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

76 showed no altitudinal trend. Fisher et al. (2013) reported that leaf N and P firstly

77 increased and then declined with increasing altitudes (200, 1000, 1500 and 3000 m) in

78 the Peruvian Andes. Zhao et al. (2014) observed that the leaf N and P of 175 plant

79 species decreased with elevation on the Changbai Mountain (540, 753, 1286, 1812,

80 2008 and 2357 m). This discrepancy of previous results indicates that the leaf N and P

81 can vary along different altitudinal ranges at regional scale. Moreover, much less

82 information was available on the vertical distribution of leaf C. Hence, the more general

83 patterns of leaf C:N:P along an extensive altitudinal gradient need to be further

84 understood.

85   While comprehensive investigations of plant stoichiometry in forestland, grassland,

86 wetland, and macrophyte ecosystems have emerged (Güsewell and Koerselman, 2002;

87 He et al., 2006; Townsend et al., 2007; Sardans et al., 2012; Xia et al., 2014), much

88 fewer studies focused on mountainous shrubs. In China, shrubland is a widely

89 distributed biome type, covering ~20% of the country. However, information on the

90 element concentrations of shrubs is very scarce (Piao et al., 2009). Thus, intensive

91 investigation of shrub stoichiometry can provide detailed information for the growing

92 global database of plant stoichiometry. As the earth's highest plateau, the Tibetan

93 Plateau exhibits one of the very few extensive elevational vegetation gradients

94 remaining in the world (Chen et al., 2013b) (Fig. 1 and Appendix B: Fig. B1). Large

95 precipitation and temperature gradients along the steep mountains bordering the plateau

96 to the east lead to a heterogeneous environment. This plateau is also considered as the

97 China's hotspot ecoregions of biodiversity (Tang et al., 2006). The shrubs here are also

98 very diverse and widely distributed along altitudinal gradients, which can endure

99 extreme cold or drought environments. Some shrub species that are unique to this

100 region have emerged in cold plateau areas (e.g., *Rhododendron telmateium* and

4

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

151 plots were 5−50 m. For each plot, mature leaves from dominant shrub species of 5−10

152 individuals were collected and mixed. After litter was removed from the soil surface,

153 nine 3-cm-diameter soil cores (0−10 cm layer) in each plot were collected and

154 combined to form one composite sample to account for any heterogeneity resulted from

155 position. After collection, the leaf samples were oven-dried at 65 ºC, and ground to fine

156 powders using a ball mill for element analysis. The fresh soils were air-dried, with

157 visible roots, stones and organic residues removed. Soil samples were sieved through

158 2-mm meshes before analysis.

159

160 **2.3 Geographic and climatic parameters**

161 The geographic locations (altitude, latitude and longitude) of sample sites were

162 recorded using a global positioning system. MAT and MAP values were obtained from

163 the China Meteorological Forcing Dataset (Yang et al., 2010; Chen et al., 2011). The

164 temporal and spatial resolutions of this dataset were every 3 h and 0.1º × 0.1º in

165 longitude and latitude from 1981 to 2008. In meteorology, MAT (°C) is the mean air

166 temperature calculated by averaging the 12 months of the calendar year. MAP (mm) is

167 the annual average value of the product of atmospheric water vapor that falls under

168 gravity.

169   Considering the mountainous areas exhibit various drought conditions (especially

170 in valley region), we herein first investigate how leaf stoichiometry varies with drought

171 index (Reconnaissance Drought Index, RDI). RDI has been widely used in meteorology

172 to powerfully assess drought severity in arid and semiarid regions (Tsakiris and

173 Vangelis, 2005). Compared to the other indices (e.g., the Palmer Drought Severity Index

174 and the Standardized Precipitation Index), the advantages of RDI are its low data

175 requirements, high resilience and sensitivity to drought events (Khalili et al., 2011).

176 The standardized form of RDI (RDI_{st}) can be calculated via the computation of potential

177 evapotranspiration (PET) based on the Thornthwaite method (Thornthwaite, 1948). The

178 detailed calculation process of RDI_{st} for a hydrological year (12-month reference period)

179 was shown in the Appendix C. In this work, RDI is used to represent RDI_{st}. Positive

180 RDI represent wet period of sample site, whereas negative values indicate dry period.

181 Using the RDI values, drought severity can be categorized as extreme (< -2.0), severe

182 (-2.0 to -1.5), moderate (-1.5 to -1.0) or mild (-1.0 to -0.5) (Vangelis et al. 2013).

183

184 **2.4 Element measurements**

185 The total C and N concentrations of leaf and soil samples were measured by dry

186 combustion using a Perkin-Elmer 2400 II elemental analyzer (Perkin-Elmer, Inc., USA).

187 Total P concentrations were determined by the ammonium molybdate method using a

188 continuous-flow analyser (AutoAnalyzer3 Continuous-Flow Analyzer; Bran Luebbe,

189 Germany) after H_2SO_4-$HClO_4$ digestion for leaves and H_2SO_4-H_2O_2-HF digestion for

190 soil (Kuo, 1996). The element concentrations are presented in units of mg g^{-1} dry

191 weight, and the element ratios are presented on a mass basis. Unfortunately, soil

192 available nutrient data were not determined, and we were unable to assess their

193 correlations with leaf elements.

194

195 **2.5 Data analysis**

196 The data were analyzed at two levels: (1) using all the shrub samples together ($n = 125$),

197 and (2) dividing the shrub dataset into four ecosystem types and four dominant shrub

198 species that located in different altitudinal belts, or three functional types classified by

199 different leaf traits. The leaf mineral concentrations and ratios were averaged at the site-

200 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

226   Leaf C, N and P contents for all shrubs ranged from 358.2 to 539.8, 9.7 to 39.4 and 0.69

227   to 3.43 mg g^{-1}, respectively (Supplementary material). The element ratios varied greatly

228   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

229   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,

230   while those for C:N, C:P and N:P were 25.3, 312.0 and 12.3, respectively.

231   The geometric means of leaf C for alpine and subalpine shrubs were 481.7 and

232   477.6 mg g^{-1}, respectively, which were higher than those of montane and valley shrubs

233   ($P < 0.001$, Table 1 and Appendix A: Table A2). Leaf N of valley shrub was the highest

234   among the ecosystem types, while the leaf P contents of subalpine and montane shrubs

235   were lower than alpine shrub ($P < 0.001$). Leaf elements also varied markedly across

236   different functional types. Deciduous broadleaf shrub showed the lowest leaf C,

237   whereas its leaf N was the largest ($P < 0.01$). Leaf P did not show significant difference

238   among the three functional types ($P = 0.323$). For dominant shrub species, the leaf

239   C:N:P in *Rhododendron telmateium* (alpine), *Quercus monimotricha* (subalpine),

240   *Coriaria sinica* (montane), and *Bauhinia brachycarpa* (valley) followed similar trends

241   to those in corresponding shrub ecosystem types.

242   The relative variability of leaf nutrients can be demonstrated by the coefficient of

243   variation (CV). Leaf P of all samples had the greatest variation (37.0%), followed by N

244   (30.4%) and C (6.3%). The relative variability of leaf elements for each shrub type also

245   showed the similar trends.

246

247   **3.2 Altitudinal patterns of leaf stoichiometry**

248   Using partial correlation analysis (Appendix A: Table A3), we found that leaf C

249   increased with the increase of altitude ($P < 0.001$), while the leaf N and P did not show

250   clear altitudinal trend ($P = 0.287$ and 0.154). The highest leaf N and P were distributed

251 at altitude of about 1500 m which belonged to valley shrub (Fig. 2).

252   The relationships between the leaf stoichiometry of shrub types and elevations

253 exhibited different patterns. For example, altitude was not correlated with the leaf C of

254 alpine and subalpine shrubs. On the contrary, leaf N and P showed obvious altitudinal

255 trends for subalpine and deciduous broadleaf shrubs ($P < 0.01$).

256

257 3.3 Climatic influence on leaf stoichiometry

258 MAP was not linearly or nonlinearly correlated with most of the leaf C:N:P traits

259 (Appendix B: Fig. B5). MAT was negatively correlated with leaf C, while the leaf P,

260 C:P and N:P were quadratically correlated with MAT ($P < 0.001$). As RDI increased

261 (i.e., wetter conditions), leaf N and P became significantly larger ($P < 0.001$). When the

262 three climatic factors were analyzed by SMR, MAP was excluded from all the analysis

263 (Table 2). MAT was negatively related with leaf C ($P < 0.001$), and only RDI was

264 entered into the SMR equations for leaf N and P.

265   The climatic factors showed large heterogeneity across different shrub types and

266 species (Appendix A: Tables A4−A6). For instance, the leaf N or P of alpine, valley

267 shrubs and *Quercus monimotricha* were correlated with MAT or MAP ($P < 0.05$), while

268 those of montane, evergreen conifer shrubs, *Rhododendron telmateium* and *Coriaria*

269 *sinica* were not affected by climate ($P > 0.05$). It indicated that the specific shrub type

270 or species exhibited diverse leaf C:N:P trends along climatic gradient and change

271 greatly to adapt to different habitats.

272

273 3.4 Soil influence on leaf stoichiometry

274 Plants take up most of the nutrients directly from soils. As usually observed elsewhere,

275 our results revealed positive correlations between the leaf and soil stoichiometry for C,

276   P, C:P and N:P ($P < 0.05$) (Appendix B: Fig. B6, Table 2). The leaf N and C:N of all

277   shrubs were not correlated with those of 0−10 cm soil layer, probably owing to

278   confounding effects of other variables along geographic gradients. Interestingly, the

279   leaf N, P, C:N, C:P and N:P of evergreen broadleaf shrub were only correlated with soil

280   variables (Appendix A: Table A5), indicating the leaf nutrients in evergreen broadleaf

281   shrub were mainly affected by root uptake from soils. By contrast, the soil elements

282   were not limiting factors for the leaf element levels in montane shrub and *Coriaria*

283   *sinica* (Appendix A: Tables A4 and A6).

284

285   **3.5 Relative effects of shrub type, soil and climate**

286   The three factors (shrub type, soil and climate) together accounted for 45.2%−54.5%

287   of the six leaf C:N:P traits (Fig. 3). The total effect of shrub type (*t+ct+st+cst*) showed

288   the largest contribution to the variations in leaf stoichiometry (37.9%−53.9%). The

289   independent effect of shrub type (*t*, 19.2%−44.7%) was also greater than those of soil

290   (*s*, 0%−34.7%) and climate (*c*, 0%−0.4%). Soil exhibited the largest independent

291   contribution (*s*, 34.7%) to the variation of leaf P. Climate (*c+ct+cs+cst*, 0%−16.1%)

292   contributed to leaf stoichiometry mainly via the interactive effects between climate and

293   shrub type (*ct*) or among the three factors (*cst*). The negative value (e.g., *cs* = −27.1%

294   for leaf P) indicated suppressive interactive effects of climate and soil.

295

296   **4 Discussion**

297   A few studies have found that the leaf elements of plants varied largely with altitudes

298   in different mountainous regions (Soethe et al., 2008; van de Weg et al., 2009; Fisher

299   et al., 2013). However, the relative effects of shrub types and environmental variables

300   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

326　probably depress available N uptake by roots.

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

336　　　The CV patterns among leaf elements are consistent with the Stability of Limiting
337　Elements Hypothesis (Sterner and Elser, 2002). It is known that plant nutrient (e.g., C)
338　that required at a high concentration should show a small variation and lower sensitivity
339　to the environment. Leaf C was less variable than leaf N and P, suggesting leaf C had
340　stronger stoichiometric homeostasis. The CV value of shrub leaf C (6.3%) was smaller
341　than those of trees, herbs and shrubs (6.9%−28.0%) in other regions, whereas those of
342　shrub leaf N (30.4%) and P (37.0%) were within the range of other ecosystems (N:
343　11.0%−50.5%; P: 13.0%−44.0%) (Tibbets and Molles, 2005; He et al., 2006; Zheng
344　and Shangguan, 2007; Ladanai et al., 2010). Consequently, the high C accumulation
345　capacity of shrub is less sensitive to the complex climate conditions on the plateau.

346

347　**4.2 Relative influences of the environment and shrub type**

348　Precipitation, temperature and soil can affect leaf elements via changing element
349　allocation among plant organs, altering plant metabolism or influencing nutrient uptake
350　by roots (Ordoñez et al., 2009). In addition to MAP, MAT and soil nutrient, we first

351 added RDI to examine the effect of local drought extent. Among the four environmental

352 parameters, it is interesting to note that RDI was positively correlated with leaf N and

353 P (Table 2). By contrast, MAP was not correlated with all the leaf C:N:P traits. This was

354 inconsistent with previous reports that MAP played an important role for the leaf

355 elements of different vegetation types (Santiago et al., 2004; Han et al., 2011). Firstly,

356 among the 125 sampling sites, only 7 sites belonged to the severe and extreme drought

357 regions (RDI < –1.5). The water conditions of other sites were mild, slight drought, or

358 wet (–1.0 < RDI < 2), which may be suitable for shrub growth and could not become a

359 limiting factor. Secondly, it is proposed that MAP could not accurately reflect the real

360 water situation due to different temperatures and evapotranspiration rates. RDI may be

361 more appropriate for evaluating the impact of water status. The wetter climatic

362 conditions (i.e., larger RDI) could provide more soluble N and P in soil and enhance

363 the nutrient transportation of shrub.

364 Increased MAT was found to be related with the decrease of leaf C in the SMR

365 analysis. This result was in agreement with a meta-analysis of C stores conducted in 13

366 different global mountains (Hoch and Körner, 2012). The large MAT gradient (–4.67

367 ºC to 22.16 ºC) on the plateau could strongly affect the shrub photosynthesis process.

368 Shrub species at higher elevations probably need to protect themselves against low

369 temperatures and make osmotic adjustments via increasing leaf C contents (Millard et

370 al., 2007). By contrast, MAT could not account for the leaf N in shrubs, which was

371 inconsistent with the opinion that leaf N contents are usually affected by temperature

372 (Wright et al., 2005). This unexpected phenomenon may result from the large

373 heterogeneity in N uptake capacities of different shrub species along the climatic

374 gradients (CV of leaf N reaches up to 30.4%). Moreover, the drought severity was so

375 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

401   species, providing further evidence that the large heterogeneity in shrub nutrient uptake

402   capacities and physiological adaptation to environments governed the leaf nutrient

403   variations.

404   For instance, alpine and subalpine shrubs had higher leaf C than the other two

405   ecosystem types (Table 1 and Appendix A: Table A2), and this trend was consistent with

406   the cold acclimation mechanism as discussed previously (Hoch and Körner, 2012).

407   Alpine shrub exhibited higher leaf N and P than subalpine and montane shrubs located

408   in low-altitude regions ($P < 0.001$). This result agreed with the Temperature-Plant

409   Physiological Hypothesis (Weih and Karlsson, 2001; Zhang et al., 2017). In high-

410   altitude area, the growing season was short, and accompanied by lower temperature.

411   Hence, shrubs might increase their nutrient absorption to compensate for lower enzyme

412   efficiency and metabolic rate. It should be also noted that the valley shrub possessed

413   the greatest leaf N and high leaf P, especially at altitude of about 1500 m. This result

414   could be explained by the remarkably different landform of valley region from those of

415   montane and subalpine areas with overlapping elevations, which caused distinctive

416   local climate and shrub species in valley. On the one hand, the uplift and geological

417   evolution of the Tibetan Plateau induced steep canyons and longitudinal range-gorge

418   regions, with towering mountains and deep valleys arranged vertically side by side

419   (Royden et al., 2008; Pan et al., 2012). The downvalley wind could result in foehn effect

420   that is characterized by an increase in evaporation rate and a decrease in relative

421   humidity (Hornsteiner, 2005; Li et al., 2007). Consequently, the MAT values of valley

422   sites were higher than montane, subalpine and alpine sites ($P < 0.05$, Appendix A: Table

423   A1), indicating faster organic matter decomposition as predicted by the Biogeochemical

424   Hypothesis (Aerts and Chapin, 1999). On the other hand, due to the special local

425   topography and climate, the shrubs in valley were mostly drought-tolerant plants (e.g.,

426 *Bauhinia brachycarpa* and *Cotinus coggygria*), which belonged to short-lived, fast-

427 growing deciduous broadleaf functional type. These valley species exhibited faster litter

428 decomposition and nutrient resorption abilities than long-lived, slow-growing

429 evergreen types (Güsewell and Koerselman, 2002; Diehl et al., 2003).

430   Large differences in leaf elements also occurred across functional types (Table 1

431 and Appendix A: Table A2). Leaf C contents in evergreen broadleaf and evergreen

432 conifer shrubs were higher than deciduous broadleaf shrub, agreeing with the higher

433 non-structural C accumulated in evergreen shrub leaves (average altitude: 3430 m) to

434 resist freezing than deciduous shrub (average altitude: 2343 m). On the contrary, leaf N

435 was larger in deciduous broadleaf shrub than in evergreen shrub types ($P < 0.01$). This

436 result was ascribed to higher nutrient resorption in deciduous species than in evergreen

437 species (Güsewell and Koerselman, 2002). Moreover, lower leaf C:N and C:P ratios

438 were observed in deciduous shrub than evergreen shrubs ($P < 0.05$), further indicating

439 faster litter decomposition process of deciduous shrub (Bui and Henderson, 2013).

440 These differences of element levels among functional types indicate the variations in

441 leaf nutrient acquisition abilities.

442   Plant nutrient acquisition strategy could also affect leaf nutrient levels of different

443 shrub species. It is well known that most plants belonging to Ericales are able to

444 associate with soil fungi and form ericoid mycorrhiza (Perotto et al., 2002). This

445 happens especially in high-altitude environment where plant litter decomposes slowly,

446 leading to acidic soils rich in recalcitrant organic matter but low in available mineral

447 nutrients (Cairney and Burke, 1998). Previous studies have reported that ericoid

448 mycorrhiza or arbuscular mycorrhizal fungi (AMF) were associated with diverse

449 rhododendrons in southwestern China and central Himalayan (Chaurasia et al., 2005;

450 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.

student Hui Yang from Peking University for calculating MAP and MAT data. The China Meteorological Forcing Dataset used in this study was developed by Data Assimilation and Modeling Center for Tibetan Multi-spheres, Institute of Tibetan Plateau Research.

References

Aerts, R., and Chapin III, F. S.: The mineral nutrition of wild plants revisited: A re-evaluation of processes and patterns, Adv. Ecol. Res., 30, 1−67, 1999.

Allen, A. P., and Gillooly, J. F.: Towards an integration of ecological stoichiometry and the metabolic theory of ecology to better understand nutrient cycling, Ecol. Lett., 12, 369−384, 2009.

Bui, E. N., and Henderson, B. L.: C:N:P stoichiometry in Australian soils with respect to vegetation and environmental factors, Plant Soil, 373, 553−568, 2013.

Cairney, J. W. G., and Burke, R. M.: Extracellular enzyme activities of the ericoid mycorrhizal endophyte *Hymenoscyphus ericae* (Read) Korf & Kernan: their likely roles in decomposition of dead plant tissue in soil, Plant Soil, 205, 181–192, 1998.

Campo, J., and Dirzo, R.: Leaf quality and herbivory responses to soil nutrient addition in secondary tropical dry forests of Yucatán, Mexico, J. Trop. Ecol., 19, 525–530, 2003.

Chaurasia, B., Pandey, A., and Palni, L. M. S.: Distribution, colonization and diversity of arbuscular mycorrhizal fungi associated with central Himalayan rhododendrons, Forest Ecol. Manag, 207, 315–324, 2005.

Chen, Y., Han, W., Tang, L., Tang, Z., and Fang, J.: Leaf nitrogen and phosphorus concentrations of woody plants differ in responses to climate, soil and plant growth form, Ecography, 36, 178–184, 2013a.

526 Chen, Y., Qu, L. Y., Ma, K. M., Yang, X. Y.: The community composition of arbuscular

527 mycorrhizal fungi in the rhizosphere of *Bauhinia faberi* var. *microphylla* in the dry

528 valley of Minjiang River, Mycosystema, 35, 39–51, 2016.

529 Chen, Y., Yang, K., He, J., Qin, J., Shi, J., Du, J., and He, Q.: Improving land surface

530 temperature modeling for dry land of China, J. Geophys. Res., 116, 999−1010, 2011.

531 Chen, H., Zhu, Q., Peng, C., Wu, N., Wang, Y., Fang, X., Gao, Y., Zhu, D., Yang, G.,

532 Tian, J., Kang, X., Piao, S., Ouyang, H., Xiang, W., Luo, Z., Jiang, H., Song, X.,

533 Zhang, Y., Yu, G., Zhao, X., Gong, P., Yao, T., and Wu, J.: The impacts of climate

534 change and human activities on biogeochemical cycles on the Qinghai-Tibetan

535 Plateau, Glob. Change Biol., 19, 2940−2955, 2013b.

536 Diehl, P., Mazzarino, M. J., Funes, F., Fontenla, S., Gobbi, M., and Ferrari, J.: Nutrient

537 conservation strategies in native Andean-Patagonian forests, J. Veg. Sci., 14, 63−70,

538 2003.

539 Elser, J. J., Fagan, W. F., Denno, R. F., Dobberfuhl, D. R., Folarin, A., Huberty, A.,

540 Interlandi, S., Kilham, S. S., McCauley, E., and Schulz, K. L.: Nutritional

541 constraints in terrestrial and freshwater food webs, Nature, 408, 578−580, 2000.

542 Elser, J. J., Fagan, W. F., Kerkhoff, A. J., Swenson, N. G., and Enquist, B. J.: Biological

543 stoichiometry of plant production: metabolism, scaling and ecological response to

544 global change, New Phytol., 186, 593−608, 2010.

545 Fisher, J. B., Malhi, Y., Torres, I. C., Metcalfe, D. B., van de Weg, M. J., Meir, P., Silva-

546 Espejo, J. E., and Huasco, W. H.: Nutrient limitation in rainforests and cloud forests

547 along a 3,000-m elevation gradient in the Peruvian Andes, Oecologia, 172, 889−902,

548 2013.

549 Güsewell, S., and Koerselman, W.: Variation in nitrogen and phosphorus concentrations

550 of wetland plants, Perspect. Plant Ecol. Evol. Syst., 5, 37−61, 2002.

Han, W., Fang, J., Guo, D., and Zhang, Y.: Leaf nitrogen and phosphorus stoichiometry across 753 terrestrial plant species in China, New Phytol., 168, 377−385, 2005.

Han, W., Fang, J., Reich, P.B., Ian Woodward, F., and Wang, Z.: Biogeography and variability of eleven mineral elements in plant leaves across gradients of climate, soil and plant functional type in China, Ecol. Lett., 14, 788−796, 2011.

He, J. S., Fang, J., Wang, Z., Guo, D., Flynn, D. F. B., and Geng, Z.: Stoichiometry and large-scale patterns of leaf carbon and nitrogen in the grassland biomes of China, Oecologia, 149, 115−122, 2006.

Hedin, L. O., Vitousek, P. M., and Matson, P. A.: Nutrient losses over four million years of tropical forest development, Ecology, 84, 2231−2255, 2003.

Heikkinen, R. K., Luoto, M., Kuussaari, M., and Pöyry, J.: New insights into butterfly-environment relationships using partitioning methods, P. Roy. Soc. B-Biol. Sci., 272, 2203−2210, 2005.

Hoch, G., and Körner, C.: Global patterns of mobile carbon stores in trees at the high-elevation tree line, Glob. Ecol. Biogeogr., 21, 861−871, 2012.

Hoch, G., Popp, M., and Körner, C.: Altitudinal increase of mobile carbon pools in *Pinus cembra* suggests sink limitation of growth at the Swiss treeline, Oikos, 98, 361−374, 2002.

Hornsteiner, M.: Local foehn effects in the upper Isar Valley, part 1: Observations, Meteorol. Atmos. Phys., 88, 175−192, 2005.

Khalili, D., Farnoud, T., Jamshidi, H., Kamgar-Haghighi, A. A., and Zand-Parsa, S.: Comparability analyses of the SPI and RDI meteorological drought indices in different climatic zones, Water Resour. Manag., 25, 1737−1757, 2011.

Koerselman, W., and Meuleman, A. F. M.: The vegetation N: P ratio: A new tool to detect the nature of nutrient limitation, J. Appl. Ecol., 33, 1441–1450, 1996.

Kuo, S.: Phosphorus. Methods of Soil Analysis. Part 3: Chemical methods. In D. L. Sparks (Ed.), Soil Science Society of America, Madison, Wisconsin, 1996.

Ladanai, S., Ågren, G. I., and Olsson, B. A.: Relationships between tree and soil properties in Picea abies and Pinus sylvestris forests in Sweden, Ecosystems, 13, 302–316, 2010.

Li, Y., Liu, X., Zheng, S., Chen, H., Yue, Y., Mu, C., and Liu, J.: Drought-resistant physiological characteristics of four shrub species in arid valley of Minjiang River, China, Acta Ecologica Sinica, 27, 870–877, 2007.

Macek, P., Klimeš, L., Adamec, L., Doležal, J., Chlumská, Z., de Bello, F., Dvorský, M., and Řeháková, K.: Plant nutrient content does not simply increase with elevation under the extreme environmental conditions of Ladakh, NW Himalaya, Arctic, Antarct Alpine Res., 44, 62−66, 2012.

Matzek, V., and Vitousek, P. M.: N:P stoichiometry and protein:RNA ratios in vascular plants: an evaluation of the growth-rate hypothesis, Ecol. Lett., 12, 765−771, 2009.

Mcavaney, B., Covey, C., Joussaume, S., Kattsov, V., Kitoh, A., Ogana, W., and Zhao, Z.: IPCC. Climate change 2001: the scientific basis. Contribution of working group I to the third assessment report of the intergovernmental panel on climate, Cambridge, UK: Cambridge University Press, 2001.

McGroddy, M. E., Daufresne, T., and Hedin, L. O.: Scaling of C:N:P stoichiometry in forests worldwide: implications of terrestrial Redfield-type ratios, Ecology, 85, 2390–2401, 2004.

Millard, P., Sommerkorn, M., and Grelet, G. A.: Environmental change and carbon limitation in trees: a biochemical, ecophysiological and ecosystem appraisal, New Phytol., 175, 11−28, 2007.

Näsholm, T., and Persson, J.: Plant acquisition of organic nitrogen in boreal forests,

601 Physiol. Plant, 111, 419−426, 2001.

602 Nogués-Bravo, D., Araújo, M. B., Romdal, T., and Rahbek, C.: Scale effects and human

603 impact on the elevational species richness gradients, Nature, 453, 216−219, 2008.

604 Ordoñez, J. C., Van Bodegom, P. M., Witte, J. P. M., Wright, I. J., Reich, P. B., and

605 Aerts, R.: A global study of relationships between leaf traits, climate and soil

606 measures of nutrient fertility, Glob. Ecol. Biogeogr., 18, 137–149, 2009.

607 Pan, T., Wu, S., He, D., Dai, E., and Liu, Y.: Ecological effects of longitudinal range-

608 gorge land surface pattern and its regional differentiation, Acta Geographica Sinica,

609 67, 13–26, 2012.

610 Perotto, S., Girlanda, M., and Martino, E.: Ericoid mycorrhizal fungi: some new

611 perspectives on old acquaintances, Plant Soil, 244, 41−53, 2002.

612 Piao, S., Fang, J., Ciais, P., Peylin, P., Huang, Y., Sitch, S., and Wang, T.: The carbon

613 balance of terrestrial ecosystems in China, Nature, 458, 1009−1013, 2009.

614 Reich, P. B., and Oleksyn, J.: Global patterns of plant leaf N and P in relation to

615 temperature and latitude, Proc. Natl. Acad. Sci., 101, 11001−11006, 2004.

616 Royden, L. H., Burchfiel, B. C., and van der Hilst, R. D.: The geological evolution of

617 the Tibetan Plateau, Science, 321, 1054−1058, 2008.

618 Santiago, L. S., Kitajima, K., Wright, S. J., and Mulkey, S. S.: Coordinated changes in

619 photosynthesis water relations and leaf nutritional traits of canopy trees along a

620 precipitation gradient in lowland tropical forest, Oecologia, 139, 495–502, 2004.

621 Sardans, J., Alonso, R., Janssens, I. A., Carnicer, J., Vereseglou, S., Rillig, M. C.,

622 Fernández-Martínez, M., Sanders, T. G. M., and Peñuelas, J.: Foliar and soil

623 concentrations and stoichiometry of nitrogen and phosphorous across European

624 Pinus sylvestris forests: relationships with climate, N deposition and tree growth,

625 Funct. Ecol., 30, 676–689, 2016.

626 Sardans, J., Rivas-Ubach, A., and Peñuelas, J.: The C:N:P stoichiometry of organisms

627   and ecosystems in a changing world: a review and perspectives, Perspect. Plant.

628   Ecol. Evol. Syst., 14, 33–47, 2012.

629 Soethe, N., Lehmann, J., and Engels, C.: Nutrient availability at different altitudes in a

630   tropical montane forest in Ecuador, J. Trop. Ecol., 24, 397−406, 2008.

631 Stern, R. W., and Elser, J. J.: Ecological stoichiometry: the biology of elements from

632   molecules to the biosphere, Princeton: Princeton University Press, 2002.

633 Tang, Z., Wang, Z., Zheng, C., and Fang, J.: Biodiversity in China's mountains, Front.

634   Ecol. Environ., 4, 347−352, 2006.

635 Thompson, K., Parkinson, J. A., Band, S. R., and Spencer, R. E.: A comparative study

636   of leaf nutrient concentrations in a regional herbaceous flora, New Phytol., 136,

637   679−689, 1997.

638 Thornthwaite, C. W.: An approach toward a rational classification of climate, Geogr.

639   Rev., 38, 55−89, 1948.

640 Tian, W., Zhang, C. Q., Qiao, P., and Milne, R.: Diversity of culturable ericoid

641   mycorrhizal fungi of *Rhododendron decorum* in Yunnan, China, Mycologia, 103,

642   703–709, 2011.

643 Tibbets, T. M., and Molles, M. C.: C : N : P stoichiometry of dominant riparian trees

644   and arthropods along the Middle Rio Grande, Freshwater Biol., 50, 1882–1894,

645   2005.

646 Townsend, A. R., Cleveland, C. C., Asner, G. P., and Bustamante, M. M.: Controls over

647   foliar N:P ratios in tropical rain forests, Ecology, 88, 107−118, 2007.

648 Tsakiris, G., and Vangelis, H.: Establishing a drought index incorporating

649   evapotranspiration, Eur. Water, 9−10, 3−11, 2005.

650 Tsakiris, G., Pangalou, D., and Vangelis, H.: Regional drought assessment based on the

651   Reconnaissance Drought Index (RDI), Water Resour. Manag., 21, 821−833, 2007.

652   van de Weg, M. J., Meir, P., Grace, J., and Atkin, O. K.: Altitudinal variation in leaf

653   mass per unit area, leaf tissue density and foliar nitrogen and phosphorus content

654   along an Amazon-Andes gradient in Peru, Plant Ecol. Divers., 2, 243−254, 2009.

655   Vangelis, H., Tigkas, D., and Tsakiris, G.: The effect of PET method on Reconnaissance

656   Drought Index (RDI) calculation, J. Arid Environ., 88, 130−140, 2013.

657   Venterink, H. O., and Güsewell, S.: Competitive interactions between two meadow

658   grasses under nitrogen and phosphorus limitation, Funct. Ecol., 24, 877−886, 2010.

659   Walbridge, M. R., Richardson, C. J., and Swank, W. T.: Vertical distribution of

660   biological and geochemical phosphorus subcycles in two southern Appalachian

661   forest soils, Biogeochemistry, 13, 61–85, 1991.

662   Weih, M., and Karlsson, P. S.: Growth response of mountain birch to air and soil

663   temperature: is increasing leaf-nitrogen content an acclimation to lower air

664   temperature? New Phytol., 150, 147–155, 2001.

665   Worboys, G. L., and Good, R. B.: Caring for our Australian Alps catchments: summary

666   report for policy makers. Department of Climate Change & Energy Efficiency,

667   Canberra, Australia, 2011.

668   Wright, I. J., Reich, P. B., Cornelissen, J. H. C., Falster, D. S., Garnier, E., Hikosaka,

669   K., Lamont, B. B., Lee, W., Oleksyn, J., Osada, N., Poorter, H., Villar, R., Warton,

670   D. I., and Westoby, M.: Assessing the generality of global leaf trait relationships,

671   New Phytol., 166, 485−496, 2005.

672   Xia, C., Yu, D., Wang, Z., and Xie, D.: Stoichiometry patterns of leaf carbon, nitrogen

673   and phosphorous in aquatic macrophytes in eastern China, Ecol. Eng., 70, 406−413,

674   2014.

675   Yang, K., He, J., Tang, W., Qin, J., and Cheng, C. C. K.: On downward shortwave and

longwave radiations over high altitude regions: observation and modeling in the Tibetan Plateau, Agr. Forest. Meteorol., 150, 38−46, 2010.

Zhang, J., Zhao, N., Liu, C., Yang, H., Li, M., Yu, G., Wilcox, K., Yu, Q., and He, N.: C:N:P stoichiometry in China's forests: From organs to ecosystems, Funct. Ecol., DOI: 10.1111/1365-2435.12979, 2017.

Zhao, N., He, N., Wang, Q., Zhang, X., Wang, R., Xu, Z., and Yu, G.: The altitudinal patterns of leaf C:N:P stoichiometry are regulated by plant growth form, climate and soil on Changbai Mountain, China, Plos One, 9, e95196, 2014.

Zheng, S., and Shangguan, Z.: Spatial patterns of leaf nutrient traits of the plants in the Loess Plateau of China, Trees, 21, 357−370, 2007.

701
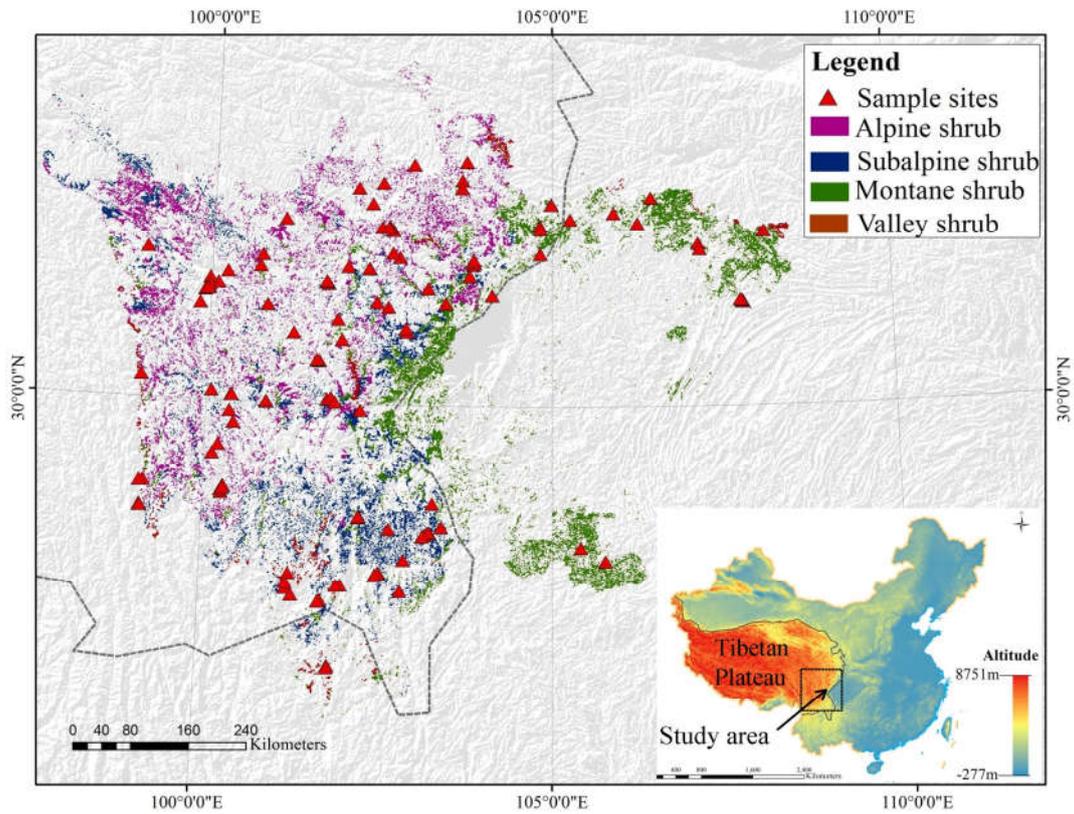
Figure 1. Locations of the southeastern Tibetan Plateau and 125 sample sites in

mountainous areas. The purple, blue, green, and brown areas stand for the distribution

of alpine, subalpine, montane and valley shrub types, respectively.

716
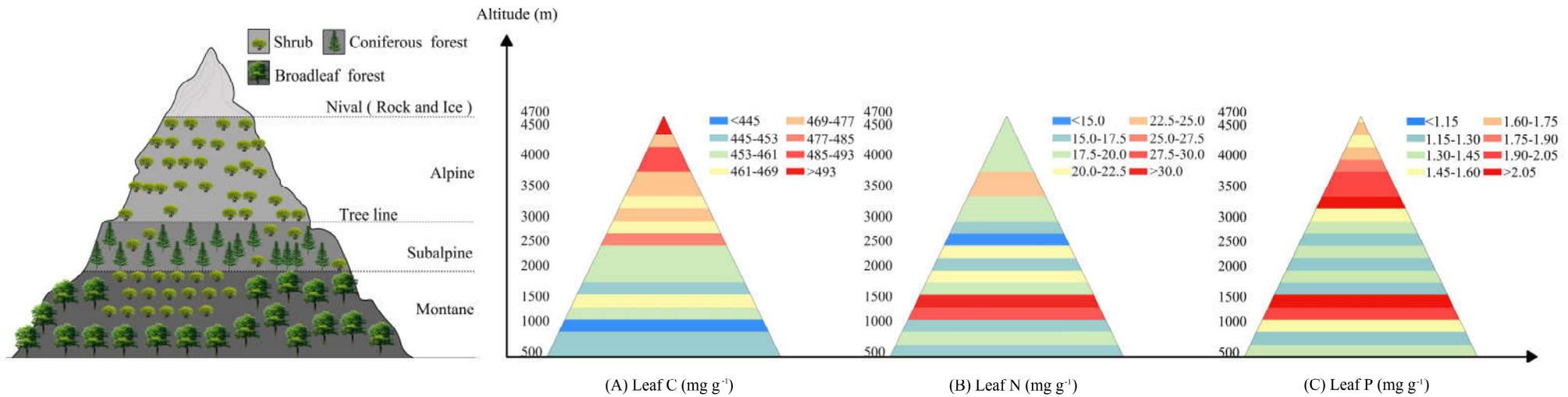
Figure 2. Vertical distribution of leaf C, N and P contents of mountainous shrubs on the Tibetan Plateau. Alpine shrub occurs at relatively higher altitude (3091−4685 m, above tree line), followed by subalpine shrub (2000−4078 m, coniferous forest zone), montane shrub (523−3342 m, broadleaf forest zone) and valley shrub (600−2350 m, valley region).

720

721

(A) Full model for leaf C: 45.2

Climate: 16.1   Soil: 11.7

c 0.1   cs 0.2   s 1.0
ct 6.7   cst 9.2   st 1.4
t 26.6

Shrub type: 43.9

(B) Full model for leaf N: 46.5

Climate: 7.8   Soil: 0

c 0.4   cs 0   s 0
ct 7.4   cst 0   st 0
t 38.7

Shrub type: 46.1

(C) Full model for leaf P: 45.5

Climate: 10.8   Soil: 21.6

c 0   cs -27.1   s 34.7
ct 4.7   cst 33.2   st -19.2
t 19.2

Shrub type: 37.9

(D) Full model for C:N ratio: 50.0

Climate: 5.3   Soil: 0

c 0.3   cs 0   s 0
ct 5.0   cst 0   st 0
t 44.7

Shrub type: 49.7

(E) Full model for C:P ratio: 46.0

Climate: 9.8   Soil: 18.5

c 0   cs 0   s 7.5
ct 4.4   cst 5.4   st 5.6
t 23.1

Shrub type: 38.5

(F) Full model for N:P ratio: 54.5

Climate: 0   Soil: 9.9

c 0   cs 0   s 0.7
ct 0   cst 0   st 9.2
t 44.7

Shrub type: 53.9

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).

738 **Table 1.** Geometric means and standard deviations of leaf element concentrations and ratios for all shrub samples, and specific shrub type and

739 species on the Tibetan Plateau. Ecosystem types include shrubs that located at different altitudinal belts. Functional types are classified based on

740 different leaf traits. Coefficients of variation (CV, %) are in parentheses. n represents the number of shrub samples. Comparisons of geometric

741 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%)

742

743 **Table 2.** Model summary for the stepwise multiple regression (SMR) of leaf element

744 concentrations and ratios of all shrub samples on climatic and soil variables (MAT, MAP,

745 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
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

746 *, **, and *** denote significance at the 0.05, 0.01, 0.001 test level, respectively. For

747 partial regression coefficients, "+" indicates a positive correlation and "−" indicates a

748 negative correlation. MAT, mean annual temperature; MAP, mean annual precipitation;

749 RDI, standardized form of Reconnaissance Drought Index. Soil represents

750 corresponding soil element or ratio relative to leaf element or ratio. Leaf element

751 concentrations and ratios were $\log_{10}$-transformed before analysis.

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762   **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

763   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

764   * 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.

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Appendix A: Additional tables

767   **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

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

769 **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*	$P = 1.000$	$P > 0.05$	$P = 0.841$	$P = 0.784$	$P > 0.05$	$P = 1.000$

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

771   **Table A3.** Partial correlation coefficients between the geographic variables and leaf

772   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

773   *, **, and *** denote significance at the 0.05, 0.01, 0.001 test level, respectively. For partial

774   correlation coefficients, "+" indicates a positive correlation and "−" indicates a negative correlation.

775   Leaf element concentrations and ratios were $\log_{10}$-transformed before analysis.

776 **Table A4.** Model summary for the stepwise multiple regression (SMR) of leaf element

777 concentrations of different ecosystem types on the climatic and soil variables (MAT,

778 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
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	–	–	–

779 *, **, and *** denote significance at the 0.05, 0.01, 0.001 test level, respectively. For partial

780 regression coefficients, "+" indicates a positive correlation and "−" indicates a negative correlation.

781 Soil represents corresponding soil element or ratio relative to leaf element or ratio. Leaf element

782 concentrations and ratios were $\log_{10}$-transformed before analysis.

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Table A5. Model summary for the stepwise multiple regression (SMR) of leaf element

784　concentrations of different functional types on the climatic and soil variables (MAT,

785　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	–	–	–

786　*, **, and *** denote significance at the 0.05, 0.01, 0.001 test level, respectively. For partial

787　regression coefficients, "+" indicates a positive correlation and "−" indicates a negative correlation.

788　MAT, mean annual temperature; MAP, mean annual precipitation; RDI, standardized form of

789　Reconnaissance Drought Index. Soil represents corresponding soil element or ratio relative to leaf

790　element or ratio. Leaf element concentrations and ratios were $\log_{10}$-transformed before analysis.

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794 **Table A6.** Model summary for the stepwise multiple regression (SMR) of leaf element

795 concentrations of dominant shrub species on the climatic and soil variables (MAT, MAP,

796 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	–	–	–	–	–	–	–	–	–

797 *, **, and *** denote significance at the 0.05, 0.01, 0.001 test level, respectively. For partial

798 regression coefficients, "+" indicates a positive correlation and "−" indicates a negative correlation.

799 MAT, mean annual temperature; MAP, mean annual precipitation; RDI, standardized form of

800 Reconnaissance Drought Index. Soil represents corresponding soil element or ratio relative to leaf

801 element or ratio. Leaf element concentrations and ratios were log_{10}-transformed before analysis.

Appendix B: Additional figures
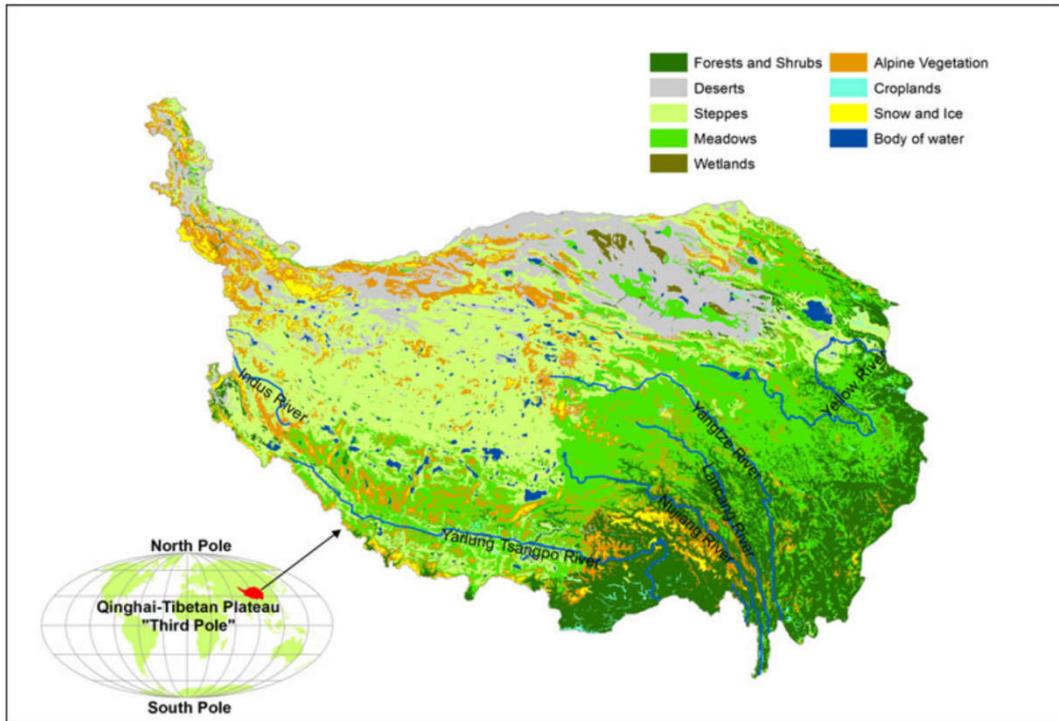
Figure B1. Distribution of vegetation types on the Tibetan Plateau, which is regarded as the "third pole" of the Earth. The complex climate conditions cause a diverse vegetation pattern, resulting in the local plant communities highly sensitive to global climate change. The southeastern margin of the plateau is dominated by shrubs and forests. This figure was originated from reference (Chen et al., 2013).
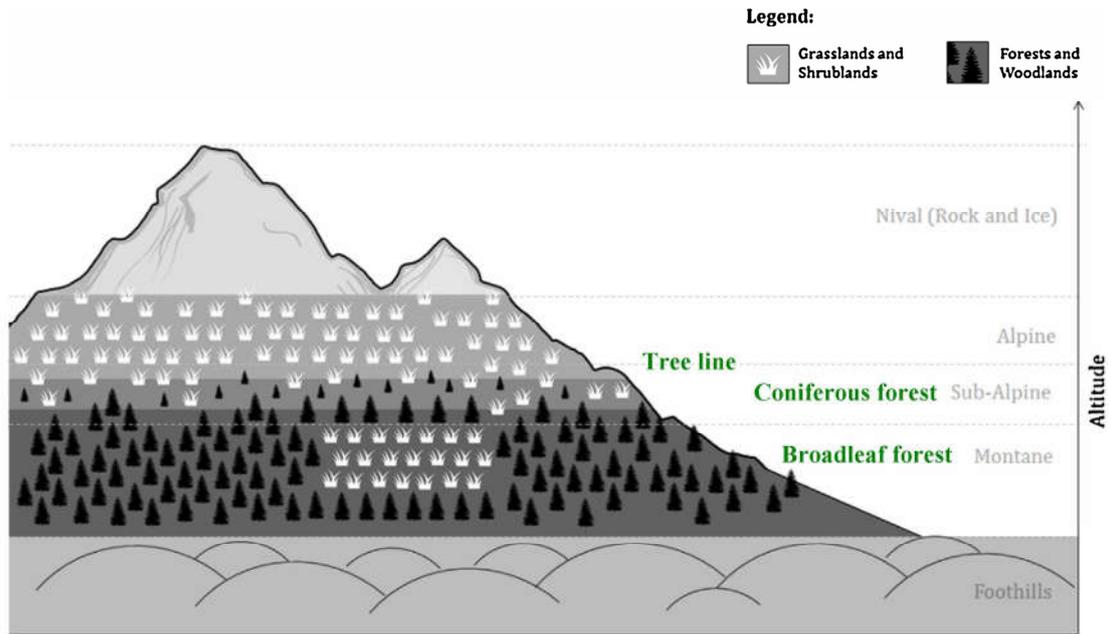
Figure B2. Diagram illustrating the delineation of montane, subalpine, alpine, and nival altitudinal belts relative to the location of shrubland and grassland ecosystems. Various shrub species are able to live in these altitudinal belts at the life form limit for shrubs, and could not be found in the nival belt. This figure was obtained from references (Mcavaney et al., 2001; Worboys and Good, 2011).

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834 **Figure B3.** Representative photos of (A) alpine, (B) subalpine, (C) montane, and (D)

835 valley shrubs on the Tibetan Plateau.

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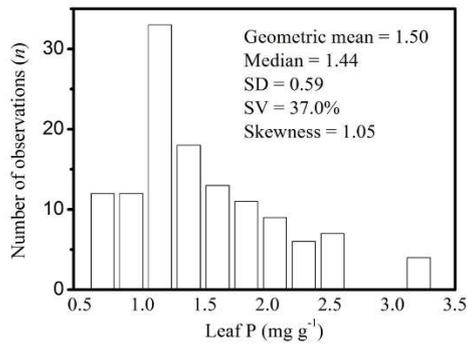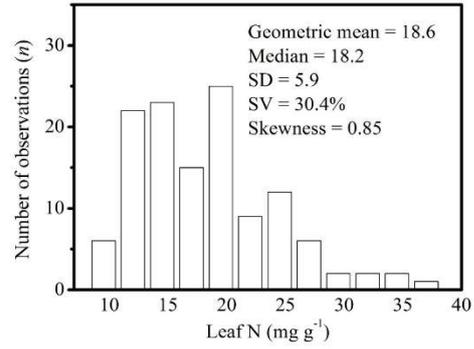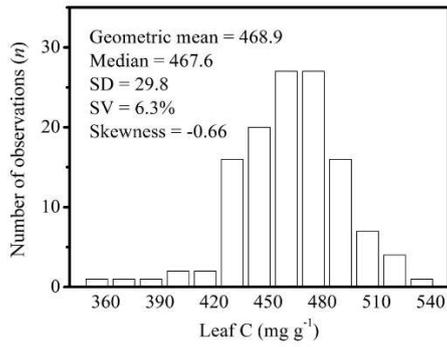
Figure B4. Distribution of leaf C, N and P concentrations of all shrubs on the Tibetan

Plateau.

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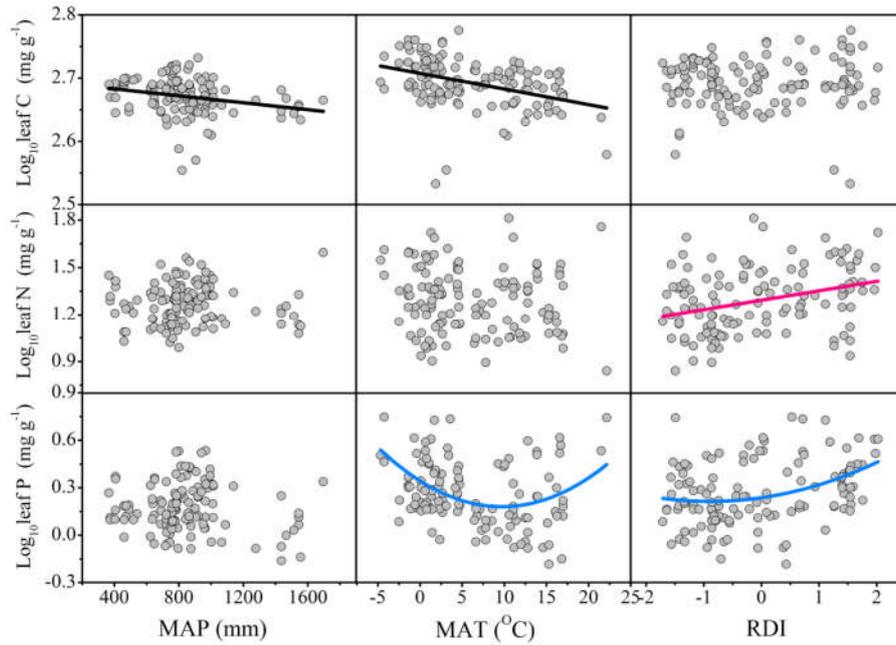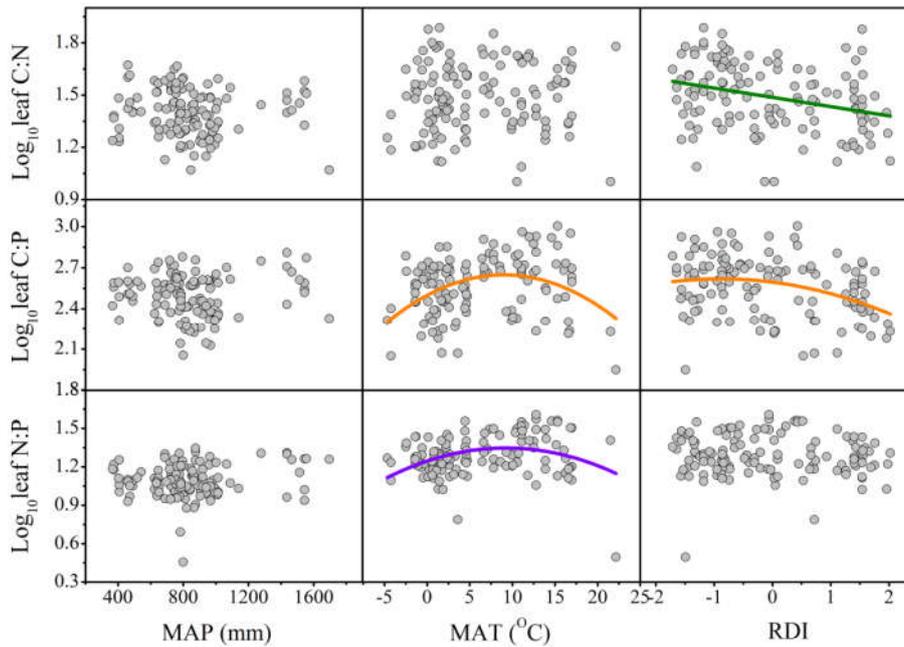
Figure B5. Variation trends of leaf C:N:P stoichiometry as a function of climatic factors.

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.

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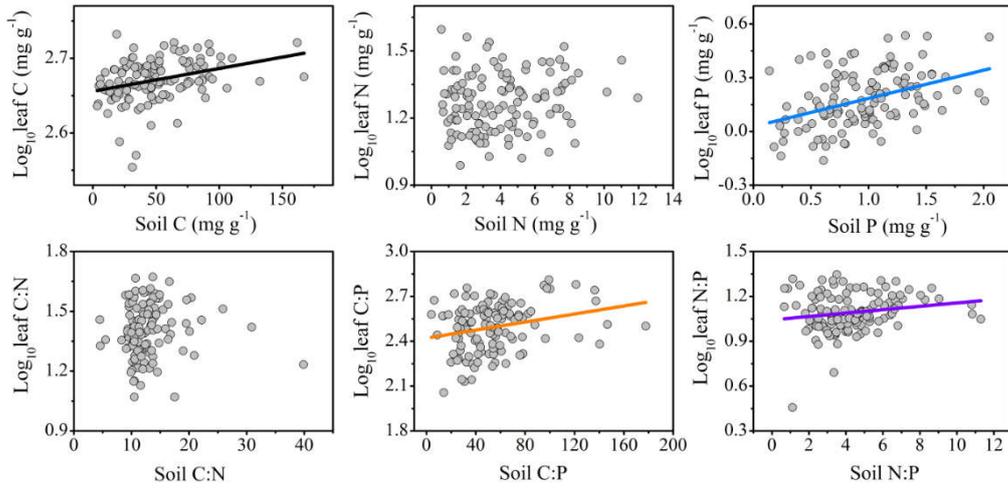
Figure B6. Variation trends of leaf C:N:P stoichiometry as a function of soil C:N:P. Data points indicate every observation of shrub stoichiometry within the sampling sites ($n = 125$). Lines are plotted if regressions were significant at $P < 0.05$. Leaf element concentrations and ratios were $\log_{10}$-transformed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

887   **Appendix C: Additional methods**

888   **Calculation of the Reconnaissance Drought Index (RDI$_{st}$)**

889   Drought severity can be evaluated via the computation of the RDI$_{st}$. RDI was proposed

890   by Tsakiris and Vangelis (2005), utilizing the ratios of precipitation over potential

891   evapotranspiration (PET) for different time scales, to be representative of the region of

892   interest (Khalili et al., 2011). The initial value of RDI (RDI$_\alpha$) is usually calculated for

893   the i-th year in a time basis of 12 consecutive months as follows:

894    $$\text{RDI}_\alpha{}^{(i)} = \frac{\sum\limits_{j=1}^{12} \text{P}_{ij}}{\sum\limits_{j=1}^{12} \text{PET}_{ij}}, \; i = 1(1)\text{N and } j = 1(1)12 \qquad (1)$$

895   where P$_{ij}$ and PET$_{ij}$ are the precipitation and potential evapotranspiration of the j-th

896   month of the i-th year, respectively, and N is the total number of years of the available

897   data (N = 25 in this study). PET was calculated using the Thornthwaite method

898   (Thornthwaite, 1948).

899   As the next step, RDI$_{st}$ for a hydrological year (12-month reference period) is

900   computed based on the following equation:

901    $$\text{RDI}_{st}{}^{(i)} = \frac{\gamma^{(i)} - \overline{\gamma}}{\sigma_\gamma} \qquad (2)$$

902   where $\gamma^{(i)}$ is the $\ln(\text{RDI}_\alpha{}^{(i)})$, $\overline{\gamma}$ is the arithmetic mean and σ_γ is the standard

903   deviation of $\ln(\text{RDI}_\alpha)$. The RDI$_\alpha$ values are assumed to follow the lognormal

904   distribution, which has been found to be the most appropriate (Tsakiris et al., 2007;

905   Vangelis et al., 2013). The calculation process was conducted by using DrinC software.

906