We highly appreciate referee #1 (Dr. Elisabeth Bui) for the helpful suggestions on our manuscript. Our responses are listed below along with the corresponding changes in the text.

Response to Comments from referee #1:

Comment 1: *In the Discussion, landform should be acknowledged as an explanatory factor; montane and valley ecosystems occupy overlapping elevations but different landforms.*

Response 1: Thank you for pointing out the effect of different landforms between the montane and valley shrubs (Fig. R1). The explanation related to landform has been provided on lines 412−429: "It should be also noted that the valley shrub possessed the greatest leaf N and high leaf P, especially at altitude of about 1500 m. This result could be explained by the remarkably different landform of valley region from those of montane and subalpine areas with overlapping elevations, which caused distinctive local climate and shrub species in valley. On the one hand, the uplift and geological evolution of the Tibetan Plateau induced steep canyons and longitudinal range-gorge regions, with towering mountains and deep valleys arranged vertically side by side (Royden et al., 2008; Pan et al., 2012). The downvalley wind could result in foehn effect that is characterized by an increase in evaporation rate and a decrease in relative humidity (Hornsteiner, 2005; Li et al., 2007). Consequently, the MAT values of valley sites were higher than montane, subalpine and alpine sites ($P < 0.05$, Appendix A: Table A1), indicating faster organic matter decomposition as predicted by the Biogeochemical Hypothesis (Aerts and Chapin, 1999). On the other hand, due to the special local topography and climate, the shrubs in valley were mostly drought-tolerant plants (e.g., *Bauhinia brachycarpa* and *Cotinus coggygria*), which belonged to short-lived, fast-growing deciduous broadleaf functional type. These valley species exhibited faster litter decomposition and nutrient resorption abilities than long-lived, slow-growing evergreen types (Güsewell and Koerselman, 2002; Diehl et al., 2003)."

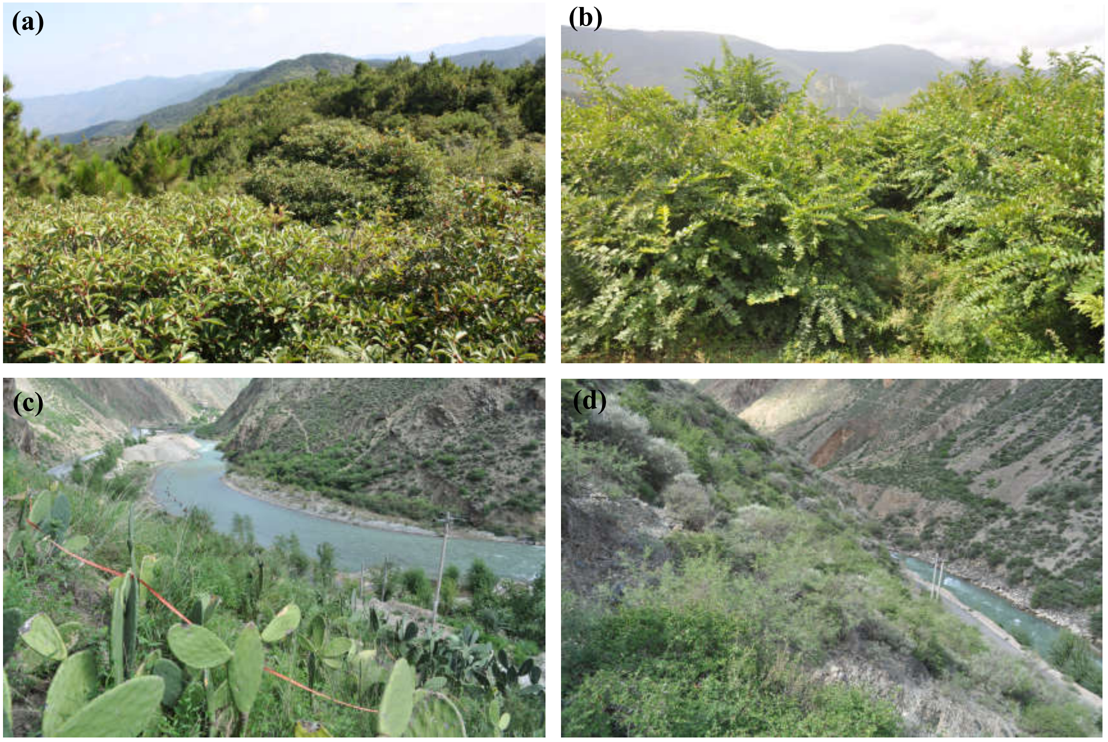

Fig. R1 Different landforms of montane (a, b) and valley (c, d) ecosystems on the Tibetan Plateau, southwest China. Photo credit: Jun Hu.

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Comment 2: *I think a key missing factor is the nutrient acquisition process of the shrubs–this may be why shrub type accounts for more of leaf nutrient variation than climate or soil. Is there a mycorrhizal association that helps Rhododendron telmatium acquire nutrients? Are there rhizobial nodules on Bauhinia brachycarpa?*

Response 2: Many thanks for the excellent suggestion on the key missing factor – nutrient acquisition strategy. This part can largely explain why the leaf nutrient levels differed among shrub species, and provide further evidence for the dominant role of shrub type in leaf element variations. We have added some discussion on lines 442−462: "Plant nutrient acquisition strategy could also affect leaf nutrient levels of different shrub species. It is well known that most plants belonging to Ericales are able to associate with soil fungi and form ericoid mycorrhiza (Perotto et al., 2002). This happens especially in high-altitude environment where plant litter decomposes slowly, leading to acidic soils rich in recalcitrant organic matter but low in available mineral nutrients (Cairney and Burke, 1998). Previous studies have reported that ericoid mycorrhiza or arbuscular mycorrhizal fungi (AMF) were associated with diverse rhododendrons in southwestern China and central Himalayan (Chaurasia et al., 2005; Tian et al., 2011). The alpine shrub species *Rhododendron telmateium* in similar regions probably also formed mycorrhizal fungal structures to enhance its survival and growth under stressed environments. *Rhododendron telmateium* may access unavailable organic N and P via the enzymatic degradation of soil organic polymers by mycorrhizal fungi (Näsholm and Persson, 2001), resulting in higher leaf N and P contents compared to *Coriaria sinica*. In addition, the valley shrub *Bauhinia brachycarpa* in our study exhibited relatively high leaf N and P levels (although insignificant), despite its low soil total nutrients relative to alpine and subalpine shrub species (Appendix A: Table A1). This leguminous species possibly interacts symbiotically with soil microorganisms to form fungal assemblages or nitrogen-fixing root nodules, improving its nutrient acquisition in infertile soil. It has been verified that a high level of AMF diversity occurred in the rhizosphere of another dominant valley shrub species (*Bauhinia faberi*) on the Tibetan Plateau (Chen et al., 2016)."

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Comment 3: *line 441, N-limited instead of N-limiting?*

Response 3: The "N-limiting" has been replaced by "N-limited" on line 472.

We want to thank referee #2 for the helpful suggestion and positive feedback on our manuscript. Dr. Adriana Grandis is correct that this work has previously been reviewed and revised elsewhere. Our responses are listed below along with the corresponding changes in the text.

Response to Comments from referee #2:

Comment 1: *Line 65: Please correct – critical.*

Response 1: We apologize for the mistake. This word has been revised as "critical" on line 65.

Comment 2: *Line 238: What is CV? Coefficient variation? Please describe if is the first time appear?*

Response 2: Yes. CV stands for the coefficient of variation. CV first appeared in part 2.5 Data analysis (line 202). We have also added this description on line 242.

Comment 3: *Line 160 and 253, 254: MAP and MAT. Please describe for the people that is not familiarized with these terms?*

Response 3: Thanks for your suggestion. MAT and MAP have been described on lines 165–168: "In meteorology, MAT (°C) is the mean air temperature calculated by averaging the 12 months of the calendar year. MAP (mm) is the annual average value of the product of atmospheric water vapor that falls under gravity".

Shrub type dominates the vertical distribution of leaf C:N:P stoichiometry across an extensive altitudinal gradient

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Abstract. Understanding the leaf stoichiometric patterns is crucial for improving predictions on plant responses to environmental changes. Leaf stoichiometry of terrestrial ecosystems has been widely investigated along latitudinal and longitudinal gradients. Still, very little is known on the vertical distribution of leaf C:N:P and the relative effects of environmental parameters, especially for shrubs. Here, we analyzed the shrub leaf C, N and P patterns in 125 mountainous sites over an extensive altitudinal gradient (523−4685 m) on the Tibetan Plateau. Results showed that the shrub leaf C and C:N were 7.3%−47.5% higher than those of other regional and global flora, whereas the leaf N and N:P were 10.2%−75.8% lower. Leaf C increased with rising altitude and decreasing temperature, supporting the physiological acclimation mechanism that high leaf C (e.g., alpine or evergreen shrub) could balance the cell osmotic pressure and resist freezing. The largest leaf N and high leaf P occurred in valley region (altitude 1500 m), likely due to the large nutrient leaching from higher elevations, faster litter decomposition and nutrient resorption ability of deciduous broadleaf shrub. Leaf N:P ratio further indicated increasing N limitation at higher altitudes. Interestingly, the drought severity was the only climatic factor positively correlated with leaf N and P, which was more appropriate for evaluating the impact of water status than precipitation. Among the shrub ecosystem and functional types (alpine, subalpine, montane, valley, evergreen, deciduous, broadleaf, and conifer), their leaf element contents and responses to environments were remarkably different. Shrub type was the largest contributor to the total variations in leaf stoichiometry, while climate indirectly affected the leaf C:N:P via its interactive effects on shrub type or soil. Collectively, the large heterogeneity in shrub type was the most important factor explaining the overall leaf C:N:P variations, despite the broad climate gradient on the plateau. Temperature- and drought-induced shift of shrub type distribution will

influence the nutrient accumulation in mountainous shrubs.

Keywords. leaf stoichiometry, mountainous shrub, altitudinal gradient, drought severity, temperature, precipitation, soil nutrient

1 Introduction

Ecological stoichiometry examines the interactions among organisms' element composition and their environments, which provides an effective way to enhance our understanding of ecosystem function and nutrient cycling (Allen and Gillooly, 2009; Venterink and Güsewell, 2010). Over the past decades, great attention has been paid to the leaf stoichiometry of terrestrial plants at regional (Townsend et al., 2007; Matzek and Vitousek, 2009), national (Han et al., 2011; Sardans et al., 2016), and global scales (Elser et al., 2000; Reich and Oleksyn, 2004). The leaf macroelements (carbon, nitrogen and phosphorus) were widely explored to indicate nutrient limitation and its response to environmental change (Elser et al., 2010). Investigating the interactions among leaf stoichiometry and the environment along geographic gradients is critical to understand the nutrient cycling process and the development of biogeochemical models.

Nowadays, it is increasingly rare to localize and work on extensive and natural altitudinal gradient varying from low to high-altitude mountaintops (Nogués-Bravo et al., 2008). A few studies have investigated the variations of leaf N and P at several elevations (Soethe et al., 2008; van de Weg et al., 2009; Fisher et al., 2013; Zhao et al., 2014); however, the scientists reported different altitudinal trends for leaf N and P. For instance, Soethe et al. (2008) found that the foliar N and P concentrations of trees, herbs and shrubs were largest at 1900 m than 2400 m and 3000 m in an Ecuadorian montane forest. van de Weg et al. (2009) observed that the foliar P along an altitudinal transect (220, 1000, 1500, 1855, 2350, 2990 and 3600 m) from lowland to montane cloud forest showed no altitudinal trend. Fisher et al. (2013) reported that leaf N and P firstly increased and then declined with increasing altitudes (200, 1000, 1500 and 3000 m) in the Peruvian Andes. Zhao et al. (2014) observed that the leaf N and P of 175 plant species decreased with elevation on the Changbai Mountain (540, 753, 1286, 1812, 2008 and 2357 m). This discrepancy of previous results indicates that the leaf N and P can vary along different altitudinal ranges at regional scale. Moreover, much less information was available on the vertical distribution of leaf C. Hence, the more general patterns of leaf C:N:P along an extensive altitudinal gradient need to be further understood.

While comprehensive investigations of plant stoichiometry in forestland, grassland, wetland, and macrophyte ecosystems have emerged (Güsewell and Koerselman, 2002; He et al., 2006; Townsend et al., 2007; Sardans et al., 2012; Xia et al., 2014), much fewer studies focused on mountainous shrubs. In China, shrubland is a widely distributed biome type, covering ~20% of the country. However, information on the element concentrations of shrubs is very scarce (Piao et al., 2009). Thus, intensive investigation of shrub stoichiometry can provide detailed information for the growing global database of plant stoichiometry. As the earth's highest plateau, the Tibetan Plateau exhibits one of the very few extensive elevational vegetation gradients remaining in the world (Chen et al., 2013b) (Fig. 1 and Appendix B: Fig. B1). Large precipitation and temperature gradients along the steep mountains bordering the plateau to the east lead to a heterogeneous environment. This plateau is also considered as the China's hotspot ecoregions of biodiversity (Tang et al., 2006). The shrubs here are also very diverse and widely distributed along altitudinal gradients, which can endure extreme cold or drought environments. Some shrub species that are unique to this region have emerged in cold plateau areas (e.g., *Rhododendron telmateium* and

Quercus monimotricha). Consequently, the Tibetan Plateau can provide a more general representation of the stoichiometry of various shrub types, which is an ideal site for examining the altitudinal patterns and environmental variables influencing shrub stoichiometry.

The objectives of this study were to (I) analyze the leaf C:N:P stoichiometric patterns of various shrub types, and (II) clarify the significant factors affecting shrub stoichiometry across an extensive altitudinal gradient. In this work, we measured the leaf C, N and P concentrations of 48 shrub species on the Tibetan Plateau. The geographic, climatic and soil data of sampling sites were recorded. Given that the Tibetan Plateau encompasses a singular region of high spatial heterogeneity and complex climatic conditions (Chen et al., 2013b) that may greatly affect shrub nutrient accumulation, we hypothesized that (I) the overall leaf C:N:P variations would be dominated by climate, and (II) the shrub leaf element contents would be different from other terrestrial ecosystems. In addition, plant types and species can greatly affect the leaf element concentrations (McGroddy et al., 2004). To reveal this effect, all shrubs were classified into four ecosystem types that located in different vertical vegetation belts (alpine, subalpine, montane and valley shrub), or three functional types based on different leaf traits (evergreen broadleaf, evergreen conifer, and deciduous broadleaf shrubs). Four dominant shrub species (*Rhododendron telmateium* – alpine, *Quercus monimotricha* – subalpine, *Coriaria sinica* – montane, and *Bauhinia brachycarpa* – valley) were also chosen to assess the leaf patterns at species level.

2 Materials and Methods

2.1 Description of the study area

Shrub is defined as a small or medium-sized woody plant, which is distinguished from a tree by its multiple stems and shorter height (below 5 m). Since shrub ecosystems are mainly distributed in the southeastern margin of the plateau (Appendix B: Fig. B1), we chose 108 mountainous sites of this region to examine the leaf stoichiometry of shrubs that included alpine, subalpine and valley areas. Additionally, the 17 neighbouring mountainous sites on the east of the Tibetan Plateau were selected to provide a representation of low-altitude montane region. In these areas, shrub is one of the most important growth forms. Evergreen broadleaf and deciduous broadleaf shrubs are the primary functional types. The mean annual temperature (MAT) and mean annual precipitation (MAP) vary from −4.67 to 22.16 ºC, and from 366.3 to 1696.3 mm, respectively.

Fig. 1 shows the distribution of shrub ecosystem types and sample sites. These sites contain extensive vertical zonation of shrubs, including alpine (3091−4685 m), subalpine (2000−4078 m), montane (523−3342 m) and valley shrubs (600−2350 m) (Appendix A: Table A1). The elevations of four ecosystem types are overlapping because of the high spatial heterogeneity and diverse vegetation that adapted to environments at different altitudes on the plateau. Alpine shrub is the main ecosystem type located above the tree line, while subalpine shrub is distributed in the subalpine coniferous forest zone (Appendix B: Figs. B2 and B3) (Worboys and Good, 2011). Montane shrub exists in the evergreen and deciduous broadleaf forests, and valley shrub occurs in the valley region.

2.2 Field sampling

During the growing seasons (from July to August) of 2011−2013, sample collection was performed in 125 mountainous sites, with shrub coverage more than 30%. At each site, three plots (5 m × 5 m) were randomly set up, and the distances among different plots were 5−50 m. For each plot, mature leaves from dominant shrub species of 5−10 individuals were collected and mixed. After litter was removed from the soil surface, nine 3-cm-diameter soil cores (0−10 cm layer) in each plot were collected and combined to form one composite sample to account for any heterogeneity resulted from position. After collection, the leaf samples were oven-dried at 65 ºC, and ground to fine powders using a ball mill for element analysis. The fresh soils were air-dried, with visible roots, stones and organic residues removed. Soil samples were sieved through 2-mm meshes before analysis.

2.3 Geographic and climatic parameters

The geographic locations (altitude, latitude and longitude) of sample sites were recorded using a global positioning system. MAT and MAP values were obtained from the China Meteorological Forcing Dataset (Yang et al., 2010; Chen et al., 2011). The temporal and spatial resolutions of this dataset were every 3 h and $0.1^{\circ} \times 0.1^{\circ}$ in longitude and latitude from 1981 to 2008. In meteorology, MAT (°C) is the mean air temperature calculated by averaging the 12 months of the calendar year. MAP (mm) is the annual average value of the product of atmospheric water vapor that falls under gravity.

Considering the mountainous areas exhibit various drought conditions (especially in valley region), we herein first investigate how leaf stoichiometry varies with drought index (Reconnaissance Drought Index, RDI). RDI has been widely used in meteorology to powerfully assess drought severity in arid and semiarid regions (Tsakiris and Vangelis, 2005). Compared to the other indices (e.g., the Palmer Drought Severity Index and the Standardized Precipitation Index), the advantages of RDI are its low data requirements, high resilience and sensitivity to drought events (Khalili et al., 2011).

The standardized form of RDI (RDI_{st}) can be calculated via the computation of potential evapotranspiration (PET) based on the Thornthwaite method (Thornthwaite, 1948). The detailed calculation process of RDI_{st} for a hydrological year (12-month reference period) was shown in the Appendix C. In this work, RDI is used to represent RDI_{st}. Positive RDI represent wet period of sample site, whereas negative values indicate dry period. Using the RDI values, drought severity can be categorized as extreme (< -2.0), severe (-2.0 to -1.5), moderate (-1.5 to -1.0) or mild (-1.0 to -0.5) (Vangelis et al. 2013).

2.4 Element measurements

The total C and N concentrations of leaf and soil samples were measured by dry combustion using a Perkin-Elmer 2400 II elemental analyzer (Perkin-Elmer, Inc., USA). Total P concentrations were determined by the ammonium molybdate method using a continuous-flow analyser (AutoAnalyzer3 Continuous-Flow Analyzer; Bran Luebbe, Germany) after H_2SO_4-$HClO_4$ digestion for leaves and H_2SO_4-H_2O_2-HF digestion for soil (Kuo, 1996). The element concentrations are presented in units of mg g^{-1} dry weight, and the element ratios are presented on a mass basis. Unfortunately, soil available nutrient data were not determined, and we were unable to assess their correlations with leaf elements.

2.5 Data analysis

The data were analyzed at two levels: (1) using all the shrub samples together ($n = 125$), and (2) dividing the shrub dataset into four ecosystem types and four dominant shrub species that located in different altitudinal belts, or three functional types classified by different leaf traits. The leaf mineral concentrations and ratios were averaged at the site-species level to control for pseudoreplication (Han et al., 2011). Because the leaf element concentrations and ratios were highly skewed (Appendix B: Fig. B4), we calculated their geometric means, standard deviations and coefficients of variation (CV) to compare the differences of leaf C:N:P among different shrubs. Besides, the arithmetic means of shrub leaf stoichiometry were also calculated to compare with prior studies that only showed arithmetic means.

After all the leaf C:N:P values were $\log_{10}$-transformed to improve the data normality, there was still no evidence for the test of homogeneity of variances. Therefore, we used Kruskal-Wallis test (nonparametric) followed by pairwise comparisons to examine the differences in leaf C:N:P among shrub types.

Partial correlation analysis allows one to distinguish the degree of the direct correlation between geography (e.g., altitude) and leaf element, with the effect of other controlling random variables removed (e.g., longitude and latitude). Linear and nonlinear regressions were utilized to show the variation trends of leaf C:N:P along climatic and soil gradients. Stepwise multiple regression (SMR) was applied to select the most influential environmental factors (MAT, MAP, RDI, soil C, soil N and soil P), and estimate their contributions to leaf stoichiometry.

To evaluate the relative effects of shrub type (ecosystem and functional types), soil (soil C, N and P) and climate (MAT, MAP, RDI), partial general linear model (GLM) analysis was applied. Partial GLM separates the total variance explained by different factors into the independent effect of each factor and their interactive effects (Heikkinen et al., 2005). The statistical analyses were conducted with SPSS v20 (SPSS Inc., USA), Origin 8.0 (OriginLab Co., USA) and R 2.15.2.

3 Results

3.1 Variations of leaf C, N, P and C:N:P ratios

Leaf C, N and P contents for all shrubs ranged from 358.2 to 539.8, 9.7 to 39.4 and 0.69 to 3.43 mg g^{-1}, respectively (Supplementary material). The element ratios varied greatly with a range of 11.7−46.9 for C:N, 113.8−646.5 for C:P, and 2.86−22.16 for N:P. The geometric means were 468.9 mg g^{-1} for C, 18.6 mg g^{-1} for N and 1.50 mg g^{-1} for P, while those for C:N, C:P and N:P were 25.3, 312.0 and 12.3, respectively.

The geometric means of leaf C for alpine and subalpine shrubs were 481.7 and 477.6 mg g^{-1}, respectively, which were higher than those of montane and valley shrubs ($P < 0.001$, Table 1 and Appendix A: Table A2). Leaf N of valley shrub was the highest among the ecosystem types, while the leaf P contents of subalpine and montane shrubs were lower than alpine shrub ($P < 0.001$). Leaf elements also varied markedly across different functional types. Deciduous broadleaf shrub showed the lowest leaf C, whereas its leaf N was the largest ($P < 0.01$). Leaf P did not show significant difference among the three functional types ($P = 0.323$). For dominant shrub species, the leaf C:N:P in *Rhododendron telmateium* (alpine), *Quercus monimotricha* (subalpine), *Coriaria sinica* (montane), and *Bauhinia brachycarpa* (valley) followed similar trends to those in corresponding shrub ecosystem types.

The relative variability of leaf nutrients can be demonstrated by the coefficient of variation (CV). Leaf P of all samples had the greatest variation (37.0%), followed by N (30.4%) and C (6.3%). The relative variability of leaf elements for each shrub type also showed the similar trends.

3.2 Altitudinal patterns of leaf stoichiometry

Using partial correlation analysis (Appendix A: Table A3), we found that leaf C increased with the increase of altitude ($P < 0.001$), while the leaf N and P did not show clear altitudinal trend ($P = 0.287$ and 0.154). The highest leaf N and P were distributed at altitude of about 1500 m which belonged to valley shrub (Fig. 2).

The relationships between the leaf stoichiometry of shrub types and elevations exhibited different patterns. For example, altitude was not correlated with the leaf C of alpine and subalpine shrubs. On the contrary, leaf N and P showed obvious altitudinal trends for subalpine and deciduous broadleaf shrubs ($P < 0.01$).

3.3 Climatic influence on leaf stoichiometry

MAP was not linearly or nonlinearly correlated with most of the leaf C:N:P traits (Appendix B: Fig. B5). MAT was negatively correlated with leaf C, while the leaf P, C:P and N:P were quadratically correlated with MAT ($P < 0.001$). As RDI increased (i.e., wetter conditions), leaf N and P became significantly larger ($P < 0.001$). When the three climatic factors were analyzed by SMR, MAP was excluded from all the analysis (Table 2). MAT was negatively related with leaf C ($P < 0.001$), and only RDI was entered into the SMR equations for leaf N and P.

The climatic factors showed large heterogeneity across different shrub types and species (Appendix A: Tables A4−A6). For instance, the leaf N or P of alpine, valley shrubs and *Quercus monimotricha* were correlated with MAT or MAP ($P < 0.05$), while those of montane, evergreen conifer shrubs, *Rhododendron telmateium* and *Coriaria sinica* were not affected by climate ($P > 0.05$). It indicated that the specific shrub type or species exhibited diverse leaf C:N:P trends along climatic gradient and change greatly to adapt to different habitats.

3.4 Soil influence on leaf stoichiometry

Plants take up most of the nutrients directly from soils. As usually observed elsewhere, our results revealed positive correlations between the leaf and soil stoichiometry for C, P, C:P and N:P ($P < 0.05$) (Appendix B: Fig. B6, Table 2). The leaf N and C:N of all shrubs were not correlated with those of 0−10 cm soil layer, probably owing to confounding effects of other variables along geographic gradients. Interestingly, the leaf N, P, C:N, C:P and N:P of evergreen broadleaf shrub were only correlated with soil variables (Appendix A: Table A5), indicating the leaf nutrients in evergreen broadleaf shrub were mainly affected by root uptake from soils. By contrast, the soil elements were not limiting factors for the leaf element levels in montane shrub and *Coriaria sinica* (Appendix A: Tables A4 and A6).

3.5 Relative effects of shrub type, soil and climate

The three factors (shrub type, soil and climate) together accounted for 45.2%−54.5% of the six leaf C:N:P traits (Fig. 3). The total effect of shrub type ($t+ct+st+cst$) showed the largest contribution to the variations in leaf stoichiometry (37.9%−53.9%). The independent effect of shrub type (t, 19.2%−44.7%) was also greater than those of soil (s, 0%−34.7%) and climate (c, 0%−0.4%). Soil exhibited the largest independent contribution (s, 34.7%) to the variation of leaf P. Climate ($c+ct+cs+cst$, 0%−16.1%) contributed to leaf stoichiometry mainly via the interactive effects between climate and shrub type (ct) or among the three factors (cst). The negative value (e.g., $cs = -27.1\%$ for leaf P) indicated suppressive interactive effects of climate and soil.

4 Discussion

A few studies have found that the leaf elements of plants varied largely with altitudes in different mountainous regions (Soethe et al., 2008; van de Weg et al., 2009; Fisher et al., 2013). However, the relative effects of shrub types and environmental variables on leaf elements have not yet been addressed. The statistical analysis proved that shrub type explained the largest fraction of the leaf C:N:P variations, and the leaf element levels differed from other terrestrial ecosystems. This work provides important information on the specific leaf patterns of various shrub types and species over a large altitudinal gradient.

4.1 Different leaf C:N:P levels of shrubs on the plateau

The leaf C, N and P of shrubs on the Tibetan Plateau confirmed our hypothesis (II) that they were different from those at regional, national and global levels (Table 3), suggesting mountainous shrubs had different ways in allocating nutrients. The arithmetic means of shrub leaf C and C:N were 7.3%−47.5% greater than those of other regional and global flora ($P < 0.05$), whereas the mean leaf N and N:P were 10.2%−75.8% lower ($P < 0.05$, except herbaceous species in central England) (Thompson et al., 1997; Elser et al., 2000; Campo and Dirzo, 2003; Reich and Oleksyn, 2004; Han et al., 2005; Tibbets and Molles, 2005; He et al., 2006; Townsend et al., 2007; Zheng and Shangguan, 2007; Chen et al., 2013a). The arithmetic mean of shrub leaf P (1.60 mg g^{-1}) were within the range of those reported in other regions (0.82−2.70 mg g^{-1}). In this study, the altitudes (523−4685 m) were much wider and higher than those investigated in other terrestrial ecosystems (Soethe et al., 2008; van de Weg et al., 2009; Fisher et al., 2013). Two classical hypotheses may account for this phenomenon. On the one hand, based on the plant physiological acclimation mechanism, it is likely that more non-structural C (e.g., starch, low molecular weight sugars and storage lipid) may accumulate in leaf (e.g., alpine shrub) to balance the osmotic pressure of cells and resist freezing (Hoch et al., 2002; Hoch and Körner, 2012). On the other hand, according to the Biogeochemical Hypothesis, low temperatures in these areas could limit soil microbe activity (Reich and Oleksyn, 2004). It may lead to slower decomposition of soil organic matter, and probably depress available N uptake by roots.

Among various mineral elements, N and P are considered the major growth-constraining nutrients (Koerselman and Meuleman, 1996). The shrub growth was relatively limited by N (mean leaf N:P = 12.8). The decreased leaf N:P with lower temperatures (Table 2) further suggested that the growth of shrubs at higher altitudes are more limited by N. However, Han et al. (2005) reported that the 547 plant species in China were strongly constrained by P, with mean leaf N:P (16.3) significantly higher than those in global flora and shrubs in this work ($P < 0.05$, Table 3). It indicated that the assessment of nutrient limitation at large scale could not reflect the pattern in mountainous areas.

The CV patterns among leaf elements are consistent with the Stability of Limiting Elements Hypothesis (Sterner and Elser, 2002). It is known that plant nutrient (e.g., C) that required at a high concentration should show a small variation and lower sensitivity to the environment. Leaf C was less variable than leaf N and P, suggesting leaf C had stronger stoichiometric homeostasis. The CV value of shrub leaf C (6.3%) was smaller than those of trees, herbs and shrubs (6.9%−28.0%) in other regions, whereas those of shrub leaf N (30.4%) and P (37.0%) were within the range of other ecosystems (N: 11.0%−50.5%; P: 13.0%−44.0%) (Tibbets and Molles, 2005; He et al., 2006; Zheng and Shangguan, 2007; Ladanai et al., 2010). Consequently, the high C accumulation capacity of shrub is less sensitive to the complex climate conditions on the plateau.

4.2 Relative influences of the environment and shrub type

Precipitation, temperature and soil can affect leaf elements via changing element allocation among plant organs, altering plant metabolism or influencing nutrient uptake by roots (Ordoñez et al., 2009). In addition to MAP, MAT and soil nutrient, we first added RDI to examine the effect of local drought extent. Among the four environmental parameters, it is interesting to note that RDI was positively correlated with leaf N and P (Table 2). By contrast, MAP was not correlated with all the leaf C:N:P traits. This was inconsistent with previous reports that MAP played an important role for the leaf elements of different vegetation types (Santiago et al., 2004; Han et al., 2011). Firstly, among the 125 sampling sites, only 7 sites belonged to the severe and extreme drought regions (RDI < –1.5). The water conditions of other sites were mild, slight drought, or wet (–1.0 < RDI < 2), which may be suitable for shrub growth and could not become a limiting factor. Secondly, it is proposed that MAP could not accurately reflect the real water situation due to different temperatures and evapotranspiration rates. RDI may be more appropriate for evaluating the impact of water status. The wetter climatic conditions (i.e., larger RDI) could provide more soluble N and P in soil and enhance the nutrient transportation of shrub.

Increased MAT was found to be related with the decrease of leaf C in the SMR analysis. This result was in agreement with a meta-analysis of C stores conducted in 13 different global mountains (Hoch and Körner, 2012). The large MAT gradient (–4.67 ºC to 22.16 ºC) on the plateau could strongly affect the shrub photosynthesis process. Shrub species at higher elevations probably need to protect themselves against low temperatures and make osmotic adjustments via increasing leaf C contents (Millard et al., 2007). By contrast, MAT could not account for the leaf N in shrubs, which was inconsistent with the opinion that leaf N contents are usually affected by temperature (Wright et al., 2005). This unexpected phenomenon may result from the large heterogeneity in N uptake capacities of different shrub species along the climatic gradients (CV of leaf N reaches up to 30.4%). Moreover, the drought severity was so dominant in leaf N that it may override any possible underlying temperature effect.

Soil nutrient was the most significant environmental factor for leaf P, C:P and N:P. Appendix B: Fig. B6 also exhibits the closest relationship between soil P and leaf P (*P* < 0.001). It was known that P mainly originates from the soil via rock weathering (Walbridge et al., 1991). Moreover, all the soil C:P ratios were less than 200 (implies net mineralization in soil), confirming the soil may provide sufficient soluble P (Bui and Henderson, 2013).

Climate, soil nutrient and vegetation type can together influence plant mineral biogeography in complex ways, while significant collinearities among these factors may potentially obscure their true impacts (Han et al., 2011). Here we used partial GLM regressions to separate the total variance into the independent effect of each factor and their interactive effects (Heikkinen et al., 2005). We found that the independent effect (*t*) of shrub type was the largest contributor to explain the leaf element variations (Fig. 3). For climate, however, the result disagreed with our hypothesis (I) that the leaf C:N:P variations would be dominated by climate. The independent effect of climate (*c*) was small, and climate mainly affected the leaf C:N:P via its interactive effects on shrub type (*ct*) or among the three factors (*cst*). Combined with SMR analysis (Table 2), this finding suggests that climate-induced (e.g., temperature and drought) changes of shrub distribution may affect the leaf nutrient contents. Soil nutrient (*s*) accounted for large parts of the variations in leaf P and C:P ratio, which was ascribed to the coupled relationships between soil P and plant P (Walbridge et al., 1991).

4.3 Large heterogeneity in leaf C:N:P patterns among various shrubs

To our knowledge, the leaf C:N:P patterns among different shrub types and species have not been sufficiently evaluated before. Our analysis suggests the leaf element contents and their responds to environments were highly heterogeneous among shrub types and species, providing further evidence that the large heterogeneity in shrub nutrient uptake capacities and physiological adaptation to environments governed the leaf nutrient variations.

For instance, alpine and subalpine shrubs had higher leaf C than the other two ecosystem types (Table 1 and Appendix A: Table A2), and this trend was consistent with the cold acclimation mechanism as discussed previously (Hoch and Körner, 2012). Alpine shrub exhibited higher leaf N and P than subalpine and montane shrubs located in low-altitude regions ($P < 0.001$). This result agreed with the Temperature-Plant Physiological Hypothesis (Weih and Karlsson, 2001; Zhang et al., 2017). In high-altitude area, the growing season was short, and accompanied by lower temperature. Hence, shrubs might increase their nutrient absorption to compensate for lower enzyme efficiency and metabolic rate. It should be also noted that the valley shrub possessed the greatest leaf N and high leaf P, especially at altitude of about 1500 m. This result could be explained by the remarkably different landform of valley region from those of montane and subalpine areas with overlapping elevations, which caused distinctive local climate and shrub species in valley. On the one hand, the uplift and geological evolution of the Tibetan Plateau induced steep canyons and longitudinal range-gorge regions, with towering mountains and deep valleys arranged vertically side by side (Royden et al., 2008; Pan et al., 2012). The downvalley wind could result in foehn effect that is characterized by an increase in evaporation rate and a decrease in relative humidity (Hornsteiner, 2005; Li et al., 2007). Consequently, the MAT values of valley sites were higher than montane, subalpine and alpine sites ($P < 0.05$, Appendix A: Table A1), indicating faster organic matter decomposition as predicted by the Biogeochemical Hypothesis (Aerts and Chapin, 1999). On the other hand, due to the special local topography and climate, the shrubs in valley were mostly drought-tolerant plants (e.g., *Bauhinia brachycarpa* and *Cotinus coggygria*), which belonged to short-lived, fast-growing deciduous broadleaf functional type. These valley species exhibited faster litter decomposition and nutrient resorption abilities than long-lived, slow-growing evergreen types (Güsewell and Koerselman, 2002; Diehl et al., 2003).

Large differences in leaf elements also occurred across functional types (Table 1 and Appendix A: Table A2). Leaf C contents in evergreen broadleaf and evergreen conifer shrubs were higher than deciduous broadleaf shrub, agreeing with the higher non-structural C accumulated in evergreen shrub leaves (average altitude: 3430 m) to resist freezing than deciduous shrub (average altitude: 2343 m). On the contrary, leaf N was larger in deciduous broadleaf shrub than in evergreen shrub types ($P < 0.01$). This result was ascribed to higher nutrient resorption in deciduous species than in evergreen species (Güsewell and Koerselman, 2002). Moreover, lower leaf C:N and C:P ratios were observed in deciduous shrub than evergreen shrubs ($P < 0.05$), further indicating faster litter decomposition process of deciduous shrub (Bui and Henderson, 2013). These differences of element levels among functional types indicate the variations in leaf nutrient acquisition abilities.

Plant nutrient acquisition strategy could also affect leaf nutrient levels of different shrub species. It is well known that most plants belonging to Ericales are able to associate with soil fungi and form ericoid mycorrhiza (Perotto et al., 2002). This happens especially in high-altitude environment where plant litter decomposes slowly, leading to acidic soils rich in recalcitrant organic matter but low in available mineral nutrients (Cairney and Burke, 1998). Previous studies have reported that ericoid mycorrhiza or arbuscular mycorrhizal fungi (AMF) were associated with diverse rhododendrons in southwestern China and central Himalayan (Chaurasia et al., 2005; Tian et al., 2011). The alpine shrub species *Rhododendron telmateium* in similar regions probably also formed mycorrhizal fungal structures to enhance its survival and growth under stressed environments. *Rhododendron telmateium* may access unavailable organic N and P via the enzymatic degradation of soil organic polymers by mycorrhizal fungi (Näsholm and Persson, 2001), resulting in higher leaf N and P contents compared to *Coriaria sinica*. In addition, the valley shrub *Bauhinia brachycarpa* in our study exhibited relatively high leaf N and P levels (although insignificant), despite its low soil total nutrients relative to alpine and subalpine shrub species (Appendix A: Table A1). This leguminous species possibly interacts symbiotically with soil microorganisms to form fungal assemblages or nitrogen-fixing root nodules, improving its nutrient acquisition in infertile soil. It has been verified that a high level of AMF diversity occurred in the rhizosphere of another dominant valley shrub species (*Bauhinia faberi*) on the Tibetan Plateau (Chen et al., 2016).

The leaf traits of shrub ecosystem, functional types and species with respect to four environmental variables differed from each other (Appendix A: Tables A4−A6). Specifically, the leaf N and P contents of montane, evergreen conifer shrubs and *Rhododendron telmateium* were not correlated with climate or soil, whereas those of evergreen broadleaf, deciduous broadleaf and *Bauhinia brachycarpa* exhibited positive relationships with soil or RDI. It revealed that the diverse shrubs showed great heterogeneity in their responses to water status and soil nutrients. Interestingly, the leaf N of evergreen broadleaf shrub had the closest correlation with soil N ($P < 0.01$). Meanwhile, the evergreen broadleaf shrub was largely limited by N (mean leaf N:P = 11.5) (Table 1), suggesting the growth of this N-limited shrub may be highly sensitive to soil N contents.

5 Conclusions

This work was the first field investigation of the leaf C:N:P stoichiometry of different shrub types along an extensive altitudinal range, providing important data for future research on global C, N and P cycling. Results highlight that different shrub leaf C:N:P contents and ratios emerged compared to other terrestrial ecosystems, and the leaf C:N:P variations were primarily explained by shrub type. This phenomenon is likely due to the large heterogeneity in nutrient uptake and physiological adaptation to extreme environments across various shrubs on the plateau. However, the underlying physiological mechanisms of specific shrub type or species require further examination. Our findings also indicated that the drought severity was the key climatic factor correlated with leaf N and P, which should be integrated into future biogeochemical models of element cycling. We should pay attention to the N shortage problem to improve the growth of shrubs. Global changes in vegetation distribution, temperature and drought severity will strongly affect the spatial patterns of shrub nutrient pools and ecosystem functioning.

Data availability. Raw data are available in the Supplementary material.

Competing interests. The authors declare that they have no conflict of interest.

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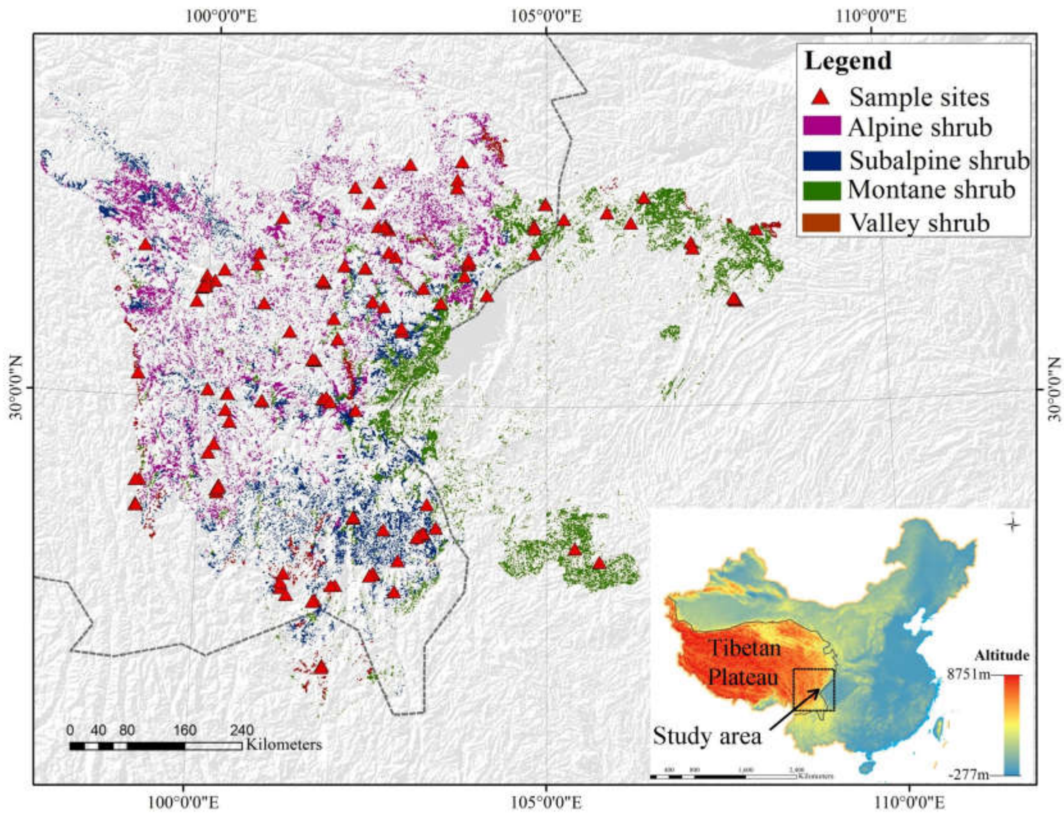
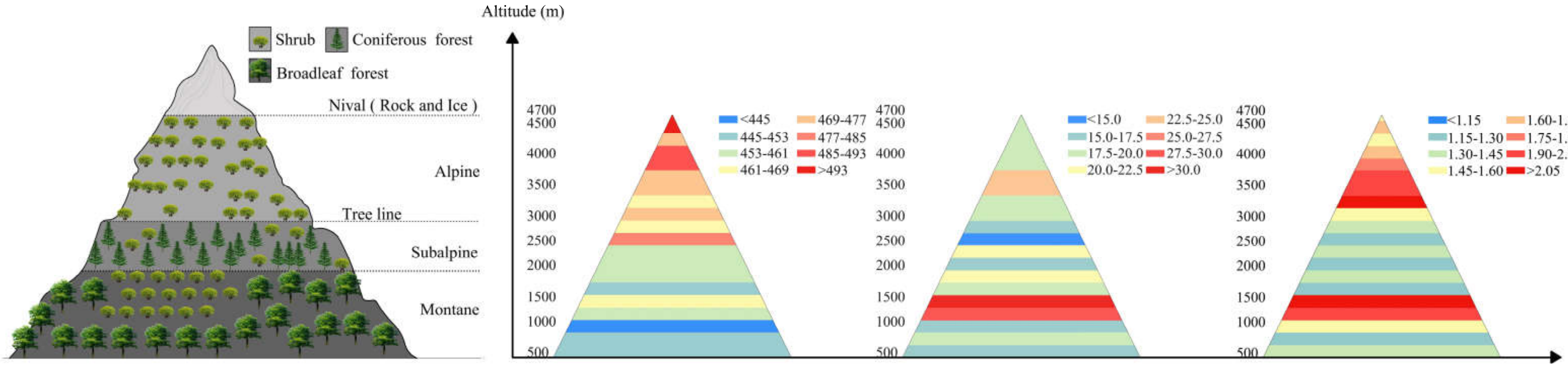


Figure 1. Locations of the southeastern Tibetan Plateau and 125 sample sites in mountainous areas. The purple, blue, green, and brown areas stand for the distribution of alpine, subalpine, montane and valley shrub types, respectively.



(A) Leaf C (mg g^{-1}) (B) Leaf N (mg g^{-1}) (C) Leaf P (mg g^{-1})

Figure 2. Vertical distribution of leaf C, N and P contents of mountainous shrubs on the Tibetan Plateau. Alpine shrub occurs at relatively higher altitude (3091−4685 m, above tree line), followed by subalpine shrub (2000−4078 m, coniferous forest zone), montane shrub (523−3342 m, broadleaf forest zone) and valley shrub (600−2350 m, valley region).

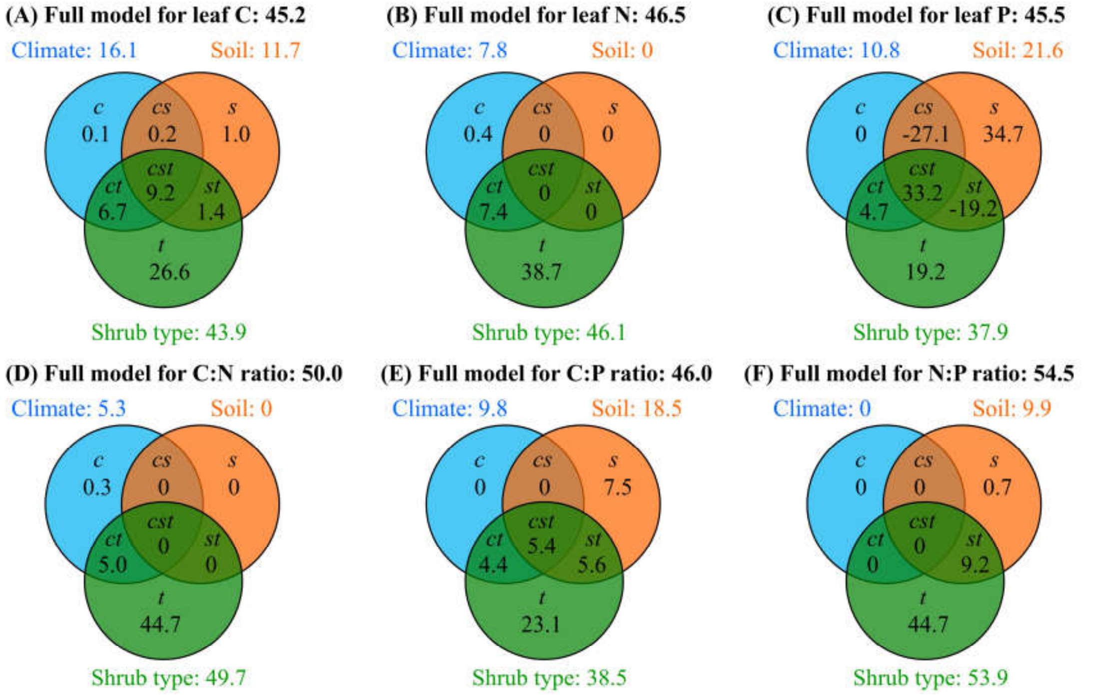


Figure 3. Summary of the partial general linear models (GLM) for the effects (R^2, %) of climate, soil and shrub type on leaf stoichiometry. *c*, *s*, and *t* represent the independent effects of climate, soil, and shrub type, respectively; *cs*, *ct*, and *st* are the interactive effects between climate and soil, climate and shrub type, soil and shrub type, respectively; *cst* denotes the interactive effect among the three factors. Leaf element concentrations and ratios were $\log_{10}$-transformed before analysis. Insignificant climatic or soil variables were not included in the partial GLM analysis. Shrub type stands for the combination of ecosystem type and functional type (e.g., montane deciduous broad-leaf shrub).

Table 1. Geometric means and standard deviations of leaf element concentrations and ratios for all shrub samples, and specific shrub type and species on the Tibetan Plateau. Ecosystem types include shrubs that located at different altitudinal belts. Functional types are classified based on different leaf traits. Coefficients of variation (CV, %) are in parentheses. *n* represents the number of shrub samples. Comparisons of geometric means of leaf C:N:P among shrub types and species (*P* values) were shown in Appendix A: Table A2.

		n	Leaf C (mg g^{-1})	Leaf N (mg g^{-1})	Leaf P (mg g^{-1})	Leaf C:N	Leaf C:P	Leaf N:P
All samples		125	468.9 ± 29.8 (6.3%)	18.6 ± 5.9 (30.4%)	1.50 ± 0.59 (37.0%)	25.3 ± 7.8 (29.7%)	312.0 ± 113.5 (34.2%)	12.3 ± 3.5 (27.5%)
Ecosystem type	Alpine shrub	58	481.7 ± 31.9 (6.6%)	19.7 ± 5.8 (28.5%)	1.75 ± 0.56 (31.0%)	24.5 ± 8.1 (31.6%)	276.0 ± 83.1 (28.8%)	11.3 ± 2.5 (21.6%)
	Subalpine shrub	20	477.6 ± 12.2 (2.6%)	14.7 ± 3.9 (25.9%)	1.24 ± 0.42 (32.6%)	32.5 ± 6.8 (20.3%)	386.4 ± 114.2 (28.3%)	11.9 ± 2.1 (17.7%)
	Montane shrub	30	448.3 ± 18.8 (4.2%)	17.6 ± 3.5 (19.3%)	1.23 ± 0.49 (37.1%)	25.4 ± 5.1 (19.8%)	357.3 ± 117.7 (31.3%)	14.1 ± 4.0 (27.3%)
	Valley shrub	17	452.9 ± 24.9 (5.5%)	21.8 ± 7.8 (34.0%)	1.56 ± 0.71 (41.9%)	20.8 ± 7.6 (34.8%)	290.1 ± 132.3 (42.0%)	14.0 ± 4.7 (31.0%)
Functional type	Evergreen broadleaf	55	485.3 ± 29.9 (6.2%)	16.5 ± 4.7 (27.5%)	1.44 ± 0.50 (33.1%)	29.4 ± 7.2 (23.6%)	337.6 ± 103.3 (29.2%)	11.5 ± 2.5 (21.3%)
	Evergreen conifer	6	488.3 ± 16.3 (3.3%)	13.7 ± 3.9 (27.9%)	1.34 ± 0.35 (25.6%)	35.6 ± 8.4 (23.0%)	363.5 ± 77.4 (20.8%)	10.2 ± 1.5 (14.6%)
	Deciduous broadleaf	64	453.5 ± 20.8 (4.6%)	21.1 ± 5.9 (27.0%)	1.58 ± 0.67 (39.3%)	21.5 ± 5.5 (24.7%)	287.4 ± 121.1 (39.1%)	13.4 ± 4.0 (28.6%)
Dominant species	*Rhododendron telmateium*	19	500.4 ± 12.7 (2.5%)	19.0 ± 4.3 (22.1%)	1.63 ± 0.37 (22.4%)	26.3 ± 5.7 (21.2%)	306.9 ± 68.7 (21.9%)	11.6 ± 1.6 (13.4%)
	Quercus monimotricha	5	464.7 ± 8.0 (1.7%)	14.9 ± 4.0 (26.4%)	1.33 ± 0.42 (30.9%)	31.1 ± 8.9 (27.6%)	350.5 ± 93.5 (25.9%)	11.3 ± 1.2 (10.5%)
	Coriaria sinica	6	426.3 ± 10.2 (2.4%)	18.4 ± 2.9 (15.4%)	1.09 ± 0.21 (19.2%)	23.2 ± 3.2 (13.5%)	391.5 ± 74.1 (18.7%)	16.9 ± 2.2 (13.1%)
	Bauhinia brachycarpa	3	443.5 ± 1.2 (0.3%)	24.7 ± 2.4 (9.6%)	1.45 ± 0.28 (19.5%)	18.0 ± 1.9 (10.3%)	306.9 ± 63.0 (20.2%)	17.1 ± 1.8 (10.8%)

Table 2. Model summary for the stepwise multiple regression (SMR) of leaf element concentrations and ratios of all shrub samples on climatic and soil variables (MAT, MAP, RDI, soil element and ratio).

Leaf	Adj. R^2	Partial regression coefficient				Contribution of predictor (%)			
element	Full mode	MAT	MAP	RDI	Soil	MAT	MAP	RDI	Soil
C	0.181	–0.001***	–	–	0.001*	61.6	–	–	38.4
N	0.097	–	–	0.037***	–	–	–	100	–
P	0.214	–	–	0.034**	0.138***	–	–	40.8	59.2
C:N	0.085	–	–	–0.036**	–	–	–	100	–
C:P	0.141	–	–	–0.043***	0.001**	–	–	54.8	45.2
N:P	0.060	0.004*	–	–	0.015*	47.8	–	–	52.2

*, **, and *** denote significance at the 0.05, 0.01, 0.001 test level, respectively. For partial regression coefficients, "+" indicates a positive correlation and "–" indicates a negative correlation. MAT, mean annual temperature; MAP, mean annual precipitation; RDI, standardized form of Reconnaissance Drought Index. Soil represents corresponding soil element or ratio relative to leaf element or ratio. Leaf element concentrations and ratios were $\log_{10}$-transformed before analysis.

Table 3. Comparison of arithmetic means of leaf C, N, P and C:N:P ratios between the shrubs on the Tibetan Plateau and other regional or global plants using Kruskal-Wallis test followed by pairwise comparisons. Standard deviations are in parentheses.

Study area	Leaf C ($mg\ g^{-1}$)	Leaf N ($mg\ g^{-1}$)	Leaf P ($mg\ g^{-1}$)	Leaf C:N	Leaf C:P	Leaf N:P	Reference
Shrubs on the Tibetan Plateau, southwestern China	469.8 (29.8)	19.4 (5.9)	1.60 (0.59)	26.4 (7.8)	331.7 (113.5)	12.8 (3.5)	This study
Shrubs in the Loess Plateau, central and northern China	437.0 (36.0)*	24.7 (8.2)*	1.55 (0.44)	19.7 (6.8)*	302.0 (84.0)*	16.1 (4.1)*	Zheng and Shangguan, 2007
Woody plants, eastern China	–	23.2 (7.2)*	1.59 (0.84)	–	–	17.6 (7.2)*	Chen et al., 2013a
Grassland biomes, China	438.0 (30.2)*	27.6 (8.6)*	–	17.9 (5.7)*	–	–	He et al., 2006
Chinese flora	–	20.2 (8.4)	1.46 (0.99)	–	–	16.3 (9.3)*	Han et al., 2005
Tropical dry forests, Mexico	–	21.3 (4.5)	1.15 (0.46)	–	–	22.2 (11.4)*	Campo and Dirzo, 2003
Tropical rain forests, Brazil, Costa Rica	–	21.6 (5.6)*	0.82 (0.34)*	–	–	28.6 (8.6)*	Townsend et al., 2007
Herbaceous species, central England	–	27.8 (9.9)*	2.70 (1.52)*	–	–	10.7 (2.8)*	Thompson et al., 1997
Dominant riparian trees along the Middle Rio Grande, USA	463.0 (0.8)	31.0 (8.0)*	1.50 (4.10)	18.4 (4.2)*	1010 (560)*	53.0 (21.0)*	Tibbets and Molles, 2005
Global flora	–	20.1 (8.7)	1.77 (1.12)	–	–	13.8 (9.5)	Reich and Oleksyn, 2004
Global flora	464.0 (32.1)	20.6 (12.2)	1.99 (1.49)*	22.5 (10.6)*	232.0 (145.0)*	12.7 (6.8)	Elser et al., 2000

* denote significant difference in leaf element traits between the shrubs on the Tibetan Plateau and other regional or global plants at the 0.05 level.

Appendix A: Additional tables

Table A1. Geographical, climatic and soil nutrient information of different shrub types and representative dominant shrub species on the Tibetan Plateau.

Shrub type	Altitude (m)	MAP (mm)	MAT (ºC)	RDI	Soil C (mg g^{-1})	Soil N (mg g^{-1})	Soil P (mg g^{-1})
Ecosystem type							
Alpine shrub	3091~4685	366.3~1013.4	–4.25~13.88	–1.36~2.02	19.0~167.1	1.41~11.95	0.58~2.05
Subalpine shrub	2000~4078	459.8~1008.5	–4.67~11.98	–1.71~–0.08	17.2~106.2	1.16~8.11	0.26~2.01
Montane shrub	523~3342	490.0~1555.4	0.11~16.97	–1.64~1.75	3.5~92.2	0.65~8.51	0.18~1.77
Valley shrub	600~2350	373.5~1696.3	2.35~22.16	–1.64~1.38	6.1~89.2	0.58~7.69	0.14~1.51
Functional type							
Evergreen broadleaf	627~4685	366.3~1555.4	–4.67~22.16	–1.71~1.76	8.9~161.8	1.00~11.95	0.23~2.01
Evergreen conifer	2145~4378	471.8~761.8	0.12~10.73	–1.33~1.54	23.0~110.3	2.23~8.32	0.46~1.64
Deciduous broadleaf	523~4212	373.5~1696.3	–4.25~21.51	–1.64~2.02	3.5~167.1	0.58~11.02	0.14~2.05
Representative species							
Rhododendron telmateium	3624~4685	366.3~993.8	–4.25~13.88	–1.36~1.54	26.7~101.2	2.07~8.13	0.61~1.60
Quercus monimotricha	2000~3325	646.5~1008.5	0.27~7.81	–1.53~–0.86	36.1~86.7	2.75~5.24	0.69~1.55
Coriaria sinica	540~3156	720.7~1435.7	6.74~15.31	–1.42~0.43	3.5~46.2	0.76~2.17	0.39~0.88
Bauhinia brachycarpa	1621~2236	688.1~918.7	4.43~11.09	–1.56~1.38	17.7~28.0	1.46~2.58	0.55~1.00

MAP, MAT and RDI indicate mean annual precipitation, mean annual temperature and Reconnaissance Drought Index, respectively.

Table A2. Comparisons of geometric means of leaf stoichiometry using Kruskal-Wallis test followed by pairwise comparisons.

Comparison pair	Leaf C	Leaf N	Leaf P	Leaf C:N	Leaf C:P	Leaf N:P
Ecosystem type						
Alpine vs Subalpine	$P = 1.000$	$P < 0.001$	$P < 0.001$	$P < 0.01$	$P < 0.01$	$P = 1.000$
Alpine vs Montane	$P < 0.001$	$P = 0.668$	$P < 0.001$	$P = 1.000$	$P < 0.01$	$P < 0.01$
Alpine vs Valley	$P < 0.001$	$P = 1.000$	$P = 1.000$	$P = 0.612$	$P = 1.000$	$P < 0.01$
Subalpine vs Montane	$P < 0.001$	$P = 0.118$	$P = 1.000$	$P < 0.05$	$P = 1.000$	$P = 0.226$
Subalpine vs Valley	$P < 0.05$	$P < 0.001$	$P = 0.229$	$P < 0.001$	$P = 0.096$	$P = 0.113$
Montane vs Valley	$P = 1.000$	$P = 0.168$	$P = 0.210$	$P = 0.335$	$P = 0.396$	$P = 1.000$
Functional type						
Evergreen broadleaf vs Evergreen conifer	$P = 1.000$	$P = 0.434$	$P > 0.05$	$P = 0.484$	$P = 1.000$	$P = 0.469$
Evergreen broadleaf vs Deciduous broad-leaf	$P < 0.001$	$P < 0.001$	$P > 0.05$	$P < 0.001$	$P < 0.05$	$P < 0.05$
Evergreen conifer vs Deciduous broad-leaf	$P < 0.01$	$P < 0.01$	$P > 0.05$	$P < 0.001$	$P = 0.299$	$P < 0.05$
Dominant species						
Rhododendron telmateium vs *Quercus monimotricha*	$P = 0.081$	$P > 0.05$	$P = 0.435$	$P = 1.000$	$P > 0.05$	$P = 1.000$
Rhododendron telmateium vs *Coriaria sinica*	$P < 0.001$	$P > 0.05$	$P < 0.01$	$P = 1.000$	$P > 0.05$	$P < 0.01$
Rhododendron telmateium vs *Bauhinia brachycarpa*	$P < 0.05$	$P > 0.05$	$P = 1.000$	$P = 0.061$	$P > 0.05$	$P < 0.05$
Quercus monimotricha vs *Coriaria sinica*	$P = 0.880$	$P > 0.05$	$P = 1.000$	$P = 0.366$	$P > 0.05$	$P < 0.05$
Quercus monimotricha vs *Bauhinia brachycarpa*	$P = 1.000$	$P > 0.05$	$P = 1.000$	$P < 0.05$	$P > 0.05$	$P = 0.076$
Coriaria sinica vs *Bauhinia brachycarpa*	$P = 1.000$	$P > 0.05$	$P = 0.841$	$P = 0.784$	$P > 0.05$	$P = 1.000$

Differences were statistically significant at the 0.05 level. Leaf element concentrations and ratios were $\log_{10}$-transformed before analysis.

Table A3. Partial correlation coefficients between the geographic variables and leaf stoichiometry of all shrubs and different shrub types.

	Variable	Leaf C	Leaf N	Leaf P	Leaf C:N	Leaf C:P	Leaf N:P
All shrubs	Altitude	0.328***	−0.097	0.129	0.163	−0.066	−0.252**
	Longitude	0.028	−0.173	−0.088	0.174	0.089	−0.069
	Latitude	−0.088	0.350***	0.097	−0.356***	−0.107	0.252**
Ecosystem type							
Alpine	Altitude	0.104	−0.238	−0.224	0.258	0.232	−0.026
	Longitude	−0.107	−0.173	0.071	0.146	−0.093	−0.287*
	Latitude	−0.164	0.319*	0.181	−0.351**	−0.207	0.190
Subalpine	Altitude	−0.083	0.485*	0.326	−0.483*	−0.319	0.004
	Longitude	−0.532*	0.580*	0.342	−0.612**	−0.369	0.128
	Latitude	−0.052	0.192	0.099	−0.191	−0.099	0.035
Montane	Altitude	−0.306	−0.107	−0.264	0.035	0.223	0.233
	Longitude	−0.221	−0.239	−0.309	0.188	0.282	0.198
	Latitude	−0.137	−0.053	−0.338	0.020	0.320	0.351
Valley	Altitude	0.216	0.429	0.322	−0.404	−0.269	0.173
	Longitude	0.165	0.258	0.408	−0.234	−0.364	−0.109
	Latitude	0.047	−0.128	−0.714**	0.137	0.697**	0.580*
Functional type							
Evergreen broadleaf	Altitude	0.212	0.012	−0.137	0.038	0.165	0.169
	Longitude	−0.175	−0.144	−0.214	0.108	0.175	0.118
	Latitude	0.103	0.315*	0.228	−0.302*	−0.200	0.040
Evergreen conifer	Altitude	−0.870	0.440	0.641	−0.512	−0.689	−0.970*
	Longitude	−0.917	0.455	0.540	−0.542	−0.613	−0.853
	Latitude	−0.379	−0.115	0.031	0.102	−0.048	−0.843
Deciduous broadleaf	Altitude	−0.016	0.270*	0.491***	−0.279*	−0.498***	−0.369**
	Longitude	−0.047	0.049	0.138	−0.059	−0.146	−0.114
	Latitude	0.148	−0.078	−0.236	0.110	0.260*	0.204

*, **, and *** denote significance at the 0.05, 0.01, 0.001 test level, respectively. For partial correlation coefficients, "+" indicates a positive correlation and "–" indicates a negative correlation. Leaf element concentrations and ratios were $\log_{10}$-transformed before analysis.

Table A4. Model summary for the stepwise multiple regression (SMR) of leaf element concentrations of different ecosystem types on the climatic and soil variables (MAT, MAP, RDI, soil element and ratio).

Leaf	Adj. R^2	Partial regression coefficient				Contribution of predictor (%)			
element	Full mode	MAT	MAP	RDI	Soil	MAT	MAP	RDI	Soil
Alpine									
C	–	–	–	–	–	–	–	–	–
N	–	–	–	–	–	–	–	–	–
P	0.059	–	0.001*	–	–	–	100	–	–
C:N	0.074	–	–	–0.037*	–	–	–	100	–
C:P	0.066	–	–	–0.036*	–	–	–	100	–
N:P	0.107	–	–	–	0.016**	–	–	–	100
Subalpine									
C	0.217	–	–0.00004*	–	–	–	100	–	–
N	0.190	–0.010*	–	–	–	100	–	–	–
P	0.212	–	–	–	0.132*	–	–	–	100
C:N	0.201	0.010*	–	–	–	100	–	–	–
C:P	0.212	–	0.001*	–	–	–	100	–	–
N:P	0.554	–	–	–	0.036***	–	–	–	100
Montane									
C	–	–	–	–	–	–	–	–	–
N	–	–	–	–	–	–	–	–	–
P	–	–	–	–	–	–	–	–	–
C:N	–	–	–	–	–	–	–	–	–
C:P	–	–	–	–	–	–	–	–	–
N:P	–	–	–	–	–	–	–	–	–
Valley									
C	–	–	–	–	–	–	–	–	–
N	–	–	–	–	–	–	–	–	–
P	0.249	0.016*	–	–	–	100	–	–	–
C:N	–	–	–	–	–	–	–	–	–
C:P	0.425	–0.020**	–	–	0.003*	60.6	–	–	39.4
N:P	0.256	–0.019*	–	–	–	100	–	–	–

*, **, and *** denote significance at the 0.05, 0.01, 0.001 test level, respectively. For partial regression coefficients, "+" indicates a positive correlation and "–" indicates a negative correlation. Soil represents corresponding soil element or ratio relative to leaf element or ratio. Leaf element concentrations and ratios were $\log_{10}$-transformed before analysis.

Table A5. Model summary for the stepwise multiple regression (SMR) of leaf element concentrations of different functional types on the climatic and soil variables (MAT, MAP, RDI, soil element and ratio).

Leaf element	Adj. R^2 Full mode	Partial regression coefficient				Contribution of predictor (%)			
		MAT	MAP	RDI	Soil	MAT	MAP	RDI	Soil
Evergreen broadleaf									
C	0.231	0.002***	–	–	–	100	–	–	–
N	0.176	–	–	–	0.022**	–	–	–	100
P	0.188	–	–	–	0.144**	–	–	–	100
C:N	0.097	–	–	–	0.017*	–	–	–	100
C:P	0.094	–	–	–	0.002*	–	–	–	100
N:P	0.259	–	–	–	0.030***	–	–	–	100
Evergreen conifer									
C	–	–	–	–	–	–	–	–	–
N	–	–	–	–	–	–	–	–	–
P	–	–	–	–	–	–	–	–	–
C:N	–	–	–	–	–	–	–	–	–
C:P	–	–	–	–	–	–	–	–	–
N:P	0.853	0.012**	–	–	–	100	–	–	–
Deciduous broadleaf									
C	–	–	–	–	–	–	–	–	–
N	0.075	–	–	0.031*	–	–	–	100	–
P	0.251	–	–	0.043*	0.159**	–	–	43.9	56.1
C:N	0.069	–	–	–0.029*	–	–	–	100	–
C:P	0.144	–	–	–0.061*	–	–	–	100	–
N:P	0.093	0.007**	–	–	–	100	–	–	–

*, **, and *** denote significance at the 0.05, 0.01, 0.001 test level, respectively. For partial regression coefficients, "+" indicates a positive correlation and "–" indicates a negative correlation. MAT, mean annual temperature; MAP, mean annual precipitation; RDI, standardized form of Reconnaissance Drought Index. Soil represents corresponding soil element or ratio relative to leaf element or ratio. Leaf element concentrations and ratios were log$_{10}$-transformed before analysis.

Table A6. Model summary for the stepwise multiple regression (SMR) of leaf element concentrations of dominant shrub species on the climatic and soil variables (MAT, MAP, RDI, soil element and ratio).

Leaf element	Adj. R^2 Full mode	Partial regression coefficient				Contribution of predictor (%)			
		MAT	MAP	RDI	Soil	MAT	MAP	RDI	Soil
Rhododendron telmateium									
C	–	–	–	–	–	–	–	–	–
N	–	–	–	–	–	–	–	–	–
P	–	–	–	–	–	–	–	–	–
C:N	–	–	–	–	–	–	–	–	–
C:P	–	–	–	–	–	–	–	–	–
N:P	0.162	–	–	–	0.013*	–	–	–	100
Quercus monimotricha									
C	0.732	–	–	0.021*	–	–	–	100	–
N	0.700	–	–	–0.318*	–	–	–	100	–
P	0.904	–0.037**	–	–	–	100	–	–	–
C:N	0.924	–	–	–	0.051**	–	–	–	100
C:P	0.919	0.039**	–	–	–	100	–	–	–
N:P	0.983	–	0.001*	–	0.070**	–	32.1	–	67.9
Coriaria sinica									
C	0.885	–	–	0.015**	–	–	–	100	–
N	–	–	–	–	–	–	–	–	–
P	–	–	–	–	–	–	–	–	–
C:N	–	–	–	–	–	–	–	–	–
C:P	0.611	–	<0.001*	–	–	–	100	–	–
N:P	–	–	–	–	–	–	–	–	–
Bauhinia brachycarpa									
C	0.991	–	0.001*	–	–0.215*	–	7.0	–	93.0
N	0.997	–	0.018*	–	0.169*	–	95.7	–	4.3
P	–	–	–	–	–	–	–	–	–
C:N	0.991	–0.373*	–0.026*	–	–	30.1	69.9	–	–
C:P	0.990	–	0.135*	–	–7.257*	–	17.9	–	82.1
N:P	–	–	–	–	–	–	–	–	–

*, **, and *** denote significance at the 0.05, 0.01, 0.001 test level, respectively. For partial regression coefficients, "+" indicates a positive correlation and "–" indicates a negative correlation. MAT, mean annual temperature; MAP, mean annual precipitation; RDI, standardized form of Reconnaissance Drought Index. Soil represents corresponding soil element or ratio relative to leaf element or ratio. Leaf element concentrations and ratios were $\log_{10}$-transformed before analysis.

Appendix B: Additional figures

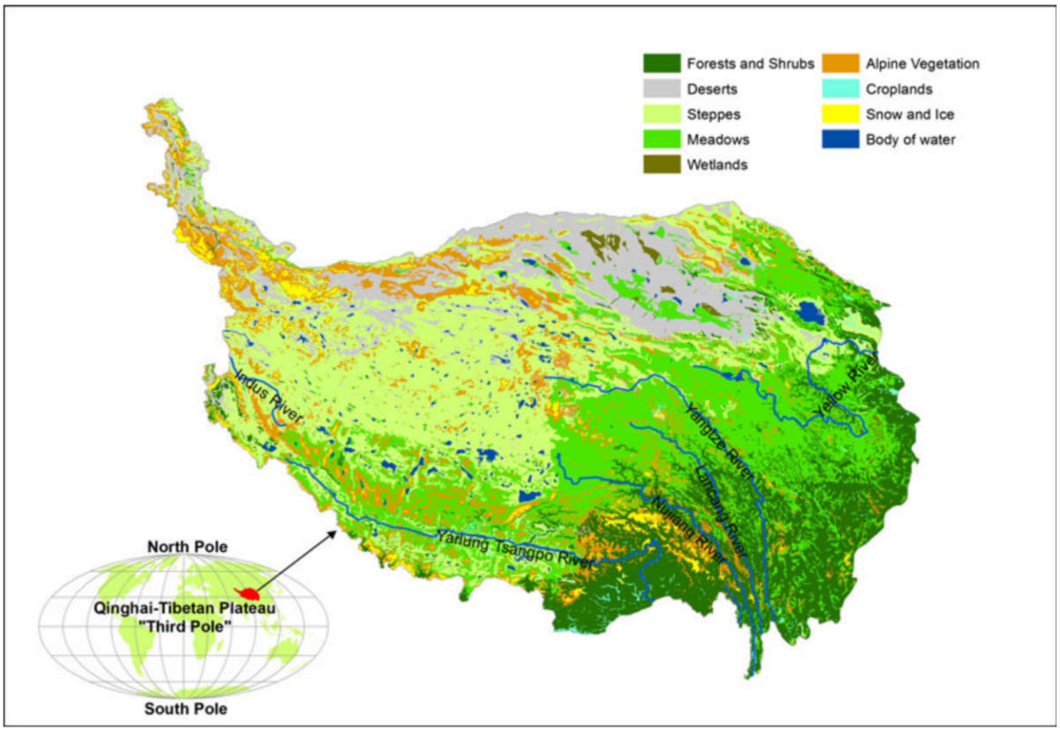


Figure B1. Distribution of vegetation types on the Tibetan Plateau, which is regarded as the “third pole” of the Earth. The complex climate conditions cause a diverse vegetation pattern, resulting in the local plant communities highly sensitive to global climate change. The southeastern margin of the plateau is dominated by shrubs and forests. This figure was originated from reference (Chen et al., 2013).

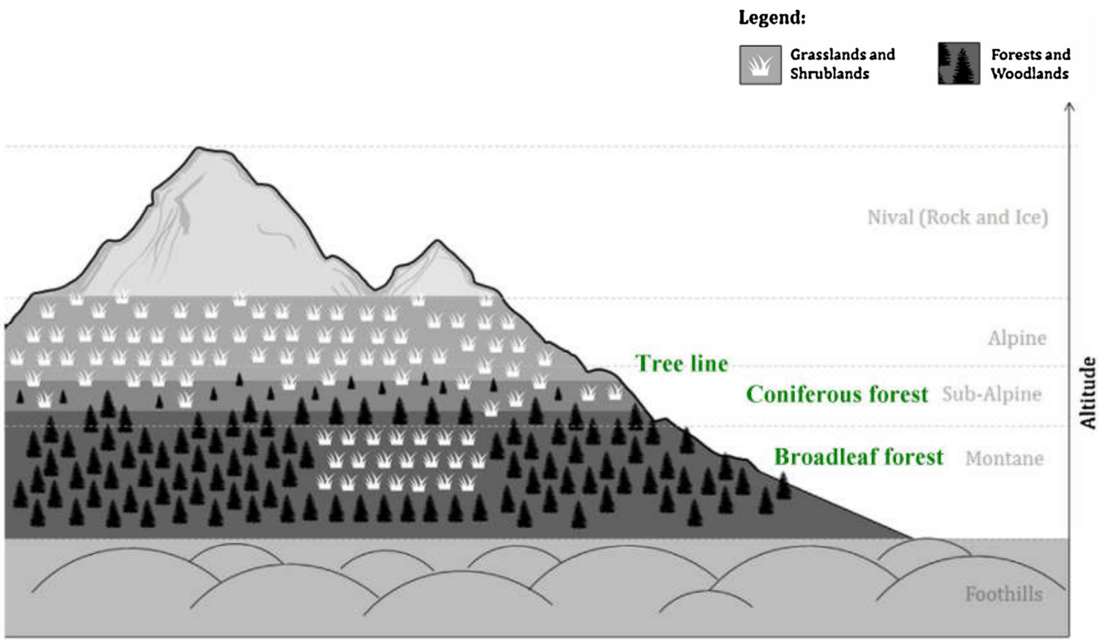


Figure B2. Diagram illustrating the delineation of montane, subalpine, alpine, and nival altitudinal belts relative to the location of shrubland and grassland ecosystems. Various shrub species are able to live in these altitudinal belts at the life form limit for shrubs, and could not be found in the nival belt. This figure was obtained from references (Mcavaney et al., 2001; Worboys and Good, 2011).

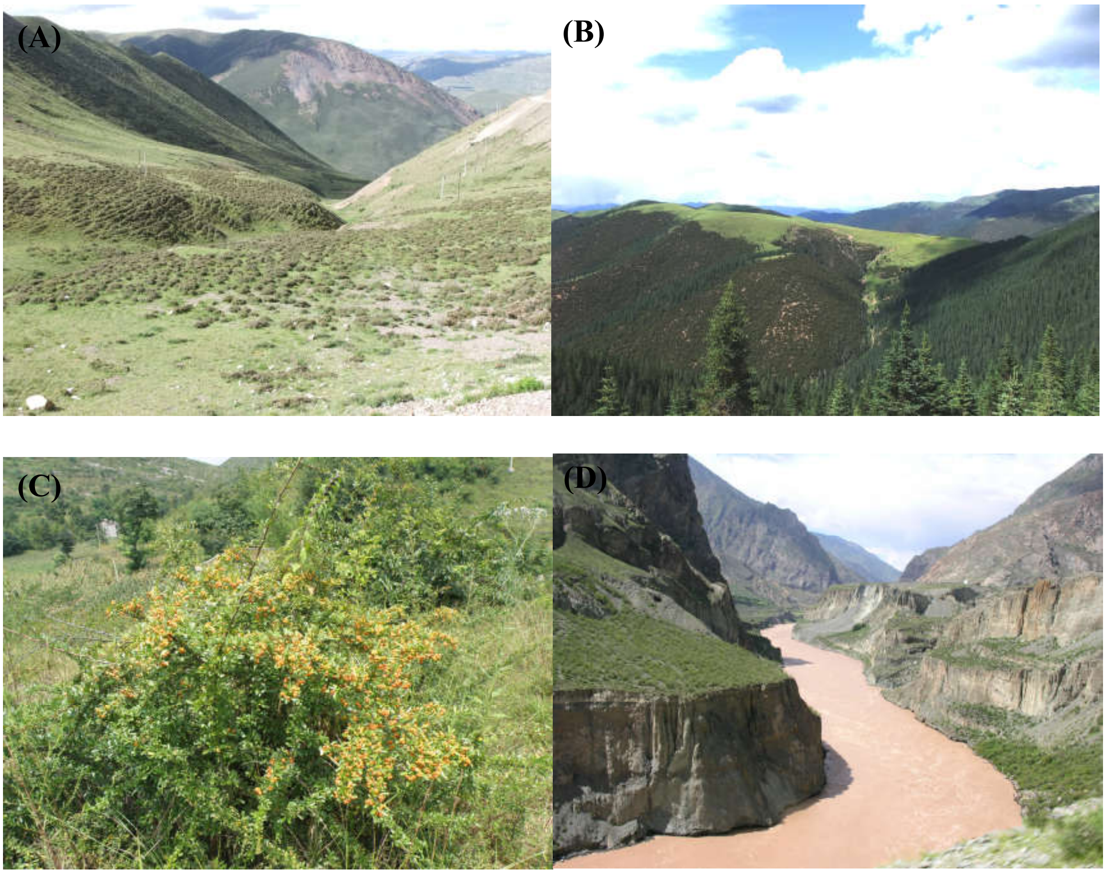


Figure B3. Representative photos of (A) alpine, (B) subalpine, (C) montane, and (D) valley shrubs on the Tibetan Plateau.

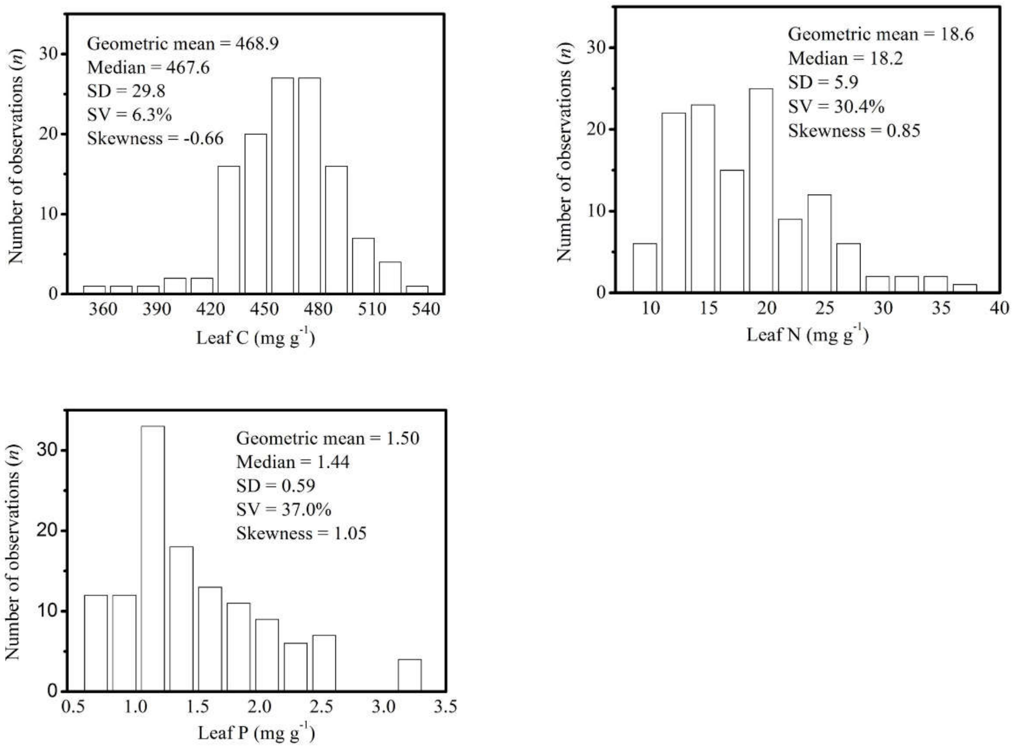
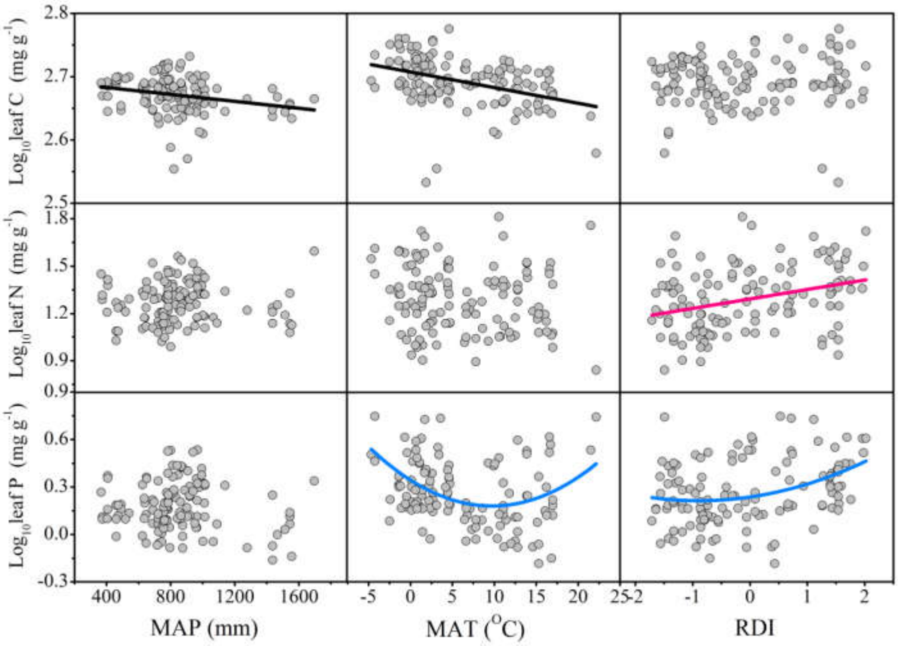


Figure B4. Distribution of leaf C, N and P concentrations of all shrubs on the Tibetan Plateau.



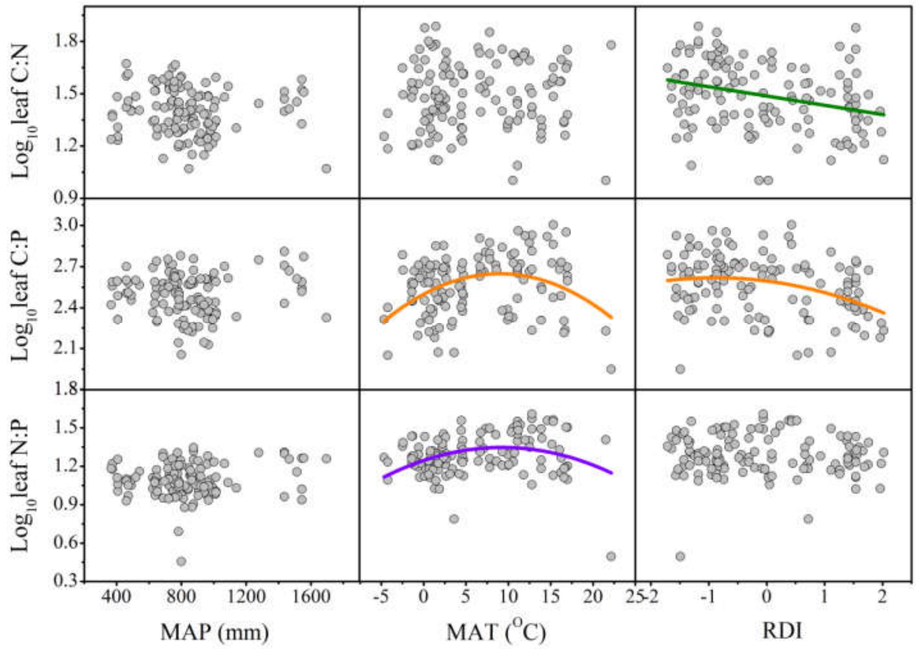


Figure B5. Variation trends of leaf C:N:P stoichiometry as a function of climatic factors. Data points indicate every observation of shrub stoichiometry within the sampling sites (n = 125). Lines are plotted if regressions were significant at $P < 0.05$. Leaf element concentrations and ratios were log$_{10}$-transformed before analysis.

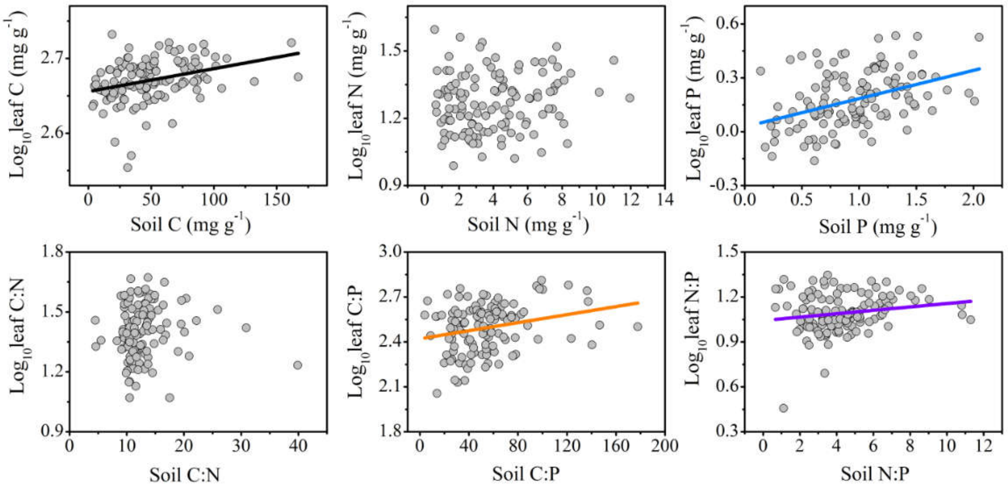


Figure B6. Variation trends of leaf C:N:P stoichiometry as a function of soil C:N:P. Data points indicate every observation of shrub stoichiometry within the sampling sites (*n* = 125). Lines are plotted if regressions were significant at $P < 0.05$. Leaf element concentrations and ratios were $\log_{10}$-transformed before analysis.

Appendix C: Additional methods

Calculation of the Reconnaissance Drought Index (RDI_{st})

Drought severity can be evaluated via the computation of the RDI_{st}. RDI was proposed by Tsakiris and Vangelis (2005), utilizing the ratios of precipitation over potential evapotranspiration (PET) for different time scales, to be representative of the region of interest (Khalili et al., 2011). The initial value of RDI (RDI_{α}) is usually calculated for the *i*-th year in a time basis of 12 consecutive months as follows:

$$RDI_{\alpha}^{(i)} = \frac{\sum_{j=1}^{12} P_{ij}}{\sum_{j=1}^{12} PET_{ij}},\ i = 1(1)N \text{ and } j = 1(1)12 \qquad (1)$$

where P_{ij} and PET_{ij} are the precipitation and potential evapotranspiration of the *j*-th month of the *i*-th year, respectively, and *N* is the total number of years of the available data (N = 25 in this study). PET was calculated using the Thornthwaite method (Thornthwaite, 1948).

As the next step, RDI_{st} for a hydrological year (12-month reference period) is computed based on the following equation:

$$RDI_{st}^{(i)} = \frac{\gamma^{(i)} - \bar{\gamma}}{\sigma_{\gamma}} \qquad (2)$$

where $\gamma^{(i)}$ is the $\ln(RDI_{\alpha}^{(i)})$, $\bar{\gamma}$ is the arithmetic mean and σ_{γ} is the standard deviation of $\ln(RDI_{\alpha})$. The RDI_{α} values are assumed to follow the lognormal distribution, which has been found to be the most appropriate (Tsakiris et al., 2007; Vangelis et al., 2013). The calculation process was conducted by using DrinC software.