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RESEARCH PAPER

A global analysis of soil microbial biomass carbon, nitrogen and phosphorus in terrestrial ecosystems

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ABSTRACT

Aim To estimate the concentrations, stoichiometry and storage of soil microbial biomass carbon (C), nitrogen (N) and phosphorus (P) at biome and global scales.

Location Global.

Method We collected 3422 data points to summarize the concentrations and stoichiometry of C, N and P in soils, soil microbial biomass at global and biome levels, and to estimate the global storage of soil microbial biomass C and N.

Results The results show that concentrations of C, N and P in soils and soil microbial biomass vary substantially across biomes; the fractions of soil elements C, N and P in soil microbial biomass are 1.2, 2.6 and 8.0%, respectively. The best estimates of C:N:P stoichiometry for soil elements and soil microbial biomass are 287:17:1 and 42:6:1, respectively, at global scale, and they vary in a wide range among biomes. The vertical distribution of soil microbial biomass follows the distribution of roots up to 1 m depth.

Main conclusions The global storage of soil microbial biomass C and N were estimated to be 16.7 Pg C and 2.6 Pg N in the 0–30 cm soil profiles, and 23.2 Pg C and 3.7 Pg N in the 0–100 cm soil profiles. We did not estimate P in soil microbial biomass due to insufficient data and insignificant correlation between soil total P and climate variables used for spatial extrapolation. The spatial patterns of soil microbial biomass C and N were consistent with those of soil organic C and total N, i.e. high density in northern high latitude, and low density in low latitudes and the Southern Hemisphere.

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Keywords

Carbon, nitrogen, phosphorus, soil microbial biomass, stoichiometry, terrestrial ecosystems.

INTRODUCTION

Global cycling of elements (carbon, C; nitrogen, N; phosphorus, P) and their interactions play an essential role in shaping earth's landscapes and climate system (Post *et al.*, 1982; Schlesinger, 1997; Thornton *et al.*, 2009). Soil microbes play a critical role in driving and regulating the cycling and interactions of these nutrients which are involved in several important feedbacks to the climate system (Chapin *et al.*, 2002, 2008; Singh *et al.*, 2010; Xu *et al.*, 2010). However, little effort has been invested in seeking patterns and drawing generalizations for soil microbial biomass due to high spatial and temporal heterogeneities in soil microbial properties and limitations of sampling and measuring methods (Cleveland & Liptzin, 2007; Joergensen *et al.*, 2011).

Nutrient regulation of soil microbial feedbacks to climate change through the carbon cycle is critically important in carbon–climate feedback (Bardgett *et al.*, 2008). The C–N–P interaction may enhance or weaken the carbon–climate feedback (Allison *et al.*, 2010; Janssens *et al.*, 2010). Ecosystem C:N:P stoichiometry has received considerable attention in the past decade (Sterner & Elser, 2002; McGroddy *et al.*, 2004; Cleveland & Liptzin, 2007; Danger *et al.*, 2008; Elser *et al.*, 2010). However, the relationship between soil elements and soil microbial

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biomass and nutrient concentrations, especially at biome level, is not well understood (Cleveland & Liptzin, 2007; Hartman, 2011).

Spatial heterogeneity of soil properties and climate conditions leads to large variations in land surface properties, especially for soil biogeochemical properties including concentrations and vertical distribution of C, N and P in soils and soil microbial biomass. The roles of soil microorganisms in regulating nutrient cycling vary across biomes (Martiny *et al.*, 2006; Hartman, 2011), implicating the role of C:N:P stoichiometry of soil microbial biomass across biomes as an important research topic. Furthermore, knowledge of spatial distribution of soil microbial biomass is critically important not only for a large-scale examination of global nutrient cycling (Allison *et al.*, 2010) but also for microbial biogeography (Martiny *et al.*, 2006).

Targeting these current knowledge gaps and research needs, this paper presents a comprehensive analysis of soil microbial biomass C, N and P at biome and global scales. Specifically, the objectives of this study are: (1) to estimate the concentrations and stoichiometry of C, N and P in soil microbial biomass at global and biome levels; (2) to estimate the global storage of soil microbial biomass; and (3) to explore the spatial distribution of soil microbial biomass across the globe. Concentrations and stoichiometries of soil elements (soil organic C, total N and total P) are also summarized.

DATA AND METHODS

Data sources

We collected publications by searching for 'soil microbial biomass' in Google Scholar. A few criteria were used to screen the data for this study. The criteria were: (1) the soil microbial biomass (at least one of soil microbial biomass C, N or P) must be reported; (2) the reported soil microbial biomass C, N and P must be less than organic C, total N and total P, respectively, in soils. Based on the second criterion, a few publications used in previous similar studies (Cleveland & Liptzin, 2007; Hartman, 2011) were excluded. Finally, 3422 data points in 14 biomes across the globe were retrieved from 315 papers (Fig. 1). Associated information for the sampling site was also retrieved, for example soil pH, sampling depth, sampling date, biome type, latitude, longitude, climate variables, etc. There is a dynamic version of this database hosted on Google Code (http://code.google.com/p/global-soil-microbial-biomass/). The data used in this study is the database created on 1 June 2012.

The date of publications used spans from the late 1970s to 2012. Since the number of data points for several biomes are insufficient for a robust statistical analysis, we aggregated biomes with few data points; specifically, savanna was combined into grassland. Several land-cover types were not included in the

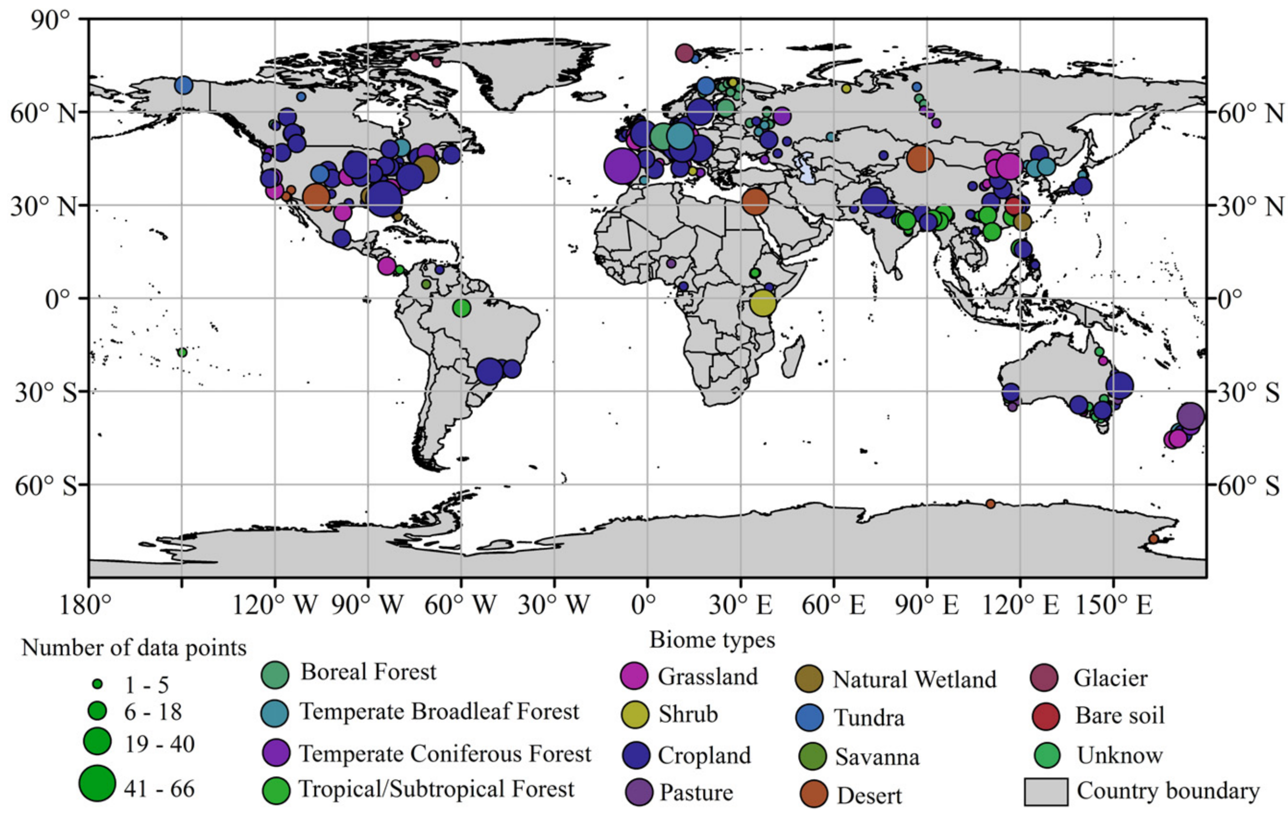

Figure 1 Distribution of the data points used in this study (3259 out of 3422 data points with geographical coordinate are shown in this map).

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analysis, for instance glacier and bare soils (mainly urban and industrial sites). Finally, surface soil data were aggregated into 11 major biome types. These data points were collected exclusively for surface soils, primarily 0–15 cm depth with some 0–30 cm; we assumed that all measurements represent the top 0–30 cm soil profile, consistent with previous datasets on global soil organic C and total N (Batjes, 1996; Jobbagy & Jackson, 2000). For those data points with no geographical coordinates reported in the literature, we searched for geographical coordinates based on the names of site, state and country. We obtained 3259 data points with geographical information. These geographical coordinates were used to locate the sites on the global map (Fig. 1) and for retrieving the long-term climate conditions associated with these observational data. We also collected any available soil microbial biomass at depth along the soil profile to 100 cm, which was used to estimate global storage of soil microbial biomass C and N in 0–30 cm and 0–100 cm soil profiles.

Global maps of vegetation distribution, soil properties and long-term climate data were used for spatial extrapolation in order to estimate global storage of soil microbial biomass C and N in terrestrial ecosystems. Climate data were provided by the University of East Anglia Climatic Research Unit (http://www.cru.uea.ac.uk/); the 1961–90 average climate data were used to represent the long-term climate conditions. The vegetation distribution data were generated by combining several data sources: global pasture and cropland data from Ramankutty *et al.* (2008); wetland coverage from global wetland distribution data (Aselmann & Crutzen, 1989); the spatial distribution of other biomes from a vegetation map developed by Ramankutty & Foley (1998). We generated a spatial map of 12 major biomes: boreal forest, temperate coniferous forest, temperate broadleaf forest, tropical/subtropical forest, mixed forest, grassland, shrub, tundra, desert, cropland and pasture (Fig. S1 in Supporting Information). The spatial distribution of soil property data is from the Harmonized World Soil Database (FAO/IIASA/ISRIC/ISSCAS/JRC, 2009) and soil element data are from the IGBP-DIS dataset [available online from Oak Ridge National Laboratory Distributed Active Archive Center (http://daac.ornl.gov/)].

Since soil data for organic C and total N in IGBP-DIS are for the 100-cm profile as a whole, we used the Harmonized World Soil Database to calculate the fraction of soil organic C and total N in the top 0–30 cm. It was then combined with the vertical distribution of soil microbial biomass to estimate the global storage of soil microbial biomass C and N in the 0–30 cm and 0–100 cm soil profiles.

Summary of the dataset

Seven different methods for measuring soil microbial biomass C, N and/or P over the past decades are presented in the dataset. These include the fumigation extraction (FE) method (Vance *et al.*, 1987), the fumigation incubation (FI) method (Jenkinson, 1966, 1988), the substrate induced respiration (SIR) method (Anderson & Domsch, 1978), the phospholipid fatty-acid analysis (PLFA) method (White *et al.*, 1979), the adenosine triphosphate (ATP) method (Jenkinson & Oades, 1979), the microwave soil extraction method (Islam & Weil, 1998) and the irradiation and incubation method (Araújo *et al.*, 2008). The FE and FI methods account for 55 and 26%, respectively, of the total measurements. The FE method was invented in 1987 (Vance *et al.*, 1987), and after several years it was broadly applied. Since 1990, the FE, FI and SIR methods have contributed 62, 19 and 16% of the reported soil microbial biomass measurements. This is consistent with a recent summary of methods used in soil microbial biomass measurements (Joergensen, 2010; Joergensen *et al.*, 2011).

In order to conduct biome-level analysis, we aggregated the data into 11 biomes based on their vegetation: boreal forest, temperate coniferous forest, temperate broadleaf forest, tropical/subtropical forest, grassland, shrub, tundra, desert, natural wetlands, cropland and pasture. We used the data for the four forest types to generate the parameters for mixed forest which is a biome type in the vegetation distribution map we used. Cropland, forest and grassland, contribute approximately 47, 24 and 10% of the dataset, while all the other biomes together contributed 19% of the dataset. Most of the field sites are located in North America, Europe, Asia, Australia and New Zealand. There are fewer observations for South America, Africa, Russian Asia and Antarctica (Fig. 1).

Statistical analysis

Almost all reported variables (soil organic C, total N, total P, soil microbial biomass C, N and P) and the calculated C:N, C:P and N:P ratios do not follow normal distribution. The log-transformation was used to convert them to a normal distribution for robust statistical analysis (Figs S2–S5); the mean and 95% confidence boundaries of concentrations and stoichiometries of C, N and P in soils and soil microbial biomass were then converted back to original values for reporting. The multiple range test was used to analyse the differences among biomes for concentrations and stoichiometries of C, N and P in soils and soil microbial biomass. Multiple linear regression was used to obtain correlations between soil microbial biomass or soil element concentrations and long-term climate variables. All statistical analyses were conducted using the R 2.12.3 program in Windows 7; Origin 8.0 was used to generate graphs and ArcGIS 10.1 was used to generate maps.

RESULTS

Concentrations of C, N and P in soils and soil microbial biomass

The concentrations of C, N and P in soils and soil microbial biomass vary by as much as three orders of magnitude even within a biome (Fig. S6). For example, the soil microbial biomass C concentration is as low as < 1 mmol C kg^{-1} but as high as > 1400 mmol C kg^{-1} in forest soils, and as low as 1 mmol C kg^{-1} but as high as 469 mmol C kg^{-1} in cropland soils. The area-weighted globally averaged soil microbial C, N and P in surface soil are 56.7 mmol C kg^{-1}, 7.5 mmol N kg^{-1} and

1.3 mmol P kg^{-1}, respectively. The area-weighted globally averaged soil organic C, total N and total P in surface soil (0–30 cm) are 4768.0 mmol C kg^{-1}, 290.5 mmol N kg^{-1} and 16.6 mmol P kg^{-1}, respectively (Fig. S6, Table 1).

At biome level, desert has the lowest concentrations of C, N and P in soils and soil microbial biomass; natural wetland and tundra have the highest organic C concentration in surface soils, natural wetland has the highest soil N concentration and tundra has the highest soil P concentration. The highest soil microbial biomass C and N concentrations concurrently occur in tundra, while the highest soil microbial biomass P concentration was observed in boreal forest (Table 1). Among the forest types, soils in boreal forest have the highest concentrations of C and N in soils and soil microbial biomass. Temperate broadleaf forest has higher, yet not statistically significant, C, N and P concentrations than temperate coniferous forest (Table 1, Fig. S6). Cropland and pasture, the human-managed biomes, have lower C, N and P concentrations in soils and soil microbial biomass than almost all naturally vegetated biomes, indicating large anthropogenic effects on soil C, N and P storage and forms (Vitousek *et al.*, 2009).

Fractions of soil elements in soil microbial biomass

Microbial biomass is the most active nutrient pool in soils but accounts for a small fraction of soil elements (Anderson & Domsch, 1989; Jonasson *et al.*, 1999; Vance & Chapin, 2001; Chapin *et al.*, 2002). There is a contrasting enriching gradient for three elements: a high-concentration element has low fraction in soil microbial biomass. For instance, compared to N and P, C has the highest concentration in soils but the lowest fraction in soil microbial biomass. The area-weighted average best estimates of contributions of soil microbial biomass to soil organic C, total N and total P are 1.2, 2.6 and 8.0% globally.

The fractions of soil nutrients in soil microbial biomass vary substantially across biomes; temperate coniferous forest has the lowest (0.99%), while desert has the highest (5.02%) fraction of soil organic C in soil microbial biomass (Fig. S7). Desert, boreal forest, grassland and tundra have a relatively large fraction of soil total N in soil microbial biomass, while temperate broadleaf forest and shrub have lower fraction of soil N into soil microbial biomass (Table 2). Natural wetlands, shrub and pasture have a large fraction of soil total P in soil microbial biomass (Table 2).

C:N:P stoichiometries in soil microbial biomass and soils

There are significant linear correlations between C, N and P in soils and soil microbial biomass (Fig. 2), which is defined as C:N:P stoichiometry. We combined the C:N and C:P ratios to estimate the C:N:P stoichiometry at global and biome levels because there are fewer data points for P and N than that for C (Table 3). For soil elements, tundra, natural wetlands and boreal forest have relatively wide C:N and C:P ratios, while cropland has narrow C:N, C:P and N:P ratios due to low C density and relatively abundant N and P inputs (Tables 1 & 3). The desert

Table 1 Summarized concentrations of C, N and P in soil and soil microbial biomass for major biomes and the global average.

Biome	Corg (mmol C kg^{-1})	Ntot (mmol N kg^{-1})	Ptot (mmol P kg^{-1})	Cmic (mmol C kg^{-1})	Nmic (mmol N kg^{-1})	Pmic (mmol P kg^{-1})
Boreal forest	8061.2^{b} (5268.8–12,333.8)	737.1^{b} (539.4–1007.3)	17.1^{b} (7.1–41.3)	86.5^{b} (59.2–126.2)	15.5^{b} (10.9–22.0)	
Temperate coniferous forest	3729.2^{c} (3120.6–4456.4)	214.8^{c} (184.1–250.6)	12.2^{b} (7.9–18.9)	42.3^{cd} (35.4–50.5)	5.7^{c} (4.8–6.9)	0.69^{de} (0.47–1.01)
Temperate broadleaf forest	4547.3^{c} (4029.5–5131.6)	289.2^{c} (262.9–318.2)	14.2^{b} (11.4–17.8)	44.7^{cd} (38.4–52.0)	5.5^{c} (4.2–7.2)	1.12^{cd} (0.79–1.58)
Tropical/subtropical forest	2357.3^{d} (1975.3–2813.2)	158.4^{d} (136.8–183.3)	12.5^{b} (10.4–15.1)	35.7^{de} (30.7–41.5)	5.1^{c} (4.3–6.0)	0.67^{de} (0.57–0.79)
Mixed forest	3802.5^{c} (3458.7–4180.5)	239.3^{c} (220.6–259.6)	13.0^{b} (11.3–15.0)	44.6^{cd} (40.6–48.9)	6.6^{c} (5.9–7.5)	0.91^{cde} (0.78–1.07)
Grassland	2070.4^{d} (1859.6–2305.0)	154.9^{d} (140.2–171.2)	21.0^{ab} (17.1–25.8)	43.4^{cd} (39.0–48.2)	5.5^{c} (4.7–6.4)	1.4^{bc} (1.1–1.7)
Shrub	3996.8^{c} (2124.8–7518.0)	255.5^{c} (136.7–477.4)	14.7^{b} (8.0–26.8)	28.5^{e} (21.4–38.0)	7.2^{c} (4.2–12.5)	0.6^{de} (0.5–0.8)
Tundra	20407.9^{a} (15,774.0–26,403.3)	837.9^{b} (641.2–1095.1)	36.9^{a} (28.1–48.5)	340.5^{a} (237.0–489.1)	34.9^{a} (29.2–41.7)	4.9^{a} (3.4–7.0)
Desert	172.7^{f} (132.6–225.1)	36.4^{f} (26.6–49.8)	12.6^{b} (11.4–14.0)	6.3^{g} (4.8–8.3)	2.4^{d} (1.9–3.0)	0.2^{f} (0.1–0.3)
Natural wetlands	22918.8^{a} (18,226.8–28,818.5)	1231.5^{a} (1036.5–1463.1)	26.5^{ab} (21–33.3)	111.4^{b} (84.4–147.0)	19.3^{b} (14.5–25.9)	2.4^{b} (1.1–5.4)
Cropland	1155.1^{e} (1117.4–1195.1)	94.4^{e} (90.5–98.6)	14.9^{b} (12.4–17.9)	20.6^{f} (19.8–21.4)	2.3^{d} (2.2–2.5)	0.5^{e} (0.4–0.6)
Pasture	3729.7^{c} (3337.2–4168.4)	235.5^{c} (203.3–272.9)	16.1^{b} (11.7–22.1)	55.2^{c} (48.2–63.3)	5.1^{c} (4.1–6.4)	2.1^{b} (1.6–2.7)
Area-weighted global average	4768.0	290.5	16.6	56.7	7.5	1.3

Values are presented as means with 95% confidence boundaries in parentheses. Different superscript letters in one column mean significant difference at a significance level of $P = 0.05$, while the same letters indicate no significant difference; it should be noted that the soil microbial biomass P in boreal forest is not reported because the data are concentrated in one site.
Corg, soil organic carbon; Ntot, soil total nitrogen; Ptot, soil total phosphorus; Cmic, soil microbial biomass carbon; Nmic, soil microbial biomass nitrogen; Pmic, soil microbial biomass phosphorus.

Table 2 Summarized percentage of soil elements contained in soil microbial biomass.

Major biomes	Cmic/Corg (%)	Nmic/Ntot (%)	Pmic/Ptot (%)
Boreal forest	1.76[bc] (1.47–2.12)	4.18[ab] (3.68–4.76)	
Temperate coniferous forest	0.99[f] (0.89–1.11)	2.62[cd] (2.29–3.00)	4.31[d] (2.85–6.51)
Temperate broadleaf forest	1.16[ef] (1.06–1.26)	2.42[d] (2.08–2.81)	8.60[bcd] (6.22–11.89)
Tropical/subtropical forest	1.79[bc] (1.63–1.96)	3.08[bcd] (2.72–3.49)	6.32[cd] (4.99–8.00)
Mixed forest	1.29[def] (1.22–1.36)	2.80[cd] (2.61–3.02)	6.72[cd] (5.61–8.04)
Grassland	2.09[b] (1.95–2.23)	4.28[ab] (3.93–4.65)	5.60[d] (4.48–7.01)
Shrub	1.43[cde] (1.11–1.84)	2.33[d] (1.74–3.12)	14.74[ab] (8.90–24.40)
Tundra	1.66[bcd] (1.27–2.17)	3.61[bc] (2.67–4.88)	4.45[d] (3.16–6.26)
Desert	5.02[a] (3.86–6.53)	5.72[a] (4.03–8.11)	
Natural wetlands	1.20[ef] (0.95–1.51)	2.58[cd] (2.04–3.27)	23.62[a] (16.54–33.73)
Cropland	1.67[bcd] (1.61–1.73)	2.53[d] (2.36–2.70)	1.60[e] (1.33–1.93)
Pasture	1.46[cde] (1.32–1.62)	2.62[cd] (2.19–3.12)	11.95[bc] (8.79–16.24)
Global average	1.2	2.6	8.0

Values are presented as means with 95% confidence boundaries in parentheses. Different superscript letters in one column mean significant difference at a significance level of $P = 0.05$, while the same letters indicate no significant difference; it should be noted that fraction of P in soil microbial biomass was not reported for boreal forest and desert due to data shortage.
Corg, soil organic carbon; Ntot, soil total nitrogen; Ptot, soil total phosphorus; Cmic, soil microbial biomass carbon; Nmic, soil microbial biomass nitrogen; Pmic, soil microbial biomass phosphorus.

soil has narrow C:N, C:P and N:P ratios due to its low C concentration (Tables 1 & 3). For soil microbial biomass, natural wetlands, tundra, tropical/subtropical forest and boreal forest have a wide C:N ratio, natural wetlands and tundra have a wide C:P ratio, while natural wetlands have the widest N:P ratio in soil microbial biomass.

The C:N:P stoichiometries at biome and global scales are summarized in the Table 3. The global averaged C:N:P stoichiometry is 287:17:1 for soil elements and 42:6:1 for soil microbial biomass. The C:N:P stoichiometry varies substantially across biomes (Table 3). The boreal forest and natural wetlands have wide ratios, while cropland has a narrow C:N:P stoichiometry for soil elements. Natural wetlands and tundra have a wide C:N:P stoichiometry, while boreal forest, cropland, pasture and desert have a narrow C:N:P stoichiometry in soil microbial biomass (Table 3). The C:N:P stoichiometry based on area-weighted globally averaged soil microbial biomass in this study is close to that of bacteria (Chapin *et al.*, 2002; Paul, 2007), indicating dominance of bacteria in the surface soil microbial community around the globe (Strickland & Rousk, 2010).

Vertical distribution of soil microbial biomass along soil profiles

Soil microbial biomass C concentration decreases exponentially with soil depth (Fig. 3). The soil microbial biomass C in the few centimetres of soil near the surface can be 100 times larger than below 100 cm, especially for cropland and grassland which usually have shallow root systems (Jackson *et al.*, 1996). There are two mechanisms contributing to the association of soil microbial biomass with root profile: first, the root exudates are the major energy sources for soil microorganisms (Helal & Sauerbeck, 2007), and second, root systems transport oxygen to the soil matrix to create a favourable soil microrhizosphere system (Chapin *et al.*, 2002). Both these mechanisms make the rhizosphere system a favourable environment for soil microbes (Helal & Sauerbeck, 2007). We hypothesize that the vertical distribution of soil microbial biomass is the same as vertical root distribution. To test this hypothesis, we fitted soil microbial biomass with soil depth using an asymptotic equation (equation 1) (Gale & Grigal, 1987) as Jackson *et al.* (1996) did for root distribution in soil profiles:

$$Y = 1 - \beta^{d} \tag{1}$$

where the Y is the cumulative soil microbial biomass fraction (a proportion between 0 and 1) from the soil surface to depth d (cm), and β is the fitted 'coefficient'. Low β corresponds to a greater proportion of soil microbial biomass near the soil surface, and vice versa (Jackson *et al.*, 1996). Similar β-values for vertical distributions of root and soil microbial biomass C would support our hypothesis.

Since no β-value for root distribution in pasture was reported in Jackson *et al.* (1996), we compared the fitted β-values for soil microbial biomass C with those reported in Jackson *et al.* (1996) for forest, cropland, grassland and desert (Fig. 3). The results show that the fitted β-values for four biomes are not different from those for root distributions at a significance level of $P = 0.05$. Therefore, we accept the hypothesis that the vertical distribution of soil microbial biomass C, N and P is the same as root distribution with soil depth. Because no vertical distribution of soil microbial biomass measurements is available for other biomes, we applied β-values for root distribution reported in Jackson *et al.* (1996) to the biomes which were not fitted in this study (Fig. 3, Table S1).

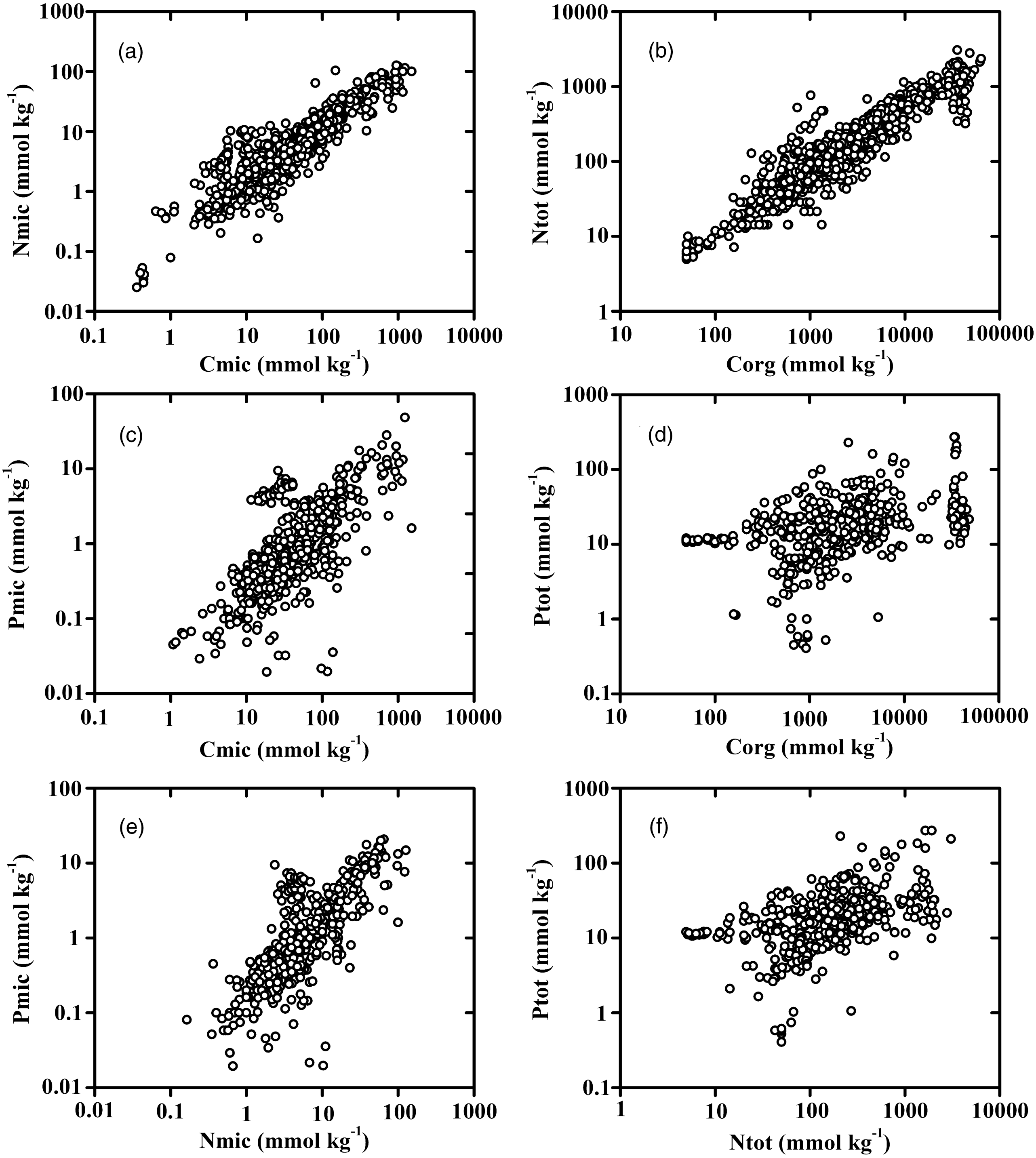

Figure 2 Stoichiometry of C, N and P in soil microbial biomass and soils. Cmic, soil microbial biomass carbon; Corg, soil organic carbon; Nmic, soil microbial biomass nitrogen, Ntot, soil total nitrogen.

Climate controls on the soil microbial biomass C and N concentrations

Climate controls on soil microbial biomass C and N were evaluated by multiple linear regressions (equations 2 & 3). The controls on the soil microbial biomass P was not fitted in our current study due to a shortage of data. The retrieved climate variables (air temperature and precipitation) are well matched to those reported in the original literature (Fig. S8). For the soil microbial biomass C, we used long-term averaged annual precipitation (PPT), long-term averaged annual temperature (T) and soil organic C (Corg) as independent variables; for the soil microbial biomass N, we used long-term averaged annual precipitation, long-term averaged annual temperature, soil organic

Table 3 Summarized atomic C:N, C:P and N:P ratios and C:N:P stoichiometry for soil elements and soil microbial biomass for major biomes and the global average.

	Soil elements				Soil microbial biomass			
Biome	C:N	C:P	N:P	C:N:P	C:N	C:P	N:P	C:N:P
Boreal forest	31.4^{a} (28.5–34.6)	1030.3^{ab} (459.1–2312.1)	31.0^{b} (19.0–50.5)	1030:33:1	8.3^{abc} (7.7–8.9)			
Temperate coniferous forest	19.9^{c} (18.5–21.4)	318.5^{cde} (214.6–472.6)	15.2^{de} (11.1–20.9)	318:16:1	6.3^{d} (5.7–7.0)	70.6^{bc} (56.1–88.9)	7.4^{b} (5.1–10.6)	71:11:1
Temperate broadleaf forest	18.7^{c} (17.9–19.6)	391.1^{cd} (306.5–499.2)	19.9^{bcd} (16.3–24.2)	391:21:1	8.3^{abc} (7.8–8.9)	46.4^{de} (37.2–57.7)	4.4^{b} (3.6–5.4)	46:6:1
Tropical/subtropical forest	15.8^{d} (14.1–17.7)	169.4^{ef} (134.2–213.7)	13.4^{de} (11.7–15.2)	169:11:1	9.0^{ab} (8.3–9.7)	56.3^{cd} (51.1–62.1)	6.9^{b} (6.0–7.9)	56:6:1
Mixed forest	18.9^{c} (18.1–19.7)	253.8^{def} (214.5–300.2)	15.7^{cde} (14.1–17.5)	254:13:1	7.8^{abcd} (7.4–8.1)	55.5^{cde} (50.8–60.6)	5.9^{b} (5.3–6.5)	55:7:1
Grassland	13.3^{e} (12.8–13.9)	143.0^{f} (127.8–160.0)	10.7^{e} (9.6–12.0)	143:111	6.6^{cd} (6.2–6.9)	50.6^{cde} (44.3–57.8)	4.8^{b} (4.2–5.4)	51:8:1
Shrub	19.4^{c} (16.1–23.4)	518.8^{bcd} (337.7–797.2)	25.3^{bc} (18.8–33.9)	519:27:1	7.2^{bcd} (5.8–9.0)	42.6^{def} (37.6–48.2)	5.2^{b} (4.3–6.3)	43:6:1
Tundra	24.4^{b} (20.0–29.6)	545.1^{bc} (445.7–666.6)	30.5^{b} (25.4–36.6)	545:22:1	9.4^{a} (7.0–12.5)	100.2^{ab} (63.7–157.5)	6.5^{b} (4.9–8.5)	100:11:1
Desert	10.5^{f} (9.4–11.8)	6.6^{h} (5.8–7.6)	0.67^{g} (0.58–.078)		7.2^{bcd} (4.5–11.3)		4.4^{b} (3.6–5.2)	31:4:1
Natural wetlands	18.6^{c} (16.7–20.7)	$1347.^{3}$a (1063.5–1706.9)	62.8^{a} (49.2–80.3)	1347:72:1	9.5^{a} (7.7–11.8)	130.7^{a} (62.1–275.0)	35.7^{a} (14.0–91.2)	131:14:1
Cropland	12.5^{e} (14.8–16.3)	63.9^{g} (53.9–75.8)	4.4^{f} (3.9–5.0)	64:5:1	7.2^{bcd} (6.8–7.6)	37.6^{ef} (32.8–43.1)	4.6^{b} (3.9–5.4)	38:5:1
Pasture	15.5^{d} (14.8–16.3)	169.3^{ef} (144.2–198.8)	11.9^{de} (10.8–13.0)	169:11:1	7.0^{bcd} (6.2–7.9)	31.6^{f} (24.3–41.1)	4.1^{b} (3.5–4.7)	32:5:1
Global average	16.4	286.5	17.5	287:17:1	7.6	42.4	5.6	42:6:1

Values are presented as mean with 95% confidence boundaries in parentheses. Different superscript letters in one column mean significant difference at a significance level of $P = 0.05$, while the same letters indicate no significant difference; it should be noted that microbial C:P ratio for boreal forest and desert and microbial N:P for boreal forest and desert and microbial C:N:P in soil microbial biomass for boreal forest were not reported due to insufficient data.

C, and soil total N (Norg) as independent variables. In equations 2 & 3, *A, B, C, D* and *E* are the fitted parameters, and the values of all parameters for each biome are listed in Table S2. The regression for desert soils was fitted by using soil elements only as independent variables.

$$\log(\text{Cmic}) = A + B\,\text{PPT} + CT + D\log(\text{Corg}) \qquad (2)$$

$$\log(\text{Nmic}) = A + B\,\text{PPT} + CT + D\log(\text{Corg}) + E\log(\text{Ntot}) \qquad (3)$$

Global storage of soil microbial biomass C and N

Based on the relationships between soil microbial biomass C and N and soil elements with long-term averaged climate data derived in the previous section, we estimated the global storage of C and N in soil microbial biomass in the soil profiles of 0–30 cm and 0–100 cm. The global soil microbial biomass C is estimated at 16.7 Pg C in the 0–30 cm profile and 23.2 Pg C in the 0–100 cm soil profile; and the global soil microbial biomass N is estimated at 2.6 Pg N in the 0–30 cm profile and 3.7 Pg N in the 0–100 cm soil profile. Taking the global estimates of soil organic C (684–724 Pg C in 0–30 cm and 1462–1548 Pg C in 0–100 cm and 133–140 Pg N in 0–100 cm soil profile) and soil total N from Batjes (1996), approximately 2.3–2.4% of soil organic C is stored in soil microbial biomass in the top 0–30 cm, and 1.5–1.6% of soil organic C is stored in soil microbial biomass in the 0–100 cm soil profile. Approximately 2.6–2.8% of soil total N is stored in soil microbial biomass in the 0–100 cm soil profile. The fractions of soil organic C and total N in microbial biomass obtained by our empirical extrapolations (Table 1) are slightly different from strict averaging across the observations. The vertical distributions of soil microbial biomass C and N with soil depth decline more steeply than that for soil organic C (Jobbagy & Jackson, 2000).

Spatial variation in soil microbial biomass C and N is large (Fig. 4). The spatial patterns of soil microbial biomass are consistent with those of soil elements: relatively high concentration in northern high latitude and relatively low concentration in low latitude and the Southern Hemisphere (Fig. 4). The biome-level analyses show that forest ecosystems make the greatest contribution to the global storage of soil microbial biomass C and N (Table 4). Natural wetlands and tundra make disproportionately large contributions to the global storage of soil microbial biomass C and N due to high C and N densities in soil, while temperate coniferous forest has the lowest contributions due to its small area (Table 4). Meanwhile, the desert has a relatively low storage of soil microbial biomass C and N due to its low C and N concentrations (Post *et al.*, 1982, 1985; Batjes, 1996).

DISCUSSION

Comparisons with previous studies

This study summarizes the concentrations and stoichiometry of C, N and P in soil microbial biomass and soil elements, and further estimates the soil microbial biomass C and N storage in

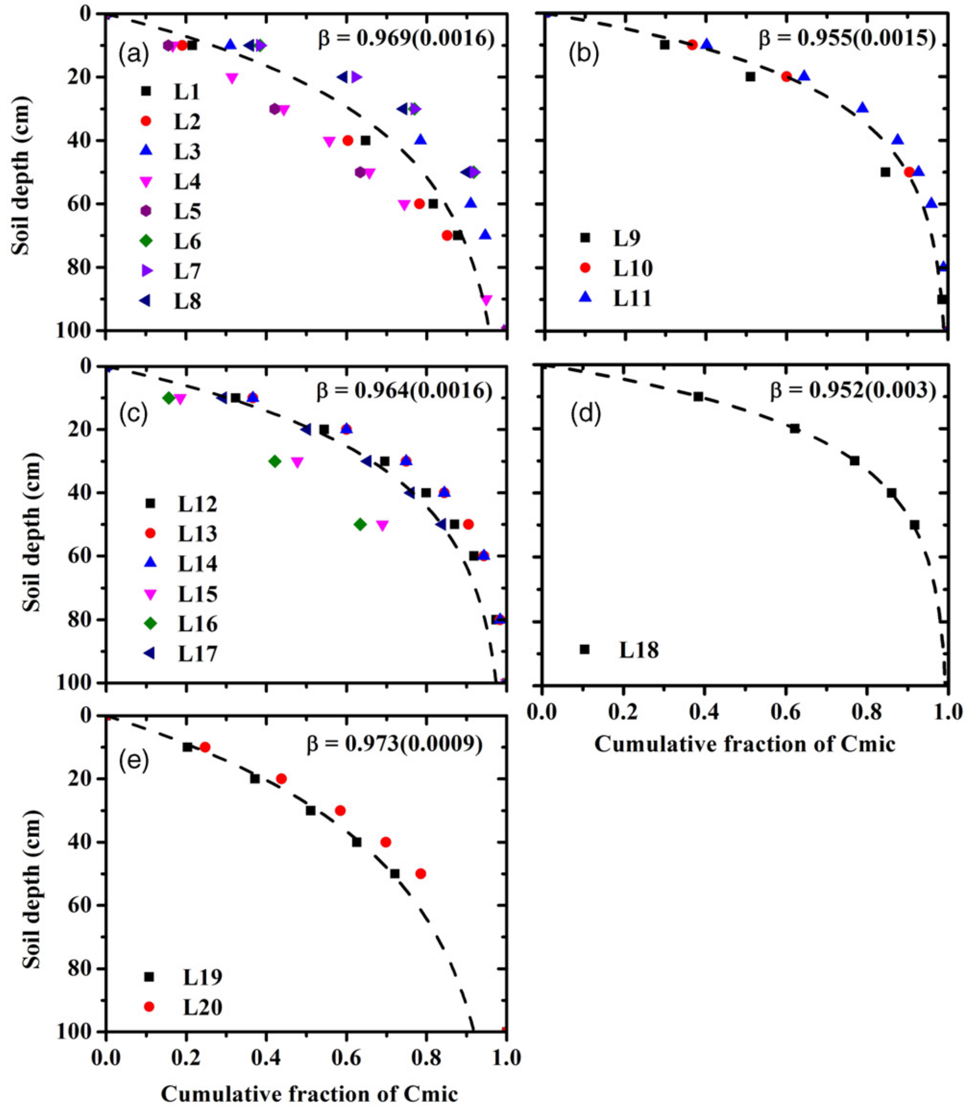

Figure 3 Vertical distribution of soil microbial biomass C, N and P in major biomes (a, forest; b, grassland; c, cropland; d, pasture; e, desert; L1, woodland–wooded grassland reported in Michelsen *et al.* (2004); L2, woodland reported in Michelsen *et al.* (2004); L3, dry deciduous forest reported in Michelsen *et al.* (2004); L4, 80-year-old plantation of *Abies alba* Mill reported in Agnelli *et al.* (2004); L5, Chinese fir reported in Li *et al.* (2007); L6, *Castanopsis kawakamii* reported in Li *et al.* (2007); L7, planted Chinese fir reported in Li *et al.* (2007); L8, planted *C. kawakamii* reported in Li *et al.* (2007); L9, Mediterranean barley and brome grass in a terrace reported in Fierer *et al.* (2003); L10, Mediterranean barley and brome grass in a valley reported in Fierer *et al.* (2003); L11, meadow reported in Lavahun *et al.* (1993); L12, oil-seed rape reported in Lavahun *et al.* (1993); L13, winter wheat reported in Lavahun *et al.* (1993); L14, sugar beet–winter wheat–winter barley reported in Kaiser & Heinemeyer (1993); L15, citrus orchard reported in Wang *et al.* (2004); L16, rice paddy reported in Wang *et al.* (2004); L17, wheat reported in Murphy *et al.* (1998); L18, clover reported in Murphy *et al.* (1998); L19, desert reported in Yu & Steinberger (2012a); L20, desert reported in Yu & Steinberger (2012b).

the 0–30 cm and 0–100 cm soil profiles at both biome and global levels. Both concentrations and stoichiometry of C, N and P in soil microbial biomass and soil elements are consistent with previous studies (Batjes, 1996; Cleveland & Liptzin, 2007; Tian *et al.*, 2010). The concentrations of organic C, total N and total P in the surface soils are reasonably consistent with previous regional and global synthesis (Batjes, 1996; Tian *et al.*, 2010); the concentrations of soil microbial biomass C, N and P are consistent with Cleveland & Liptzin (2007). Tian *et al.* (2010) summarized soils across China and estimated 134 ± 8.5 mmol N kg^{-1} total N in the 0–10 cm soil profile which is less than half of the area-weighted soil total N in the present study (Table 1). However, the arithmetic mean of soil N concentration in this study is 143.6 mmol N kg^{-1} with a 95% confidence boundary of 137.6–149.9 mmol N kg^{-1}, consistent with Tian *et al.*, (2010). Therefore, the large discrepancy in total N between this study and Tian *et al.* (2010) indicates a potential substantial bias when dealing with a largely skewed or varied dataset by using different approaches. The total P in China estimated by Tian *et al.* (2010) is much higher than that derived in this study; the discrepancy is

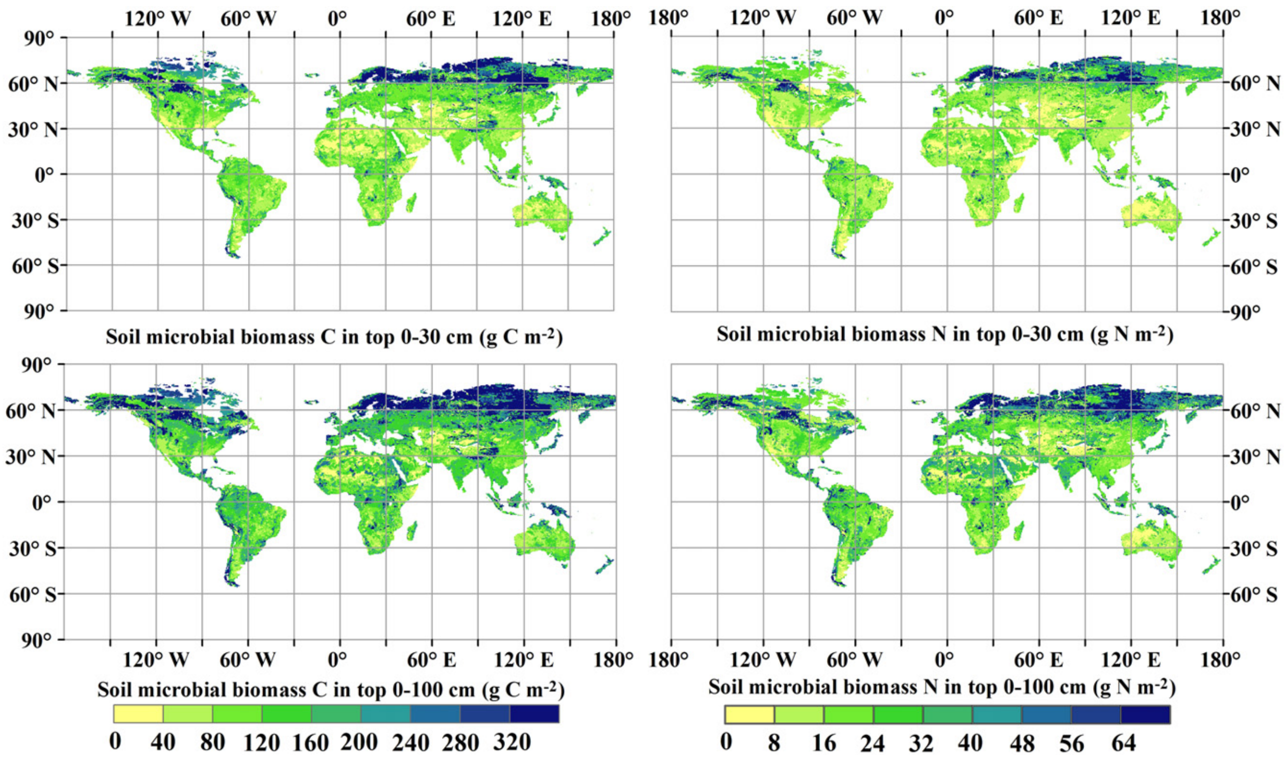

Figure 4 Global distribution of soil microbial C and N in terrestrial ecosystems: top left, soil microbial biomass C in top 0–30 cm; bottom left, soil microbial biomass C in top 0–100 cm; top right, soil microbial biomass N in top 0–30 cm; bottom right, soil microbial biomass N in top 0–100 cm.

Table 4 Storage of soil microbial C and N for major biomes.

Major biomes	Area (million km^2)	Soil microbial C (Pg C) 0–30 cm	Soil microbial C (Pg C) 0–100 cm	Soil microbial N (Tg N) 0–30 cm	Soil microbial N (Tg N) 0–100 cm
Boreal forest	7.0	3.38	4.08	388.54	469.21
Temperate coniferous forest	2.5	0.25	0.49	59.13	114.26
Temperate broadleaf forest	3.6	0.37	0.57	61.25	94.86
Tropical/subtropical forest	15.6	1.83	2.63	276.94	397.43
Mixed forest	11.9	1.76	2.89	332.02	543.21
Grassland	12.2	1.64	2.20	269.89	360.45
Shrub	8.1	0.53	0.80	73.09	109.57
Tundra	5.7	1.50	1.61	145.22	155.71
Desert	13.5	1.00	1.79	226.85	405.03
Natural wetlands	6.7	0.70	1.00	168.57	241.91
Cropland	14.8	1.44	2.16	244.14	365.97
Pasture	26.8	2.30	2.99	338.47	438.79
Total	128.3	16.72	23.20	2584.10	3696.39

Biome-based estimates may not sum to totals because of the effects of rounding in reporting those estimates.

the result of three factors. First, the soil total P in Tian *et al.* (2010) is exclusively from China while the data in this study have global coverage; second, log-transformation was not applied to the total P in Tian *et al.* (2010) – an arithmetic mean will result in an overestimate when dealing with a highly right-skewed data population. Actually, the arithmetic mean of untransformed total P in this study is 24.4 mmol P kg^{-1} which is close to 25.0 mmol P kg^{-1}, the estimate in the 0–10 cm soil profile by Tian *et al.* (2010).

The global average of C:N:P stoichiometry in soils is largely wider than that obtained by Cleveland & Liptzin (2007). We attribute this discrepancy to different approaches to summarizing the results. For example, the arithmetic average of the reported global average C:P ratio in this study is 133.1, with a 95% confidence interval of (118.1, 149.9), which is not significantly different from the 136 ± 11 reported in Tian *et al.* (2010), while slightly lower than 186 ± 12.9 reported in Cleveland & Liptzin (2007). However, the C:N:P stoichiometry estimated in this study is based on the area-weighted globally averaged C, N and P concentrations in soils and soil microbial biomass. This study estimates a soil C:N ratio of *c.* 17 at global level and *c.* 19 for forest, values which are consistent with previous summaries at global (Post *et al.*, 1985; Cleveland & Liptzin, 2007) and regional scales (Tian *et al.*, 2010).

This study reported a wide range in the fractions of total soil elements contained in soil microbial biomass. For example, the biome-level fraction of soil organic C in soil microbes varies from 0.9 to 6.5%; the biome-level fraction of soil total N in soil microbial biomass could be as low as 1.7% and as high as 8.1%, values consistent with previous studies (Chapin *et al.*, 2002). The biome-level fraction of soil total P in soil microbial biomass could be as low as 1.3% and as high as 33.7%, which is a slightly wider range than a previous estimate of 20–30% (Jonasson *et al.*, 1999;

Chapin *et al.*, 2002). However, global averages of the fractions of soil elements contained in soil microbial biomass reported in this study are slightly lower than previously reported. This is because the previous summaries are based on limited site observations, while the current estimates are based on a larger and more complete dataset covering all major biomes across the globe (Fig. 1).

Environmental controls on concentrations and stoichiometries of C, N and P in soil microbial biomass and soils

In this study we estimated the influences of environmental factors and climate on storage of soil microbial biomass C and N. No significant influence was found for soil pH on soil microbial biomass density. A recent study found pH value to be a controlling factor for soil bacterial communities (Fierer & Jackson, 2006). This indicates that the soil bacterial communities might not be able to represent all soil microbial groups. We found significant correlations with long-term climate factors for some biomes, consistent with the idea that soil microbial growth was influenced by soil moisture and temperature (Paul, 2007). We found that concentrations of C, N and P in soil elements and soil microbial biomass significantly increase with latitude (Figs S9–S11), consistent with Post *et al.* (1982).

Similar to a recent study (Cleveland & Liptzin, 2007), we did not find a significant correlation between C:N:P ratios and soil pH values, indicating weak controls from soil physical factors on soil microbial biomass. Yet this study does find latitudinal gradients of C:N:P ratios in soils and soil microbial biomass (Figs S12–S14), indicating temperature effects on C:N:P stoichiometry.

Soil microbial biomass as an indicator for ecosystem nutrient limitation

Studies have suggested that soil N:P ratio or foliar N:P ratio could be used to indicate nutrient limitation on the basis of the Liebig's law of the minimum (Güsewell, 2004; Cleveland & Liptzin, 2007). Using the N:P ratio as an indicator for ecosystem limitation is based on the assumption that a higher N:P ratio than an optimal value indicates a P deficiency for plant acquisition, and vice versa.

A recent meta-analysis suggests using soil microbial biomass N:P as an indicator for ecosystem limitation since a more constrained N:P ratio in microbial biomass than the reported plant and soil N:P ratio was found (Cleveland & Liptzin, 2007); this is confirmed by our analysis. However, we argue that the N:P ratio in soil microbial biomass may not suitable as an indicator for ecosystem nutrient limitation. The growth of soil microorganisms is normally limited by C, rather than by N or P as indicated by previous studies (Allison *et al.*, 2010). Compared with plants, soil microorganisms are able to thrive in P-depleted conditions (Chapin *et al.*, 2002; Paul, 2007). When the availability of P in the ecosystem declines, relatively more P will be stored in soil microbial biomass, which will enhance the P limitation for plants. This results in a relatively lower microbial N:P ratio and severe P limitation for plants, indicating the inappropriateness of N:P ratio in soil microbial biomass as an indicator for ecosystem limitation.

The varied fractions of soil elements in soil microbial biomass across biomes may imply N or P limitation of specific biomes. The mechanism is on the basis of higher efficiency of soil microbes in assimilating nutrients. Soil microbes are more efficient in obtaining nutrients than plants from soil to keep their own biological mechanisms functioning well (Bardgett *et al.*, 2003). In nutrient-depleted ecosystems, the relatively high fraction of specific nutrients in microbial biomass implies a strong limitation of this element to plants (Jonasson *et al.*, 1999). For example, natural wetland, a severe P-limiting ecosystem (Elser *et al.*, 2007; Xu *et al.*, 2011), has a large fraction of soil total P in soil microbial biomass (Table 2); boreal forest, a severe N-limiting ecosystem (DeLuca *et al.*, 2008), and slightly P-limiting ecosystem (Giesler *et al.*, 2002), has a large fraction of soil total N and P in soil microbial biomass (Table 2).

Uncertainties and research needs

Sources of uncertainties should be noted when interpreting the results of this study. First, a mixture of various methods in reporting soil microbial biomass introduces uncertainties in estimation because different methods in measuring soil microbial biomass C, N and P may result in differences as large as the reported soil microbial biomass (Beck *et al.*, 1997; Anderson & Domsch, 2010; Joergensen *et al.*, 2011). Second, differences in the number of data and the land area for each biome would also be a source of uncertainty. In this study almost half of the data are from cropland (Fig. 1), while the land area of cropland is approximately 14% of the global land area (Ramankutty & Foley, 1998); this contributes bias to the global summaries even though land area-weighted averages were reported. Third, the seasonality of soil microbial biomass could be another source of uncertainty; the spatial dataset of soil microbial biomass used in this study is collected in field measurements conducted in various seasons and locations. Further studies on seasonal variation of soil microbial C, N and P would be a large improvement on current knowledge. Fourth, the different methods in measuring soil P are another source of uncertainty. The relatively large variations in P might be partially caused by different methods which are usually targeted at distinct P forms (Yang & Post, 2011). Last, but not least, a new study reported that the northern circumpolar permafrost region contains more than double the amount of soil organic C in the top 1 m than previous estimates (Tarnocai *et al.*, 2009), indicating we might have underestimated the soil microbial biomass in the soils in northern permafrost region.

Concluding remarks

We summarized the concentrations of C, N and P in soils and soil microbial biomass across biomes and gave a global average. The best estimates of C:N:P stoichiometry for soil elements and soil microbial biomass are 287:17:1, and 42:6:1, respectively, at a global scale. The global storage of soil microbial biomass C and N was estimated to be 16.7 Pg C and 2.6 Pg N in the 0–30 cm soil profiles and 23.2 Pg C and 3.7 Pg N in the 0–100 cm soil profiles.

This study represents the first attempt to examine the C:N:P stoichiometry in soil microbial biomass at biome level and to estimate the global storage of soil microbial biomass. Although there are a number of uncertainties, this study contributes to ecological stoichiometry, global change research and microbial geography, and improves our understanding of the roles of microbes in land–atmosphere interaction and its feedbacks to the climate system. Many studies have identified soil microbial biomass as both a major source of uncertainties and an important component of large-scale earth system models (Bardgett *et al*., 2008). Incorporating soil microbial roles in biogeochemical cycles of elements into earth system models is an urgent task.

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SUPPORTING INFORMATION

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

Figure S1 Spatial distribution of major biomes across the globe.
Figure S2 Histograms showing frequency of soil elements.
Figure S3 Histograms showing frequency of soil microbial biomass C, N and P.
Figure S4 Histograms showing frequency of ratios between soil elements.
Figure S5 Histograms showing frequency of ratios between soil microbial biomass C, N and P.
Figure S6 Box and scatter charts showing distributions and magnitudes of C, N and P in microbial biomass and soil and fractions of soil nutrient in soil microbial biomass.
Figure S7 Box and scatter charts showing distributions and magnitudes of C, N and P in microbial biomass and soil and fractions of soil nutrient in soil microbial biomass in 11 major biomes.
Figure S8 Observed versus retrieved climate variables for the sampling sites.
Figure S9 Scatterplot showing soil organic C and soil microbial biomass C along latitude.
Figure S10 Scatterplot showing soil organic N and soil microbial biomass N along latitude.
Figure S11 Scatterplot showing soil organic P and soil microbial biomass P along latitude.
Figure S12 C:N ratios for soil elements and soil microbial biomass along latitude.
Figure S13 C:P ratios for soil elements and soil microbial biomass along latitude.
Figure S14 N:P ratios for soil elements and soil microbial biomass along latitude.
Table S1 The values of parameters describing vertical distribution of soil microbial biomass C and N in soil profile.
Table S2 Values of parameters used to estimate global soil microbial biomass C and N (standard errors in the brackets; *N* is the numbers of data points used in multiple linear regression).

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