequence, vegetation influences the growth, distribution, and stoichiometry of microorganisms in soils, as demonstrated by the close

relationships of microbial biomass with plant root biomass and litter input (Jing et al., 2021; Kara et al., 2008). The relative effects of climate, soil physico-chemical properties, and vegetation on soil microbial biomass and stoichiometry are difficult to disentangle and are thus rarely reported at the global scale. Further, global patterns are obscured by seasonal variations in soil microbial biomass C, N, and P, possibly related to temporal changes in climate, nutrient availability, and vegetation input (Bargali et al., 2018; Lepcha and Devi, 2020; Patel et al., 2010).

Almost all of the above-mentioned soil physical and chemical factors change with soil depth, affecting the vertical distribution of soil organisms (Liu et al., 2020). Although soil microbial biomass has been found to exhibit an exponential decrease with increasing soil depth (Xu et al., 2013; Chen et al., 2021), the information available on microbial biomass in deeper soils is still scarce, and a global-scale three-dimensional mapping of soil microbial biomass C, N, and P and their stoichiometry is still not available.

On the global scale, soil microbial biomass shows distinct patterns among biomes. Tundra and boreal forests generally have a larger microbial biomass than tropical or subtropical biomes (Wang et al., 2021c; Xu et al., 2013). One reason for this phenomenon could be that soil microorganisms in areas with lower temperatures maintain a larger microbial biomass at lower levels of metabolic activity compared with values observed in warmer regions (Li et al., 2014; Reich and Oleksyn, 2004), resulting in a higher carbon use efficiency (Wang et al., 2021b). Another reason might be that colder regions have larger SOM stocks, which are associated with larger microbial biomass (Crowther et al., 2019). Soil microbial biomass also varies across vegetation types within a single climate zone, but the observed patterns have not been consistent. For example, in subtropical regions forests have been found to have a larger microbial biomass than that of grasslands and croplands

(Tiwari et al., 2019), while in temperate regions grasslands have been reported to have a larger microbial biomass than that of forest and cropland biomes (van Leeuwen et al., 2017).

The stoichiometric ratios of soil microbes reflect the physiological and structural adaptations of microorganisms, at the community level, to their environment (Zhu et al., 2022). Therefore, soil microbial stoichiometry has been found to be related to soil physical and chemical properties, which drives soil nutrient availability and mineralization (Griffiths et al., 2012), and to the stoichiometry of the SOM on which microbes feed (Cleveland and Liptzin, 2007). However, compared with the large stoichiometry gradient in the resources used by soil microbes, microbial biomass C/N remains rather stable, ranging from 8:1 to 12:1, and is thus regarded as relatively homeostatic (Cleveland and Liptzin, 2007; Xu et al., 2013; Zechmeister-Boltenstern et al., 2015). In comparison, recent findings indicate that C/P and N/P ratios in microbial biomass vary more widely, demonstrating a greater stoichiometric plasticity of microorganisms with respect to P (Camenzind et al., 2021; Zhang and Elser, 2017). The authors of these studies proposed that this plasticity might be the result of a physiological adaptation modulating P storage and the building of cell walls.

Changes in microbial stoichiometry can also result from shifts in the microbial community (Heuck et al., 2015), climate conditions, or plant input. For example, the ratio of fungi to bacteria can be important, as soil fungi are characterized by higher C/N/P ratios than bacteria (Strickland and Rousk, 2010). Further, climate can affect the availability and mineralization of nutrients in soils and SOM, thereby influencing the composition of the microbial community and thus the ratios of soil microbial C, N, and P (Nielsen et al., 2009). Plants may affect microbial stoichiometry through rhizodeposition, litter stoichiometry, and their impact on nutrient cycling. This results in an overall close coupling in the stoichiometry of C, N, and P among plants, soils, and microorganisms

(McGroddy et al., 2004).

It remains unclear as to which factor is decisive for microbial stoichiometric ratios, especially at the global scale. Previous assessments have indicated that microbial C/N and microbial N/P are higher at higher latitudes than at lower latitudes (Chen et al., 2016; Cleveland and Liptzin, 2007; Wang et al., 2021c). In contrast, Li et al. (2014) reported a decreasing trend in microbial N/P with increasing latitude. The inconsistency of these results may be partially attributed to the various methods used to measure microbial C/N/P ratios (Xu et al., 2013) or to other factors that vary with latitude, such as aridity (Liu et al., 2020). Consequently, there is still considerable uncertainty in the estimates of microbial stoichiometry reported in global studies.

In this study, we created a global database of the C, N, and P concentrations and C/N/P ratios of soil microbial biomass, measured in all cases by the fumigation-K<sub>2</sub>SO<sub>4</sub> extraction method (Vance et al., 1987). We then used the ensemble learning method to extrapolate unmeasured points. Subsequently, we mapped variations in soil microbial biomass C, N, and P concentrations and their stoichiometric ratios at the 1 km × 1 km latitude–longitude resolution, as well as vertical patterns down to 1 m soil depth, using the random forest method. The objectives of this study were: (1) to statistically evaluate the climatic, edaphic, and vegetation factors predicting the three-dimensional variations in soil microbial C, N, and P concentrations, and their stoichiometric ratios at the global scale; (2) to analyze the driving factors of spatio-temporal variations in soil microbial biomass C, N, and P concentrations and their stoichiometric ratios in different biomes and seasons; and (3) to estimate the flexibility and patterns of microbial stoichiometry, such as C/P versus C/N ratios, at the global scale.

## 2 Material and methods

### 2.1 Data sources and processing

We searched for data from peer-reviewed journal articles (publication year before 2022) using the keyword “soil microbial biomass” in Google Scholar and Web of Science. The criteria for selecting eligible data were as follows: (i) at least one variable of soil microbial biomass C, N, or P was reported; (ii) soil microbial biomass was determined with the chloroform fumigation- $K_2SO_4$  extraction method (Vance et al., 1987), given its wide application and high reliability; (iii) only soil microbial biomass data from control plots was used in the case of manipulation experiments. Following these criteria, our database included 7747, 3635, and 863 observations of soil microbial biomass C, N, and P, respectively, from 1626 published studies (Fig. 1, Table S1). Besides soil microbial biomass C, N, and P concentrations, associated information on the sampling sites was also extracted from the original articles and included in our database: site location (latitude and longitude), climate variables (mean annual temperature and precipitation), biome type, and soil physico-chemical properties (e.g., soil organic carbon (SOC), total nitrogen (TN), total phosphorus (TP), pH, soil bulk density, soil sand, silt, and clay contents, sampling time, and sampling soil depth). The original data was either obtained directly from the tables and supplementary information of the articles or extracted indirectly using GetData Graph Digitizer (<http://www.getdata-graph-digitizer.com/index.php>) when the results were shown in the form of figures in the original publication. In addition to the three soil microbial biomass variables, the ratio of microbial biomass C to microbial biomass N (MBC/MBN), the ratio of microbial biomass C to microbial biomass P (MBC/MBP), and the ratio of microbial biomass N to microbial biomass P (MBN/MBP) were calculated or taken directly from the original articles. The sampling season for MBC was marked as

spring (March to May), summer (June to August), autumn (September to November), or winter (December to February). To conduct a biome-level analysis, the data was aggregated into 11 terrestrial biomes: boreal forest, montane grassland, temperate broadleaf forest, temperate coniferous forest, temperate grassland, tropical/subtropical coniferous forest, tropical/subtropical broadleaf forest, tropical/subtropical grassland, tundra, cropland, and wetland.

## **2.2 Data analysis**

Soil microbial biomass is thought to be mainly affected by soil physico-chemical properties, vegetation, and climate (Liu et al., 2020; Mooshammer et al., 2014b; Xu et al., 2013). We selected eight soil parameters (SOC, TN, TP, pH, silt and clay contents, cation exchange capacity (CEC), and base saturation (Bsat), and five climate/vegetation parameters [mean annual temperature (MAT), mean annual precipitation (MAP), potential evapotranspiration (PET), relative humidity (humidity), and normalized difference vegetation index (NDVI)] as predictors (Table S2). Almost none of the considered studies reported every one of these predictors. We obtained values directly from the original articles if the relevant data was presented there. In cases where studies did not report a given predictor, we extracted the missing data from global data maps or satellite remote sensing data according to the geographical coordinates of the measurement sites. In addition to the above predictors, we also considered soil depth as a covariate in order to predict the concentration of soil microbial biomass at different soil depths (He et al., 2021; Hengl et al., 2017). Further, five climate/vegetation parameters from the four seasons were used to predict soil microbial biomass C for each season. However, due to a lack of seasonal data and small seasonal variations for the eight soil parameters, the average values for the whole year were used in this case.



To identify the best model for predicting soil microbial biomass and stoichiometric ratios, we selected four linear regression models [multiple linear regression model, multiple stepwise regression model (Friedman et al., 2001), least angle regression model (Efron et al., 2004), and elastic net model (Kuhn and Johnson, 2013; Zou and Hastie, 2005)] and four nonlinear models [cubist model (Quinlan, 1992), boosted tree model (Friedman, 2001), bagged tree model (Breiman, 1996), and random forest model (Breiman, 2001)] (Table S3). For all models, we evaluated the strength of prediction using a five-fold cross-validation method implemented with the R package “caret” (v. 6.0-86; Kuhn et al., 2020). Based on this method, the entire dataset was randomly split into five groups. We used 80% of the data for training and the rest for validation.  $R^2$  and root mean square error (RMSE) were used to evaluate model accuracy and performance (Shcherbakov et al., 2013). According to the results of the five-fold cross-validation, the random forest model performed best among all models and was therefore selected to extrapolate the correlations of soil microbial biomass C, N, and P and their ratios with the 14 predictors across the globe. In order to minimize multicollinearity effects, the variable inflation factor (VIF) was calculated for all variables. The variable with the largest VIF was eliminated if its VIF exceeded five, and this step was repeated until all variables had a VIF of less than five (Gareth et al., 2013). The global bulk density obtained from the Harmonized World Soil Database was used to calculate the global stocks of MBC, MBN, and MBP. The mean decrease in accuracy (% IncMSE) was used to assess the relative importance of each variable (Du et al., 2020). The relative uncertainty of the predicted soil microbial biomass C, N, or P or of their stoichiometric ratios was estimated by dividing the absolute error by the global mean of microbial biomass C, N, or P or their stoichiometric ratios. We performed all statistical analyses and created all plots in ArcGIS 10.5 and the R environment v. 4.0.2 (R Core Team, 2018).

## 3 Results

### 3.1 Global patterns of soil microbial biomass carbon, nitrogen, and phosphorus

Based on the five-fold cross-validation, the random forest machine learning algorithm resulted in the highest prediction accuracy for MBC ( $R^2 = 0.79$ ), MBN ( $R^2 = 0.85$ ), and MBP ( $R^2 = 0.63$ ) in the comparison of four linear and four nonlinear models (Fig. S1, Table S3). According to the random forest model, SOC was the most important factor determining soil MBC at the global scale. SOC and TN had the strongest influences on MBN, whereas SOC and PET were the two most important variables influencing soil MBP (Fig. S1). Partial regression analysis indicated that soil MBC and MBN had significantly positive relationships with SOC, TN, TP, MAP, soil silt and clay contents, and NDVI, and significantly negative correlations with MAT, pH, CEC, Bsat, PET, humidity, and soil depth. MBP had significantly positive correlations with SOC, TN, TP, and humidity, and significantly negative relationships with PET, soil depth, MAT, MAP, Bsat, pH, and CEC (Figs. 2, S7-S9).

We present global soil MBC, MBN, and MBP in the 0–30 cm, 30–100 cm, 0–15 cm, and 0–100 cm depth layers (Figs. 3, S5). The modeled global average concentrations of MBC, MBN, and MBP were 673.5 mg C kg<sup>-1</sup>, 97.6 mg N kg<sup>-1</sup>, and 43.7 mg P kg<sup>-1</sup> at 0–30 cm depth (Table S4). The observed average concentrations corresponded to 2.24%, 3.09%, and 5.45% of the total SOC, TN, and TP concentrations, respectively. Soil MBC, MBN, and MBP all exhibited distinct variations across global biomes and climate zones (Fig. 3, Table S4). Among biomes, MBC, MBN, and MBP were generally highest in tundra, followed by boreal forests and wetland. Tropical/subtropical grasslands had the lowest concentrations. Among forest biomes, MBC, MBN, and MBP were highest in boreal regions, followed by temperate and finally tropical/subtropical areas. Among grasslands, MBC,

MBN, and MBP concentrations were significantly higher in montane grasslands than in temperate and tropical/subtropical grasslands. Overall, forests had significantly higher MBC, MBN, and MBP compared with grasslands, whereas there was no significant difference in MBC between broadleaf forests and coniferous forests. MBC, MBN, and MBP decreased with soil depth, and this decrease was more pronounced at higher than at lower latitudes (Fig. 3). Consequently, at 30–100 cm soil depth, temperate coniferous forests had the highest MBC, MBN, and MBP, followed by boreal forests and temperate broadleaf forests (Fig. S4).

The modeled global stocks of soil MBC, MBN, and MBP at 0–30 cm depth were 27.3 Pg C, 4.06 Pg N, and 1.91 Pg P (Table 1). Similar to the patterns observed for the concentrations of C, N, and P in soil microbial biomass, the largest global stocks of MBC, MBN, and MBP were found in tundra, followed by boreal forests, while the smallest stocks occurred in tropical/subtropical coniferous forests, which have the smallest total global area.

### **3.2 Seasonal variation in soil microbial biomass carbon**

The random forest model also had the highest prediction accuracy for MBC in different seasons ( $R^2 = 0.83, 0.77, 0.65$ , and  $0.77$  for MBC in spring, summer, autumn, and winter, respectively; Fig. S2). SOC concentration remained the most important factor affecting MBC in spring, summer, and autumn, whereas TN was the most important in winter (Fig. S2).

The modeled concentration of MBC varied significantly over the four seasons only in tundra and boreal forest, with higher MBC in winter ( $P < 0.05$  for biome  $\times$  season interaction; Fig. 4). Tundra soils had the largest seasonal variation in MBC, with 4.7 times higher concentrations in summer than in winter (Table S5). Soils from temperate coniferous and broadleaf forests also tended to have a lower MBC in winter, while tropical forests, grasslands, and croplands had the highest MBC in

autumn rather than in summer.

### 3.3 Stoichiometric ratios of soil microbial biomass carbon, nitrogen, and phosphorus

The random forest machine learning algorithm had the highest prediction accuracy for MBC/MBN ( $R^2 = 0.51$ ), MBC/MBP ( $R^2 = 0.70$ ), and MBN/MBP ( $R^2 = 0.49$ ) in the five-fold cross-validation comparison of four linear and four nonlinear models (Fig. S3). Compared with the great importance of soil factors for MBC, MBN, and MBP concentrations, climatic factors such as MAP and MAT played a more dominant role in determining microbial stoichiometry (Fig. S3). Based on the partial regression analysis, we found significantly positive relationships between microbial C/N/P ratios and MAP, and significantly negative correlations between microbial ratios and MAT (Figs. 5, S14–S16).

The modeled global mean mass ratios of MBC/MBN, MBC/MBP, and MBN/MBP were 10, 48, and 6.7, respectively, at 0–30 cm depth (Table 2). Microbial stoichiometric ratios were generally higher at higher altitudes (e.g., montane grasslands) and higher latitudes (e.g., tundra and boreal forests) than at lower altitudes and latitudes (e.g., tropical/subtropical forests and grasslands; Fig. 6). For MBC/MBN, a higher ratio was found in tundra, wetland, and boreal forests, while the ratio was smallest in temperate coniferous forests. For MBC/MBP and MBN/MBP, tundra, wetland, boreal forests, and montane grasslands had the highest ratios. Croplands and tropical/subtropical grasslands had the lowest ratios of MBC/MBP and MBN/MBP, respectively. Negligible differences in microbial C/N/P ratios were found between forests and grasslands within a given climate zone. The variation in MBC/MBP was substantially greater than that in MBC/MBN (Table 2). Among biomes, MBC/MBP varied from 36 in croplands to 68 in tundra and had an overall coefficient of variance (CV) of 24%. MBC/MBN varied only slightly, from 9.1 in temperate coniferous forests to

10.8 in tundra, and had an overall CV of 11%.

## **4 Discussion**

### **4.1 Concentrations of microbial biomass carbon, nitrogen, and phosphorus**

Our extensive analysis and modeling of data from 1626 articles revealed distinct global patterns regarding the concentration and stoichiometry of microbial biomass. Microbial biomass C, N, and P concentrations were highest in cold biomes such as tundra, boreal forest, and mountain grassland. In agreement with this finding, microbial biomass C, N, and P concentrations were negatively related to mean annual temperature, which is consistent with results from a previous meta-analysis in which climate was found to exert the strongest effects on microbial C, N, and P (Xu et al., 2013). One reason for this pattern might be the physiological adaptation of soil microorganisms to climatic conditions, with lower metabolic activity but a relatively large microbial biomass at lower temperatures (Li et al., 2014; Reich and Oleksyn, 2004). However, our random forest modeling indicated a dominant influence of SOC concentration on microbial biomass C, N, and P at the global scale. We therefore attribute the global patterns of microbial biomass C, N, and P to an indirect effect of climate, resulting from greater SOM concentration in colder biomes and wetlands, rather than to direct effects on microbial physiology and activity (Crowther et al., 2019). Higher SOM contents in colder biomes and wetlands may, however, also result from a distinct microbial processing of SOM under harsh conditions. At low temperatures and under water-saturated conditions, decomposition is slow while the formation of microbial biomass remains relatively high; as microbial necromass strongly contributes to SOM, this leads to a high SOM content (Liang et al., 2019; Wang et al., 2021a).

Our results demonstrate that, in addition to having larger concentration, colder biomes also have greater seasonal variation in microbial biomass C concentration than warmer biomes in the tropics and subtropics. Our synthesis based on data from various sites with soils sampled at various times is supported by assessments of seasonal patterns at specific sites. Specifically, a larger microbial biomass has been observed in summer than in winter in cold biomes (Bargali et al., 2018; Lepcha and Devi, 2020; Patel et al., 2010), while microbial biomass has been found to be largest in autumn in warmer biomes (Babur et al., 2021; da Silva et al., 2012; Yao et al., 2011). The likely reason for this contrasting pattern is the greater seasonal variation in temperature at higher than at lower latitudes, with microbial biomass peaking in the active warm season but decreasing during prolonged and intensive frost periods (Gao et al., 2021). In contrast, in tropical and subtropical regions, the rainfall distribution appears to be more decisive (Marañón-Jiménez et al., 2022).

Less data was available from deeper soils, but the observed global patterns indicate that the vertical decline in the concentrations of MBC, MBN, and MBP with increasing soil depth is less pronounced in tropical and temperate biomes than in boreal forests and in tundra. Consequently, the relative importance of deeper soils in harboring microbial biomass is greater under warmer climatic conditions. We relate this finding to the more advanced development of soils at greater depths and the occurrence of deeper-rooting plants in temperate and tropical zones than in subpolar and polar zones (Schenka and Jackson, 2005; Yang et al., 2016), strongly suggesting that global patterns of microbial C, N, and P result from the long-term interplay of climate, vegetation, and soil formation.

#### **4.2 Spatial patterns of C/N/P ratios in microbial biomass**

Our study gives evidence that, along with the increasing concentrations of microbial biomass C, N, and P towards colder biomes, microbial C/N/P ratios increase with increasing latitude and are

highest in tundra and boreal forests (Fig. 6). These patterns in microbial stoichiometry parallel the global patterns of decreasing N availability and decreasing N content in plant detritus, as well as an increasing soil C/N ratio, with decreasing MAT and MAP (Augusto et al., 2017). This signifies a pronounced microbial adaptation on the cellular and/or community level to N scarcity despite the notion of a general homeostasis of soil microorganisms (Manzoni et al., 2021; Zechmeister-Boltenstern et al., 2015). Nonetheless, soil microorganisms can adjust their cell constituents in response to nutrient-poor conditions, for instance by modifying the chemical structure of cell walls or altering nutrient storage (Mooshammer et al., 2014a; Zechmeister-Boltenstern et al., 2015).

Our global assessment revealed that the N/P ratio in microbial biomass increases towards colder ecosystems. This contrasts with global patterns in nutrient availability of a stronger latitudinal decline in N than in P (Vitousek and Farrington, 1997; Augusto et al., 2017). We regard this opposing pattern as an indication of a shift in microbial community composition with latitude, suggesting that community shifts are more important than direct physiological adjustments to nutrient availability (Camenzind et al., 2021) in driving microbial stoichiometry at the global scale. Towards higher latitudes, microbial communities shift at the group level, with an increasing fungi:bacteria ratio (He et al., 2020). As soil fungi have wider stoichiometric ratios, including N/P, than bacteria (Keiblinger et al., 2010), this implies that the higher C/N/P ratios in microbial biomass in colder, more humid and nutrient-poorer biomes very likely mirror increasing fungi:bacteria ratio. The contribution of fungi has been found to increase with decreasing temperature (Yang et al., 2022), decreasing precipitation (He et al., 2020), and increasing latitude (Bahram et al., 2018). Also, within fungal communities, there is a shift in tree-associated mycorrhizae from AM-fungi to ECM-fungi towards higher latitudes (Steidinger et al., 2019) where soils are richer in SOM and more N-limited (Averill

et al., 2014), with ECM being more adapted to N-poor environments and having higher C/N/P ratios than other fungal guilds (Zhang and Elser, 2017).

### **4.3 Higher plasticity of microbial C/P than C/N ratio**

The data compiled here indicate that the global average of C/N/P mass ratios in microbial biomass of 48:7:1 is substantially smaller than values reported for plant detritus and SOM (e.g., Cleveland and Liptzin, 2007; Xu et al., 2013). Adjustment of stoichiometry is one of the strategies microorganisms use to overcome the elemental differences in their resources during microbial decomposition (Manzoni et al., 2021). Observations of a rather rigid C/N ratio in microbial biomass have suggested that microbial communities are rather homeostatic, and adjustment of microbial stoichiometry has therefore been regarded to be of minor importance (Mooshammer et al., 2014a; Zechmeister-Boltenstern et al., 2015). However, our global dataset indicates a substantially greater plasticity of the C/P ratio compared with the C/N ratio in microbial biomass. While the microbial C/N ratio varies by only 11% across all major biomes, the C/P ratio approximately doubles from subtropical to tundra biomes. This considerable span supports recent mechanistic studies demonstrating that the C/P ratio differs widely among fungal species (Spohn, 2016) and guilds (Zhang and Elser, 2017) and even varies greatly within fungal species in response to the P supply (Camenzind et al., 2021).

Reasons for this greater variation in the C/P ratio include a physiological adaptation of microorganisms in adjusting P storage as polyphosphates and/or modifying the chemical structure of cell walls (Kulakovskaya, 2015). Moreover, the difference between bacteria and fungi is greater for C/P than for C/N (Mouginot et al., 2014), implying that microbial community shifts at the global scale (Crowther et al., 2019) are also associated with larger changes in microbial C/P than in C/N.



We cannot rule out that the greater range in the microbial C/P ratio may be partially attributed to methodological difficulties in the analysis of microbial P. Specifically, internal standards have to be used to correct for the sorption of released phosphate during the fumigation-extraction procedure (McLaughlin et al., 1986). Nonetheless, we speculate that the greater plasticity of microbial P could be one of the reasons why terrestrial ecosystems are less limited by P than by N (Vitousek et al., 2010), except in situations where P availability is constrained by the extremely strong binding of phosphate to secondary minerals, such as in tropical soils (Augusto et al., 2017).

#### **4.4 Limitations**

Some limitations and prediction uncertainties exist in this study. First, more than 70% of the data originated from croplands, forests, and grasslands, while much less data was available for tundra and boreal forests, especially for Eastern Russia. Data was also limited from tropical rainforests in Western Africa and deserts, which might have induced biases in global estimates. Second, the number of observations was smaller for winter than for other seasons, especially at high latitudes and altitudes. Further, seasonal data on microbial biomass was retrieved from various studies conducted in multiple years, seasons, and locations, which might have yielded different results compared with repeated assessments at the same locations. Moreover, seasonal data was too scarce to analyze the seasonality of microbial stoichiometry. Third, the number of observations in subsoils (>30 cm depth) was substantially smaller than in topsoils (0–30 cm depth), contributing to the fact that deeper soils remain a major unknown in terrestrial ecology. Finally, some predictors (e.g., cation exchange capacity, base saturation, potential evapotranspiration, relative humidity, and normalized difference vegetation index) were not available in all studies, and filling in missing values with global raster data leads to greater uncertainties.

In summary, our study contributes to the three-dimensional mapping of soil microbial biomass C, N, and P concentrations and their stoichiometric ratios at the global scale. Our results show that soil properties, climate, and vegetation jointly determine the C, N, and P concentrations and their ratios. Tundra and boreal forest biomes have the highest concentrations, stocks, and seasonal variations in microbial C, N, and P, as well as the highest C/N/P ratios. We relate this pattern to the high SOM content in these cold regions and their N-poor and/or water-logged conditions, promoting fungal communities with high stoichiometric ratios. Physiological adaption may also contribute to a high C/P ratio in microbial biomass. Consequently, we suggest that high microbial C/P and N/P ratios are indicative of oligotrophic conditions, although soil microorganisms are generally regarded as been primarily limited by carbon and energy (e.g., Gunina and Kuzyakov, 2022). However, understanding microbial stoichiometry appears to be insufficient to disentangle N and P limitation, as the highest N/P ratios occur in primarily N-limited high-latitude systems. Our study reveals that microbial communities are highly homeostatic with respect to their C/N ratio at the global scale but show a comparatively greater flexibility in their C/P ratio. We relate this greater plasticity of microbial C/P to physiological adjustment and to microbial community shifts, which have consequences for the processing of organic matter in nutrient-poor environments. These findings challenge current approaches to modeling microbial adaptations to nutrient limitation, which primarily builds on knowledge of the N cycle (e.g., Manzoni et al., 2021) and assumes a pronounced homeostasis of microbial communities.

#### **Code and data availability**

The R code and global maps generated in this study are available at <https://doi.org/10.5281/zenodo.6615713>. Soil microbial C, N, and P from any depth range are

available from the authors upon request.

#### **Author contributions**

DG and EB developed the original idea for the study. DG completed the literature search. DG, EB, YW, FH and SZ conducted data analysis. The manuscript was written by DG, EB, and FH and was revised and discussed by all of the coauthors.

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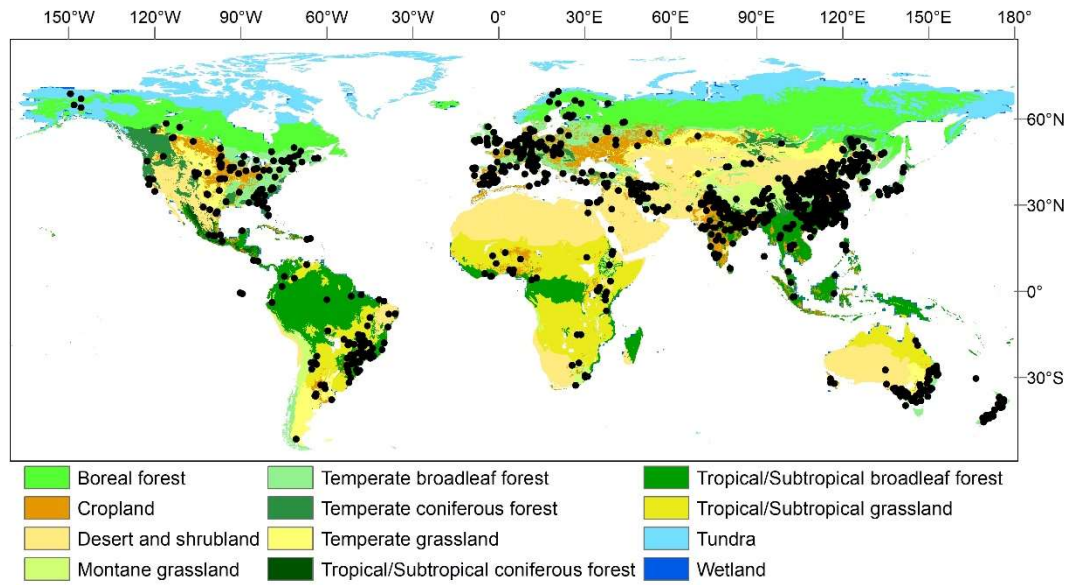
**Table 1 Modeled global stocks of soil microbial biomass carbon (MBC), nitrogen (MBN), and phosphorus (MBP) at 0–30 cm soil depth in major biomes.**

Biome	Area (million km <sup>2</sup> )	MBC (Pg C)	MBN (Pg N)	MBP (Pg P)
Boreal forest	15.1	6.12	0.98	0.45
Montane grassland	5.1	0.87	0.12	0.07
Temperate broadleaf forest	9.7	1.45	0.24	0.12
Temperate coniferous forest	3.9	0.63	0.11	0.06
Temperate grassland	7.2	0.80	0.12	0.06
Tropical/subtropical broadleaf forest	20.2	3.10	0.43	0.18
Tropical/subtropical coniferous forest	0.6	0.10	0.01	0.01
Tropical/subtropical grassland	19.4	1.99	0.30	0.13
Tundra	11.5	7.58	1.10	0.45
Cropland	11.6	1.46	0.21	0.10
Wetland	1.5	0.47	0.07	0.03
Global total	132.7	27.3	4.06	1.91

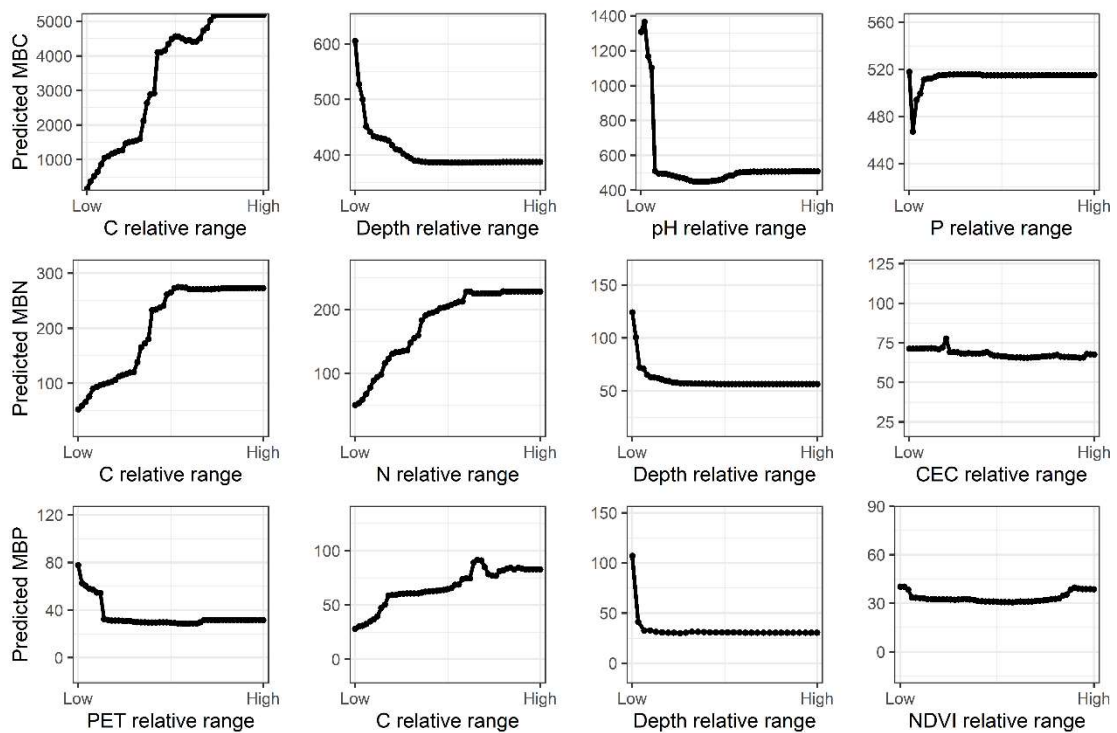
**Table 2 Modeled mean stoichiometric ratios and their coefficients of variance (CV) of soil microbial biomass carbon, nitrogen, and phosphorus at 0–30 cm soil depth in different major biomes.** Values are reported as mean  $\pm$  standard deviation. Different lowercase letters in a column indicate significant differences among biomes ( $P < 0.05$ ). MBC/MBN, ratio of microbial biomass carbon to microbial biomass nitrogen; MBC/MBP, ratio of microbial biomass carbon to microbial biomass phosphorus; MBN/MBP, ratio of microbial biomass nitrogen to microbial biomass phosphorus.

Biome	MBC/MBN	CV (%)	MBC/MBP	CV (%)	MBN/MBP	CV (%)
Boreal forest	10.2 $\pm$ 0.8 <sup>d</sup>	8	59 $\pm$ 11 <sup>c</sup>	19	8.8 $\pm$ 0.9 <sup>a</sup>	10
Montane grassland	9.3 $\pm$ 1.3 <sup>h</sup>	14	62 $\pm$ 25 <sup>b</sup>	40	8 $\pm$ 1.9 <sup>c</sup>	24
Temperate broadleaf forest	9.2 $\pm$ 0.9 <sup>i</sup>	10	37 $\pm$ 7.8 <sup>i</sup>	21	6.2 $\pm$ 1.4 <sup>g</sup>	23
Temperate coniferous forest	9.1 $\pm$ 0.9 <sup>j</sup>	10	43 $\pm$ 15 <sup>g</sup>	34	7 $\pm$ 1.7 <sup>e</sup>	24
Temperate grassland	9.3 $\pm$ 1.2 <sup>h</sup>	13	45 $\pm$ 12 <sup>f</sup>	27	6.7 $\pm$ 1.3 <sup>f</sup>	19
Tropical/subtropical broadleaf forest	9.7 $\pm$ 1.3 <sup>g</sup>	13	38 $\pm$ 7.3 <sup>h</sup>	19	5.3 $\pm$ 1.1 <sup>i</sup>	21
Tropical/subtropical coniferous forest	9.8 $\pm$ 1.2 <sup>f</sup>	12	38 $\pm$ 5.5 <sup>hi</sup>	15	5.8 $\pm$ 0.9 <sup>h</sup>	16
Tropical/subtropical grassland	9.9 $\pm$ 1.2 <sup>e</sup>	12	37 $\pm$ 8.1 <sup>j</sup>	22	5.1 $\pm$ 0.9 <sup>i</sup>	18
Tundra	10.8 $\pm$ 0.6 <sup>a</sup>	6	68 $\pm$ 9.7 <sup>a</sup>	14	8.4 $\pm$ 0.7 <sup>b</sup>	8
Cropland	9.8 $\pm$ 1.4 <sup>f</sup>	14	36 $\pm$ 6.3 <sup>k</sup>	18	5.9 $\pm$ 1.1 <sup>h</sup>	19
Wetland	10.4 $\pm$ 1.2 <sup>c</sup>	12	56 $\pm$ 18 <sup>d</sup>	32	7.4 $\pm$ 1.6 <sup>d</sup>	22
Global mean	10	11	48	24	6.7	18

**Figure legends:**

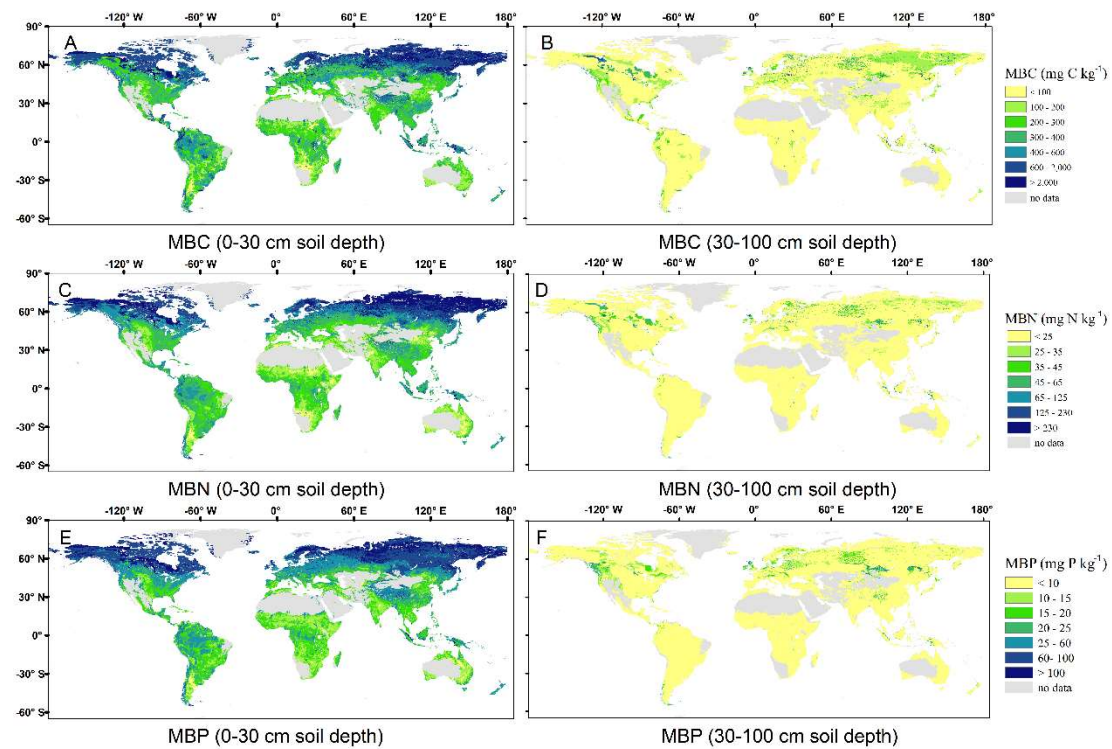


**Figure 1 The spatial distribution of the sampling sites (black dots) considered in this study.**

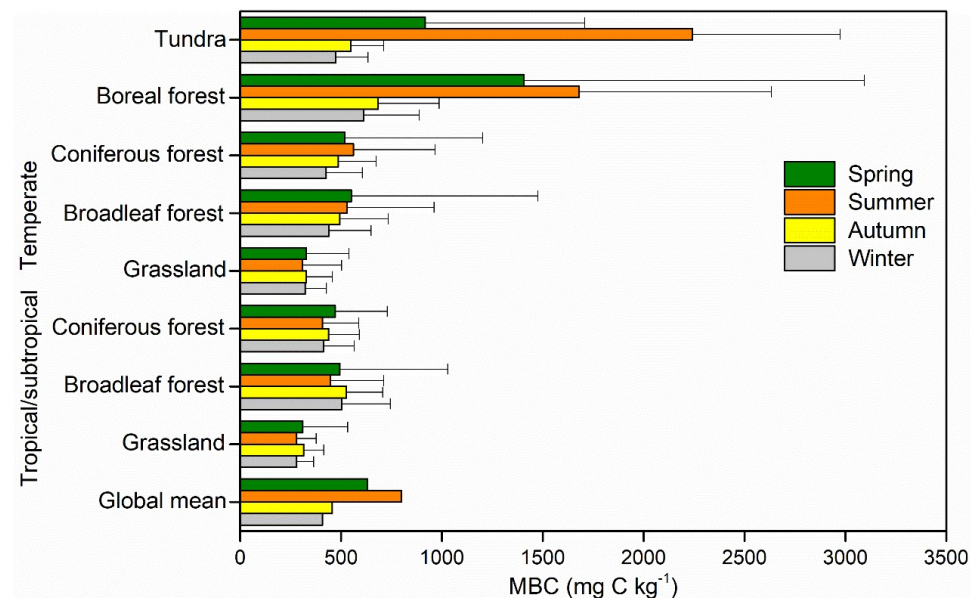


**Figure 2 Partial dependence plots indicating the dependence on different predictors of microbial biomass carbon (MBC), microbial biomass nitrogen (MBN), and microbial biomass phosphorus (MBP) at 0–30 cm soil depth. C, soil organic carbon (%); N, soil total nitrogen ( $\text{g N kg}^{-1}$ ); P, soil total phosphorus ( $\text{mg P kg}^{-1}$ ); pH, soil pH; CEC, cation exchange capacity ( $\text{cmol kg}^{-1}$ ); PET, potential evapotranspiration (mm); NDVI, normalized difference vegetation index; depth, soil depth (cm).**

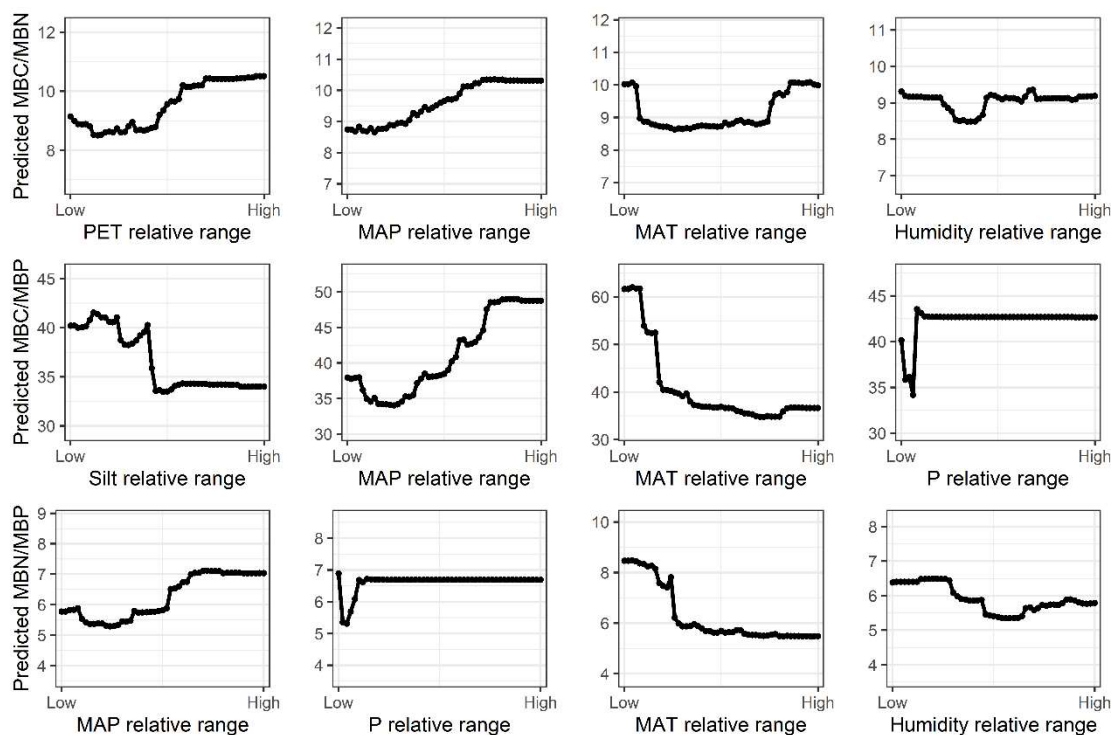




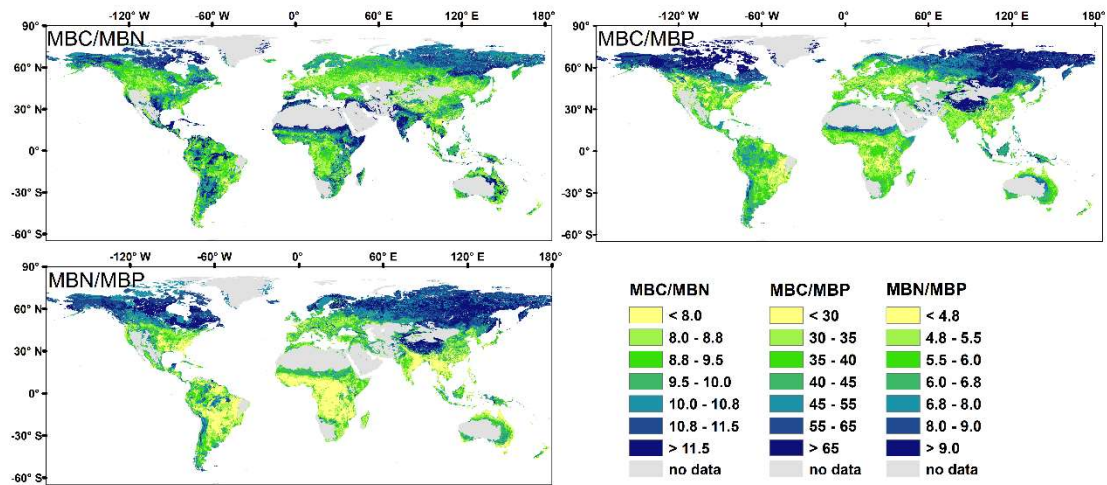
**Figure 3 Modeled global patterns of microbial biomass carbon (MBC), microbial biomass nitrogen (MBN), and microbial biomass phosphorus (MBP) at soil depths of 0–30 cm and 30–100 cm.**



**Figure 4 Modeled global patterns of microbial biomass carbon (MBC) at 0–30 cm soil depth in different seasons.**



**Figure 5** Partial dependence plots indicating the dependence on different predictors of the microbial stoichiometric ratios at 0–30 cm soil depth. MBC/MBN, ratio of microbial biomass carbon to microbial biomass nitrogen; MBC/MBP, ratio of microbial biomass carbon to microbial biomass phosphorus; MBN/MBP, ratio of microbial biomass nitrogen to microbial biomass phosphorus; MAP, mean annual precipitation (mm); MAT, mean annual temperature (°C); P, soil total phosphorus (mg P kg<sup>-1</sup>); silt, soil silt content (%); PET, potential evapotranspiration (mm); humidity, average annual relative humidity (%).



**Figure 6 Modeled global ratios of microbial biomass carbon to microbial biomass nitrogen (MBC/MBN), microbial biomass carbon to microbial biomass phosphorus (MBC/MBP), and microbial biomass nitrogen to microbial biomass phosphorus (MBN/MBP) at 0–30 cm soil depth.**