

# Consistent profile pattern and spatial variation of soil C/N/P stoichiometric ratios in the subalpine forests

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## Abstract

**Purpose** The vertical patterns of soil carbon (C), nitrogen (N), and phosphorus (P) stoichiometry are still controversial, and relative contribution of their controlling factors also is rarely understood for the whole soil profile. This study aimed to assess the vertical variation of both C/N, N/P, C/P ratios and their determining factors along soil profiles in subalpine forests of the eastern Tibetan Plateau.

**Materials and methods** Soil samples at five depths (0–10, 10–20, 20–30, 30–50, and 50–100 cm) were collected from 132 forest sites to evaluate the vertical distribution of soil C/N, N/P, and C/P ratios. Eleven relevant environmental factors (e.g., altitude, latitude, longitude, soil pH, soil bulk density, relative stone contents, soil order, slope, position, forest type, and dominant tree species) were measured to examine their relative contribution on stoichiometric ratios within each soil layer using boosted regression tree (BRT) analysis.

**Results and discussion** Soil C/N, N/P, and C/P ratios consistently decreased with increasing soil depth. BRT models

accurately predicted the soil C/N, N/P, and C/P ratios in the upper four layers ( $R^2 = 49\text{--}97\%$ ). For soil C/N and N/P ratios, altitude associated with latitude had the highest contribution across five soil layers, while the contributions of soil pH and bulk density were significant within soil layers closer to the surface. Independently, soil bulk density and altitude were the most important factors of C/P ratios in 0–30- and 30–100-cm soil layers.

**Conclusions** This study indicated that soil C/N/P stoichiometric ratios, and the relative importance of their controlling factors, shifted within soil profiles across Tibetan Plateau forests. Further research will be needed to understand the regulatory mechanism of soil stoichiometry and biogeochemistry in response to environmental change at whole soil profiles.

**Keywords** BRT · Soil profile · Soil stoichiometry · Subalpine forest · Tibetan Plateau

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## 1 Introduction

Soil carbon (C), nitrogen (N), and phosphorus (P) stoichiometry can mirror ecological processes, for example the retention and release of C (Aitkenhead and McDowell 2000) and N (Klemetsson et al. 2005; Gundersen et al. 2009; Vesterdal et al. 2008), the determination of tree species (Lovett et al. 2002), and the regulation of vegetation composition (Fanelli et al. 2008; Bui and Henderson 2013). Previous evaluation of nutrient pools has suggested that the relationship of C/N ratios in soil was largely dependent upon climate and soil texture (Callesen et al. 2007; Homann et al. 2007). Soil C/N/P stoichiometric flexibility plays a role in governing biogeochemical cycles (Sistla and Schimel 2012) and carbon sequestration (Hessen et al. 2004; Kirkby et al. 2013) in terrestrial ecosystems;

therefore, exploring the pattern and variation of soil C/N/P ratios will greatly improve our understanding of forest dynamics and soil C sequestration in response to environmental change.

The relative change of soil C, N, and P concentrations along soil profiles are influenced by the distribution of belowground biomass, as well as microbial decomposition and disturbance. Thus, diverse vertical patterning of soil C/N, N/P, and C/P ratios across various ecosystems has been described. In forest ecosystems, Callesen et al. (2007) observed that C/N ratios decreased with increased soil depth within a boreal forest. Meanwhile, Tischer et al. (2014) found that the C/N ratio remained relatively stable but N/P and C/P ratios both decreased with increasing soil depth in tropical mountain rainforests. In grasslands, there are several reports of an unusual increase of soil C/N ratios along a soil profile (Dumig et al. 2009; Watt and Palmer 2012; Liu et al. 2014; Tischer et al. 2014); yet, Yang et al. (2010) found the soil C/N ratio remained relatively stable along soil profiles in the Tibetan Plateau grassland. In wetlands, Zhang et al. (2012) reported that C/N ratios remained relatively stable but both N/P and C/P ratios decreased with increasing soil depth. Tian et al. (2010) also demonstrated that C/N, N/P, and C/P ratios always decline with increasing soil depth across various climate regions in mainland China. With all considerations, the vertical pattern of C/N ratios along soil profiles still remains unclear, and the vertical trends of soil N/P and C/P ratios have not been sufficiently documented. In-depth exploration of the variation and pattern of soil stoichiometric ratios will allow for new insights into biogeochemical cycles.

Previous studies have revealed that many environmental factors, including temperature, precipitation, elevation, latitude, soil texture, vegetation types, and disturbance (nitrogen deposition and grazing) can regulate the spatial pattern of soil C/N/P ratios (Cleveland and Liptzin 2007; Tian et al. 2010). Temperature and precipitation are negatively related to soil C/N ratio (Callesen et al. 2007; Vesterdal et al. 2008), while elevation typically has a positive correlation with C/N ratios in tropical forests (Schawe et al. 2007; Moser et al. 2011; Whitaker et al. 2014). As latitude increases, soil C/N and C/P ratios also increase (Xu et al. 2013) since higher latitudes are associated with lower temperatures, less precipitation, and a lower nutrient mineralization rate. Soil texture with relatively high clay content often corresponds to a decreased C/N ratio (Homann et al. 2007; Vesterdal et al. 2008). Vegetation composition can also have a remarkable effect on surface soil C/N, N/P, and C/P ratios (Xu et al. 2013; Cools et al. 2014). The C/N ratio is higher in coniferous forests than in broadleaf forests and is higher in temperate forests compared to tropical forests (Yang and Luo 2011).

Because these environmental factors also influence each other, their relative contribution on the spatial pattern variation of soil C/N/P stoichiometry at a regional scale remains unclear.

Many studies have indicated that the effects of external environmental factors, such as temperature, precipitation, and vegetation, are lessened with increasing soil depths (Jobbagy and Jackson 2000; Yang et al. 2010). Thus, the factor with the highest relative contribution to stoichiometric ratios may differ between the surface and deep soil layers. Cools et al. (2014) found that the largest sources of influence on the C/N ratio in European forest soils shifted from tree species to soil type along soil profiles. Gao et al. (2014) also reported that the effect of land use change on C/N ratios between surface and deep soil layers was contrasting in subtropical ecosystems. However, current research into the soil stoichiometry has predominantly focused on surface soil layers rather than whole soil profiles. Obviously, it will be very important to determine how environmental factors influence the variation of soil stoichiometric ratios along soil profiles in different regions and ecosystems. Therefore, such effort would greatly improve our knowledge of the soil processes and biochemical cycles at whole soil profiles (Rumpel and Kogel-Knabner 2011; Wang et al. 2014).

The Tibetan Plateau ecosystem is fragile and susceptible to future global change. Soil stoichiometry tends to control the relative C allocation between plant biomass and soil organic matter (Alberti et al. 2015), which impacts soil C sequestration (Kirkby et al. 2013). The pattern and variation of soil C/N ratio in grasslands are well documented at local and regional scales across the Tibetan Plateau (Tian et al. 2010; Yang et al. 2010; Liu et al. 2014). Forest ecosystems with approximately 27 % of the area of the Tibetan Plateau had the highest biomass and soil C storage (Zhang et al. 2015). Subalpine forests are widely distributed in the eastern Tibetan Plateau and are critical for regional C sequestration and biogeochemistry in response to global climate change. However, there are only a few case studies of soil C/N ratios in the mountain forests of the eastern Tibetan Plateau (e.g., Gongga Mountain) (Yang et al. 2014). As a consequence, the vertical pattern of soil C/N/P and major factors influencing their spatial variation at the regional scale remain unclear. In this study, we explored the vertical patterns of C/N, N/P, and C/P ratios along soil profiles in the subalpine forests and evaluated the change of determinants controlling soil C/N, N/P, and C/P ratios across different soil depths. Here, we asked the following questions: (1) Are the vertical distributions of three stoichiometric (C/N, N/P, and C/P) ratios along soil profiles consistent or do the ratios decrease with increasing depth? (2) What are the main factors that determine the spatial pattern of soil C/N, C/P, and N/P ratios? (3) Do the regulating factors differ with soil depths and among C/N, N/P, and C/P ratios?

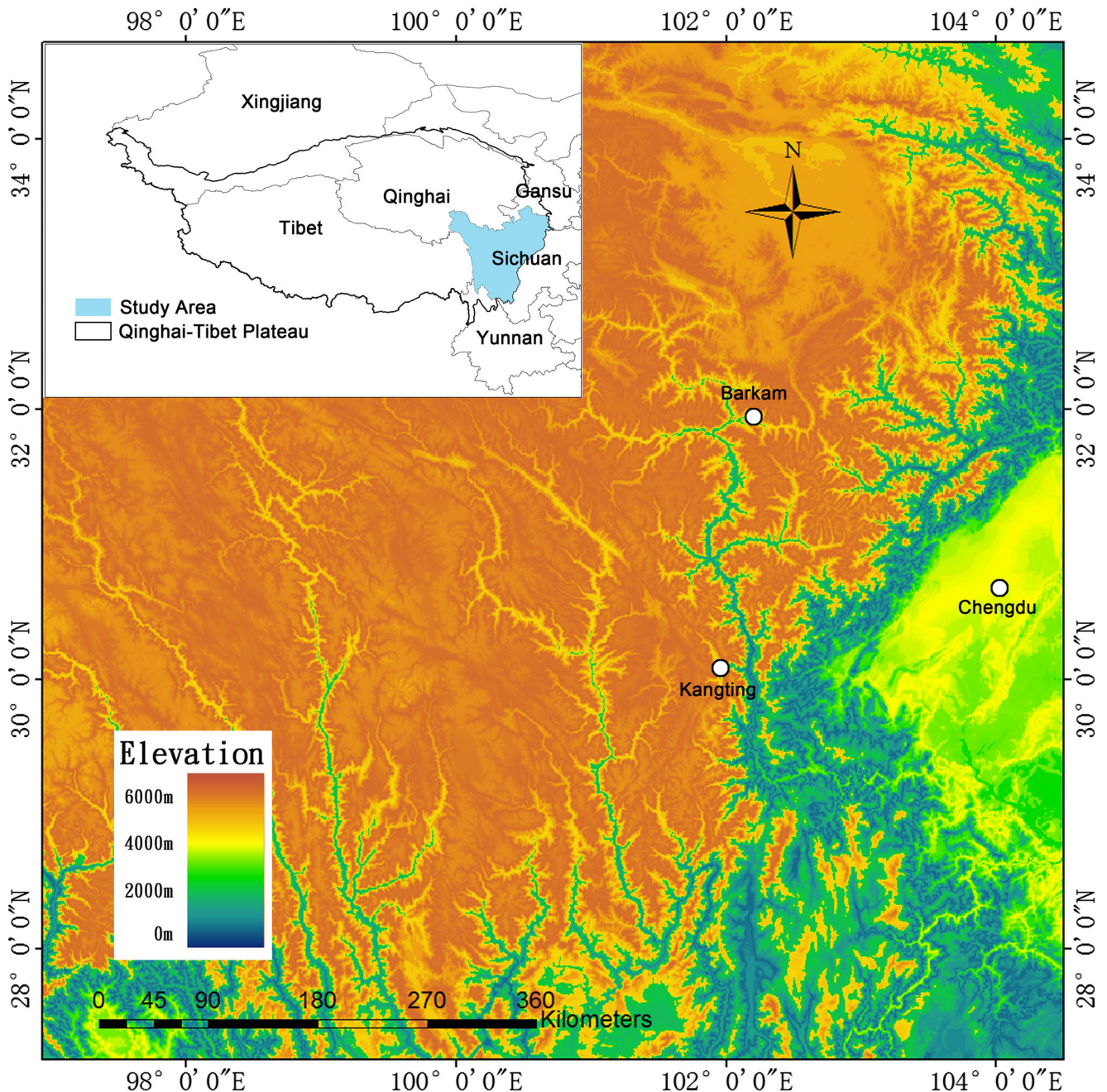


## 2 Materials and methods

### 2.1 Study area

The study area ranged from 27° 27' N to 33° 37' N and from 99° 23' E to 103° 54' E, with an altitude of 1779 m to 4292 m a.s.l. (Fig. 1), which covered about 254,000 km<sup>2</sup> in the western region of Sichuan province in the eastern Tibetan Plateau (Zhang et al. 2002). It is a part of the Southwestern National Forest Region in China. The climate is temperate with an annual rainfall of 700–1100 mm and a mean annual

temperature of 6–13 °C. The frost-free period in this region is less than 110 days. Coniferous and broadleaf forests are widely distributed in the subalpine region. Typically, subalpine coniferous forests are dominated by spruce trees (*Picea* spp.), fir trees (*Abies* spp.), and pine trees (*Pinus* spp.). The pine forests mostly consist of *Pinus yunnanensis*, *Pinus armandii*, *Pinus tabulaeformis*, and *Pinus densata*. The typical subalpine broadleaf forests include deciduous mixed forests and sclerophyllously evergreen oak forests. The deciduous broadleaf forests are comprised of birch (*Betula utilis*, *Betula albosinensis*, and *Betula platyphylla*), aspen (*Populus*



**Fig. 1** Location of the 132 sites in subalpine forests of eastern Tibetan Plateau, China

spp.), and some maple trees (*Acer* spp.). The evergreen broad-leaf forests are dominant by sclerophyllous evergreen oak (*Quercus aquifolioides*, *Quercus pannosa*, and *Quercus senescens*). Soil order under these forests is generally Alfisols, while a few pine forests (*P. yunnanensis*) are characterized as Inceptisols according to soil developmental time series described by Shi et al. (2004).

## 2.2 Sampling design and data collection

We conducted the field forest inventory of Sichuan Province during July and August of 2011–2013. In order to survey the vertical pattern of soil C/N, N/P, and C/P ratios and unveil their controlling factors in subalpine forests of eastern Tibetan Plateau, we selected 132 soil profiles of natural forests without disturbance in the western Sichuan Province. In reference to the dominant tree species, these sites were classified as five typical subalpine forests: 12 sites for spruce forests, 43 sites for fir forests, 37 sites for pine forests, 26 sites for birch forests, and 14 sites for sclerophyllous evergreen oak forests.

Forest plots had an area of 20 m × 30 m or 20 m × 50 m for each site. The geographic location (altitude, longitude, and latitude) and the degree and position of the slopes were recorded. Then, each forest plot was divided into six or nine subplots (10 m × 10 m) to identify tree species. Three subplots were systematically selected to establish a quadrat (2 m × 2 m) in its top-left corner. So, the measurement of understory plants and soil sampling by soil auger (20 cm high and 5 cm in diameter) was conducted in three quadrats for each forest plot. In each quadrat, three duplicate soil samples for each depth interval were collected according to five fixed depth intervals (i.e., 0–10, 10–20, 20–30, 30–50, and 50–100 cm). We collected nine soil samples at each depth interval in each forest plot. After picking out the root and coarse stone, the nine soil samples were mixed into one composite sample. Thus, for each forest plot, we transported the composite soil samples of the five depth intervals to determine nutrient concentrations and pH in laboratory. All soil samples were air-dried at room temperature for 2 weeks and sieved through a 2-mm mesh for further chemical analysis. The total C (TC) and total N (TN) concentration were measured by a CHN-elemental analyzer (Vario MACRO, Elementar Analysesyteme GmbH, Hanau, Germany). The total P (TP) concentration was determined with ICP-OES 8300 (PerkinElmer, USA.) after digestion with H<sub>2</sub>SO<sub>4</sub>-HClO<sub>4</sub>. Soil pH was measured by pH meter in the suspension (soil/water = 1:2.5).

Additionally, we excavated a soil profile in the forest plot by soil cores to measure soil bulk density and to cut a soil hexahedron with the same volume at five intervals mentioned above. Soil hexahedrons were dried and successively sieved through 10-, 2-, and 1-mm mesh to separately measure their mass according to four diameter classes of coarse stone (<1, 1–2, 2–10, and >10 mm).

For each diameter, the mass of coarse stone was divided by the total mass of the soil hexahedrons and this was considered the relative stone content (%). Ultimately, we tested the soil nutrient concentration across five soil depths and for 11 dependent environmental factors (14 variables) from 132 forest sites (Table 1).

## 2.3 Statistical analyses

We transformed the concentrations (g kg<sup>-1</sup>) of TC, TN, and TP to mole per kilogram, then calculated three stoichiometric ratios (C/N, N/P, and C/P) in soil as atomic ratio, rather than mass ratio. The soil C/P ratios needed to improve their normal distribution by log<sub>10</sub>-transformed prior to these statistics analyses but following analyses transformed back to the original units. The coefficient of the variations (CV = standard deviation/mean, %) was used for indicating the vertical variation degree. We calculated the CV of each soil profile and then averaged the CV of each nutrient stoichiometric ratio from 132 soil profiles. The lower average CV indicated more stable values along soil profiles. We employed Pearson correlation to analyze the relationships between the CV of nutrient stoichiometric ratios and the CV of nutrient concentrations. Further, we used a one-way analysis of variance (ANOVA) with least significant difference (LSD) post hoc test of significance to compare C/N, N/P, and C/P ratios among five soil depths (Cleveland and Liptzin 2007; Tian et al. 2010). We also assessed the relationship between stoichiometric ratios (C/N, N/P, and C/P) and soil depth by curve estimation independently. The power function with a higher coefficient of determination ( $R^2$ ) was considered as the best-fit model. Standardized major axe approach (SMA) (Warton et al. 2006) was used to compare the differences in slopes of power function among three stoichiometric ratios. These statistical analyses were performed using SPSS 20.0 for Windows statistical software package (SPSS Inc., Chicago, IL, USA) and SMATR 2.0 (<http://www.bio.mq.edu.au/ecology/SMATR/>). All differences were considered to be significant at the  $p < 0.05$  level.

In order to thoroughly understand changes in soil stoichiometric ratios and obtain reliable statistical results, it is critical to explore the roles of factors that influence these ratios. Boosted regression tree (BRT) is a powerful modeling method that combines regression trees and boosting algorithms. The BRT model is a robust method to measure variable colinearity, variable outliers, missing data, variable type (numeric, binary, or categorical), and distributional characteristics (Bernoulli, Poisson, Gaussian, etc.). For these reasons, its use has become increasingly popular within the field of ecology (De'ath 2007; Aertsen et al. 2012; Cools et al. 2014). Thus, we



**Table 1** Explanatory variables used in the boosted regression tree (BRT) models for soil C/N/P ratios in subalpine forests of eastern Tibetan Plateau

Variable (14)	Abbreviation	Type	Unit	Description (mean and/or range)
Forest type	Forest	Factor (2) <sup>a</sup>	Null	Coniferous and broadleaf forests
Tree species	tree	Factor (5)	Null	Spruce ( <i>Picea</i> spp.) forests; fir ( <i>Abies</i> spp.) forests Pine ( <i>Pinus</i> spp.) forests; birch ( <i>Betula</i> spp.) forests Oak ( <i>Quercus</i> spp.) forests (Appendix 2)
Altitude	Al	Numeric	m	Elevation of the site above sea level (1179–4292 m.a.s.l)
Latitude	La	Numeric	Degree	27.45–33.62
Longitude	Lo	Numeric	Degree	99.38–103.90
Slope		Numeric	Degree	0–58
Position		Factor (4)	Null	Footslope, lowslope, upslope, and mountaintop
Soil pH		Numeric	Null	Mean = 5.8; range from 3.8 to 8.8
Bulk density	BD	Numeric	g/cm <sup>3</sup>	Mean = 1.12; range from 0.21 to 1.98
Coarse stone content ( $d > 10$ mm)	X.10	Numeric	%	The percentage of coarse stone with diameter larger than 10 mm (0–81)
Coarse stone content (10 mm $> d > 2$ mm)	X2.10	Numeric	%	The percentage of coarse stone with diameter between 10 and 2 mm (0–84)
Coarse stone content (2 mm $> d > 1$ mm)	X1.2	Numeric	%	The percentage of coarse stone with diameter between 2 and 1 mm (0–93)
Coarse stone content ( $d < 1$ mm)	X.1	Numeric	%	The percentage of coarse stone with diameter less than 1 mm (0–92)
Soil order		Factor (2)	Null	Alfisols and Inceptisols (Shi et al. 2004)

<sup>a</sup> Number of levels are given between brackets

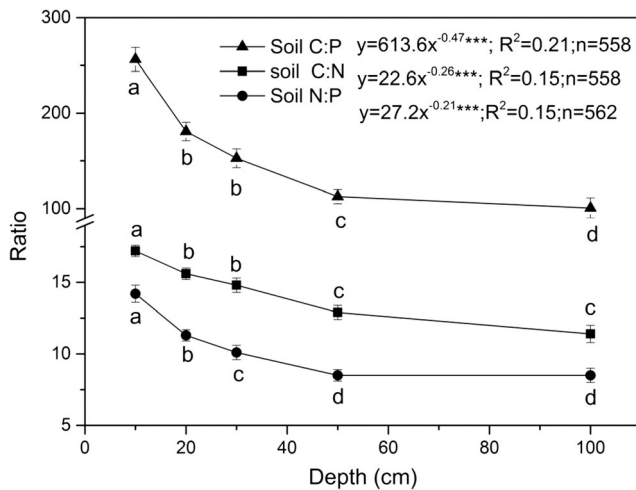
selected BRT model analysis to partition the independent influence of environmental factors on soil C/N, N/P, and C/P ratios for five soil depth (0–10, 10–20, 20–30, 30–50, and 50–100 cm intervals). These factors were divided into 14 variables: altitude, latitude, longitude, soil pH, soil bulk density, relative stone contents of four diameter classes (diameter  $< 1$  mm,  $1 < \text{diameter} < 2$  mm,  $2 < \text{diameter} < 10$  mm, and diameter  $> 10$  mm), soil order, slope, position, forest type, and dominant tree species. Forest type was classified into coniferous and broadleaf forests. The dominant tree species were spruces (*Picea* spp.), firs (*Abies* spp.), pines (*Pinus* spp.), birch (*Betula* spp.), and sclerophyllous evergreen oak (Table 1). BRT models were operated in R-software, version 3.1.13 (R Development Core Team 2015), using the “gbm” package (Ridgeway 2006) and its extensions “dismo” package (Elith et al. 2008). Models were fitted using the *gbm.step* function and a Gaussian response type, with the following effective settings: learning rate (0.005), bag fraction (0.5), and cross-validation (10). Given our relatively small forest sites, we set tree complexity at 3, according to reported recommendations (Elith et al. 2008). We used the *gbm.simplify* function to drop insignificant variables from the original model without affecting predictive performance. Finally, model fit and predictive performance of the stoichiometric ratios at each soil layer after 10-fold cross-validation were quantified by the coefficient of determination ( $R^2$ ) (Aertsen et al. 2012). BRT analysis

output demonstrated the relative influence of the predictor variables in the model. The relative influence or contribution of each variable was scaled so that the sum was equal to 100, with higher numbers indicating stronger influence on the response.

### 3 Results

#### 3.1 Vertical change of soil C/N, N/P, and C/P ratios along soil profiles

Three stoichiometric ratios (C/N, N/P, and C/P) all dramatically declined with increasing soil depth as a power function formulation (Fig. 2). The C/N, N/P, and C/P ratios significantly decreased from 16.9 to 11.3, 14.1 to 8.5, and 241.2 to 98.7 at five depths, respectively ( $p < 0.001$ ). For all soil depths,  $CV_{C/P}$  (72 %) was bigger than  $CV_{C/N}$  (35 %) and  $CV_{N/P}$  (51 %) in subalpine forests of eastern Tibetan Plateau (Appendix 1, [Electronic Supplementary Material](#)). The mean  $CV_{C/P}$  (43.2 %) was also higher than  $CV_{C/N}$  (17.8 %) and  $CV_{N/P}$  (30.3 %) across 132 soil profiles ( $p < 0.001$ ). This result reflected that the vertical variation of C/P ratio was larger than that of N/P and C/N ratios along all soil profiles. Pearson correlation analysis showed that  $CV_{C/N}$  was closely related to  $CV_C$  but not to  $CV_N$  along soil depth gradients (Fig. 3a).  $CV_{N/P}$  and  $CV_{C/P}$  were more relevant to  $CV_N$  and  $CV_C$  rather than  $CV_B$ , respectively ( $p < 0.001$ ) (Fig. 3b, c).



**Fig. 2** The vertical change and its fitted vertical distribution of soil C/N, N/P, and C/P ratios across soil profiles in subalpine forests of eastern Tibetan Plateau. The *geometry* and *error bar* represent the mean and SE across all sites in each depth, respectively; the *different lowercase letters* meant significantly different among soil depth intervals ( $p < 0.05$ ), while the *same lowercase letters* indicated no significant difference by one-way ANOVA and post hoc LSD tests. In fitted functions,  $y$  and  $x$  represent soil stoichiometric ratios and soil depth (cm), respectively; \*\*\* $p = 0.001$

These results showed a faster exponential decrease in C/P ratio (SMA,  $p = 0.001$ ), which was primarily due to the sharply decreasing C concentrations along the profiles.

### 3.2 Main factors influencing soil C/N, N/P, and C/P ratios at different soil depths

#### 3.2.1 Soil C/N ratio

Altitude, latitude, longitude, soil pH and bulk density, slope, position, dominant tree composition, and the relative contents of four stone classes were successfully entered into the final BRT models for soil C/N ratio (Table 2a). These 12 variables together explained 77, 86, 97, 97, and 88% of spatial variation for C/N ratios at 0–10, 10–20, 20–30, 30–50, and 50–100 cm soil intervals, respectively. Altitude had the highest contribution (18.1–29.5 %) at 0–10, 20–30, and 50–100 cm intervals, while soil pH (20.9 %) and longitude (17.2%) separately had the highest contribution at 10–20 and 30–50 cm intervals in the subalpine forest region. Relative stone content and position with low contribution (1.6–8.2 %) had less impact on the C/N ratios along soil profiles. Moreover, the relative contribution of altitude on the C/N ratio was higher than that of latitude and longitude in the upper three soil layers (0–30 cm) and the deepest soil layer (50–100 cm). The effect of soil pH on the C/N ratio was consistently larger than that of bulk density and had a greater influence than the slope in the upper three soil layers.

Partial plots showed that C/N ratios in the upper three soil layers sharply decreased from 3000 to 3500 m a.s.l. but

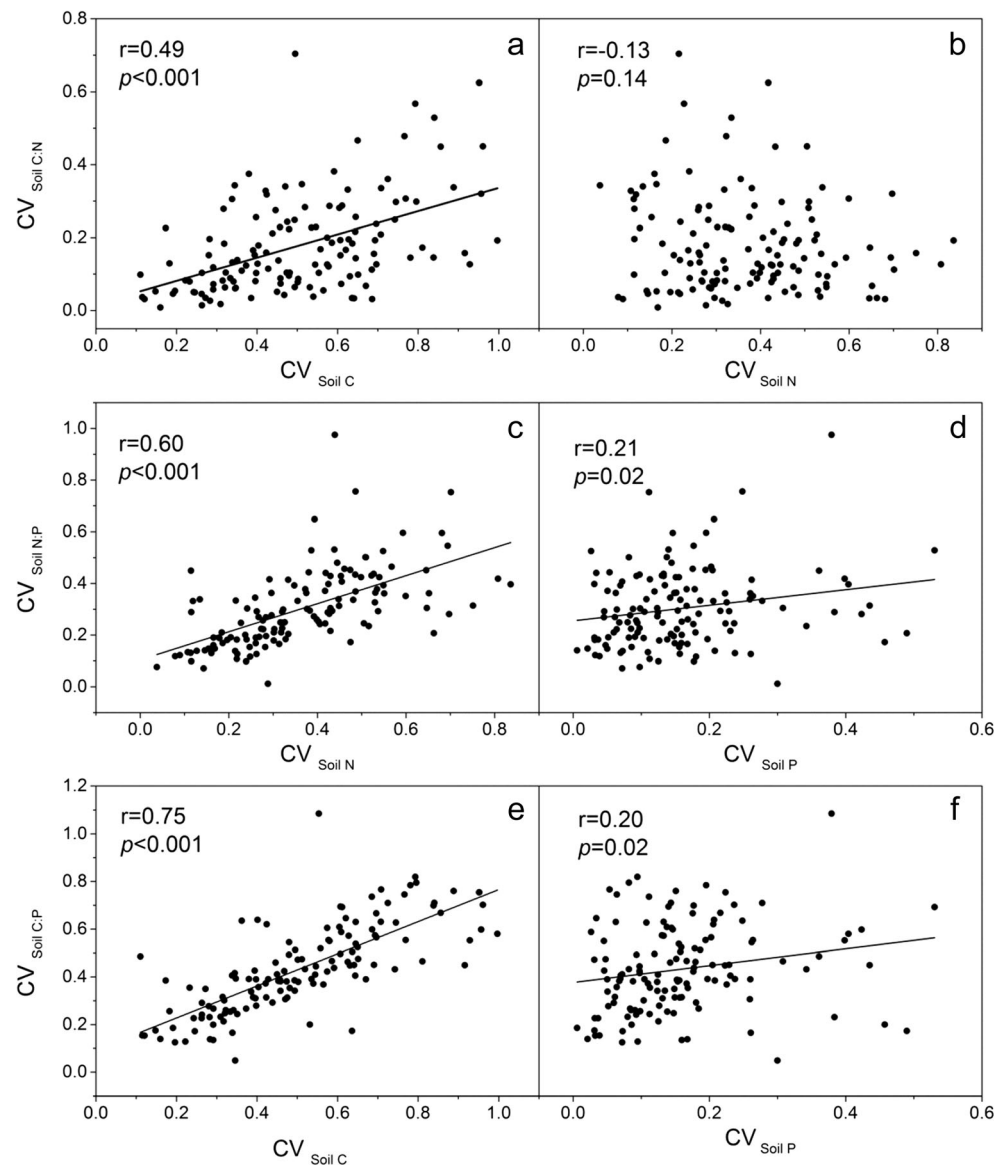
increased in other elevation ranges (Fig. 4 and Appendixes 3c and 4a in the [Electronic Supplementary Material](#)). Interestingly, the C/N ratios in the two deeper soil layers (30–50 and 50–100 cm) always increased with rising elevation (Table 2a and; Appendixes 3b and 6a in the [Electronic Supplementary Material](#)) and the trend of soil C/N ratio with longitude shifted from positive to negative at approximate 102 E (Fig. 4c and Appendixes 3d, 4b, and 5a in the [Electronic Supplementary Material](#)). Soil C/N ratio decreased with increasing latitude (Table 2a, Fig. 4d, and Appendixes 3e and 4e in the [Electronic Supplementary Material](#)) and soil bulk density (Fig. 4e and Appendixes 3b, 5d, and 6c in the [Electronic Supplementary Material](#)) but increased with rises in slope (Appendixes 4f, 5d, and 6b). Soil C/N ratios were negatively correlated with pH values in the two upper soil layers (0–20 cm) (Table 2a, Fig. 1b, and Appendix 3a in the [Electronic Supplementary Material](#)). However, in the three deeper soil layers (20–100 cm), there were positive relationships between C/N ratio and pH, when soil pH was higher than six (Appendixes 4c, 5e, and 6d in the [Electronic Supplementary Material](#)). Consistently, soil C/N ratios in the pine forest were always lower than other forests (Fig. 6f).

#### 3.2.2 Soil N/P ratio

In comparison with the 12 variables for soil C/N ratio, except for the position, the other 11 variables together explained 64, 95, 66, 63, and 29 % of spatial variation for N/P ratios at 0–10, 10–20, 20–30, 30–50, and 50–100 cm soil intervals, respectively (Table 2b). Latitude possessed the highest contribution at 0–10 (25.5 %) and 30–50 cm (35.5 %) intervals, while soil pH, bulk density, and altitude independently contributed at 10–20 (17.1 %), 20–30 (19.4 %), and 50–100 cm (66.7 %) intervals. The relative contribution of longitude (7.0–1.2 %), dominant tree species (2.5–7.6 %), or relative stone contents (2.5–12.2 %) was low among the soil profiles. Moreover, the effect of latitude on soil N/P ratio in the four surface soil layers (0–50 cm) was relatively stronger than the altitude and longitude. The relative contribution of soil pH was higher than bulk density in the shallow two layers (0–20 cm) but was lower in the deeper layers (20–50 cm). At a depth over 30 cm, slope had a stronger influence than soil pH and bulk density.

Soil N/P ratios increased with latitude between 28 N and 31 N (Fig. 5a and Appendixes 7b, 8b, and 9a in the [Electronic Supplementary Material](#)). N/P ratios at the two deepest soil intervals (30–50 and 50–100 cm) increased at elevations between 3000 and 3500 m a.s.l. and decreased in other elevation ranges (Appendixes 9c and 10a, [Electronic Supplementary Material](#)). N/P ratio in 0–10 cm soil layer declined with increasing pH value (Table 2b and Fig. 5e). In deep soil layers (below 10 cm), the change of N/P ratios sharply shifted from a downward trend to upward trend when the pH was 6 (Appendixes 7a, 8d, and 9d, [Electronic Supplementary](#)

**Fig. 3** Correlation between the CV of soil C/N, N/P, and C/P ratio and the CV of soil C, N, and P concentration in subalpine forests of eastern Tibetan Plateau



Material). Moreover, soil N/P ratios were positively related to slope (Fig. 5b and Appendixes 7d, 8c, 9b, and 10b) and negatively related to bulk density (Appendixes 7c, 8a, and 9e, [Electronic Supplementary Material](#)) along soil profiles. Soil N/P ratios of pine forests were relative lower than that of other forests (Fig. 5d).

### 3.2.3 Soil C/P ratio

As mentioned above, several variables were included into the final BRT models for soil C/P ratios (Table 2c) and collectively explained 49, 77, 79, 57, and 44 % of spatial variation at 0–10, 10–20, 20–30, 30–50, and 50–100 cm soil depths, respectively. Soil bulk density had the greatest influence on C/P ratios accounting for 22.0 to 26.5 % in the upper three layers (0–10, 10–20, and 20–30 cm), whereas altitude had the

highest contribution and accounted for 33.9 to 39.9 % in the deepest two layers (30–50 and 50–100 cm). Dominant tree species and slope were the second most influential independent variables for C/P ratios in 0–10 and 20–100 cm soil intervals (Table 2c). The contributions of relative stone content (2.3–13.1 %) and longitude (2–7 %) were relative low among soil profiles.

Soil C/P ratio showed a decreasing trend with bulk density (Fig. 6a and Appendixes 11a and 12a in the [Electronic Supplementary Material](#)) and an increasing trend with both elevation (Appendixes 11e, 12a, and 14a) and slope (Fig. 6d and Appendixes 11c, 12b, 13b, and 14b in the [Electronic Supplementary Material](#)). C/P ratio also declined with increasing pH value but only in 0–10 and 10–20 cm soil layers (Fig. 6e and Appendix 11b in the [Electronic Supplementary Material](#)). Soil C/P ratio of pine forests was lower than that of

**Table 2** Relative influence [RI (%)] of environmental variables on soil C/N, N/P, and C/P ratios at five soil depth intervals in subalpine forests of eastern Tibetan Plateau following a boosted regression tree (BRT) analysis

	Variable	RI (%)	Variable	RI (%)	Variable	RI (%)	Variable	RI (%)	Variable	RI (%)
(a) C/N										
	0–10 cm (n = 132)		30–50 cm (n = 115)		20–30 cm (n = 115)		30–50 cm (n = 115)		50–100 cm (n = 57)	
1	Al↗↘↗	29.5	pH↘	20.9	Al↗↘↗	18.1	Lo↗↘	17.2	Al↗	25.1
2	pH↘	16.0	BD↘	18.6	Lo↗↘	12.8	BD↘	13.0	Slope↗	21.1
3	Lo↗	10.4	Al↗↘↗	14.7	pH↘↗	11.7	Al↗	13.0	Tree	18.2
4	La↘	9.8	Lo↗↘	13.1	BD↘	10.6	Slope↗	10.9	pH↘	16.8
5	BD↘	8.2	La↘	6.6	La↘	10.5	pH↘↗	9.0	La↘↗	12.1
6	Tree	7.1	Tree	5.7	Slope↗	8.3	X.10↗	7.4	BD	6.7
7	X.10↗	5.4	X.10↘	4.9	X.1↗	8.2	La↘	7.0		
8	Slope↗	4.3	Slope↗	4.4	X1.2↘	6.7	X1.2↘	6.2		
9	X2.10↘	3.3	X.1↘	4.3	X2.10↗	5.1	X.1↗	6.0		
10	X.1↗	3.1	X1.2↗	3.6	X.10↘	5.1	X2.10↗	5.0		
11	X1.2↘	3.1	X2.10↗	3.3	Tree	2.1	Tree	3.8		
12							Position	1.6		
(b) N/P										
	0–10 cm (n = 128)		10–20 cm (n = 132)		20–30 cm (n = 115)		30–50 cm (n = 115)		50–100 cm (n = 57)	
1	La↗↘	35.9	pH↘↗	17.1	BD↘	19.4	La↗	25.5	Al↘↗↘	66.7
2	Slope↗	13.2	La↗	14.5	La↗	16.7	Slope↗	20.1	Slope↗	33.3
3	X.10↗	9.7	BD↘	10.6	Slope↗	13.4	Al↘↗↘	18.1		
4	Tree	7.6	Slope↗	9.9	pH↘↗	12.7	BD↘	7.8		
5	X2.10↗	6.0	X.10↗	9.5	X.10↗	12.2	pH↗	7.8		
6	pH↘	6.0	X.1↗	8.6	X2.10↗	6.0	Tree	7.6		
7	BD↘	5.9	X1.2↗↘	7.3	X1.2↘	4.8	X1.2↘	5.6		
8	X.1↘	5.2	Lo↘	7.0	Tree	4.8	X2.10↗	5.1		
9	X1.2↘	4.5	Al↘↗↘	6.4	X.1↘	4.4	X.10↗	2.5		
10	Al↘↗	3.4	X2.10↗	5.4	Al↘↗	3.9				
11	Lo↘	2.6	Tree	2.5	Lo↘	1.2				
(c) C/P										
1	BD↘	26.5	BD↘	22.0	BD↘	25.1	Al↗	39.9	Al↗	33.9
2	Tree	16.6	pH↘	12.6	Slope↗	14.5	Slope↗	32.4	Slope↗	27.6
3	X.10↗	13.1	Slope↗	11.5	X2.10↗	8.9	La↗	11.5	pH↘↗	12.0
4	Slope↗	12.5	Tree	11.1	Tree	8.3	pH↘	7.4	La↗	11.6
5	pH↘	8.6	Al↗	10.9	X.1↗	7.2	Tree	2	Tree	3.8
6	X2.10↗	5.1	X.10↗	8.4	pH↘↗	7.1	Lo↘	2	X2.10↘	3.7
7	X.1↘	4.9	Lo↘	7.0	Al↗	6.7			Lo↘	3.3
8	Al↗	4.4	X.1↗	6.5	X1.2	6.2			BD↘	2.1
9			X1.2↘	3.6	X.10↗	5.6			X.1↗	2.3
10					La	5.2				

More details of the abbreviated variables were in Table 1

Al altitude; La latitude; Lo longitude; BD soil bulk density; the percentage of coarse stone (%), X.10 the percentage of coarse stone with diameter larger than 10 mm; X2.10 the percentage of coarse stone with diameter between 2 and 10 mm; X1.2 the percentage of coarse stone with diameter between 1 and 2 mm; X.1 the percentage of coarse stone with diameter less than 1 mm, ↗↘↗ gradual increase/decrease trends

other forest (Fig. 6b and Appendix 11d in the [Electronic Supplementary Material](#)).

### 4 Discussion

In this study, we found that CV for C/P ratio was larger than C/N and N/P ratios (Fig. 3), which demonstrated that the C/P ratio has higher stoichiometric flexibility than the other two ratios across soil profiles in subalpine forests. Our results also showed that the ranges of soil C/N, N/P, and C/P ratios in subalpine forests of eastern Tibetan Plateau were narrower than that of analogous forests at global scale (Xu et al. 2013)

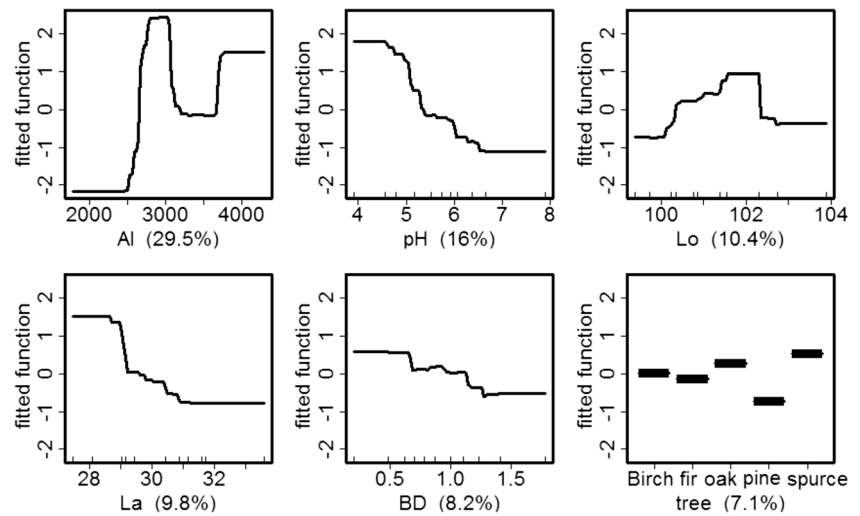
but were consistent with the observations of soil C/N/P stoichiometry across mainland China (Tian et al. 2010). The average ratios of soil C/N, N/P, and C/P (Fig. 2) were higher than those of corresponding layers from national scales (Tian et al. 2010), as well as those from adjacent grasslands in the Tibetan Plateau (Yang et al. 2010; Liu et al. 2014).

#### 4.1 Vertical pattern of C/N/P ratios along soil profile

We confirmed that the vertical pattern of soil C/N, N/P, and C/P ratios in the subalpine forest region consistently decreased with soil depths (Fig. 2), in agreement with previous reports in other forest ecosystems (Callesen et al. 2007; Li et al. 2013;



**Fig. 4** Partial dependence plots of the most six important predictor variables in the BRT model of soil C/N ratio (0–10 cm) in subalpine forests of eastern Tibetan Plateau. The fitted function shows the relationship between soil C/N ratio and an explanatory variable, while all other explanatory variables are constant at their mean level. The details of explanatory variables were in Table 2



Tischer et al. 2014). Here, C/P ratio decreased faster than C/N and N/P ratio with increasing soil depth (Fig. 2). This result was consistent with previous findings in China (Tian et al. 2010) and distinctly showed that soil C and N couples well, while soil P progressively disconnects from organic matter among soil profiles (Tischer et al. 2014). Interestingly, the significant decline of C/N ratios along soil profiles was not consistent with the results obtained from adjacent grasslands with relatively stable trends of soil C/N ratios (Yang et al. 2010). The difference in root distribution between grassland and forests provides one potential reason. The deeper root profiles present in forests over grasslands cause a shallower distribution of soil C with increasing soil depth (Jobbagy and Jackson 2000). In contrast to the isometric change between soil C and N along soil profiles in grasslands (Yang et al. 2010), our results demonstrated that the vertical change of soil C (CV = 50.5%) was larger than that of soil N (CV = 35.6%). Further, the vertical change of soil C/N ratio was greatly

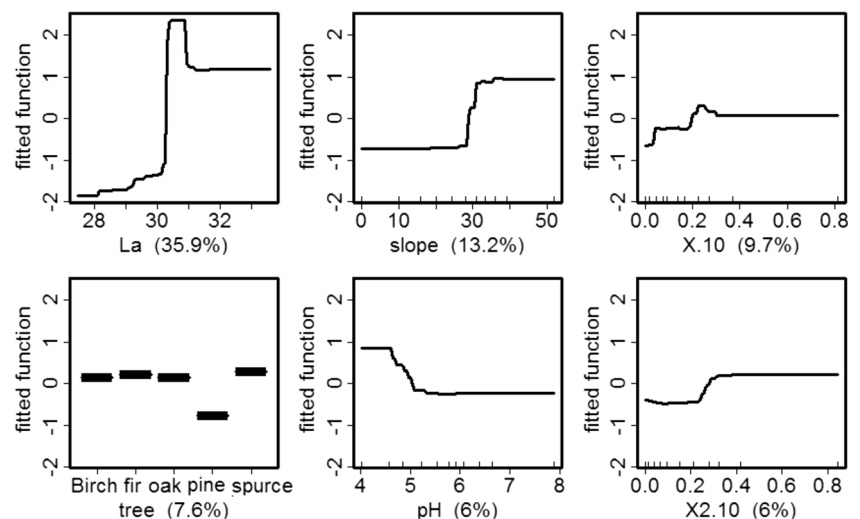
affected by the vertical change of soil C in subalpine forests (Fig. 3a).

#### 4.2 Major factors explaining C/N/P ratios along soil profiles

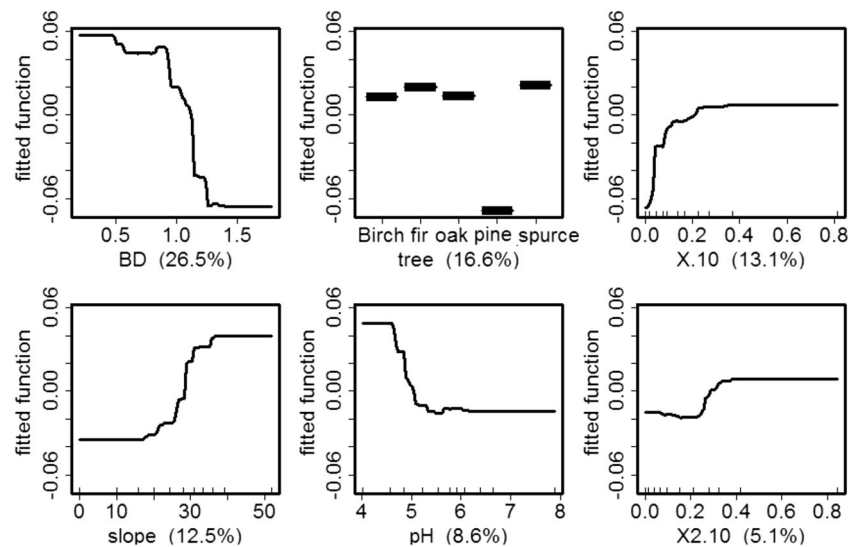
Our results (Table 2) clearly showed that the eight factors, namely altitude, latitude, longitude, soil pH, bulk density, relative stone content, slope, and dominant tree species, together determined the most variation (49–97 %) for the three ratios in the upper four soil layers (0–10, 10–20, 20–30, and 30–50 cm) in the subalpine forest region. BRT analysis also demonstrated that the factor with the highest influence was different among the five soil layers.

Altitude and latitude generally served as the proxies of climate (Cleveland and Liptzin 2007) and primarily governed the distribution of forest and soil type in the eastern Tibetan

**Fig. 5** Partial dependence plots of the most six important predictor variables in the BRT model of soil N/P ratio (0–10 cm) in subalpine forests of eastern Tibetan Plateau (cf. Fig. 4 for details)



**Fig. 6** Partial dependence plots of the most six important predictor variables in the BRT model of soil C/P ratio (0–10 cm) in subalpine forests of eastern Tibetan Plateau (cf. Fig. 4 for details)



Plateau. As expected, our results demonstrated that altitude and latitude were the factors with the highest contribution to C/N and N/P ratio variability in most soil layers (Table 2a, b) and to C/P ratios in the two deepest soil layers (Table 2c). Soil C/N ratio (0–30 cm) increased at low (1800–3000 m a.s.l.) and high altitudes (3500–4200 m a.s.l.) (Fig. 4a), which was consistent with previous results in tropical forests (Schawe et al. 2007; Unger et al. 2010; Moser et al. 2011; Whitaker et al. 2014). Notably, N/P ratios in 30–100 cm soil layers presented a significant decline at low (1800–3000 m a.s.l.) and high altitudes (3500–4200 m a.s.l.). These findings indicated that a gradual increase in N limitation is present with such altitude ranges, a likely result of the decline in decomposition of litter and soil organic matter due to the lower temperature. Intriguingly, soil C/N ratio declined at intermediate altitudes (3000–3500 m a.s.l.) (Fig. 4a), indicating an increase in soil N availability with altitude. This decreasing trend of soil C/N ratios was similar to observations made in the tropical montane cloud forests of Peruvian Andes along elevation gradient (3000–3800 m a.s.l.) (Zimmermann et al. 2010). This downward trend was due to changes in the dominant vegetation rather than the changes in elevation per se. Indeed, the dominant tree species with most frequently distributed between 3000 and 3500 m a.s.l. was birch in same region (Appendix 2, [Electronic Supplementary Material](#)). Fast-growing birch forests with lower leaf C/N ratio could improve soil N availability and accelerate the rate of N turnover. Therefore, subalpine forests between 3000 and 3500 m a.s.l. had a weaker N limitation. In contrast with the results from Europe and Australia forests (Bui and Henderson 2013; Cools et al. 2014), we found subalpine forests at a higher latitude had the lowest soil C/N ratios and the highest N/P and C/P ratios, suggesting subalpine forests probably underwent stronger P rather than N limitations with an increasing latitude across eastern Tibetan Plateau region.

We found that soil pH and bulk density had the strongest influence on C/N/P ratios in more superficial (0–30 cm) soil layers, and their effect was similar among C/N, N/P, and C/P ratios (Table 2). The C/N, N/P, and C/P ratios in surface soil (0–10 cm) linearly decreased with pH value (Figs. 4b, 5e, and 6e), which was consistent with the corresponding soil layers of plantations in China (Gao et al. 2014, Wang et al. 2014). However, this negative linear relationship in surface soil layers did convert to nonlinear in deeper soil layers (Appendixes 2–14, [Electronic Supplementary Material](#)). This complex result indicated that soil pH may be a regulatory mechanism of stoichiometric ratios in deep layers and should be further explored. We initially reported that soil bulk density strongly regulates the spatial variations of stoichiometric ratios across different soil layers, particularly since it was the most influential to C/P ratios in the upper three layers (Table 2c). Several researches have previously demonstrated that coarse texture soil can increase C/N ratios (Homann et al. 2007, Vesterdal et al. 2008). Soil bulk density was generally low in coarse texture soil with relatively less clay content (Manrique and Jones 1991). Thus, similar to previous findings (Zimmermann et al. 2010; Wang et al. 2014), subalpine forest soil with lower bulk density has higher C/N, N/P, and C/P ratios (Figs. 4e and 6a).

In our study, we also demonstrated that the slope and tree species could impact the spatial variations of soil C/N, N/P, and C/P ratio. However, unlike European forests (Cools et al. 2014) where the most important factor to C/N ratios in topsoil and deep soil was tree species and soil order, these factors had only a slight effect in the subalpine region. Usually, slope is closely related to soil moisture along soil profiles. Soil nutrients leaching were positively associated with soil moisture, which possibly accounted for the slope effect on spatial variation of soil C/N/P ratios (Suo et al. 2016). Thus, the effect of slope may become stronger as soil depth increased (Table 2).

Consequently, altitude and latitude that associated with soil pH and bulk density accounted for most of the spatial variation of soil C/N and N/P ratios in 0–50 cm layers; whereas, soil bulk density associated with pH and dominant tree species accounted for most spatial variation of soil C/P ratio in 0–30 cm layers (Table 2a, b). Altitude associated with slope invariably explained the spatial variation of three ratios in the deepest (50–100 cm) soil layers (Table 2). Therefore, we confirmed that the most influential factors that determine spatial patterns of soil C/N/P stoichiometry differed for all three stoichiometric ratios and varied with the soil depths.

## 5 Conclusions

This study showed that C/P ratio declined faster than C/N and N/P ratio with increasing soil depth in subalpine forests. Eight factors including altitude, latitude, longitude, soil pH, bulk density, relative stone content, slope, and dominant tree species accounted for the majority of variation in soil C/N/P ratios in the upper four layers. For soil C/N and N/P ratios, altitude and latitude exhibited the largest influence across soil profiles. In contrast, soil pH and bulk density were the most important factors in some upper soil layers. Soil bulk density and altitude separately had the highest contribution on C/P ratio in 0–30 and 30–100 cm soil layers. The influence of slope increased with soil depths. As a consequence, altitude and latitude associated with soil pH and bulk density together explained the majority of spatial variation in soil C/N and N/P ratios in 0–50 cm deep soil. Soil bulk density and pH also associated with dominant tree species to account for the spatial variation of soil C/P ratio in 0–30 cm layers. Altitude combined with slope to invariably explain the spatial variation of three ratios in deepest (50–100 cm) soil layers. Therefore, our study suggested that the geographical location (altitude and latitude) and the soil properties (pH and bulk density) control the majority of spatial variation of soil C/N/P ratios across eastern Tibetan Plateau forests. These results confirmed that the relative influence of factors varied among soil depths and the three soil stoichiometric ratios.

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