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Soil properties rather than climate and ecosystem type control the vertical variations of soil organic carbon, microbial carbon, and microbial quotient

Tingting Sun [a,b,c], Yugang Wang [a,b,c,**], Dafeng Hui [d], Xin Jing [e], Wenting Feng [f,*]

[a] *State Key Laboratory of Desert and Oasis Ecology, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Urumqi, Xinjiang, 830011, China*
[b] *University of Chinese Academy of Sciences, Beijing, 100049, China*
[c] *National Fukang Station of Desert Ecosystem Ecology, Field Sciences Observation and Research Station, Chinese Academy of Sciences, Fukang, Xinjiang, 831505, China*
[d] *Department of Biological Sciences, Tennessee State University, Nashville, TN, 37209, USA*
[e] *Department of Earth and Environmental Sciences, KU Leuven, Celestijnenlaan 200E, 3001, Leuven, Belgium*
[f] *Institute of Agricultural Resources and Regional Planning, Chinese Academy of Agricultural Sciences, Beijing, 100081, China*

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ABSTRACT

Small changes in soil organic carbon (SOC) may have great influences on the climate-carbon (C) cycling feedback. However, there are large uncertainties in predicting the dynamics of SOC in soil profiles at the global scale, especially on the role of soil microbial biomass in regulating the vertical distribution of SOC. Here, we developed a database of soil microbial biomass carbon (SMBC), SOC, and soil microbial quotient (SMQ = SMBC/SOC) from 289 soil profiles globally, as well as climate, ecosystem types, and edaphic factors associated with these soil profiles. We assessed the vertical distribution patterns of SMBC and SMQ and the contributions of climate, ecosystem type, and edaphic condition to their vertical patterns. Our results showed that SMBC and SMQ decreased exponentially with soil depth, especially within the 0–40 cm soil depth. SOC also decreased exponentially with depth but in different magnitudes compared to SMBC and SMQ. Edaphic factors (*e.g.*, soil clay content and C/N ratio) had the strongest control on the vertical distributions of SMBC and SMQ, probably by mediating substrate and nutrient supplies for microbial growth in soils. Mean annual temperature and ecosystem types (*i.e.*, forests, grasslands, and croplands) had weak influences on SMBC and SMQ. In contrast, the vertical distribution of SOC was significantly affected by climate and edaphic factors. Climate and ecosystem types likely simultaneously affected multiple factors that control SMBC, such as the distribution of soil clay and nutrients along soil profiles. Overall, our data synthesis provides quantitative information of how SMBC, SMQ, and SOC changed along soil profiles at large spatial scales and identifies important factors that influence their vertical distributions. The findings can help improve the prediction of C cycling in terrestrial ecosystems by incorporating the contribution of soil microbes in Earth system models.

1. Introduction

Since soil organic carbon (SOC) is the largest carbon (C) reservoir in terrestrial ecosystems (Jones et al., 2005; Lal, 2018), small changes in SOC may have great impacts on terrestrial C-climate feedback. Soil microbial biomass is an active component of SOC and sensitive to environmental changes (Feng et al., 2009; Wardle, 1992; Xu et al., 2013). Its spatial and vertical variations may greatly influence SOC change. There are large uncertainties in predicting the global SOC change along soil profiles (Jobbágy and Jackson, 2000; Koven et al., 2013; Shi et al., 2018). One of the main sources of this uncertainty is our poor understanding of the vertical distribution of soil microbial biomass carbon (SMBC) and its controls at large spatial scales (Fterich et al., 2011; Xu et al., 2013).

Soil microorganisms are important in regulating SOC dynamics along soil profiles by mediating the decomposition and formation of SOC. SOC changes are tightly coupled to the size and activity of soil microbial population. For instance, soil microbial biomass is part of labile organic C and influences the decomposition of existing old SOC (Fontaine et al., 2007; Liang et al., 2011). In newly developed soil C models that explicitly represent the roles of microbial communities and vertical SOC changes, SMBC is a key parameter and assumed to be proportional with

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* Corresponding author.
** Corresponding author. Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, Urumqi, Xinjiang, 830011, China.
E-mail addresses: wangyg@ms.xjb.ac.cn (Y. Wang), fengwenting@caas.cn (W. Feng).

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the pools of soil enzyme and labile organic C (Koven et al., 2013; Wang et al., 2013, 2017). The central roles of SMBC in soil C models suggest that changes in SMBC would substantially affect SOC dynamics. Meanwhile, SMBC is the precursor of organic substances to form stable SOC (Cotrufo et al., 2013; Kallenbach et al., 2016; Liang et al., 2017). The microbial necromass and byproducts in soils account for ~80% of SOC and are proportional to living microbial biomass in soils (Liang et al., 2011, 2019a), thus potentially controlling soil C sequestration.

Given the dual roles of SMBC in regulating the vertical change of SOC, the ratio of SMBC to SOC, known as soil microbial quotient (SMQ) (Liu et al., 2018; Xu et al., 2013), could be a potential regulator of SOC dynamics. However, large variations in SMQ have been observed along soil profiles. Globally, SMBC accounts for <5% of SOC in surface soils (Cleveland and Liptzin, 2007; Fterich et al., 2011) and the ratio of SMBC and SOC (*i.e.*, SMQ) varied with soil depth in the top 10 cm (Fterich et al., 2011; Liu et al., 2018). The biotic (*e.g.*, plant root and microbial community) and abiotic factors (*e.g.*, O_2, soil clay content, pH, and nutrient) may control the vertical distributions of SMBC and SMQ with soil depth (Jackson et al., 1996; Jiao et al., 2018; Joergensen and Raubuch, 2003; Nielsen and Ball, 2015). Moreover, the biotic and abiotic factors interact with each other, but their overall effects on the spatial heterogeneity of SMBC were not well explored. For example, plant root distribution could influence soil physiochemical properties (*e.g.*, substrates and pH) along soil profiles (Paul et al., 2008; Pietri and Brookes, 2008). Meanwhile, the vertical variations of soil clay content and roots may affect the preferential flows of moisture, substrates, nutrients, and soil microbes (Fterich et al., 2011; Gross and Harrison, 2019; Jackson et al., 1996). However, studies that characterize and quantify the global patterns of vertical distributions of SMBC and SMQ and their controls remain rare. More knowledge of the spatial pattern of vertical distribution of SMBC is critically important for understanding global C cycling (Powlson et al., 1987) and microbial biogeography (Martiny et al., 2006).

In this study, we built a comprehensive database of the vertical distributions of SMBC and SMQ at the global scale. Specifically, the study aimed to (1) explore the vertical distribution patterns of SMBC and SMQ along soil profiles across ecosystem types, climatic zones, and soil textures and (2) identify the primary controls on the vertical distribution patterns of SMBC and SMQ and quantify their relative importance globally. We hypothesized that: (1) SMBC and SMQ would decrease with soil depth but in different magnitudes at large spatial scales, because microbial growth depends on substrates and nutrients that generally decrease with soil depth (Ma et al., 2020; Rumpel and Kögel-Knabner, 2011). (2) SMBC and SMQ would be more likely regulated by ecosystem types in surface soils and by soil clay content in subsoils. This is because plant roots, a main source of substrates for soil microbial growth, are mainly allocated in surface soils and vary with ecosystem types (Jackson et al., 1996). In contrast, fine soil particles (*e.g.*, soil clay content) that can preserve substrates and nutrients for microbial growth are generally higher in subsoils than in surface soils (Bu et al., 2012; Fterich et al., 2011; Wiesmeier et al., 2012; Zhao et al., 2016a,b).

2. Materials and methods

2.1. Data source

We compiled a database of the vertical distribution of soil microbial biomass from the Web of Science and the China National Knowledge Infrastructure which is a comprehensive literature database of papers published in Chinese (1970–2019). The keywords used to search relevant literature were microbial biomass, soil depth, soil profile, deep soil (s), subsoil(s), and vertical. All studies included in our database met the following criteria: 1) a soil profile was reported with at least three soil layers. The litter or soil organic layer was not included in this study, because the variations of soil properties in the organic layers were large across studies and most studies focused on mineral soils. 2) SMBC was measured using the chloroform-fumigation extraction method. We found that common approaches to estimate SMBC included chloroform-fumigation extraction method (Vance et al., 1987), phospholipid fatty acid (PLFA) technique (Frostegård and Bååth, 1996), deoxyribonucleic acid (DNA) extraction (Marstorp et al., 2000), and substrate induced respiration (SIR) (Anderson and Domsch, 1978). We only included studies using the chloroform-fumigation extraction method, as it was the most commonly used method to determine SMBC and SMBC measured by this method were more available compared to the other three methods. In total, we collected 1040 data points of SMBC from 289 soil profiles in 59 publications. The geographic locations varied from 39°S to 55°N in latitude and from 122°W to 140°E in longitude (Figs. 1 and S1). Mean annual temperature (MAT, ^{o}C) ranged from −1.7 to 30 °C and precipitation (MAP, mm) ranged from 119 to 2200 mm yr^{-1} (Fig. S1).

We examined the first 1 m of soil profiles because this was the depth in which most studies measured SMBC (Xu et al., 2013). The unit of SMBC was unified and expressed as mg C per kg dry soil. In those studies where SMBC were not available but SOC and SMQ were reported, we calculated SMBC through multiplying SOC by SMQ.

To investigate the influencing factors of SMBC distribution, we also compiled a suite of climate, ecosystem type, and edaphic factors (Fterich et al., 2011; Liu et al., 2018; Nielsen and Ball, 2015; Wang et al., 2004; Zhao et al., 2016a,b). MAT and MAP were compiled from each study. When the climate data at the study sites were not reported, they were obtained from the World Weather information service (https://worldweather.wmo.int/en/home.html) based on the longitude and latitude of the locations. Ecosystem types of soil profiles in our database were divided into three groups: grasslands, croplands, and forests, accounting for 22, 48, and 30% of all the soil profiles, respectively.

Soil properties, such as SOC, soil total nitrogen (STN), the ratio of SOC to STN (soil C/N), soil pH, soil clay content, SMQ ratio, and soil depth were collected from each study site. In some cases when soil clay content and pH were not available, the data were obtained from SoilGrids at a spatial resolution of 250 m (version 0.5.3, https://soilgrids.org) according to the coordinates of the soil profiles. In some studies where soil organic matter (SOM) content instead of SOC was reported, SOM was transformed to SOC by multiplying a coefficient of 0.58 (Howard and Howard, 1990; Read and Ridgell, 1922). Soil texture was classified into sandy soil (sand ≥70%, clay ≤15%), loamy soil (sand ≤85%, clay ≤40%) and clay soil (sand ≤65%, clay ≥35%) according to the USDA Soil Texture Classification system (U.S. Department of Agriculture, 1951), each of which included 22, 232, and 35 soil profiles, respectively. Soil depth was calculated by arithmetic mean value of the upper and lower boundaries of each soil layer reported in literature. For example, the mean depth of a soil layer from 10 to 30 cm was 20 cm. The data of the above variables were obtained from tables and texts from literature directly, and the data in figures were extracted using GetData Graph digitizer software version 2.25 (Fedorov, 2013).

2.2. Statistical analysis

The data of all continuous variables were plotted in histogram to show their relative frequency distribution. Correlations among environmental variables (*e.g.*, climate), soil properties (*e.g.*, pH and clay content), soil depth, SMBC and SMQ were estimated using Spearman correlation analysis (Rebekic et al., 2015).

SMBC and SMQ vary with soil depth and are influenced by environmental variables, such as climate, ecosystem types, and soil properties. The exponential function was used to examine the vertical distribution patterns of SOC, SMBC, and SMQ with soil depth, according to the parsimonious principle of model selection. The exponential function was widely used in literature (Bai et al., 2016; Eilers et al., 2012; Stone et al., 2014) and had similar goodness of fit (*e.g.*, R^2 and root mean square error) compared to the power function (Table S1). To test whether climate, ecosystem types, and soil textures influenced the vertical distribution patterns of SOC, SMBC and SMQ, we compared the

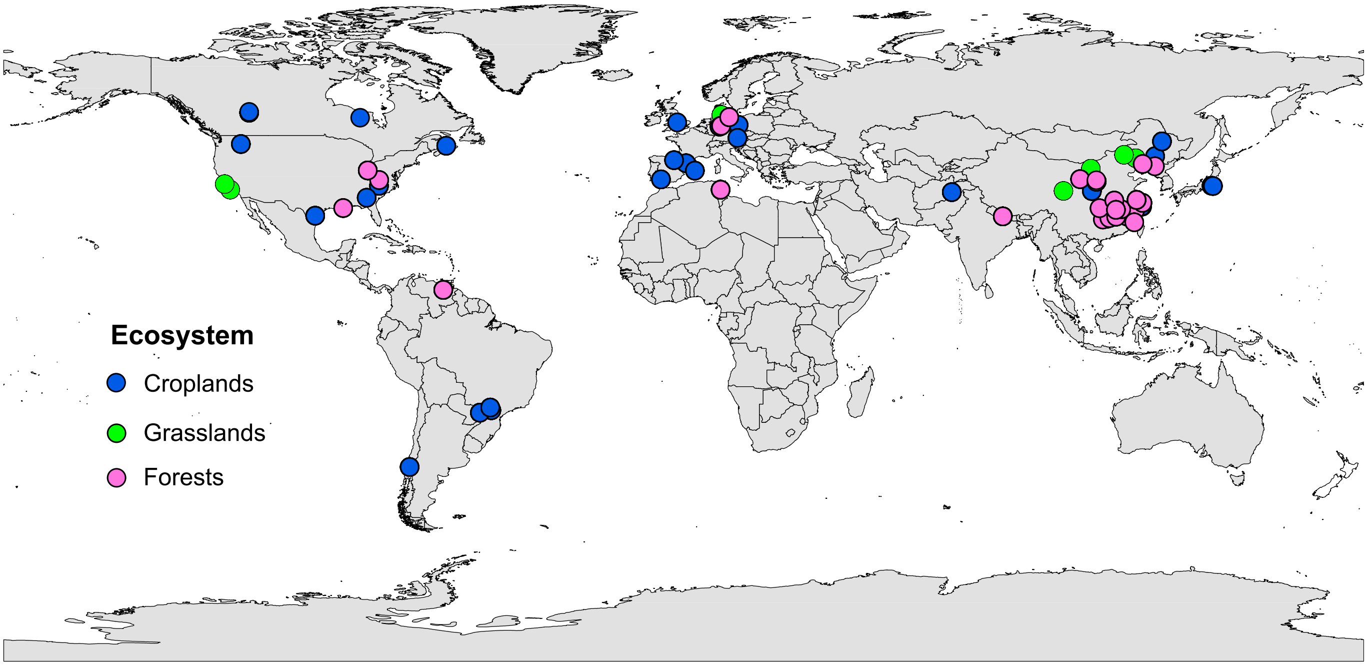

Fig. 1. Geographic locations of soil profiles across three ecosystem types in this study (n = 289).

patterns of their vertical distributions across climate zones, ecosystem types, and soil texture types. Climate zones were divided into three MAT groups (<10, 10–20, and >20 °C) and three MAP groups (<400, 400–800, and >800 mm) according to the criteria that are commonly used in other studies (Jobbágy and Jackson, 2000; Mi et al., 2008). The MAP values of 400 mm and 800 mm were the cutoff points s to distinguish the semiarid, semi-humid, and humid climate (Compiler Group of Physical Geography of China, 1993).

Since SOC, SMBC, and SMQ were significantly different in the surface soils (0–40 cm) and subsoils (40–100 cm), their main control factors might be different. To quantify the relative importance of environmental variables on SOC, SMBC, and SMQ at different soil depths (0–40 cm vs. 40–100 cm vs. 0–100 cm), we conducted the random forest (RF) modeling with bootstrap samples and random feature selection in regression trees using the randomForest package in R version 3.5.3 (Cutler et al., 2007; Svetnik et al., 2003). We also assessed the significance of each predictor in the RF modeling using the A3 package (Fortmann-Roe, 2015) and rfPermute package (Archer, 2016). The partial dependence was applied to examine how a single environmental variable affected SOC, SMBC, and SMQ while other environmental variables were controlled. This analysis was performed using pdp package in R version 3.5.3 (Greenwell, 2017).

To evaluate the direct and indirect effects of environmental variables on SMBC and SMQ along soil profiles, we performed the structural equation modeling analyses (SEMs) based on the hierarchical pathways of prior knowledge and conceptual models (see summaries in Table S5) (Grace et al., 2016). Prior to SEMs, some environmental variables were excluded for this analysis due to their insignificant effects or collinearity according to the results of RF and correlation analyses. To run SEMs for SMBC, we excluded soil pH as it was a non-significant predictor for SMBC ($P > 0.05$, Fig. 3f) and STN because of its collinearity with SOC ($r = 0.87$, $P < 0.01$, Table S4). To run SEMs for SMQ, we excluded soil C/N ratio and pH as they were non-significant predictors ($P > 0.05$, Fig. 3i) and SMBC due to its collinearity with SOC ($r = 0.66$, $P < 0.01$, Table S4). Eventually, MAT, MAP, ecosystem type, depth, soil clay content, SOC, and soil C/N were selected to perform SEMs for SMBC. MAT, MAP, ecosystem, depth, soil clay content, and SOC were selected to perform SEMs for SMQ. The contributions of these variables in the SEMs were evaluated using the Chi-square test (χ^2, $P > 0.05$) and the root mean square error of approximation (RMSEA <0.05, $P > 0.05$) (Schermelleh-Engel et al., 2003). The ecosystem types, such as croplands, grasslands, and forests were coded as 1, 2, and 3, respectively, for SEMs and the RF analyses. The data of these variables were natural logarithm transformed to increase the goodness of SEMs (*i.e.*, χ^2 and RMSEA).

The correlation and regression analyses were conducted in SPSS 20.0 (IBM Corp., Armonk, NY). The SEMs were conducted using AMOS 23.0 (SPSS Inc., Chicago, IL, USA). All figures were prepared using Origin 8.5 and the geographic locations of soil profiles collected in this study were visualized using ArcGIS 10.2.

3. Results

3.1. Vertical distributions of soil properties

Globally, soil nutrients (*i.e.*, STN and soil C/N) decreased exponentially with increasing soil depth, particularly in the surface soil layer (0–40 cm). Soil pH increased with depth, but they were relatively stable in the subsoils (40–100 cm) (Fig. S2). The degrees of vertical changes of soil properties with depth differed across climate zones, ecosystems, and soil textures. MAT and MAP significantly affected the vertical distribution of STN. STN declined from surface soils to subsoils by 65.9% in the warm climate zone (MAT, 10–20 °C) and by 76.4% in the high rainfall zone (MAP >800 mm), both of which were higher than those in other climate zones (Fig. S2).

3.2. Vertical distributions of SOC, SMBC, and SMQ

SOC decreased sharply with increasing soil depth, especially in the surface soils. SOC in forests declined by 66.9% from the surface soils to subsoils, which were faster than those in croplands and grasslands (Figs. 2 and S3). Climate and soil texture significantly influenced the magnitudes of decreases in SOC with depth (Fig. S3). SOC was significantly different among the MAT regions in the surface soils but not in the subsoils, while SOC differed considerably among soil texture types and the MAP regions in both the surface and subsoils (Fig. S3).

SMBC decreased exponentially with increasing soil depth (Figs. 2 and S4). The largest declines in SMBC occurred in the surface soils with small changes in the subsoils (Fig. 2). At large spatial scales, the means

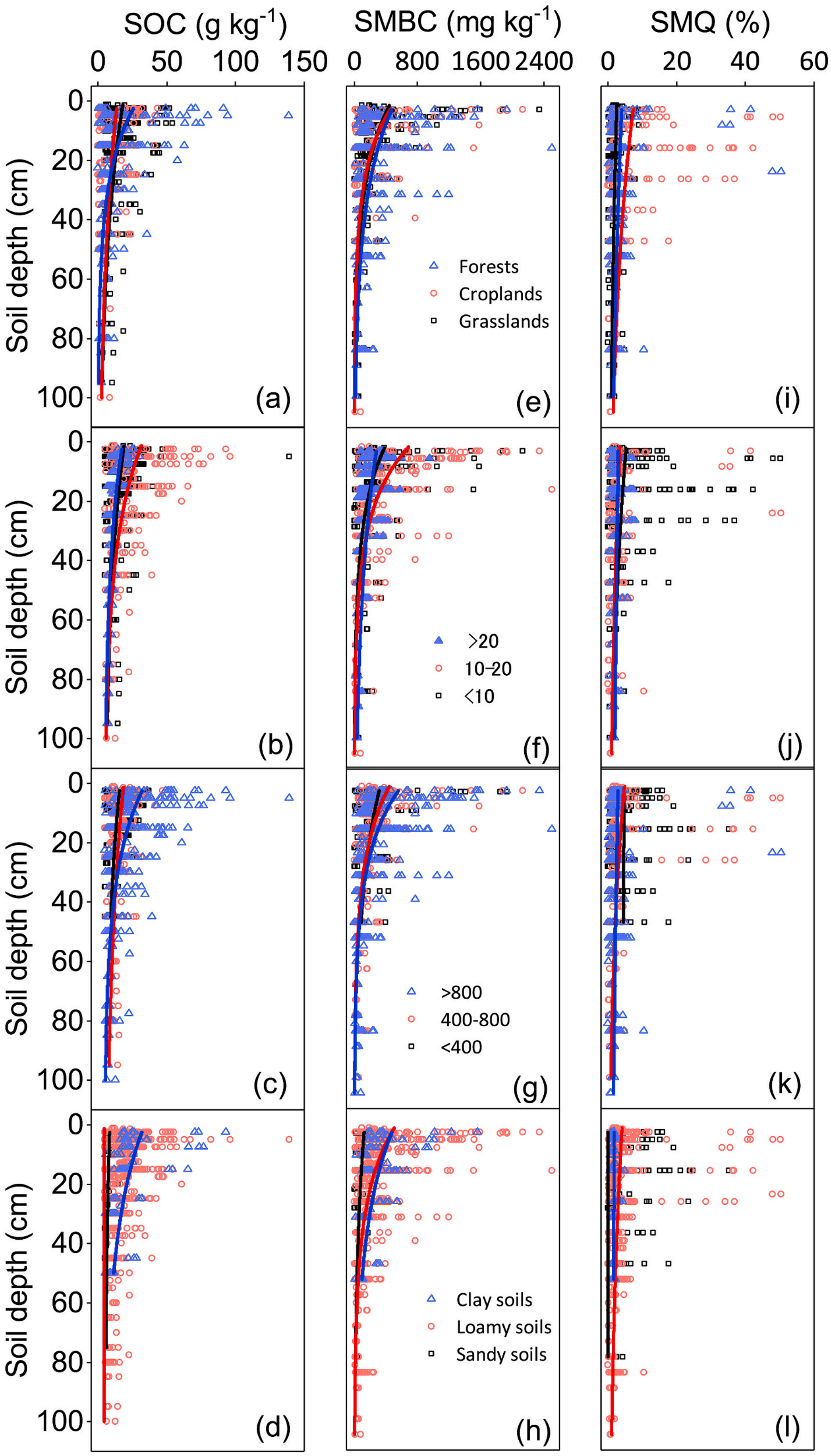

Fig. 2. Vertical variations of SOC, SMBC, and SMQ across ecosystems, climate zones, and soil textures at large spatial scales. (a–d) SOC: soil organic carbon (g kg^{-1}); (e–h) SMBC: soil microbial biomass carbon (mg kg^{-1}), (i–l) SMQ: the ratio of SMBC to SOC (%); ecosystem type was classified into croplands, grasslands, and forests; mean annual temperature (MAT) was classified into <10, 10–20, and >20 °C; mean annual precipitation (MAP) was classified into <400, 400–800, and >800 mm; soil texture was grouped to sandy, loamy, and clay soils. Lines represented the exponential fitting curves of soil properties with soil depth.

of SMBC were 274.6 ± 10.5 and 90.0 ± 6.0 mg kg^{-1} at 0–40 cm and 40–100 cm depths, respectively (Fig. S4). In addition, the vertical distribution of SMBC differed with climate (MAT and MAP) and soil texture. SMBC decreased by 77.4% and 75.1% from the surface soils to subsoils in the warm region (MAT, 10–20 °C) and the high precipitation region (MAP, >800 mm) compared to other climatic regions (decreased by 55.5% on average) (Figs. 2 and S4; Table S3). Meanwhile, SMBC declined by 71.2% from the surface to subsoil layers in the loamy soils, which was nearly 2-fold higher than that in the sandy soils (declined by 37.9%) (Figs. 2 and S4; Table S3).

Like SOC and SMBC, SMQ decreased exponentially with increasing soil depth but in slower rates (Figs. 2 and S5). Globally, SMQ averaged at

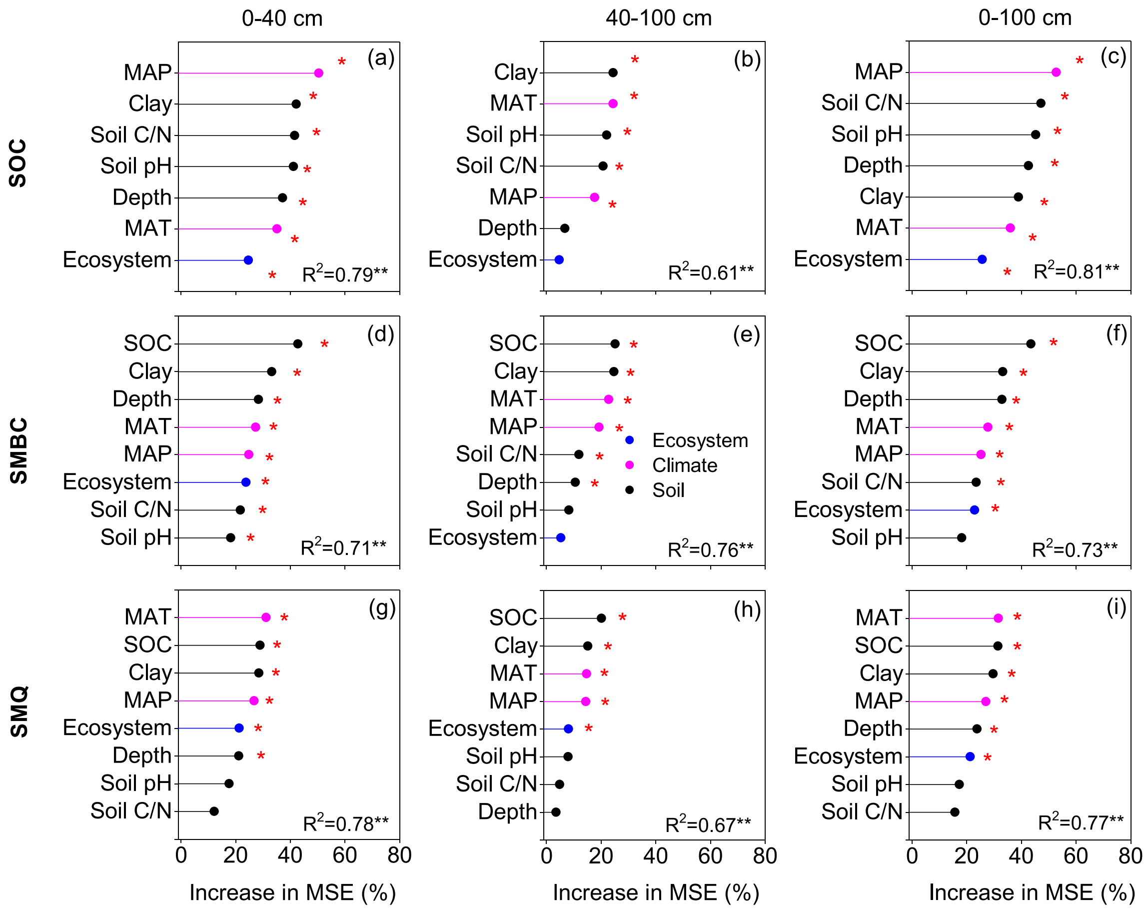

Fig. 3. Relative importance of soil properties, climate, and ecosystem types on SMBC and SMQ at different soil depths. The relative importance of predictors was denoted by the percentage of increased mean square error (%MSE). Ecosystem type was classified into croplands, grasslands, and forests and numbered as 1, 2, and 3, respectively. SOC: soil organic carbon (g kg^{-1}); soil C/N: the ratio of SOC to soil total nitrogen (STN); MAP: mean annual precipitation (mm); MAT: mean annual temperature (°C). SMBC: soil microbial biomass carbon (mg kg^{-1}); SMQ: the ratio of SMBC to SOC (%). Significance levels: *P < 0.05.

3.32% ± 0.18% in the entire soil profile (0–100 cm) and decreased exponentially from 3.56% ± 0.20% in the surface soils to 2.13% ± 0.17% in the subsoils. The vertical distribution pattern of SMQ was significantly different among MAT, MAP, ecosystems, and soil textures (Fig. 2).

3.3. Controls of the vertical distributions of SOC, SMBC, and SMQ

The results of random forest modeling showed that the most important predicators for SOC along soil profiles were MAP, followed by soil clay, C/N ratio, pH, and depth (Figs. 3, S6, and S7). For SMBC along soil profiles, SOC was its predominant predictor and explained 25–44% of its variations (Fig. 3). Soil depth, clay content, and climate were also important predictors, explaining 11–33% of the variation in SMBC along soil profiles (Fig. 3d–f). For SMQ along soil profiles, SOC and MAT were predominant predicators, explaining 20–32% and 15–32% variation in SMQ along soil profiles, respectively (Fig. 3g–i). Soil clay content and MAP were also important predicators for SMQ (Fig. 3g–i). The important predictors for the variations of SOC, SMBC, and SMQ in the surface soils were also important predictors for the variations in the entire soil profile of 1 m. The important predictors generally explained larger variations in SOC, SMBC, and SMQ in the surface than in the subsoils (Fig. 3). Soil pH had weak influences on SMBC and SMQ along soil profiles.

The results of SEMs showed that SOC had the largest direct positive impact on SMBC (path coefficient = 0.58), followed by soil depth (path coefficient = −0.37), C/N ratio (path coefficient = −0.21), and MAP (path coefficient = −0.18), all of which negatively influenced SMBC along soil profiles (Fig. 6a–c). The partial dependence plots further indicated that SMBC increased with increasing SOC when it was below 50 g kg^{-1} and decreased with soil C/N ratio (<20) and depth (<40 cm) (Fig. 4). MAT and soil pH had no significant influences on SMBC along soil profiles (Fig. 4). In addition, SOC had the largest direct negative impact on SMQ along soil profiles (path coefficient = −0.52, Fig. 6b–d) when SOC was less than 25 g kg^{-1} (Fig. 5). Soil depth (path coefficient = −0.36), MAP (path coefficient = −0.16), and ecosystem (path coefficient = 0.10) also directly influenced SMQ (Figs. 5, 6b and 6d). In contrast, soil C/N ratio, pH, and clay content had no significant impacts on SMQ (Figs. 5–6b).

4. Discussion

4.1. SMBC and SMQ decreased with soil depth

SMBC content was 1.5–3 times greater in the surface soils (274.57 ± 10.47 mg kg^{-1}) than in the subsoils (89.97 ± 6.00 mg kg^{-1}) (Fig. S4), which is within the range of previous studies. Xu et al. (2013) found that SMBC in top 30 cm (0.25–3.38 Pg C) was ~1–3 times higher than that in deep soil layers (30–100 cm) (0.49–4.08 Pg C) across different ecosystems globally. In this study, SMBC decreased exponentially with soil depth at large spatial scales, with rapid decline in the top 40 cm and relatively constant values in the subsoils (Figs. 2 and S4). This pattern has been found in many early studies (Adrover et al., 2017; Fierer et al., 2003; Liu et al., 2018; Tian et al., 2017). It is probably because substrates and nutrients, the primary controls of microbial growth, are more abundant in the surface soils than in the subsoils. Our results indeed showed that SOC and STN decreased with soil depth, mainly in the top

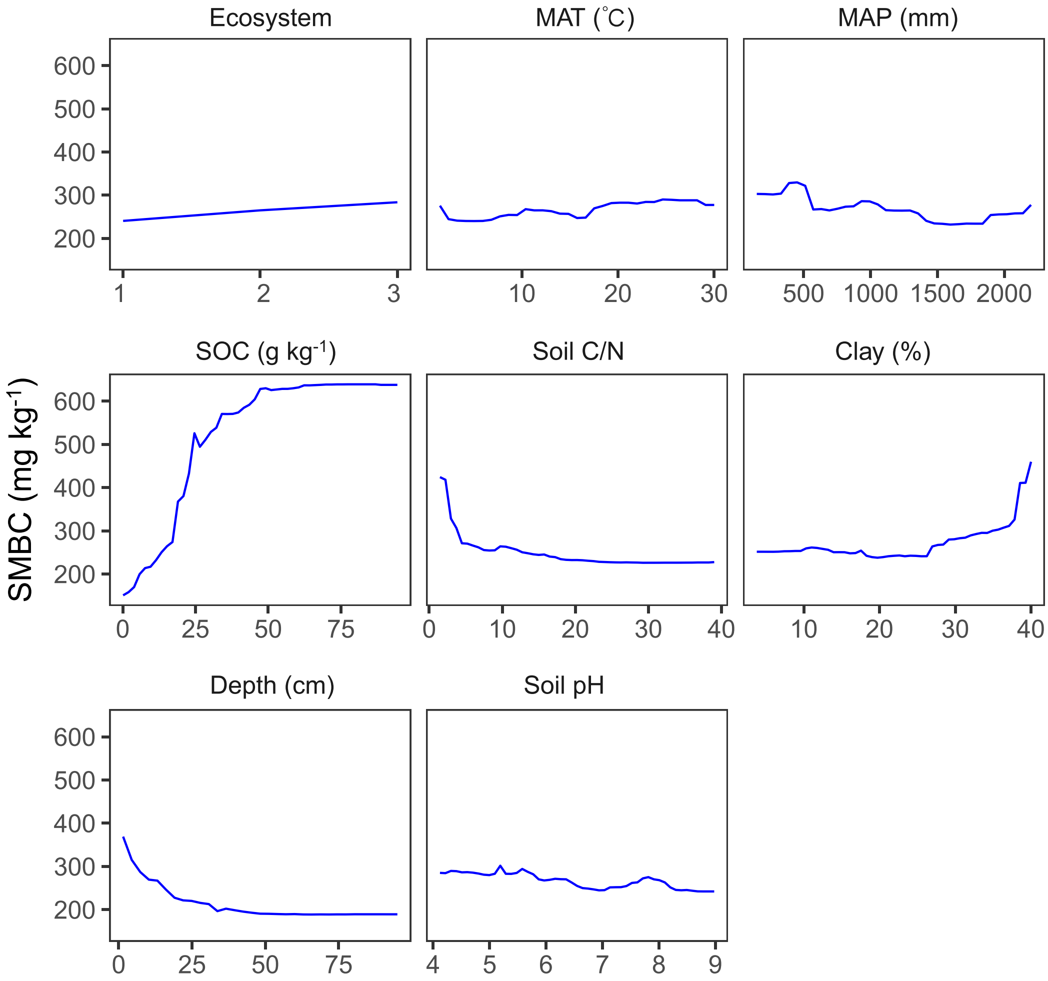

Fig. 4. Partial dependence of environmental factors, soil depth, and soil properties on soil microbial biomass C. Ecosystem type is classified into croplands, grasslands, and forests which are numbered as 1, 2, and 3, respectively. MAT, mean annual temperature (°C); MAP: mean annual precipitation (mm); Depth, soil sampling depth (cm); SOC, soil organic carbon (g kg^{-1}); soil C/N: the ratio of SOC to soil total nitrogen. SMBC: soil microbial biomass carbon (mg kg^{-1}).

40 cm (Figs. 2 and S2). Other studies also found that plant roots, SOC, and STN displayed the same patterns at the regional and global scales (Eilers et al., 2012; Jackson et al., 1996). Additionally, living conditions (*e.g.*, O_2 level) are more favorable for microbial growth in the surface than in the subsoils (Jiao et al., 2018).

SMQ decreased with soil depth globally (Fig. 2), implying that microbial abilities to assimilate soil C reduced with soil depth. Although numerous studies have shown that SMBC is more easily altered by changes in climate, ecosystem types, and edaphic factors (*e.g.*, pH and N) than SOC (Anderson and Domsch, 1989; Dick and Tabatabai, 1993), few studies have compared the vertical changes of SMBC with those of SOC at the regional and global scales. This synthesis showed that SMBC decreased more rapidly with soil depth than SOC, suggesting that the proportion of SOC that corresponds to SMBC is more sensitive than SOC to the biotic and abiotic changes not only geographically but also vertically at large spatial scales. Moreover, the decreased SMQ with soil depth could be the result of more rapid decreases of SMBC with soil depth relative to SOC, confirming that SMBC is more sensitive to environmental changes along soil profiles than SOC.

We found that SMQ ratio was 3.56% ± 0.20% in the surface soils and 2.13% ± 0.17% in the subsoils at large spatial scales, with the average of 3.32% ± 0.18% for 1-m soil profiles (Fig. S5). These values were in the ranges of 1–5% at the depth of top 7.5 cm as reported previously (Sparling, 1992). Our estimate of SMQ ratios of the 1-m soil layers were nearly 3 times of the values (~1.20) reported by Xu et al. (2013) in another global synthesis. One potential explanation for the discrepancy is due to different methods and the sample size of soil profiles used. In our synthesis, we included 1040 data points of SMBC from 289 soil profiles that were measured only by the chloroform-fumigation extraction method. Xu et al. (2013) investigated the vertical patterns of SMBC based on data from 23 soil profiles in 10 peer-published studies. In addition, they included SMBC estimated by a variety of different methods. Different methods yield different SMBC values and enlarge the uncertainties in characterizing the vertical distribution pattern of SMBC at large spatial scales (Anderson and Joergensen, 1997). For instance, Anderson and Joergensen (1997) found that the estimates of SMBC by the chloroform-fumigation extraction method were lower than those by the substrate induced respiration, and both estimates were positively correlated with increasing soil pH from 3 to 8. Thus, the values and patterns of SMBC and SMQ estimated by the same method with a large sample size in the present study is more robust and representative than previous studies.

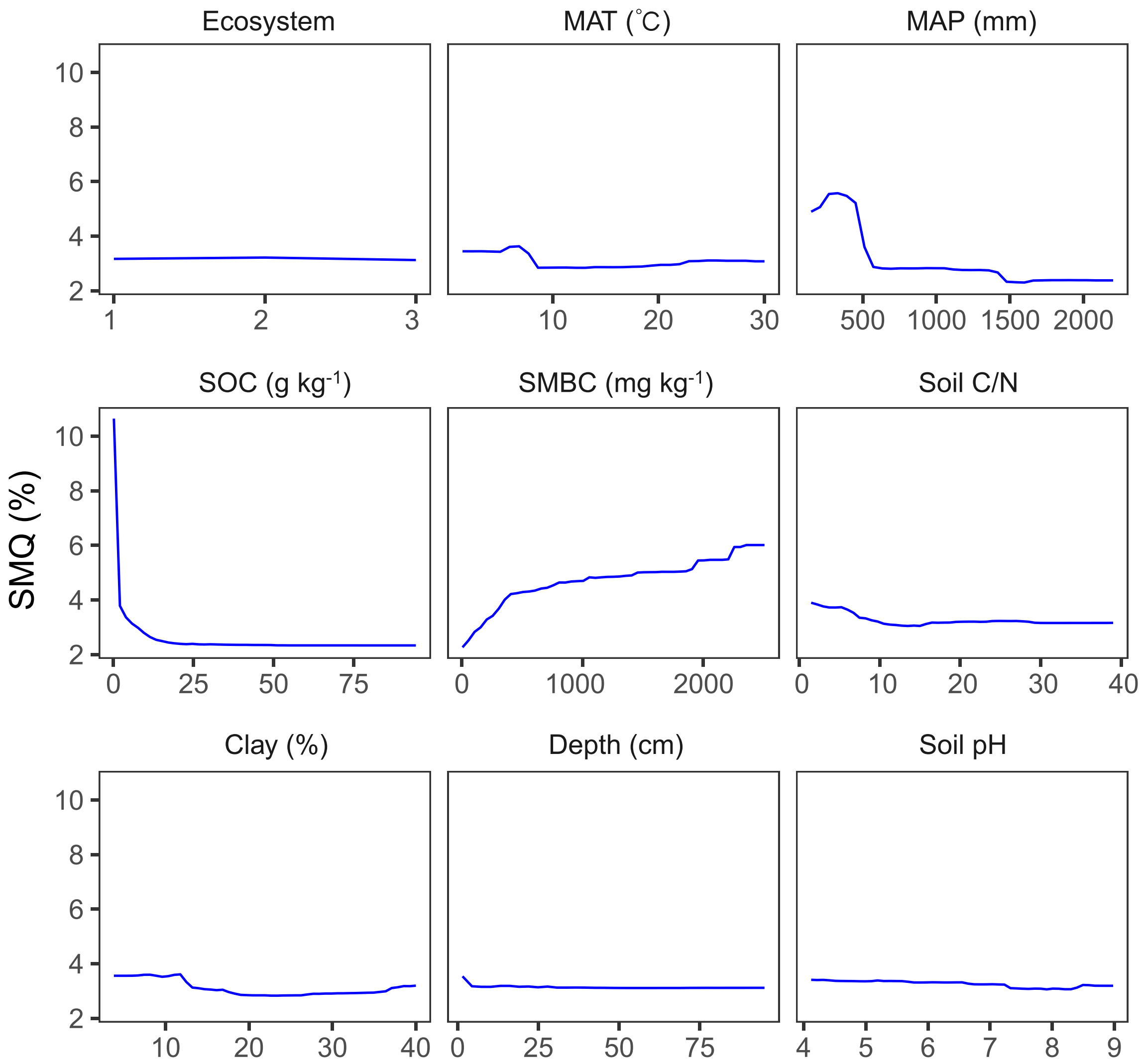

Fig. 5. Partial dependence of environmental factors, soil depth, and soil properties on the ratios of soil microbial biomass C to soil organic C (SMQ) using the Random forest modeling. Ecosystem type is classified into croplands, grasslands, and forests which are numbered as 1, 2, and 3, respectively. MAT, mean annual temperature (°C); MAP: mean annual precipitation (mm); Depth, soil sampling depth (cm); SOC, soil organic carbon (g kg^{-1}); soil C/N: the ratio of SOC to soil total nitrogen. SMBC: soil microbial biomass carbon (mg kg^{-1}). SMQ: the ratio of SMBC to SOC (%).

4.2. Impacts of climate and ecosystem type on vertical distributions of SMBC and SMQ

Although SMBC is known to be influenced by climate (Joergensen and Raubuch, 2003; Nielsen and Ball, 2015) and ecosystem type (Liu et al., 2018; Xu et al., 2013), it is still not clear whether climate and ecosystem type substantially affect the vertical distributions of SMBC and SMQ at large spatial scales. We originally hypothesized that the vertical distributions of SMBC and SMQ would be different across ecosystem types (*i.e.*, forests, grasslands, and croplands), because these three ecosystem types vary in root distributions and have distinct vertical patterns of substrates and nutrients (*e.g.*, SOC and STN) along soil profiles (Jackson et al., 1996; Jobbágy and Jackson, 2000; McKenna and Sala, 2016). We found that ecosystem type affected the vertical distribution of SOC, as SOC of the top 40 cm was higher and decreased more rapidly with soil depth in croplands and forests than in grasslands (Figs. 2 and S3; Table S3). However, the vertical distribution pattern of SMBC did not differ substantially among ecosystems (Figs. 2 and S4), although it was strongly correlated with SOC (Figs. 3d–f and 6a). This result implies that factors other than SOC could also play important roles in regulating SMBC along soil profiles. For example, soil C/N ratio might regulate SMBC based on the results of random forest analysis and SEMs (Figs. 3 and 6a). In this study, soil C/N ratio was predominantly in the range of 10–20 (Fig. S2). SMBC did not change substantially when soil C/N ratio was within this range (Fig. 4), which is supported by the results of Schimel and Weintraub (2003). They found that microbial biomass remains constant when soil C/N is below 30. Although the mean values of soil C/N ratio were similar among different ecosystems, they varied considerably in each ecosystem type mainly due to different plant species within the same ecosystem type. In a previous study, Xu et al. (2013) reported the highest soil C/N ratios in boreal forests (31.4) and the lowest in tropical/subtropical forests (15.8). The vertical distribution pattern of SMQ also differed among ecosystems, particularly in grasslands vs. croplands and grasslands vs. forests. This difference was likely due to distinct vertical distribution patterns of SOC among ecosystem types (Figs. 2 and S3).

We found that the vertical distributions of SMBC and SMQ showed different patterns among climate zones, as SMBC was higher and decreased more rapidly in the warm regions (10–20 °C) than in the cold (<10 °C) or hot (>20 °C) regions (Figs. 2 and S4). It was in contrast with previous studies, suggesting that SMBC decreased with increasing temperature (Capek et al., 2019; Joergensen and Raubuch, 2003). The effect of temperature on the vertical distribution of SMBC was likely due to differences in soil texture rather than temperature itself, as soils in the

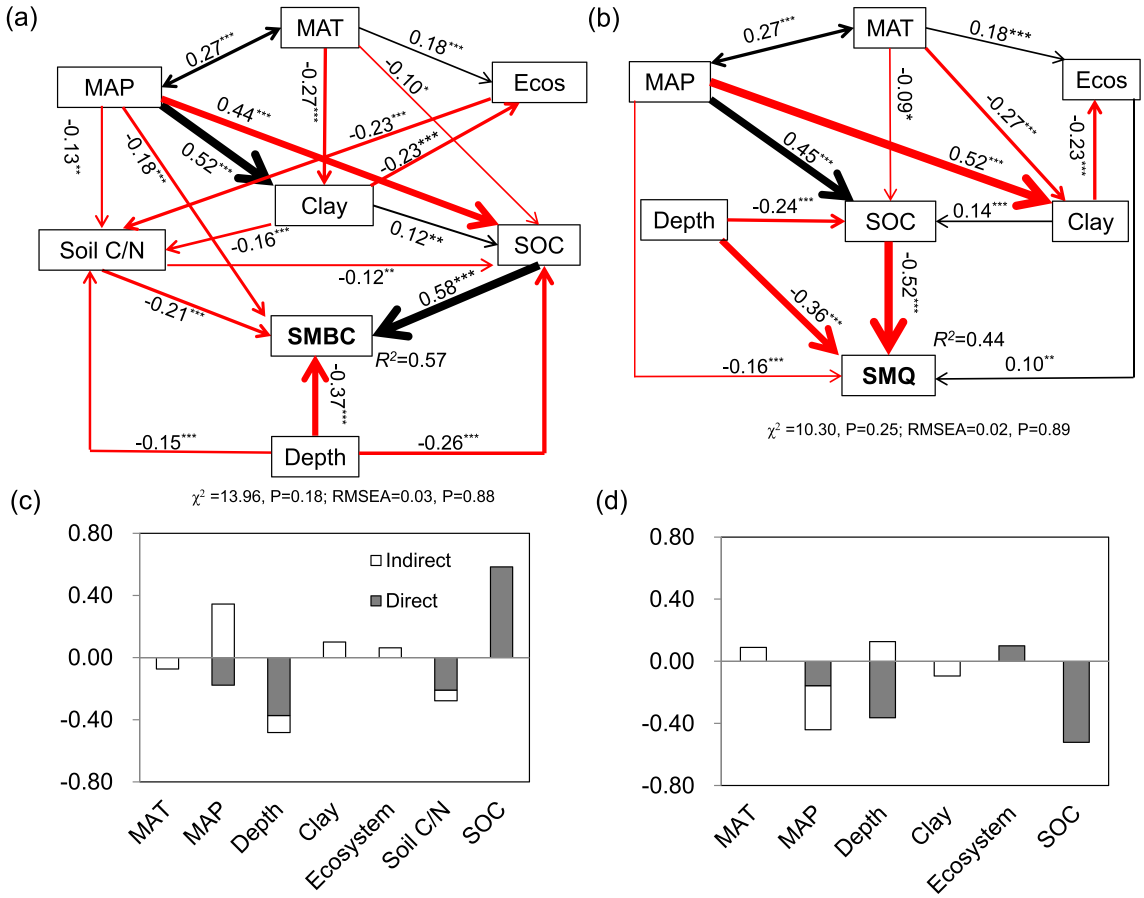

Fig. 6. Direct and indirect effects of climate and soil properties on (a, c) SMBC and (b, d) SMQ at large spatial scales (n = 553). Black and red solid arrows represent the positive and negative relationships, respectively. Numbers adjacent to arrows are standardized path coefficients. The path widths are in proportion to the path coefficient. SOC: soil organic carbon (g kg^{-1}); soil C/N: the ratio of SOC to soil total nitrogen (STN); MAP: mean annual precipitation (mm); MAT: mean annual temperature (°C). SMBC: soil microbial biomass carbon (mg kg^{-1} soil); SMQ: the ratio of SMBC to SOC (%). Ecos: ecosystem type, namely croplands, grasslands, and forests which are numbered as 1, 2, and 3, respectively. MAT, MAP, SOC, soil C/N, soil depth, soil clay content, SMBC, and SMQ were natural logarithm transformed. Significance levels: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

warm regions were dominated by the fine-textured soils (Figs. S4 and S10).

The vertical distribution pattern of SMBC was not significantly different among MAP regions but that of SOC was different in the MAP>800 mm region than the other two regions (Fig. 2). MAP also had smaller contributions to the variation in SMBC compared to SOC based on the results of random forest analysis (Fig. 3). The different effects of MAP on the vertical distribution patterns of SMBC and SOC likely resulted from the transport of organic C inputs and nutrient along soil profiles by water. High SOC in the high MAP regions could be caused by high C inputs and low microbial decomposition. Plant productivity is generally higher in the regions with high rainfall (Cui et al., 2019). Meanwhile, high rainfall could lead to anaerobic conditions in soils, which may impede microbial growth and decomposition (Haroon et al., 2013; Jiao et al., 2018). This was confirmed by the negative correlations between SMBC and MAP in this synthesis (Fig. 6a). Additionally, high rainfall could facilitate the transport of labile substrates and microbes from surface to subsoils (Gross and Harrison, 2019). This migration process may weaken the difference of soil microbes and substrates in the surface soils and subsoils, leading to similar vertical distributions of SMBC among MAP zones found in the present study (Fig. 2).

4.3. Impacts of edaphic factors on vertical distributions of SMBC and SMQ

This synthesis showed that soil texture strongly affected the vertical distributions of SMBC and SMQ at large spatial scales and both SMBC and SMQ were significantly higher in the fine-textured than in the coarse-textured soils (Figs. 2 and S4 and S5). SMBC decreased more rapidly along soil profiles in the clay soils than in the sandy soils, a pattern similar to that of SOC (Figs. 2 and S4). Higher SMBC in the surface soils indicated that there was a high potential of fast SOC decomposition and there were more nutrients for plants. Many studies reported that SMBC is positively correlated with soil clay content (Hassink, 1992; Moyano et al., 2012; Wardle, 1992). It is likely that high soil clay content can preserve substrates and nutrients in small soil pores or onto mineral surfaces for microbial growth and provide habitats for soil microbes (Liang et al., 2019a,b; Postma and Vanveen, 1990). In addition, our analysis showed that soil clay content was the second most important factor in regulating SMBC along soil profiles, especially in the top 40 cm (Fig. 3), confirming the importance of soil clay content in regulating SMBC (Fig. 6a). It was notable that the vertical distribution pattern of SMBC in loamy soils was not significantly different from those in clay soils. This is probably because there was no substantial difference in clay content between the loamy and clay soils. In some literature the data of soil clay content were absent, we extracted the data from Soil-Grids (https://soilgrids.org) according to the longitude and latitude of the study sites with the resolution of 250 m. As a result, the study sites within the same grid cell have the same value of soil clay content and this may underestimate the influences of soil texture on SMBC.

Soil texture had smaller impacts on SMQ along soil profiles compared to SMBC, given that the vertical distribution pattern of SMQ was not different among soil texture types at large spatial scales and soil clay content was not as important as SOC in controlling SMQ (Figs. 3 and 5). The reason is that soil clay has similar contributions to SOC (24–42%) as to SMBC (25–33%) (Fig. 3), leading to the relatively weak influence on their ratio (SMQ). This result suggests that soil microbial assimilation of C among soil texture types remains relatively stable. Our finding is supported by a previous study that reported soil clay content is positively associated with SOC ($r = 0.61$) and SMBC ($r = 0.65$) (Fterich et al., 2011). As a result, the ratio of SOC and SMBC may not be correlated with soil clay content along soil profile.

In addition to soil texture, we found that soil C/N ratio influenced SMBC along soil profiles (Figs. 3 and 6a). According to the results of partial dependence plot and SEMs, SMBC decreased with increasing soil C/N ratio when it was <15 (Figs. 4 and 6), suggesting that changes in soil N could substantially regulate SMBC, because soil C and N are considered as limiting factors of microbial biomass due to microbial demands for both C and N (Wardle, 1992). This synthesis also showed that soil C/N ratio generally decreased with soil depth (Fig. S2). This pattern has been found at the regional scale (Awad et al., 2019; Chen et al., 2019; Creamer et al., 2016) and is confirmed here. Decreased soil C/N ratio with depth was potentially due to the gradual decrease of plant-derived C (high C/N ratio, ranging from 57 to 690) (Zechmeister-Boltenstern et al., 2015) and the enrichment of microbial-derived C (Ma et al., 2020; Rumpel and Kögel-Knabner, 2011) from surface to susoils.

Soil pH showed little impacts on SMBC and SMQ along soil profiles at large spatial scales (Figs. 3–5). It was positively correlated with SMBC in a UK arable soil with pH ranging from 3.7 to 8.3 (Pietri and Brookes, 2008). In a global analysis, soil pH drives the diversity and richness of soil bacteria across sampling sites in North and South America (Fierer and Jackson, 2006). No significant impact of soil pH on SMBC found in this synthesis might be due to that soil pH of the same soil profile only varied within the range of two pH units across climate zones, ecosystems, and soil textures at large spatial scales (Fig. S2). The small changes in soil pH might not lead to a remarkable change in SMBC. It could be that soil pH only altered the composition and diversity rather than the biomass of soil microbial community.

5. Conclusion

Given the important roles of soil microbial biomass in regulating both the decomposition and formation of SOC, understanding the global pattern of vertical distribution of SMBC and its controls can improve our understanding of soil C dynamics in terrestrial ecosystems. This synthesis revealed the vertical distribution patterns of SMBC, SOC, and SMQ based on 289 soil profiles globally, and quantified the contributions of climate, ecosystem type, and edaphic factors to them. Two major findings were generated from this synthesis. 1) SMBC, SOC, and SMQ decreased exponentially with soil depth, especially in the top 40 cm. 2) The vertical distributions of SMBC and SMQ differed significantly only among soil texture types, with higher SMBC in the fine-textured than in the coarse-textured soils. Edaphic factors such as soil C/N ratio influenced SMBC along soil profiles, but climate and ecosystem type did not significantly influence SMBC. These results highlight the important contributions of soil microbial biomass to the changes of soil C pool and help predict the responses of SOC to environmental changes in earth system models. Therefore, future studies should examine the vertical changes of plant C inputs, soil clay content, and the transport of substrates and microbes along soil profiles in addition to SMBC and SOC and their interactions with climate, ecosystem, and edaphic factors.

Declaration of competing interest

The authors state no conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2020.107905.

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