



Global patterns and predictors of soil microbial biomass carbon, nitrogen, and phosphorus in terrestrial ecosystems

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ARTICLE INFO

Keywords:

Soil microbial biomass carbon
Soil microbial biomass nitrogen
Soil microbial biomass phosphorus
Spatial pattern
Terrestrial ecosystems

ABSTRACT

Soil microbes play key roles in driving and regulating nutrient cycling in terrestrial ecosystems. However, a lack of global-scale information regarding the distribution of soil microbial biomass carbon (SMB C), nitrogen (SMB N), and phosphorus (SMB P) in terrestrial ecosystems has limited our ability to incorporate the broad-scale soil microbial nutritional properties and the associated processes into biogeochemical models. Here, we synthesized a global dataset including 3801 observations for SMB C, 3154 observations of SMB N, and 2429 observations of SMB P in the top 0–30 cm soil depth. Based on this comprehensive global dataset, we generated quantitative and spatially explicit maps of SMB C, N, and P across terrestrial ecosystems using a random forest approach. We also quantified the relative importance of multiple environmental variables in predicting the spatial variation of SMB C, N, and P concentrations and then made further predictions at a global scale. Soil organic carbon (SOC) was the most important factor in predicting SMB C, N, and P at a global scale. At the global scale, the storage of SMB C, N, and P were estimated to be 23.13 Pg C, 3.93 Pg N and 2.16 Pg P in the top 0–30 cm soil surface, respectively. Our global maps of SMB C, N, and P presented here can be used to constraint Earth system models, and provide the first step forward to predict the roles of soil microbial nutrients in terrestrial nutrient cycling.

1. Introduction

Carbon (C), nitrogen (N), and phosphorus (P) are generally regarded as the most important elements in terrestrial ecosystems because their interactions play key roles in global biogeochemical cycling and ecosystem function (Marschner, 2012). Soil microbes, as the main decomposers within terrestrial ecosystems, perform major roles in driving and regulating terrestrial ecosystem processes (Bardgett and van der Putten, 2014) and important nutrient cycling, such as soil C sequestration (Mooshammer et al., 2014; Spohn, 2016), soil organic matter decomposition (Heuck et al., 2015), soil N mineralization (Li et al., 2019a), and nutrient recycling (Bardgett et al., 2008; Handa et al., 2014)

as well as soil formation (Rillig and Mummey, 2006), and then affect the pattern and dynamics of ecosystem productivity (van der Heijden et al., 2008). Soil microbial biomass carbon (SMB C), nitrogen (SMB N) and phosphorus (SMB P) are crucial elemental components of the soil microbial biomass (Singh and Gupta, 2018; Chen et al., 2021). Given the spatial heterogeneity of SMB C, N, and P across major biomes, the knowledge of spatial distribution of SMB C, N, and P is important for global nutrient cycling (Martiny et al., 2006). In addition, due to the important roles of soil microbes in plant-soil-microbe systems and soil microbial biomass as a major reservoir of soil available C, N and P, spatially-explicit information about SMB C, N, and P at a global scale will improve our understanding of nutrient cycling and terrestrial

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<https://doi.org/10.1016/j.catena.2022.106037>

Received 29 September 2021; Received in revised form 13 December 2021; Accepted 10 January 2022

Available online 19 January 2022

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ecosystem dynamics, particularly in the contexts of global environmental changes. Yet to date, we still lack a quantitative and spatially explicit understanding of SMB C, N, and P that could lay the foundation work in predicting future changes in terrestrial nutrient cycling.

It is generally assumed that abiotic factors, such as climate and soil chemical properties, play important if not the most important roles in regulating SMB C, N, and P at a global scale (Xu et al., 2013; Li et al., 2014). For example, Xu et al. (2013) proposed that climate variables (mean annual temperature, MAT; mean annual precipitation, MAP) regulated SMB C and N, whereas Li et al. (2014) reported that soil chemical properties (e.g. soil N and P contents, and soil pH) explained most of the variation in SMB N and P in global forest ecosystems. The relative importance of climatic and soil chemical properties in determining SMB C, N, and P remain unresolved at a global scale. In addition, a myriad of different methods have been used to determine soil microbial biomass, which could cause uncertainty (Joergensen et al., 2011) regarding the evaluation of the variation in SMB C, N, and P at a global scale (Cleveland and Liptzin, 2007; Hartman and Richardson, 2013; Xu et al., 2013).

In addition to the effects of climate and soil chemical properties, soil physical properties (e.g., soil order and texture) can also influence nutrient availability and water-holding capacity (de Vries et al., 2012; Chen et al., 2016), and therefore drive changes in SMB C, N, and P (Griffiths et al., 2011; Delgado-Baquerizo et al., 2013). For instance, soil organic carbon and structure regulated SMB C across the arid and semi-arid grasslands in northern China (Hu et al., 2014). Moreover, soil depth and land cover type are also important factors controlling SMB C, N, and P cycling processes (Fanin et al., 2013; Bahram et al., 2018). For example, shifts in soil microbial C:N:P stoichiometry are related to changes in soil depth and aboveground biomass at regional scales (Liu et al., 2020). Nonetheless, the relative importance of climatic, plant, or soil chemical and physical properties controlling spatial distribution of SMB C, N, and P at a global scale remains relatively unclear. Most importantly, yet to date, we still lack a quantitative and spatially explicit understanding of SMB P at a global scale due to the limited data. Collectively, an improved global understanding of the determinants of SMB C, N, and P would offer a unique opportunity to benchmark and improve C, N, and P dynamics in terrestrial ecosystems. To address these knowledge gaps, we compiled a comprehensive global dataset of chloroform fumigation-extraction (CFE) derived SMB C, N, and P concentrations from surface soil horizons (at a depth of 0–30 cm). The CFE protocol was used because it is the most frequently used protocol across a wide range of soil types and provides an index of total soil microbial biomass which contains all bacteria and fungi (Fierer et al., 2009).

The objectives of the present study were to generate quantitative and spatially explicit maps of SMB C, N, and P at a global scale using a machine learning algorithm approach and quantify the relative importance of climate, plant, and soil variables for predicting the spatial variation of SMB C, N, and P in the top 0–30 cm soil depth. We answer the following questions: (1) Which factors are the most important for predicting the spatial variation of SMB C, N, and P in the top 0–30 cm soil depth? (2) How much SMB C, N, and P is stored in the top 0–30 cm of soil for major biomes and globally?

2. Materials and methods

2.1. Data compilation

A large dataset of SMB C, N, and P was compiled from a broad range of published literature by searching for ‘soil microbial biomass’ in Google Scholar (<http://scholar.google.com>), Web of Science (<http://apps.webofknowledge.com>), and the China National Knowledge Infrastructure Database (<http://cnki.net>) from the earliest publication. To avoid bias in selecting publications, the criteria for selecting eligible data were: (1) at least one of SMB C, N, or P concentrations must be reported; (2) the data reported for SMB C, N, and P concentrations were

measured using the chloroform fumigation-extraction (CFE) technique (Vance et al., 1987). The CFE technique quantifies SMB C, N and P concentrations were calculated as the difference between non-fumigated and fumigated extracts using a conversion factors of 0.45, 0.54, and 0.4, respectively (Joergensen and Mueller, 1996) (Brookes et al., 1982); (3) the data had to come from control plots if the reported results are based on manipulation experiments; (4) the data had to come from the top 0–30 cm soil depth (data from unspecified soil depths were excluded). We also included data provided by Wang et al. (2021) and by Xu et al. (2013) that met these criteria.

Site descriptors were also recorded in the dataset from the original articles, including geographic location (i.e., latitude and longitude), climate variables (i.e., mean annual temperature MAT, mean annual precipitation MAP), soil physical attributes (i.e., sand and clay content, and soil order), soil chemical properties (i.e., soil pH, soil organic carbon; SOC, soil total N and P), and land cover type. The original data were obtained from the text, tables and appendices of the original publications, or extracted from figures using GetData Graph Digitizer (version 2.22). When the geographical coordinates and climatic factors were unavailable in the original articles, we sourced our data from the Global Gazetteer Version 2.2 (<http://www.fallingrain.com/world/index.html>) and the WorldClim global climatic database (<http://worldclim.org/bio-clim>) with a grid precision of 30×30 arc sec according to geographic location. Missing soil physical–chemical properties and soil-types were evaluated using the global harmonized database with high resolution of 30×30 arc sec (<http://openlandmap.org>) (Batjes, 2016). Land cover type was determined from the database of socioeconomic data and applications with a resolution of 30×30 arc sec (<https://sedac.ciesin.columbia.edu>). To standardize the data, we converted all SMB C, N, and P concentrations values into units of mg kg^{-1} dry soil. A total of 789 distinct sites worldwide from 279 published studies composed the dataset (Fig. 1; A list of data sources is provided in the supplementary material). The observations came from nine major terrestrial biomes, including cropland, boreal forest, tropical/subtropical forest, temperate forest, shrubland, grassland, desert, tundra and wetland.

2.2. Data analyses

The total dataset of SMB C ($n = 3801$), N ($n = 3154$) and P ($n = 2429$) was used to examine the environmental controls and geospatial distribution of these essential elements in soil microbes, and to further generate the corresponding spatially explicit global maps. The machine-learning algorithm Random Forest, an ensemble regression tree approach (Breiman, 2001), was used to extrapolate the relationships of the SMB C, N, and P with the 10 predictors across the globe, and to generate spatially explicit, quantitative maps at a global scale. The 10 predictors were suggested to be important by previous studies (Xu et al., 2013; Li et al., 2014; Chen et al., 2016; Zechmeister-Boltenstern et al., 2015; Liu et al., 2020) and were derived from the original studies or global map layers that include soil physical–chemical properties (i.e., soil clay and sand content, SOC, soil pH, soil total N and P) and soil type (soil order), climate variables (i.e., MAT, MAP), and biotic factors (i.e., vegetation land cover). The strength of prediction was evaluated using 5-fold cross validation which was performed using the R package caret (v. 6.0–86) (Kuhn, 2020). In this method, the whole dataset was randomly classified into five folds, each of which contained 20% of the data. One fold was used for validation data, whereas the other four folds were used for training data. Then another fold of data was used for validation, and the remaining four were used for training, generating five validation trials (He et al., 2021). The final models were used to generate the global maps at 0.5° resolution. To predict the uncertainty of each map cell, we used the bootstrap samples with quantile regression forests technique to map the conditional standard deviations (SDs) (Meinshausen, 2006). SDs were calculated to represent the uncertainty using the `quantregForest` function in the `quantregForest` R package (Meinshausen, 2017).

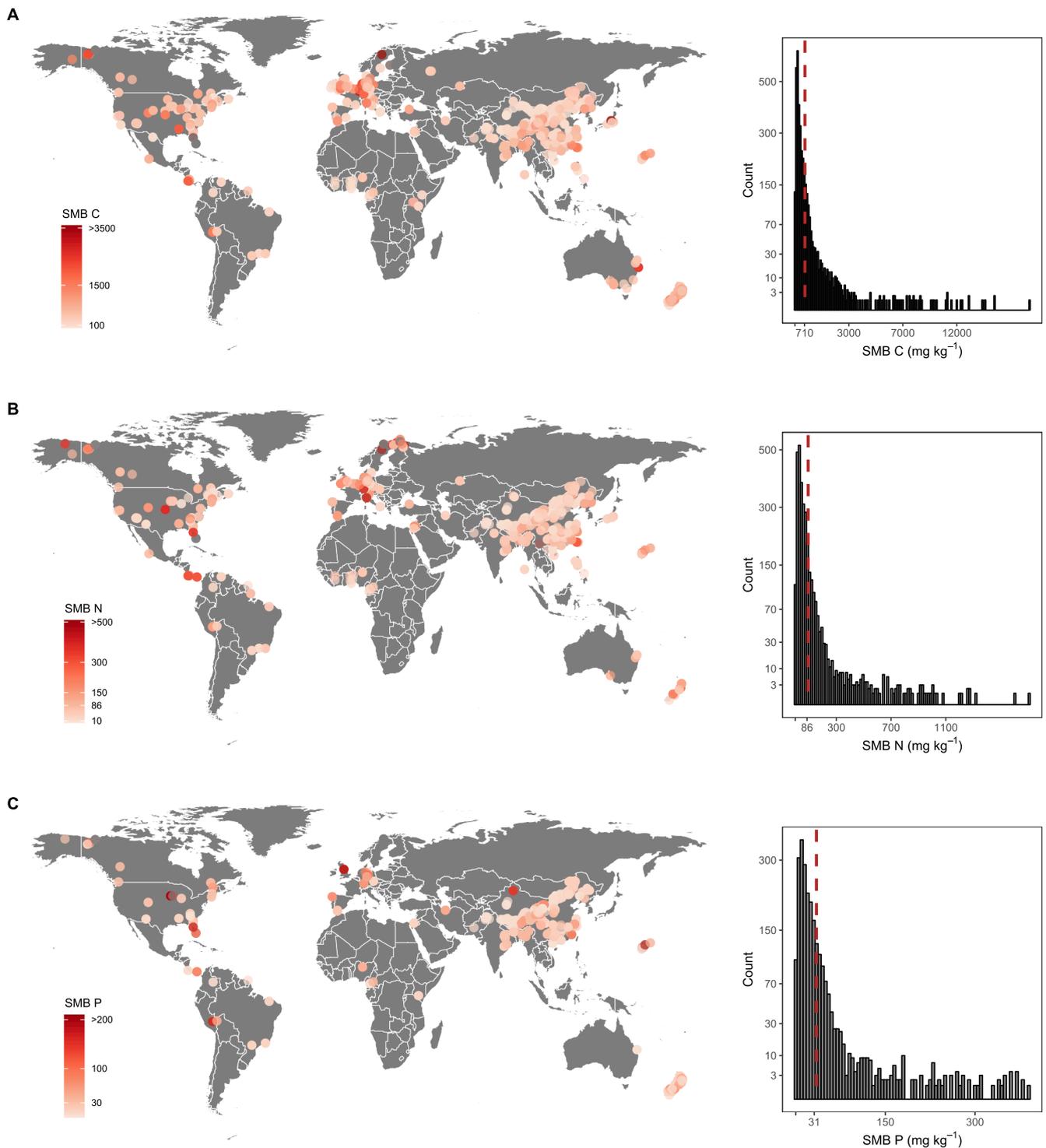


Fig. 1. Global distributions of sampling sites. (A) soil microbial biomass carbon (SMB C), (B) soil microbial biomass nitrogen (SMB N), and (C) soil microbial biomass phosphorus (SMB P).

To examine the 10 potential predictors hypothesized to control SMB C, N, and P at a global scale, machine learning algorithms (random forest) were then used to determine the relative importance of each variable (Du et al., 2020). Mean decrease in accuracy (% IncMSE) was used as a criterion of success, and the variables with greater values of % IncMSE were identified as important in influencing SMB C, N, and P. Pearson correlation coefficients were calculated for all pairwise combinations of variables to evaluate their interrelationship structure. We

calculate SMB C, N, and P storage in 0–30 cm based on our predicted SMB C, N, and P concentration maps, a global soil density map (0–30 cm depth), and a global terrestrial surface area map (antarctica excluded) (Hengl et al., 2017). The global terrestrial surface area map (including areas of different land cover) is generated by computing the approximate surface area of cells ($0.5^\circ \times 0.5^\circ$ in our study) in a longitude/latitude projection, which was carried out using the area function in the raster R package (Hijmans et al., 2021). Statistical analyses were

Table 1

Summary of total soil organic carbon, nitrogen, and phosphorus, and soil microbial biomass C, N, and P concentrations in the top 0–30 cm soil depth layer at the global scale and across nine major biomes.

Biomes	SOC (g kg ⁻¹)	STN (g kg ⁻¹)	STP (g kg ⁻¹)	SMB C (mg kg ⁻¹)	SMB N (mg kg ⁻¹)	SMB P (mg kg ⁻¹)
Boreal Forest	107.7 ^c (18.3–501.3)	5.1 ^b (0.1–222.4)	0.7 ^b (0.5–1.4)	2062.8 ^b (37.0–7985.0)	234.3 ^b (4.0–996.0)	174.3 ^a (30.0–329.0)
Cropland	27.3 ^c (0.6–496.0)	2.2 ^c (0.1–27.0)	0.6 ^b (0.0–2.2)	716.2 ^c (19.0–5623.0)	70.9 ^c (1.5–459.0)	30.9 ^c (0.9–226.0)
Desert	50.9 ^d (0.3–272.4)	0.3 ^d (0.2–1.0)	0.6 ^b (0.1–0.9)	172.3 ^c (0.5–979.1)	57.1 ^f (0.3–260.0)	20.9 ^c (14.8–25.9)
Grassland	31.1 ^e (0.6–447.8)	2.8 ^c (0.1–24.9)	0.6 ^b (0.0–2.2)	489.7 ^d (8.7–3412.0)	58.1 ^f (0.4–499.9)	24.0 ^c (0.2–239.0)
Shrubland	55.9 ^d (1.0–523.0)	2.6 ^c (0.1–24.9)	0.6 ^b (0.0–1.1)	799.0 ^c (56.0–6948.0)	157.7 ^c (5.0–541.2)	61.4 ^b (0.7–168.4)
Temperate Forest	46.6 ^d (1.7–227.0)	2.9 ^c (0.2–19.5)	0.6 ^b (0.0–2.0)	707.2 ^c (4.3–9285.0)	109.3 ^d (0.4–732.1)	27.8 ^c (0.5–271.0)
Tropical/Subtropical Forest	53.2 ^d (2.6–329.0)	3.7 ^c (0.2–22.0)	0.6 ^b (0.1–1.6)	400.5 ^d (8.0–3151.0)	68.4 ^c (3.4–578.8)	25.6 ^c (0.6–368.6)
Tundra	187.9 ^a (10.1–584.0)	9.4 ^a (1.1–23.2)	0.9 ^a (0.1–2.1)	3407.6 ^a (130.0–9390.0)	443.8 ^a (15.0–960.0)	181.5 ^a (2.0–390.0)
Wetland	149.5 ^b (14.6–338.9)	9.0 ^a (0.2–18.9)	0.9 ^a (0.1–1.8)	1782.1 ^b (115.0–9000.0)	137.0 ^c (9.0–897.0)	71.0 ^b (0.6–345.0)
Global	37.8 ^c (0.3–584.0)	2.6 ^c (0.2–27.0)	0.6 ^b (0.0–2.2)	693.0 ^c (185.0–812.0)	89.5 ^c (27.3–104.0)	35.5 ^c (10.5–39.7)

Values are means with minimum and maximum value intervals in parentheses. Different letters indicate significant differences at the 0.05 level. SOC, Soil organic carbon; STN, Soil total nitrogen; STP, Soil total phosphorus; SMB C, soil microbial biomass C; SMB N, soil microbial biomass N; SMB P soil microbial biomass P.

performed and maps were drawn using R 4.0.2 (R Core Team, 2018).

3. Results

The mean SMB C, N, and P concentrations in the global dataset were 693.0 mg kg⁻¹, 89.5 mg kg⁻¹, and 35.5 mg kg⁻¹, respectively (Table 1). There was 10-fold variation in mean SMB C, N, and P concentrations across biomes (Table 1). At biome level, tundra had the highest SMB C, N, and P concentrations, whereas deserts had the lowest SMB C, N, and P concentrations (Table 1). Among the forest types, boreal forest has the highest, whereas tropical/subtropical forest has the lowest SMB C, N, and P concentrations (Table 1).

Clear latitudinal trends were observed at the global scale, with SMB C, N, and P increasing from low- to high-latitude regions (Fig. 2). Machine learning algorithms (random forest) demonstrated good predictions regarding SMB C ($r^2 = 0.77$ in 5-fold cross validation; Supplementary Fig. S1A), N ($r^2 = 0.71$ in 5-fold cross validation; Supplementary Fig. S1B), and P concentrations ($r^2 = 0.73$ in 5-fold cross validation; Supplementary Fig. S1C) with high predictive accuracy, and showed their standard deviation maps (Fig. S2). The random forest model revealed that SOC was the most important factor affecting SMB C, N, and P concentrations at a global scale (Fig. 3). Partial regression analysis showed that SMB C, N, and P increased significantly with SOC, soil total N and P, MAP, MAT, and soil clay content, but decreased significantly with MAP, soil pH, and soil sand content (Fig. S3).

Based on the relationships of SMB C, N, and P and environmental factors, the global storage of SMB C, N, and P were estimated as 23.13 Pg, 3.93 Pg, and 2.16 Pg, respectively, in the top 0–30 cm soil depth. The storage of SMB C, N, and P varied among major biomes (Table 2). For example, SMB C and N ranged from 0.58 Pg C and 0.13 Pg N for shrubland to 4.97 Pg C and 0.86 Pg N for boreal forest, respectively, whereas SMB P ranged from 0.03 Pg for wetland to 0.57 Pg for boreal forest.

4. Discussion

Previous studies of SMB C, N, and P have provided important, but incomplete insights (especially due to limited data for soil microbial biomass P) into the importance of soil microbes in biogeochemical cycles at a global scale. To our knowledge, this study provides quantitatively and spatially explicit distribution maps and estimates the global storage of SMB C, N, and P in the top 0–30 cm soil depth. These high-resolution maps and numerical estimates provide insight into biogeochemical and ecosystem models under current and future climate scenarios.

4.1. Variation in SMB C, N, and P concentrations across biomes

The data presented here provide information regarding SMB C, N,

and P concentrations in the top 0–30 cm soil depth at both the biome and global levels. Compare with previous studies, the means of SMB C, N, and P concentrations were similar to those reported by Wang et al. (2021). These mean values, however, were lower than those reported by Xu et al. (2013). The discrepancies may be attributed to the differences in the soil depths sampled and the methods used to measure the soil microbial biomass. Specifically, the data presented here were obtained from a specific range of surface soil horizons (depths of 0–30 cm), whereas the dataset used by Xu et al. (2013) included a significant proportion of data extracted from unspecified soil depth or 30–100 cm soil profiles. Furthermore, SMB C, N, and P concentrations were estimated using a single protocol (i.e., chloroform fumigation-extraction method; Vance et al., 1987) in our study, whereas the data emerging from seven different methods for measuring these variables were incorporated in the dataset of Xu et al. (2013). These differences presumably resulted in the lower SMB C and N concentrations reported in this study.

SMB C, N, and P concentrations varied significantly across biomes (Table 1). This result is identical to that reported by Xu et al. (2013). However, the SMB C, N, and P concentrations in boreal forest, shrubland, cropland, and desert are higher, whereas grassland and tropical/subtropical forest are lower than that reported by Xu et al. (2013). These large discrepancies between our study and Xu et al. (2013) are largely because previous summaries are based on limited site observations in different biomes, whereas our estimates are based on a larger and more complete global dataset covering all major biomes. Among all major biomes, the highest SMB C, N, and P concentrations are observed in tundra, supporting the notion that soil microbes at high latitudes with low temperatures may increase C, N, and P content to compensate for their lower metabolic activity (Reich and Oleksyn, 2004; Li et al., 2014). Deserts are observed to have the lowest SMB C, N, and P concentrations, suggesting that the lower soil organic carbon in deserts is correlated with lower soil microbial biomass C, N, and P concentrations (Batjes, 1996; Fierer et al., 2009).

4.2. Global mapping of SMB C, N, and P

At the global scale, SMB C, N, and P exhibited significant latitudinal trends (i.e., these three nutrients increase in colder, higher latitudes) (Fig. 2). These trends are consistent with global patterns reported by other relevant studies (Xu et al., 2013; Li et al., 2014; Crowther et al., 2019), and with the temperature-biogeochemistry hypothesis and/or the latitudinal/temperature compensation hypothesis (Levinton, 1983; Reich and Oleksyn, 2004), stating that offset reduced rates of biochemical reactions caused by the diminished efficiency of N-rich enzymes and P-rich RNA at low temperatures.

Our analyses show that SOC is the most important factor to affect SMB C, N, and P in the top 0–30 cm soil depth at a global scale. This finding is inconsistent with previous studies, in which climate and soil

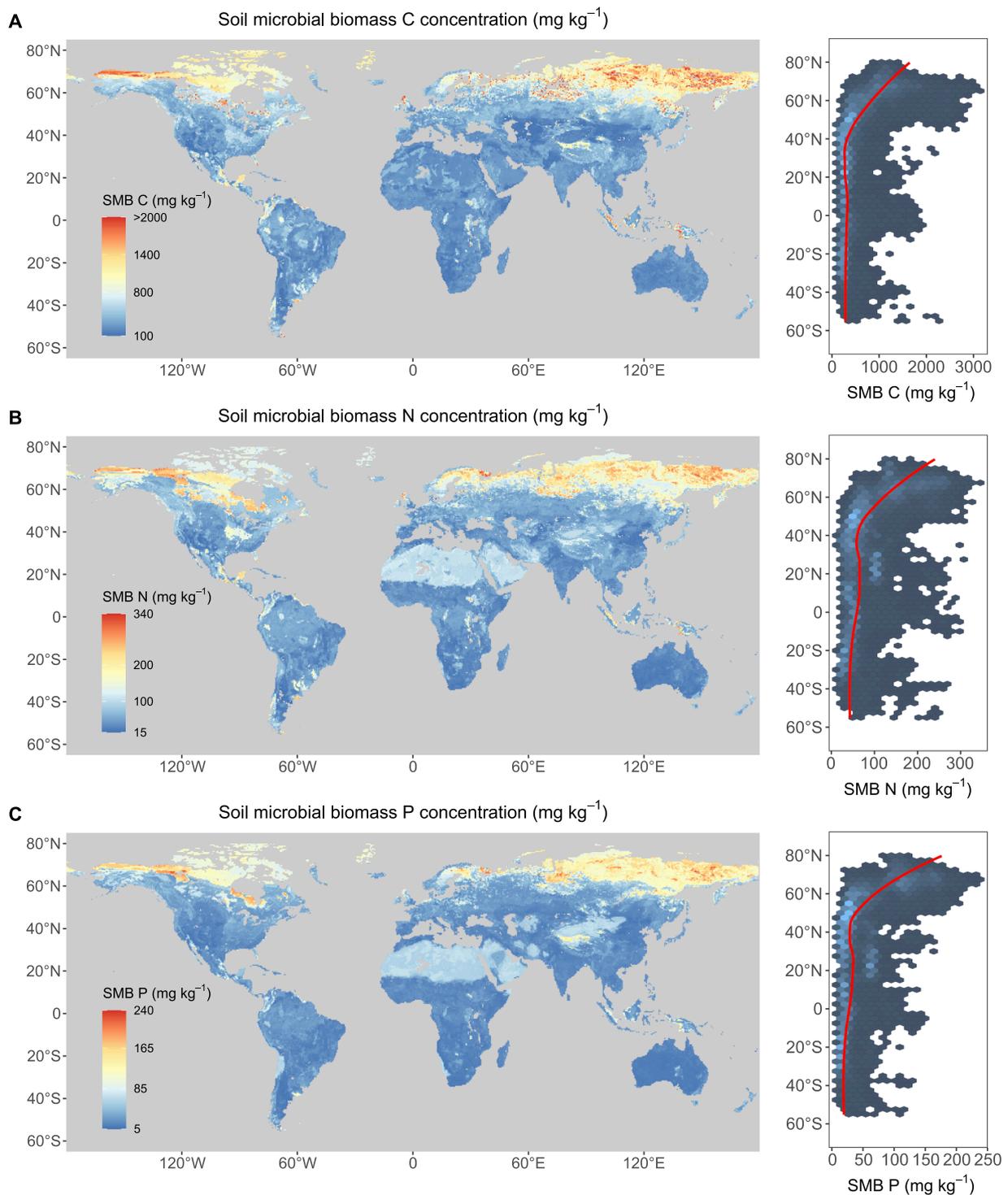


Fig. 2. Global maps of soil microbial biomass carbon (A), nitrogen (B), and phosphorus (C) at the 30 arc sec (approximately 1 km) pixel scale using the pooled dataset.

chemical properties are reported to be the primary ‘drivers’ (Xu et al., 2013; Li et al., 2014). As an important substrate and a product of microbial activity for soil microbes (Paul, 2016; Tashi et al., 2016; He et al., 2019), it is well known that soils with high organic matter usually contain a higher microbial biomass (Traoré et al., 2016; Camenzind et al., 2018). Microbial necromass C can make up more than half of SOC (Liang et al., 2019), and in cold regions, low metabolic activity of heterotrophic organisms induces the accumulation of large organic matter stocks (van den Hoogen et al., 2019). Thus, the greatest accumulation of

SOC occurs in Arctic and sub-Arctic soils (Crowther et al., 2019). Moreover, an increase in the SOC stock in mineral-rich soils (which have a significant effect on global C cycle) requires the sequestration of large amounts of P (Minasny et al., 2017). For example, it is estimated that the storage of 1000 kg C in the topsoil of temperate and tropical cropland would require the sequestration of 8.4 and 4.1 kg P, respectively (Spohn, 2020). Hence, compared to other environmental variables, it seems reasonable to suggest that SOC is a better variable in predicting the spatial variation of SMB C, N, and P at a global scale. In addition, our

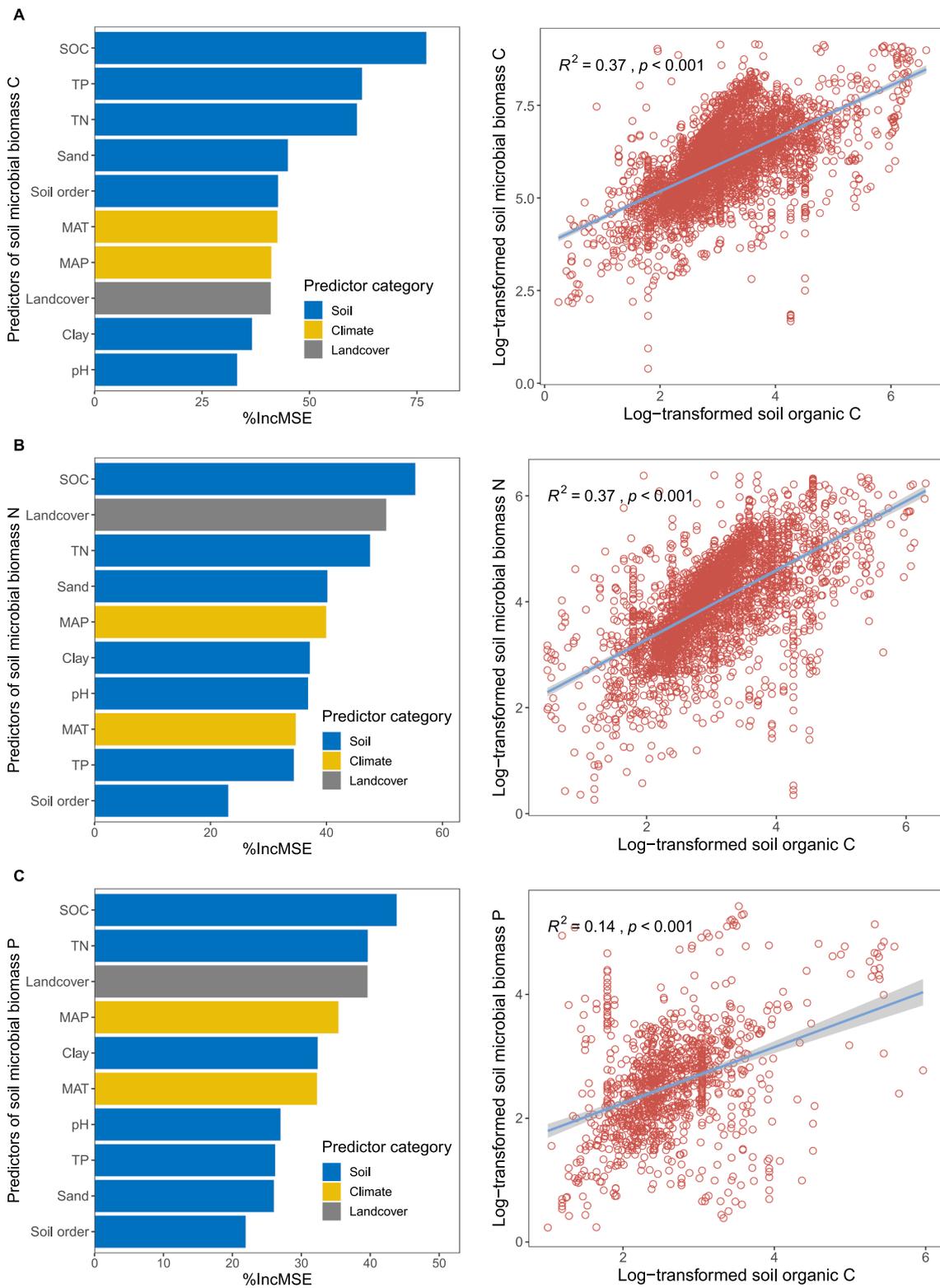


Fig. 3. Potential predictors of soil microbial biomass carbon (A), nitrogen (B), and phosphorus (C). In the left panel, the relative importance of climate variables, soil properties and land cover on SMB C, N and P was quantified by the partial regression with the IncMSE. In the right panel, the relationships of soil organic carbon (SOC) with the SMB C, N and P were determined by the partial regression. Data were log-transformed before the statistical analyses. Climate variables include mean annual temperature (MAT) and mean annual precipitation (MAP). Soil properties include SOC, soil total nitrogen (TN), soil total phosphorus (TP), soil sand and clay content, soil pH and soil order.

Table 2

Summary of the storage of soil microbial biomass C, N, and P in the top 0–30 cm soil depth layer at the global scale and across nine major biomes.

Major biomes	SMB C (Pg C)	SMB N (Pg N)	SMB P (Pg P)	Area (million km ²)
Boreal forest	4.97	0.86	0.57	10.86
Tropical/Subtropical Forest	3.55	0.50	0.31	20.03
Temperate forest	3.23	0.69	0.21	10.85
Shrubland	0.58	0.13	0.16	9.77
Grassland	3.46	0.47	0.31	18.21
Cropland	2.66	0.40	0.19	25.27
Desert	1.48	0.45	0.21	14.88
Wetland	1.21	0.17	0.03	7.18
Tundra	1.99	0.26	0.07	8.82
Global	23.13	3.93	2.16	125.87

SMB C, soil microbial biomass C; SMB N, soil microbial biomass N; SMB P soil microbial biomass P.

data indicate that SMB C, N, and P are highly associated with one another (Fig. 4), which indirectly supports the conclusion that SOC provides a surrogate measure of not only SMB C, but also SMB N and P at a global scale. Interestingly, our results revealed that land cover is another important factor in predicting SMB N and P (Fig. 3). One possibility is that vegetation structure and composition exert a control on SMB N and P through immobilization and mineralization of both N and P from plant residues (Kara et al., 2008; Aponte et al., 2010).

Overall, these accurate spatially explicit global maps of SMB C, N, and P can help improve understanding of the Earth system dynamics by facilitating fundamental studies on carbon storage, nutrient acquisition and land–atmosphere interaction. For example, the close correlation between SOC and SMB C, N, and P at a global scale could make more accurate predictions of carbon dynamics and facilitate the improvement in prediction of large scale terrestrial carbon budget.

4.3. The storage of SMB C, N, and P at the global and major biome level

The global storage of SMB C, N, and P in the top 0–30 cm soil depth were estimated as 23.13 Pg C, 3.93 Pg N and 2.16 Pg P, respectively. The SMB C and N were higher than those of Xu et al. (2013) (i.e., 16.7 Pg C and 2.6 Pg N). This difference may be attributed to the smaller sample size used by Xu et al. (2013), whereas our current estimates are based on a larger and more comprehensive dataset. At the biome level, boreal forest stored the highest SMB C, N, and P (i.e., 4.97 Pg C and 0.86 Pg N). These values are consistent with those reported by Xu et al. (2013), indicating that boreal forest ecosystems are the largest reservoirs of SMB

C and N. Shrubland appears to be the lowest reservoirs of SMB C (0.58 Pg C) and N (0.13 Pg N), whereas wetlands contain the lowest SMB P (0.03 Pg P), most likely because of their small areas across all the biomes (Table 2). These results are similar to those reported by Xu et al. (2013). Previous study has proved that SMB C, N, and P concentrations decreased exponentially with soil depth as a result of a favourable soil microrrhizosphere system created by root systems transport oxygen to soil matrix (Chapin et al., 2002; Xu et al., 2013). However, due to the limited data, our maps do not estimate the storage of SMB C, N, and P in the 30–100 cm soil depth, but an outcome on its aggregated effects. We therefore suggest that further studies on vertical distribution of SMB C, N, and P at a global scale are valuable.

4.4. Limitations and uncertainties

Some limitations and uncertainties must be recognized when interpreting our results. First, approximately 75% of the SMB C, N, and P concentrations in our dataset were extracted from croplands, grasslands, and forest ecosystems. This disproportionate number of data points from different biomes likely biases global summaries and spatial extrapolations. Second, our study presents a spatial analysis of SMB C, N, and P that neglect the effects of temporal variation that can regulate the spatial patterns at the global level (e.g., seasonal changes in concentrations). For example, data indicate that seasonal variations can shift SMB C, N, and P concentrations in forest ecosystems (Li et al., 2019b). This possibility indicates that the sampling and measurement time for the SMB C, N, and P data should be reported. Future studies on temporal dynamics of SMB C, N, and P are needed. Third, environmental changes (e.g. warming, N deposition) could lead to variations in SMB C, N, and P at a global scale (Guo et al., 2018; Xu et al., 2020). Therefore, the underlying mechanisms governing the dynamics of SMB C, N, and P under changing environments merits need to be further investigated.

5. Conclusions

Our results reported here provide detailed information regarding SMB C, N, and P concentrations in the top 0–30 cm soil depth at a global level and across contrasting biomes. By constructing a database of SMB C, N, and P globally, we generated the quantitative and spatially explicit maps in the top soil 0–30 cm depth layer in the global terrestrial ecosystems. The SMB C, N, and P showed clear latitudinal patterns at a global scale. The global storage of SMB C, N, and P are estimated to be 23.13 Pg C, 3.93 Pg N and 2.16 Pg P in the top 0–30 cm soil depth. In addition, we also quantified the relative importance of multiple variables for predicting the spatial variation of SMB C, N, and P. We found

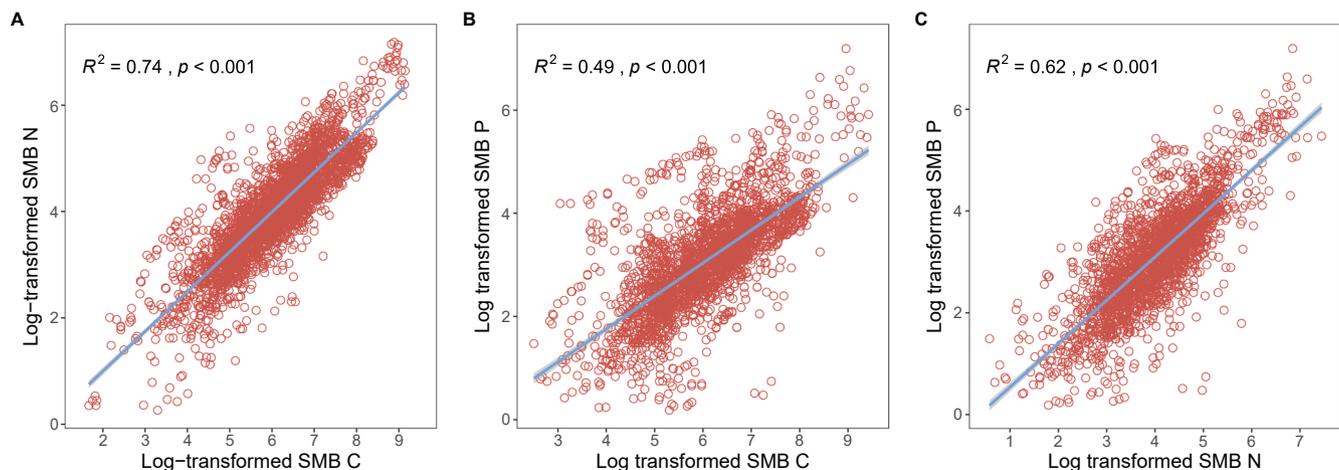


Fig. 4. Relationships among soil microbial biomass carbon (SMB C), nitrogen (SMB N), and phosphorus (SMB P) concentrations. Relationship of SMB C and SMB N (A), SMB C and SMB P (B), and SMB N and SMB P (C).

that SOC plays a dominant role in predicting SMB C, N, and P at a global scale. Our improved global maps of SMB C, N, and P will be future attempts to model the effects of SMB C, N, and P on nutrient cycling and ecosystem functioning, and could provide valuable insights into understanding ecosystem dynamics associated with a changing environment.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This study was financially supported by the National Natural Science Foundation of China (31470498), the National Key Research and Development Program (2015CB954200), the Fundamental Research Funds for the Central Universities (2020NQN27), and the China Postdoctoral Science Foundation (2020M673123).

Data availability statement

The dataset is archived from published articles. The list of references for dataset is publicly available and can be accessed in the [supplementary material](#). All data presented in this manuscript are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.xd2547dhk> (Wang 2021).

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.catena.2022.106037>.

References

- Aponte, C., Marañón, T., García, L.V., 2010. Microbial C, N and P in soils of Mediterranean oak forests: influence of season, canopy cover and soil depth. *Biogeochemistry* 101 (1-3), 77–92.
- Bahram, M., Hildebrand, F., Forslund, S.K., Anderson, J.L., Soudzilovskaia, N.A., Bodegom, P.M., Bengtsson-Palme, J., Anslan, S., Coelho, L.P., Harend, H., Huerta-Cepas, J., Medema, M.H., Maltz, M.R., Mundry, S., Olsson, P.A., Pent, M., Pöhl, S., Sunagawa, S., Ryberg, M., Tedersoo, L., Bork, P., 2018. Structure and function of the global topsoil microbiome. *Nature* 560 (7717), 233–237.
- Bardgett, R.D., van der Putten, W.H., 2014. Belowground biodiversity and ecosystem functioning. *Nature* 515 (7528), 505–511.
- Bardgett, R.D., Freeman, C., Ostle, N.J., 2008. Microbial contributions to climate change through carbon cycle feedbacks. *ISME J.* 2 (8), 805–814.
- Batjes, N.H., 1996. Total carbon and nitrogen in the soils of the world. *Eur. J. Soil Sci.* 47 (2), 151–163.
- Batjes, N.H., 2016. Harmonized soil property values for broad-scale modelling (WISE30sec) with estimates of global soil carbon stocks. *Geoderma* 269, 61–68.
- Breiman, L., 2001. Random forests. *Mach. Learning* 45, 5–32.
- Brookes, P.C., Powlson, D.S., Jenkinson, D.S., 1982. Measurement of microbial biomass phosphorus in soil. *Soil Biol. Biochem.* 14 (4), 319–329.
- Camenzind, T., Hättenschwiler, S., Treseder, K.K., Lehmann, A., Rillig, M.C., 2018. Nutrient limitation of soil microbial processes in tropical forests. *Ecol. Monogr.* 88 (1), 4–21.
- Chapin, F.S., Matson, P.A., Mooney, H.A. (Eds.), 2002. *Principles of Terrestrial Ecosystem Ecology*. Springer New York, New York, NY.
- Chen, X.Y., Zhang, H.J., Yao, X.D., Zeng, W.J., Wang, W., 2021. Latitudinal and depth patterns of soil microbial biomass carbon, nitrogen, and phosphorus in grasslands of an agro-pastoral ecotone. *Land Degrad. Dev.* 32, 3833–3846.
- Chen, Y.-L., Chen, L.-Y., Peng, Y.-F., Ding, J.-Z., Li, F., Yang, G.-B., Kou, D., Liu, L.-i., Fang, K., Zhang, B.-B., Wang, J., Yang, Y.-H., 2016. Linking microbial C:N: P stoichiometry to microbial community and abiotic factors along a 3500-km grassland transect on the Tibetan Plateau. *Glob. Ecol. Biogeogr.* 25 (12), 1416–1427.
- Cleveland, C.C., Liptzin, D., 2007. C:N: P stoichiometry in soil: is there a 'Redfield ratio' for the microbial biomass? *Biogeochemistry* 85 (3), 235–252.
- Crowther, T.W., van den Hoogen, J., Wan, J., Mayes, M.A., Keiser, A.D., Mo, L., Averill, C., Maynard, D.S., 2019. The global soil community and its influence on biogeochemistry. *Science* 365, eaav0550.
- Delgado-Baquerizo, M., Maestre, F.T., Gallardo, A., Bowker, M.A., Wallenstein, M.D., Quero, J.L., Ochoa, V., Gozalo, B., García-Gómez, M., Soliveres, S., García-Palacios, P., Berdugo, M., Valencia, E., Escolar, C., Arredondo, T., Barraza-Zepeda, C., Bran, D., Carreira, J.A., Chaieb, M., Conceição, A.A., Derak, M., Eldridge, D.J., Escudero, A., Espinosa, C.I., Gaitán, J., Gatica, M.G., Gómez-González, S., Guzman, E., Gutiérrez, J.R., Florentino, A., Hepper, E., Hernández, R. M., Huber-Sannwald, E., Jankju, M., Liu, J., Mau, R.L., Miriti, M., Monerris, J., Naseri, K., Noumi, Z., Polo, V., Prina, A., Pucheta, E., Ramírez, E., Ramírez-Collantes, D.A., Romão, R., Tighe, M., Torres, D., Torres-Díaz, C., Ungar, E.D., Val, J., Wamití, W., Wang, D., Zaady, E., 2013. Decoupling of soil nutrient cycles as a function of aridity in global drylands. *Nature* 502 (7473), 672–676.
- Du, E., Terrer, C., Pellegrini, A.F.A., Ahlström, A., van Lissa, C.J., Zhao, X., Xia, N., Wu, X., Jackson, R.B., 2020. Global patterns of terrestrial nitrogen and phosphorus limitation. *Nat. Geosci.* 13 (3), 221–226.
- Fanin, N., Fromin, N., Buatois, B., Hättenschwiler, S., Cleland, E., 2013. An experimental test of the hypothesis of nonhomeostatic consumer stoichiometry in a plant litter-microbe system. *Ecol. Lett.* 16 (6), 764–772.
- Fierer, N., Strickland, M.S., Liptzin, D., Bradford, M.A., Cleveland, C.C., 2009. Global patterns in belowground communities. *Ecol. Lett.* 12 (11), 1238–1249.
- Griffiths, R.I., Thomson, B.C., James, P., Bell, T., Bailey, M., Whiteley, A.S., 2011. The bacterial biogeography of British soils. *Environ. Microbiol.* 13, 1642–1654.
- Guo, X., Feng, J., Shi, Z., Zhou, X., Yuan, M., Tao, X., Hale, L., Yuan, T., Wang, J., Qin, Y., Zhou, A., Fu, Y., Wu, L., He, Z., Van Nostrand, J.D., Ning, D., Liu, X., Luo, Y., Tiedje, J.M., Yang, Y., Zhou, J., 2018. Climate warming leads to divergent succession of grassland microbial communities. *Nat. Clim. Change* 8 (9), 813–818.
- Handa, I.T., Aerts, R., Berendse, F., Berg, M.P., Brunder, A., Butenschoten, O., Chauvet, E., Gessner, M.O., Jabiol, J., Makkonen, M., McKie, B.G., Malmqvist, B., Peeters, E.T.H.M., Scheu, S., Schmid, B., van Ruijven, J., Vos, V.C.A., Hättenschwiler, S., 2014. Consequences of biodiversity loss for litter decomposition across biomes. *Nature* 509 (7499), 218–221.
- Hartman, W.H., Richardson, C.J., Mormile, M.R., 2013. Differential nutrient limitation of soil microbial biomass and metabolic quotients (qCO₂): is there a biological stoichiometry of soil microbes? *PLoS ONE* 8 (3), e57127.
- He, X.J., Hou, E.Q., Veen, G.F., Farnon Ellwood, M.D., Dijkstra, P., Sui, X.H., Zhang, S., Wen, D.Z., Chu, C.J., 2019. Soil microbial biomass increase along elevational gradients in the tropics and subtropics but not elsewhere. *Glob. Ecol. Biogeogr.* 29, 345–354.
- He, X.J., Augusto, L., Goll, D.S., Ringeval, B., Wang, Y.P., Helfenstein, J., Huang, Y.Y., Yu, K.L., Wang, Z.Q., Yang, Y.C., Hou, E.Q., 2021. Global patterns and drivers of soil total phosphorus concentration. *Earth Syst. Sci. Data Discuss.* <https://doi.org/10.5194/essd-2021-166>.
- van der Heijden, M.G.A., Bardgett, R.D., van Straalen, N.M., 2008. The unseen majority: Soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. *Ecol. Lett.* 11 (3), 296–310.
- Hengl, T., Mendes de Jesus, J., Heuvelink, G.B.M., Ruiperez Gonzalez, M., Kilibarda, M., Blagotić, A., Shangguan, W., Wright, M.N., Geng, X., Bauer-Marschallinger, B., Guevara, M.A., Vargas, R., MacMillan, R.A., Batjes, N.H., Leenaars, J.G.B., Ribeiro, E., Wheeler, I., Mantel, S., Kempen, B., Bond-Lamberty, B., 2017. SoilGrids250m: Global gridded soil information based on machine learning. *PLoS ONE* 12 (2), e0169748.
- Heuck, C., Weig, A., Spohn, M., 2015. Soil microbial biomass C:N: P stoichiometry and microbial use of organic phosphorus. *Soil Biol. Biochem.* 85, 119–129.
- van den Hoogen, J., Geisen, S., Routh, D., Ferris, H., Trausperger, W., Wardle, D.A., de Goede, R.G.M., Adams, B.J., Ahmad, W., Andriuzzi, W.S., Bardgett, R.D., Bonkowski, M., Campos-Herrera, R., Cares, J.E., Caruso, T., de Brito Caixaeta, L., Chen, X., Costa, S.R., Creamer, R., Mauro da Cunha Castro, J., Dam, M., Djigal, D., Escuer, M., Griffiths, B.S., Gutiérrez, C., Hobbeg, K., Klinkina, D., Kardol, P., Kergunteuil, A., Korthals, G., Krashevskaya, V., Kudrin, A.A., Li, Q.i., Liang, W., Magilton, M., Marais, M., Martín, J.A.R., Matveeva, E., Mayad, E.H., Mulder, C., Mullin, P., Neilson, R., Nguyen, T.A.D., Nielsen, U.N., Okada, H., Rius, J.E.P., Pan, K., Peneva, V., Pellissier, L., Carlos Pereira da Silva, J., Pitteloud, C., Powers, T. O., Powers, K., Quist, C.W., Rasmann, S., Moreno, S.S., Scheu, S., Setälä, H., Sushchuk, A., Tiunov, A.V., Trap, J., van der Putten, W., Vestergård, M., Villenave, C., Waeyenberge, L., Wall, D.H., Wilschut, R., Wright, D.G., Yang, J.-i., Crowther, T.W., 2019. Soil nematode abundance and functional group composition at a global scale. *Nature* 572 (7768), 194–198.
- Hijmans, R.J., 2021. raster: Geographic Data Analysis and Modeling. R package version 3.4-13. <https://CRAN.R-project.org/package=raster>.
- Hu, Y., Xiang, D., Veresoglou, S.D., Chen, F., Chen, Y., Hao, Z., Zhang, X., Chen, B., 2014. Soil organic carbon and soil structure are driving microbial abundance and community composition across the arid and semi-arid grasslands in northern China. *Soil Biol. Biochem.* 77, 51–57.
- Joergensen, R.G., Mueller, T., 1996. The fumigation-extraction method to estimate soil microbial biomass: Calibration of the ¹⁴C value. *Soil Biol. Biochem.* 28 (1), 33–37.
- Joergensen, R.G., Wu, J., Brookes, P.C., 2011. Measuring soil microbial biomass using an automated procedure. *Soil Biol. Biochem.* 43 (5), 873–876.
- Kara, Ö., Bolat, I., Çakıroğlu, K., Öztürk, M., 2008. Plant canopy effects on litter accumulation and soil microbial biomass in two temperate forests. *Biol. Fertil. Soils* 45 (2), 193–198.
- Kuhn, M., 2020. caret: Classification and Regression Training. R package version 6.0-86. <https://github.com/topepo/caret/>.
- Levinton, J.S., 1983. The latitudinal compensation hypothesis: growth data and a model of latitudinal growth differentiation based upon energy budgets. I. Interspecific comparison of *Ophryotrocha* (Polychaeta; Dorvilleidae). *Biol. Bull.* 165 (3), 686–698.
- Li, P., Tuerhanbai, M., Tian, D., Feng, Z.Z., 2019a. Seasonal dynamics of soil microbial biomass carbon, nitrogen and phosphorus stoichiometry across global forest ecosystems. *Chinese J. Plant Ecol.* 43, 532–542.

- Li, P., Yang, Y., Han, W., Fang, J., 2014. Global patterns of soil microbial nitrogen and phosphorus stoichiometry in forest ecosystems. *Glob. Ecol. Biogeogr.* 23 (9), 979–987.
- Li, Z., Tian, D., Wang, B., Wang, J., Wang, S., Chen, H.Y.H., Xu, X., Wang, C., He, N., Niu, S., 2019b. Microbes drive global soil nitrogen mineralization and availability. *Glob. Change Biol.* 25 (3), 1078–1088.
- Liang, C., Amelung, W., Lehmann, J., Kästner, M., 2019. Quantitative assessment of microbial necromass contribution to soil organic matter. *Glob. Change Biol.* 25 (11), 3578–3590.
- Liu, Y.Q., Ma, W.H., Kou, D., Niu, X.X., Wang, T., Cheng, Y.L., Chen, D.M., Zhu, X.Q., Zhao, M.Y., Hao, B.H., Zhang, J.B., Yang, Y.H., Hu, H.F., 2020. Comparison of patterns of microbial C:N: P stoichiometry between topsoil and subsoil along an aridity gradient. *Biogeosciences* 17, 2009–2019.
- Marschner, P., 2012. *Marschner's mineral nutrition of higher plants*, 3rd ed. Elsevier, Amsterdam.
- Martiny, J.B.H., Bohannan, B.J.M., Brown, J.H., Colwell, R.K., Fuhrman, J.A., Green, J. L., Horner-Devine, M.C., Kane, M., Krumins, J.A., Kuske, C.R., Morin, P.J., Naeem, S., Øvreås, L., Reysenbach, A.-L., Smith, V.H., Staley, J.T., 2006. Microbial biogeography: putting microorganisms on the map. *Nature Rev. Microbiol.* 4 (2), 102–112.
- Meinshausen, N., 2006. Quantile Regression Forests. *J. Mach. Learning Res.* 7, 983–999.
- Meinshausen, N., 2017. *quantregForest: Quantile Regression Forests*, <https://CRAN.R-project.org/package=quantregForest>.
- Minasny, B., Malone, B.P., McBratney, A.B., Angers, D.A., Arrouays, D., Chambers, A., Chaplot, V., Chen, Z.-S., Cheng, K., Das, B.S., Field, D.J., Gimona, A., Hedley, C.B., Hong, S.Y., Mandal, B., Marchant, B.P., Martin, M., McConkey, B.G., Mulder, V.L., O'Rourke, S., Richer-de-Forges, A.C., Odeh, I., Padarian, J., Paustian, K., Pan, G., Poggio, L., Savin, I., Stolbovoy, V., Stockmann, U., Sulaeman, Y., Tsui, C.-C., Vågen, T.-G., van Wesemael, B., Winowiecki, L., 2017. Soil carbon 4 per mille. *Geoderma* 292, 59–86.
- Mooshammer, M., Wanek, W., Zechmeister-Boltenstern, S., Richter, A., 2014. Stoichiometric imbalances between terrestrial decomposer communities and their resources: mechanisms and implications of microbial adaptations to their resources. *Front. Microbiol.* 4, 22.
- Paul, E.A., 2016. The nature and dynamics of soil organic matter: Plant inputs, microbial transformations, and organic matter stabilization. *Soil Biol. Biochem.* 98, 109–126.
- Team, R.C., 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria <https://www.R-project.org/> 2018.
- Reich, P.B., Oleksyn, J., 2004. Global patterns of plant leaf N and P in relation to temperature and latitude. *Proc. Natl. Acad. Sci. USA* 101 (30), 11001–11006.
- Rillig, M.C., Mummey, D.L., 2006. Mycorrhizas and soil structure. *New Phytol.* 171 (1), 41–53.
- Singh, J.S., Gupta, V.K., 2018. Soil microbial biomass: A key soil driver in management of ecosystem functioning. *Sci. Total Environ.* 634, 497–500.
- Spohn, M., 2016. Element cycling as driven by stoichiometric homeostasis of soil microorganisms. *Basic Appl. Ecol.* 17 (6), 471–478.
- Spohn, M., 2020. Increasing the organic carbon stocks in mineral soils sequesters large amounts of phosphorus. *Glob. Change Biol.* 26, 4169–4177.
- Tashi, S., Singh, B., Keitel, C., Adams, M., 2016. Soil carbon and nitrogen stocks in forests along an altitudinal gradient in the eastern Himalayas and a meta-analysis of global data. *Glob. Change Biol.* 22 (6), 2255–2268.
- Traoré, O.Y.A., Kiba, D.I., Arnold, M.C., Fließbach, A., Oberholzer, H.R., Nacro, H.B., Lompo, F., Oberson, A., Frossard, E., Bünenmann, E.K., 2016. Fertilization practices alter microbial nutrient limitations after alleviation of carbon limitation in a Ferric Acrisol. *Biol. Fertil. Soils* 52 (2), 177–189.
- Vance, E.D., Brookes, P.C., Jenkinson, D.S., 1987. An extraction method for measuring soil microbial C. *Soil Biol. Biochem.* 19, 703–707.
- de Vries, F.T., Manning, P., Tallwin, J.R.B., Mortimer, S.R., Pilgrim, E.S., Harrison, K.A., Hobbs, P.J., Quirk, H., Shipley, B., Cornelissen, J.H.C., Kattge, J., Bardgett, R.D., Johnson, N., 2012. Abiotic drivers and plant traits explain landscape-scale patterns in soil microbial communities. *Ecol. Lett.* 15 (11), 1230–1239.
- Wang, Z., Wang, M., Yu, K., Hu, H., Yang, Y., Ciais, P., Ballantyne, A.P., Niklas, K.J., Huang, H., Yao, B., Wright, S.J., 2021. Global synthesis for the scaling of soil microbial nitrogen to phosphorus in terrestrial ecosystems. *Environ. Res. Lett.* 16 (4), 044034. <https://doi.org/10.1088/1748-9326/abed78>.
- Xu, X., Thornton, P.E., Post, W.M., 2013. A global analysis of soil microbial biomass carbon, nitrogen and phosphorus in terrestrial ecosystems. *Glob. Ecol. Biogeogr.* 22 (6), 737–749.
- Xu, X., Wang, N., Lipson, D., Sinsabaugh, R., Schimel, J., He, L., Soudzilovskaia, N.A., Tedersoo, L., Algar, A.C., 2020. Microbial macroecology: In search of mechanisms governing microbial biogeographic patterns. *Glob. Ecol. Biogeogr.* 29 (11), 1870–1886.
- Zechmeister-Boltenstern, S., Keiblinger, K.M., Mooshammer, M., Peñuelas, J., Richter, A., Sardans, J., Wanek, W., 2015. The application of ecological stoichiometry to plant-microbial-soil organic matter transformations. *Ecological Monographs* 85 (2), 133–155.