



Climate and vegetation together control the vertical distribution of soil carbon, nitrogen and phosphorus in shrublands in China

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Abstract

Aims Carbon (C), nitrogen (N) and phosphorus (P) in soil are characterized by decreasing patterns with soil depth. However, these patterns and their driving factors have rarely been investigated in shrublands.

Methods We conducted extensive sampling of the top 100 cm of soil in 1120 shrublands across China to measure the soil organic C (SOC), total N (STN) and total P (STP) concentrations and densities.

Results We found that in shrublands, the geometric means (and geometric standard errors) of SOC, STN and STP concentrations were 5.62 (0.09), 0.66 (0.07),

and 0.31 (0.07) mg g⁻¹, respectively, and those of their densities were 5.46 (0.08), 0.67 (0.08), and 0.30 (0.08) kg m⁻³, respectively. The decrease along soil depth for nutrients could be parameterized by a power function. The rates of decrease with depth differed between shrubland types and were negatively correlated with temperature but positively correlated with biomass. Climatic factors tended to have a relatively stronger effect than vegetation factors on the vertical distribution patterns of soil nutrients.

Conclusions Our findings reveal nutrient limitations in shrublands in terms of the total pools, suggest the necessity of soil protection for vegetation conservation and restoration, and provide an important supplement for the accurate prediction of terrestrial element cycles.

Yanpei Guo and Minwei Jiang contributed equally to this work.

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Introduction

Soil is the largest carbon (C) pool in terrestrial ecosystems (Jobbágy and Jackson 2000; Jackson et al. 2017), and 56% of the total soil organic C (SOC) (within the top 3 m) is located in the top 1 m of soil (Kern 1994). CO₂ emitted by soil respiration accounts for a large proportion of the terrestrial C cycle (Post et al. 1982). Global changes such as nitrogen deposition and climate warming can influence the soil C pool and further the global C cycle through biological and chemical processes (Waldrop et al. 2004; Knorr et al. 2005). Soil nitrogen

(N) and phosphorus (P) are coupled with SOC in terrestrial material cycles (Vitousek 2004; Tian et al. 2010). The turnover of SOC is constrained by N and P availability (Oren et al. 2001; Yuan and Chen 2015).

Taking the vertical distributions of nutrients into account is necessary for the estimation of soil nutrient pools. For example, Jackson et al. (2017) recalculated a global soil C pool with a vertical distribution and found a reduction of one-third compared to a prior study (Batjes 2016) due to the overestimated C pool in deep soil. It is commonly acknowledged that nutrient contents decrease with soil depth (Jobbágy and Jackson 2000; Hobbey et al. 2013; Groppo et al. 2015; Nie et al. 2017). The descending curves of nutrients along soil depth depend on the origins of the nutrients (Chai et al. 2015). In addition, climate and vegetation also shape the curves by the controlling the input from above (e.g. litter production and decomposition) and downward nutrient transport (e.g. leaching), while vegetation characteristics determine litter and root properties that influence nutrient input to soil (Weltzin and Coughenour 1990; Jobbágy and Jackson 2000, 2001; Wang et al. 2004). Meanwhile, soil nutrients in different depths can be differentially affected by these factors, because of the more stable physicochemical conditions in deeper soil and the vertical distribution pattern of roots (Jobbágy and Jackson 2000; Yang et al. 2007).

Previous studies on large-scale patterns of vertical distributions of soil nutrients mainly focused on forests and grasslands, neglecting shrublands, a typical vegetation type in harsh or degraded habitats where forests and grasslands cannot be maintained. Along with ongoing climate change and anthropogenic habitat destruction, shrublands show a trend of expanding and taking the place of other vegetation types (Sturm et al. 2001; Briggs et al. 2005; Bühlmann et al. 2016), and subsequent changes in the local dynamics of C storage caused by shrub invasion and vegetation transformation are expected (Jackson et al. 2002). Considering that shrublands could play an increasingly important role in C and nutrient cycles in the future, there is an urgent need to study the soil pools in shrublands comprehensively. Estimating C, N and P stocks and exploring their vertical distributions in shrubland soil are necessary for understanding C, N and P cycles in shrublands as well as their responses to global changes. Furthermore, the comparison between these soil characteristics of shrublands and those of other vegetation types could reveal the driving force of vegetation change in terms of soil conditions, facilitate the accurate prediction of soil C, N and P

dynamics under global changes, and provide guidance for management measures for habitat conservation and restoration.

Shrublands cover approximately one-fifth of the land area in China (Editorial Committee of Vegetation Map of China 2007), and their area is still growing in recent years (Brandt et al. 2013; Peng et al. 2013; Wang et al. 2016). In this study, we explored the vertical distributions of SOC, soil total N (STN) and soil total P (STP) in Chinese shrublands to answer the following three questions.

- 1) What are the concentrations and densities of SOC, STN and STP in shrublands?
- 2) How do SOC, STN and STP change with soil depth in shrublands?
- 3) How do climatic and vegetation factors affect the vertical distributions of SOC, STN and STP?

Materials and methods

Study area and sample measurements

The field work was conducted in the summer (July–September) from 2011 to 2015. The sampling sites were chosen based on the distribution map of shrublands from the *Vegetation Map of P. R. China* (1:1,000,000) (Editorial Committee of Vegetation Map of China 2007). The study region was divided into 35,800 grids of different areas (100–900 km²) according to the biogeographic regions (see Fig. S1 in Tang et al. 2018). For each province in China, 3–5% of the qualified grids that have a shrubland coverage $\geq 30\%$ were randomly chosen, and the coordinates of field sites were determined based on historical records of local vegetation. In practice, the shrubland was defined as the vegetation dominated by shrubs with a canopy height ≤ 5 m and a shrub coverage $\geq 10\%$. All sites were set at the location with a shrubland area ≥ 1 ha and a buffering distance to other patches ≥ 10 m. Meanwhile, the habitat conditions, structure and species composition were required to be relatively homogeneous at each site. In total, we investigated 1120 shrubland sites across China, including 233 evergreen broadleaf shrubland (EBS) sites, 10 evergreen coniferous shrubland (ECS) sites, and 877 deciduous broadleaf shrubland (DBS) sites (Fig. S1). These sites have a geographic span from 18.2 to 48.1°N in latitude and

from 75.6 to 132.8°E in longitude. At each site, we set three plots of 5 × 5 m to investigate species composition, biomass and soil properties. Plots were set at the place that represents the local community composition within each site, and the edge-to-edge distance between plots at each site was between 5 m to 50 m. At each plot, we also collected all the litter in one 1 × 1 m quadrat, weighed the fresh weight and brought samples to the laboratory. Samples of litter were oven dried at 65 °C and weighed dry.

For the measurements of the focused elements, we sampled soils in three one-meter-deep pits (or deep to bedrock) along the diagonal of each plot at the depths of 0 ~ 10 (layer a), 10 ~ 20 (layer b), 20 ~ 30 (layer c), 30 ~ 50 (layer d), 50 ~ 70 (layer e) and 70 ~ 100 (layer f) cm. A soil sample with an estimated dry weight of 100 g was collected with a small scraper at each depth of each pit. We mixed the samples from the same depth in each plot, air dried them and removed roots and gravel. Soil samples were ground to pass through a 100 µm mesh sieve. One 100 cm soil profile was excavated outside each site to measure the soil bulk density (BD, g/cm³) and the gravel (> 2 mm) content (GC, volume percentage), and soil cores were sampled using a 100 cm³ cutting ring at the same depths as the soil samples for element measurements. Three soil cores were collected at each depth on the three surfaces of each soil profile, respectively. Soil cores were oven-dried at 105 °C for 48 h. We measured soil total C concentration by an elemental analyzer (2400 II CHNS/O; PerkinElmer, Boston, USA), and the inorganic C concentration by an inorganic C analyzer (Calcimeter 08.53, Eijkelkamp, Giesbeek, Netherlands). The difference between these two values was the SOC concentration. We also measured STN concentration by an elemental analyzer (2400 II CHNS/O; PerkinElmer, Boston, USA) and STP concentration using the molybdate/ascorbic acid method after H₂SO₄-H₂O₂ digestion (Jones Jr 2001). Please refer to Yang et al. (2014) and Guo et al. (2017) for detailed sampling and measuring descriptions.

Climate data

We obtained mean monthly temperature and precipitation data at a resolution of 30 arc-second from the WorldClim database (Hijmans et al. 2005) and calculated mean annual temperature (MAT) and precipitation (MAP) for each site.

Data analysis

We calculated concentrations (mg g⁻¹) of SOC, STN and STP for each of the six soil layers for each site. We then calculated the soil nutrient densities of each layer using Eq. 1.

$$\text{Density} = \text{Concentration} \times \text{BD} \times (1 - \text{GC}) \quad (1)$$

We applied Student's *t* tests to contrast log-transformed soil nutrients between the EBS and the DBS. We did not consider the ECS when comparing different vegetation types because of their scarcity (*n* = 10).

Following Jobbágy and Jackson (2000), we applied the following equation to describe the general vertical distribution patterns of soil nutrients.

$$Y = \alpha' D^{-\beta} \quad (2)$$

which can be log-transformed to

$$\log Y = -\beta \log D + \alpha \quad (3)$$

where *Y* represents the concentration or density of soil nutrients (SOC, STN or STP), and *D* represents soil depth measured as the midpoint depth of each layer, i.e., 5 cm for layer a, 15 cm for layer b, 25 cm for layer c, 40 cm for layer d, 60 cm for layer e, and 85 cm for layer f. The coefficient *β* stands for the rate of decrease in soil nutrients with depth, and a larger value indicates a larger difference between surface and bottom soils in nutrient concentrations or densities. We applied Eq. 3 with all sites pooled together to calculate the overall rates of decrease in SOC, STN and STP in shrublands, and we also applied this equation to every site where soil depth reached 1 m to obtain site-specific *β* values. We selected the sites with significant *β* (*P* < 0.05) to compare among SOC, STN and STP and between the EBS and the DBS. Then, we tested the correlations between site-specific *β* and climatic and vegetation factors.

To distinguish climatic and vegetation effects on the vertical distributions of SOC, STN and STP, we performed partial redundancy analysis (RDA) at sites where soil depth reached 1 m. The response matrix contains six columns, i.e., concentrations or densities of SOC, STN or STP in six soil layers with increasing depth. Climatic explanatory variables include MAT and MAP, while vegetation explanatory variables include shrubland type, aboveground biomass (AGB), belowground biomass (BGB) and litter biomass (LB).

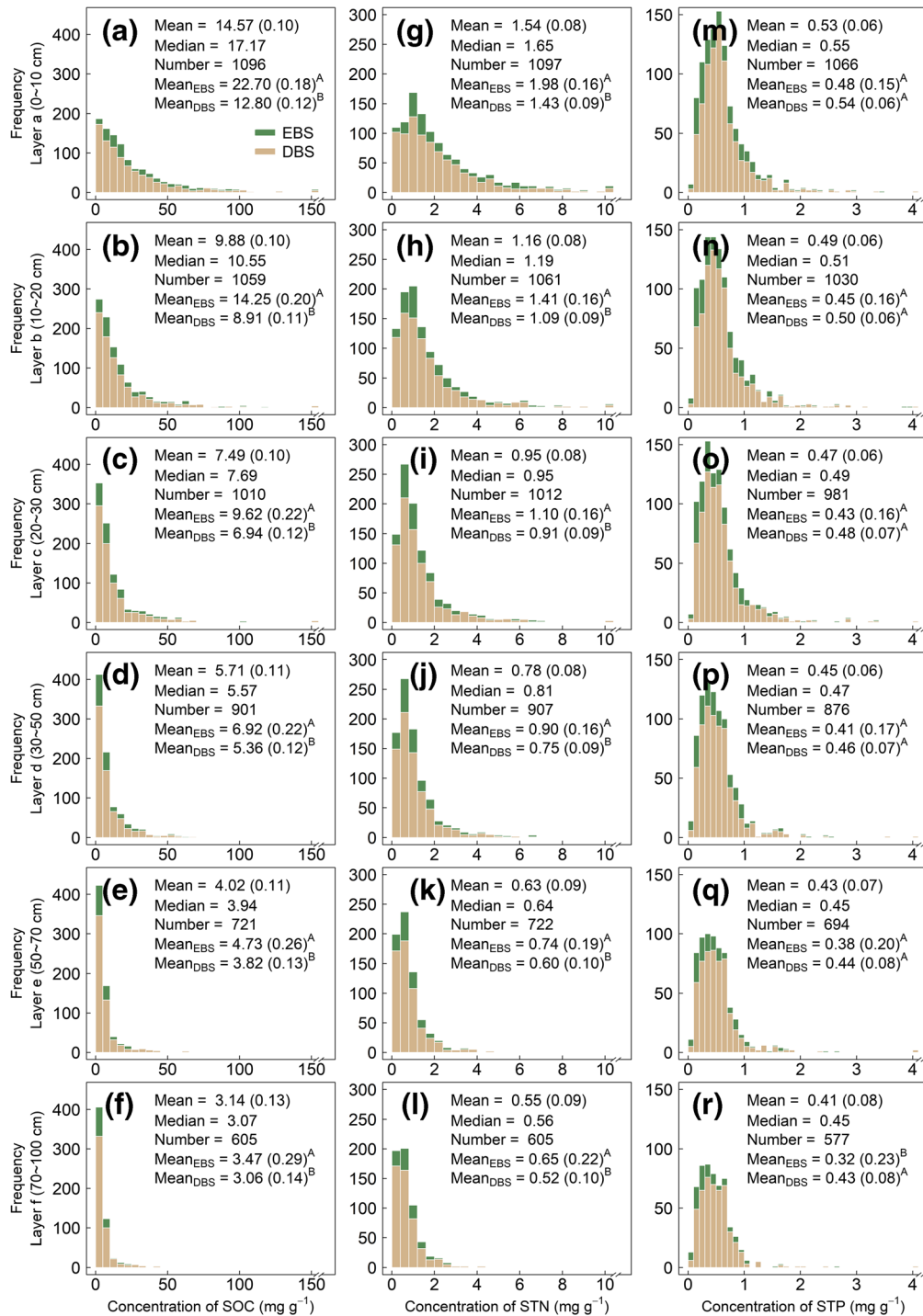


Fig. 1 Histograms of concentrations of soil organic C (SOC) (A–F), total N (STN) (G–L) and total P (STP) (M–R) in different layers within the top 100 cm of soil. Geometric means (geometric standard errors), medians and sampling numbers were shown.

EBS, evergreen broadleaf shrublands; DBS, deciduous broadleaf shrublands. Different letters denoted significant differences at $P < 0.05$ between the EBS and the DBS

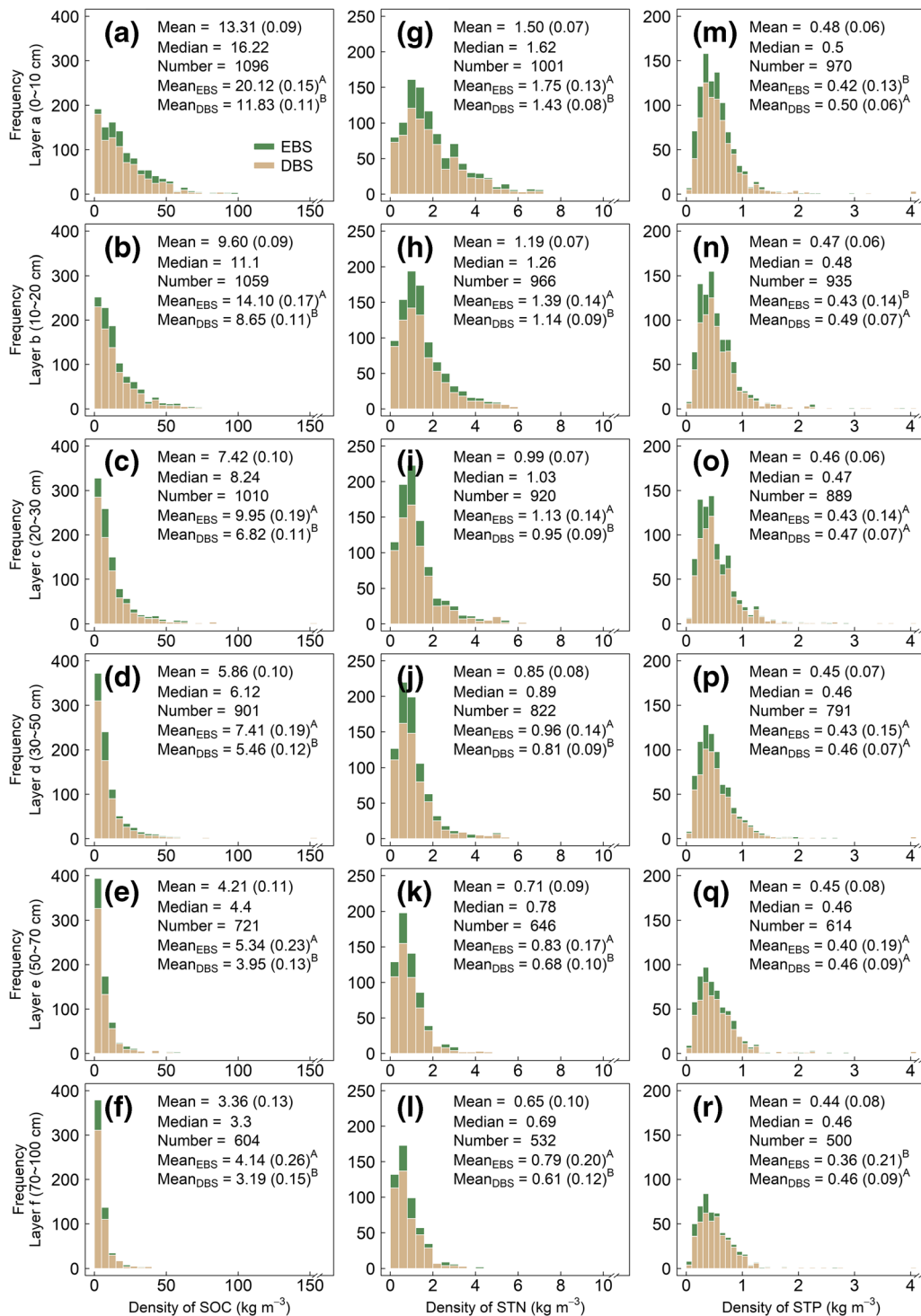


Fig. 2 Histograms of densities of soil organic C (SOC) (A–F), total N (STN) (G–L) and total P (STP) (M–R) in different layers within the top 100 cm of soil. Geometric means (geometric

standard errors), medians and sampling numbers were shown. For abbreviations and letters after geometric means, see Fig. 1

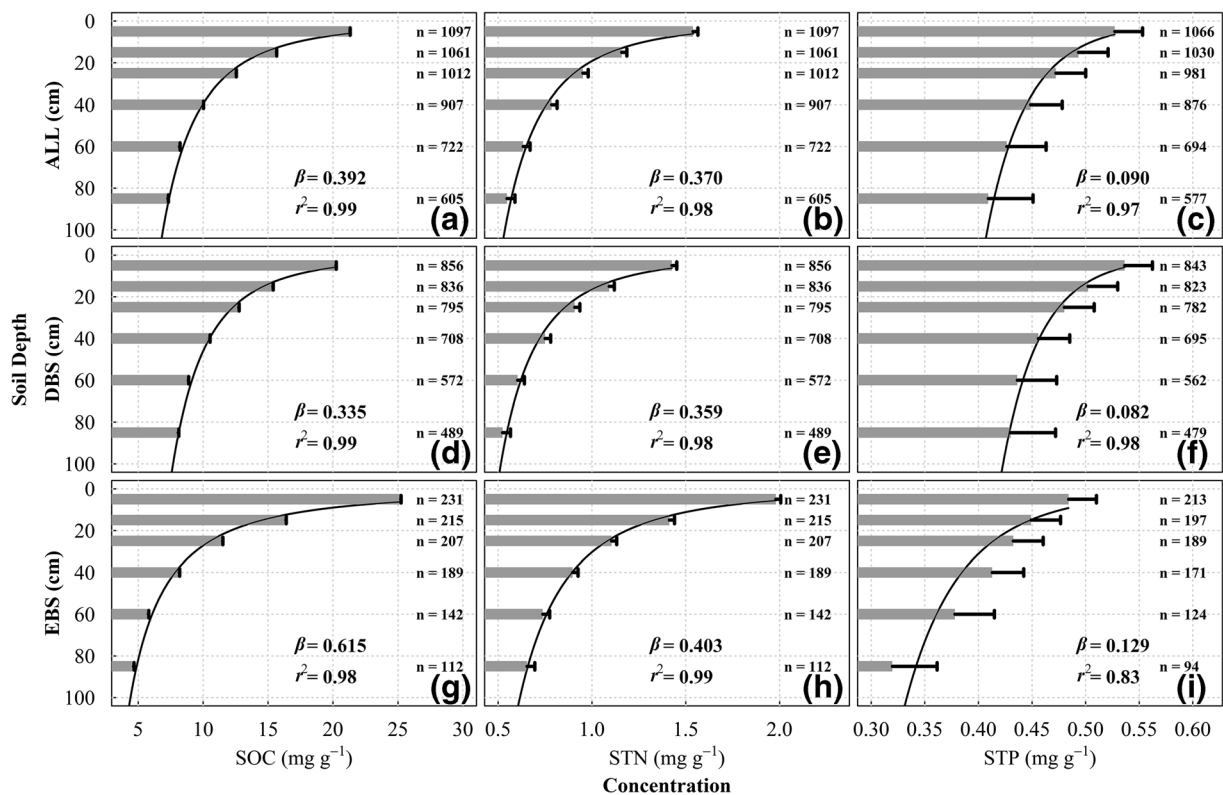


Fig. 3 Vertical distributions of concentrations of soil organic C (SOC), total N (STN) and total P (STP) in the top 100 cm for all shrublands (A–C), the deciduous broadleaf shrublands (DBS) (D–F) and the evergreen broadleaf shrublands (EBS) (G–I). Error bars

denote standard errors divided by five. β denoted the decreasing rate of soil nutrients along depth as calculated based on Eq. 3. All β values were significant at $P < 0.05$

Results

The vertical distribution patterns of soil nutrient concentrations and densities

The geometric means (and geometric standard errors) of SOC, STN and STP concentrations were 5.62 (0.09), 0.66 (0.07), and 0.31 (0.07) mg g^{-1} , respectively, within the top 100 cm of soil in shrublands (see the supplementary dataset for site-specific values). The concentrations of SOC, STN and STP significantly decreased with increasing soil depth (Fig. 1). The concentrations of SOC decreased from 14.57 (0.10) mg g^{-1} in the topsoil (0–10 cm) to 3.14 (0.13) mg g^{-1} in the bottom soil (70–100 cm). Similarly, the STN and STP concentrations decreased from 1.54 (0.08) mg g^{-1} and 0.53 (0.06) mg g^{-1} in the topsoil to 0.55 (0.09) mg g^{-1} and 0.41 (0.08) mg g^{-1} in the bottom soil, respectively. For SOC and STN concentrations, the EBS were higher than the DBS in all layers. For STP concentrations, the EBS were similar to the DBS in all layers except for the layer f.

The geometric means (and geometric standard errors) of SOC, STN and STP densities were 5.46 (0.08), 0.67 (0.08), and 0.30 (0.08) kg m^{-3} , respectively, within the top 100 cm of soil in shrublands (see the supplementary dataset for site-specific values). The densities of SOC decreased from 13.31 (0.09) kg m^{-3} in the topsoil to 3.36 (0.13) kg m^{-3} in the bottom soil (Fig. 2). The STN and STP densities decreased from 1.50 (0.07) kg m^{-3} and 0.48 (0.06) kg m^{-3} in the topsoil to 0.65 (0.10) kg m^{-3} and 0.44 (0.08) kg m^{-3} in the bottom soil, respectively. For SOC and STN densities, the EBS were higher across all layers than DBS. For STP densities, the EBS were lower in the layers a, b and f, and similar in the layers c, d and e compared to the DBS.

The rates of decrease in soil nutrient concentrations and densities with soil depth

With all shrubland sites pooled, the decreasing rates, β , for SOC, STN and STP concentrations were 0.54, 0.37 and 0.09, respectively (Fig. 3), and β for SOC, STN and

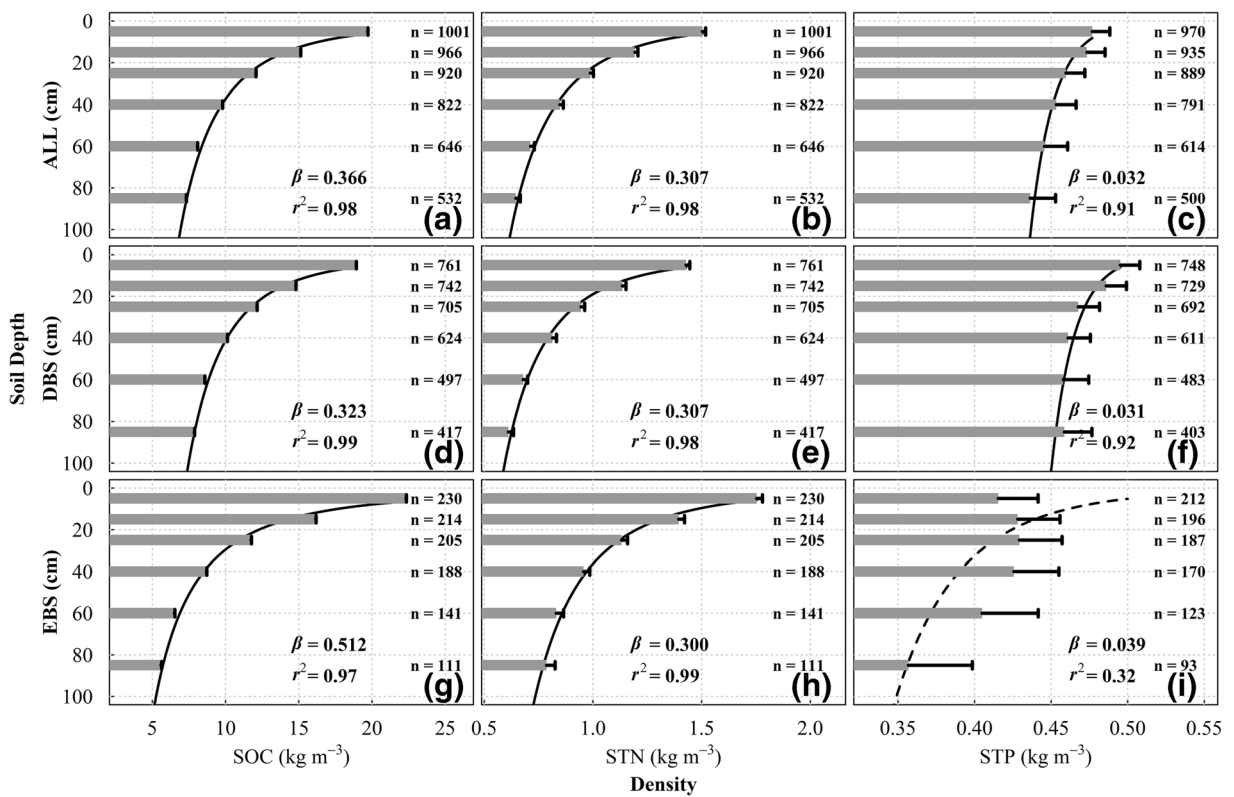


Fig. 4 Vertical distributions of densities of soil organic C (SOC), total N (STN) and total P (STP) in the top 100 cm for all shrublands (A–C), the deciduous broadleaf shrublands (DBS) (D–F) and the evergreen broadleaf shrublands (EBS) (G–I). Error

bars denote standard errors divided by five. β denoted the decreasing rate of soil nutrients along depth as calculated based on Eq. 3. All β values were significant at $P < 0.05$, except for STP in the EBS, which was denoted by a dashed line

STP densities were 0.49, 0.31 and 0.03, respectively (Fig. 4).

After calculating site-specific β for SOC, STN and STP (see the supplementary dataset), we found $\beta_{SOC} > \beta_{STN} > \beta_{STP}$ ($P < 0.05$) for both concentration and density (Fig. 5A & B). This meant that the difference between deep soil and surface soil was larger in SOC but smaller in STP. For concentration, β_{SOC} and β_{STP} in the DBS were similar to those in the EBS, while β_{STN} in the DBS was larger than β_{STN} in the EBS; for density, β_{SOC} in the DBS was similar to that in EBS, while β_{STN} and β_{STP} in DBS were larger than those in the EBS ($P < 0.05$) (Fig. 5C & D). In fact, β_{STP} for density in the EBS was not significantly different from 0 ($P = 0.29$). In other words, the differences between deep soil and surface soil in the STN and the STP densities were larger in the DBS than in the EBS.

The site-specific β values for soil nutrients were all negatively correlated with MAT, but not correlated with MAP except the β_{STN} for concentration

and density (Table 1). The β values were not or only weakly correlated with the AGB, but positively correlated with the BGB except for the β_{STP} for density. The β values for concentration and β_{SOC} for density were also positively correlated with the LB.

Environmental influences on the vertical distributions of soil nutrients

The results of partial RDA divided the total variance of vertical distributions of soil nutrients into four components: variance explained by the climatic matrix independently, by the vegetation matrix independently, by the climatic and vegetation matrices jointly and the unexplained variance (Fig. 6). Climatic and vegetation factors explained the vertical variations in STN concentration (40%) and density (30%) best and the vertical variation in STP concentration (13%) and density (4%) most poorly. For all three elements,

Table 1 Correlation coefficients between the decreasing rates of soil nutrients along depth and climatic and vegetation factors

	MAT	MAP	ln AGB	ln BGB	ln LB
Concentration					
β_{SOC} ($n = 371$)	-0.20*	0.03	0.09·	0.23*	0.16*
β_{STN} ($n = 436$)	-0.36*	-0.17*	-0.04	0.13*	0.13*
β_{STP} ($n = 228$)	-0.26*	0.05	0.06	0.15*	0.14·
Density					
β_{SOC} ($n = 320$)	-0.22*	-0.01	0.08	0.25*	0.13*
β_{STN} ($n = 334$)	-0.35*	-0.26*	-0.06	0.13*	0.09
β_{STP} ($n = 125$)	-0.17·	-0.11	-0.08	-0.10	-0.03

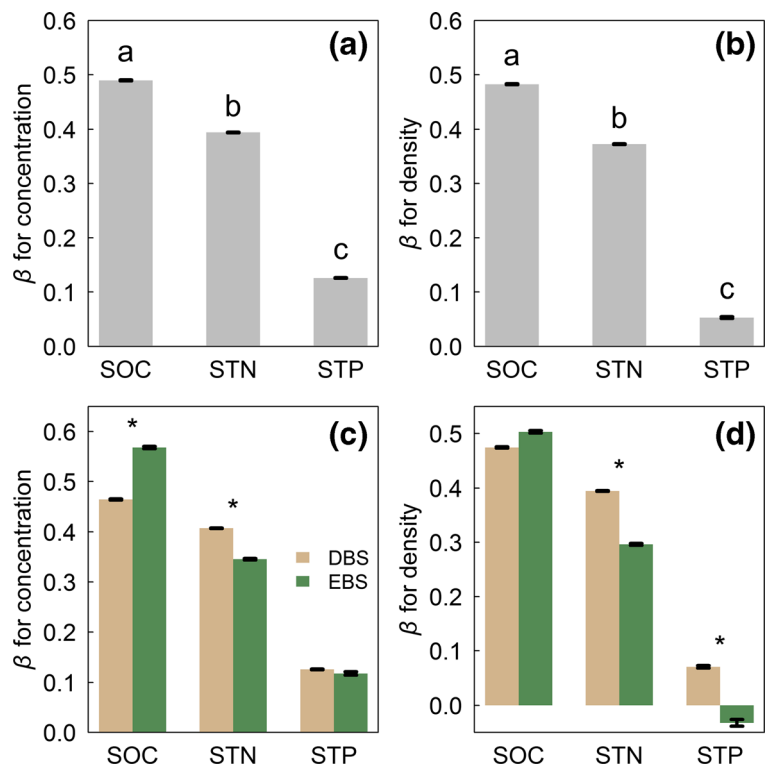
The rates of decrease in soil organic C (β_{SOC}), total N (β_{STN}) and total P (β_{STP}) were calculated based on the Eq. 3

Abbreviations: MAT, mean annual temperature; MAP, mean annual precipitation; AGB, aboveground biomass; BGB belowground biomass; LB, litter biomass

*, $P < 0.05$; ·, $P < 0.1$

climatic factors had stronger independent explanatory power than vegetation factors, except for the STP density, for which neither climatic nor vegetation factors exhibited independent explanatory component.

Fig. 5 Comparisons of decreasing rates in soil nutrients along depth (β) among soil organic C (SOC), total N (STN) and total P (STP) and between the deciduous broadleaf (DBS) and the evergreen broadleaf shrublands (EBS) (C–D). Error bars denoted standard errors. Different letters denoted significant differences at $P < 0.05$ among nutrients, while asterisks denoted significant differences at $P < 0.05$ between shrubland types

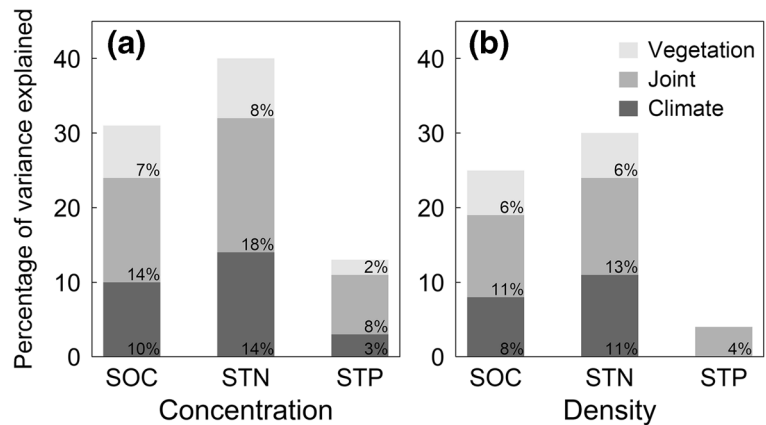


Discussion

Soil nutrient pools in shrublands

Within the top 100 cm, the average SOC density in our study (5.46 kg m^{-3}) is lower than the result from a previous study with far fewer sampling records of shrublands based on the second Chinese national soil survey (6.93 kg m^{-3}), and much lower than that in forests (13.5 kg m^{-3}) or grasslands (17.3 kg m^{-3}) (Wang et al. 2004). The STN density in Chinese shrublands (0.67 kg m^{-3}) is less than the Chinese average (0.84 kg m^{-3}), and that in forests (1.01 kg m^{-3}), steppes (0.77 kg m^{-3}) and meadows (1.64 kg m^{-3}) (Yang et al. 2007). The STP density in Chinese shrublands (0.30 kg m^{-3}) is even less than the half of the Chinese average (0.83 kg m^{-3} , Zhang et al. 2005). In summary, shrublands occupy habitats with lower stocks of SOC, STN and STP, compared with other vegetation types. Therefore, the transformation from other vegetation to shrublands indicates the degradation of soil conditions, while an inverse change probably suggests the improvement of soil conditions.

Fig. 6 Variance partitioning of the influences of climate and vegetation on soil nutrient concentrations (A) and densities (B). Percentages of corresponding components were the adjusted R^2



Vertical distribution patterns of soil nutrients in shrublands

Consistent with previous studies in other ecosystems (Jobbágy and Jackson 2000, 2001; Hobbey et al. 2013; Groppo et al. 2015; Nie et al. 2017), the concentrations and densities of SOC, STN and STP in shrublands generally decreased with soil depth, which could be parameterized by a power equation (Eq. 3, Figs. 3 and 4). Although STP in the EBS density did not follow the equation, it also exhibited a decreasing trend with soil depth. SOC and STN had larger β than STP, probably because of their different sources. C and N in soil originate mainly from the atmosphere and biomass input from above the soil or in topsoil, leading to the accumulation of nutrients in surface soil (Tian et al. 2010). However, P can originate both from the top by biomass input and from the bottom by weathering of soil parent material (Vitousek 2004), leading to the more complex and diverse vertical distribution patterns of STP (Weil and Brady 2016). In our case, this variability is shown as a more uniform vertical distribution of STP.

The decreasing rate of nutrient concentrations with soil depth is higher in shrublands (0.54) than that in forests (0.44) or grasslands (0.42) for the SOC, while that for the STN (0.37) is similar to that in forests (0.37) but lower than that in grasslands (0.41) in China (Chai et al. 2015). We found that SOC in surface soil accounted for a larger fraction of total SOC in shrublands than in forests or grasslands, implying that shrublands can suffer soil C loss more easily because of their lower plant cover that may cause more severe weathering of surface soil.

It has been frequently reported that the vertically decreasing patterns of soil nutrients differ among vegetation types (Jobbágy and Jackson 2000; Yang et al. 2007; Chai et al. 2015). On the one hand, this difference could be attributed to the divergent root distribution and biomass input from above- and belowground because of different life history strategies of dominant plant life forms (Jobbágy and Jackson 2000). On the other hand, from the viewpoint of habitat differences, the lower β of STN and STP densities in the EBS than in the DBS from our study may be resulted from stronger leaching in subtropical and tropical regions where evergreen shrubs dominate (Reich and Oleksyn 2004), which transfers more nutrients from the topsoil to the bottom soil.

Influences of climate and vegetation on the vertical distributions of soil nutrients

The positive correlation between β and the BGB confirms the role of root input in determining soil nutrient distribution (Jobbágy and Jackson 2000), while the positive correlations between β and the LB probably indicates that a larger amount of litter input could facilitate the accumulations of these elements in the topsoil (Lugo et al. 1990; Sayer et al. 2012; Lafleur et al. 2015), increasing the relative difference in nutrient contents between the topsoil and deeper soil. The negative relationship between β and MAT may reflect higher decomposition rates in surface soil in warmer regions. Although higher precipitation can cause more litterfall (Zhou et al. 2009), it can also increase leaching intensity, which could be the reason for its negative correlation with β_{STN} . The non-significant correlation for SOC or STP might be attributed to their lower soluble fraction

that caused lower mobility in the process of leaching (Pirainen et al. 2007).

The influence of climate and vegetation on the soil nutrients varies at different depths, because of different activity levels of decomposition, leaching, root absorption and above- and belowground material inputs along the soil depth, contributing to the vertical patterns of soil nutrients (Jobbágy and Jackson 2000, 2001; Yang et al. 2007). Meanwhile, effects of climate and vegetation can be confounded. For instance, climate controls plant turnover or physiological conditions and indirectly influence nutrient uptake and input in soil (Raich and Schlesinger 1992; He and Dijkstra 2014), while vegetation could form microhabitats to mediate the effects of climate on soil (Smith and Johnson 2004; D’Odorico et al. 2013). Thus, distinguishing the intensities of their specific influences on soil nutrients using a variance partitioning method is necessary.

We found a relatively stronger effects of climate than vegetation in controlling soil nutrient vertical distribution, which emphasizes the importance of climate-related processes such as decomposition and leaching. The vertical distribution of STP was less affected by climatic and vegetation factors, probably due to the more stable source from parent material (Vitousek 2004). In contrast, STN showed a stronger plasticity, reflecting a more sensitive and flexible source from the metabolism of plants and microbes (Bernal et al. 2012). In addition, climatic and vegetation factors played stronger roles on nutrient concentrations than densities that were the products of concentrations and soil bulk density, reflecting that concentrations could be more sensitive to external influences, while soil bulk density could potentially be determined by other inherent soil properties (da Silva et al. 1997).

Conclusions

Shrublands are much poorer in the top 100 cm soil C, N and P than other vegetation types. The concentrations and densities of SOC, STN and STP decrease with soil depth, which can be modeled by a power equation ($\log Y = -\beta \log D + \alpha$ after logarithm transformation). Climate and vegetation have a combined influence on the vertical distributions of soil nutrients, while the independent influence of the former tends to be relatively stronger. STP is more uniformly distributed vertically and less affected by both kinds of factors because of its

unique source from parent material. The infertility of shrubland soil suggests that soil nutrient conditions can be an important determinant of vegetation physiognomy. Therefore, the management of ecosystems for conservation and restoration should pay special attention to soil protection.

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