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1 **Shrub type dominates the vertical distribution of leaf C:N:P stoichiometry across**

2 **an extensive altitudinal gradient**

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26   **Abstract.** Understanding the leaf stoichiometric patterns is crucial for improving

27   predictions on plant responses to environmental changes. Leaf stoichiometry of

28   terrestrial ecosystems has been widely investigated along latitudinal and longitudinal

29   gradients. Still, very little is known on the vertical distribution of leaf C:N:P and the

30   relative effects of environmental parameters, especially for shrubs. Here, we analyzed

31   the shrub leaf C, N and P patterns in 125 mountainous sites over an extensive altitudinal

32   gradient (523−4685 m) on the Tibetan Plateau. Results showed that the shrub leaf C

33   and C:N were 7.3%−47.5% higher than those of other regional and global flora,

34   whereas the leaf N and N:P were 10.2%−75.8% lower. Leaf C increased with rising

35   altitude and decreasing temperature, supporting the physiological acclimation

36   mechanism that high leaf C (e.g., alpine or evergreen shrub) could balance the cell

37   osmotic pressure and resist freezing. The largest leaf N and high leaf P occurred in

38   valley region (altitude 1500 m), likely due to the large nutrient leaching from higher

39   elevations, faster litter decomposition and nutrient resorption ability of deciduous

40   broadleaf shrub. Leaf N:P ratio further indicated increasing N limitation at higher

41   altitudes. Interestingly, the drought severity was the only climatic factor positively

42   correlated with leaf N and P, which was more appropriate for evaluating the impact of

43   water status than precipitation. Among the shrub ecosystem and functional types (alpine,

44   subalpine, montane, valley, evergreen, deciduous, broadleaf, and conifer), their leaf

45   element contents and responses to environments were remarkably different. Shrub type

46   was the largest contributor to the total variations in leaf stoichiometry, while climate

47   indirectly affected the leaf C:N:P via its interactive effects on shrub type or soil.

48   Collectively, the large heterogeneity in shrub type was the most important factor

49   explaining the overall leaf C:N:P variations, despite the broad climate gradient on the

50   plateau. Temperature- and drought-induced shift of shrub type distribution will

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51   influence the nutrient accumulation in mountainous shrubs.

52   **Keywords.** leaf stoichiometry, mountainous shrub, altitudinal gradient, drought

53   severity, temperature, precipitation, soil nutrient

54

55   **1 Introduction**

56   Ecological stoichiometry examines the interactions among organisms' element

57   composition and their environments, which provides an effective way to enhance our

58   understanding of ecosystem function and nutrient cycling (Allen and Gillooly, 2009;

59   Venterink and Güsewell, 2010). Over the past decades, great attention has been paid to

60   the leaf stoichiometry of terrestrial plants at regional (Townsend et al., 2007; Matzek

61   and Vitousek, 2009), national (Han et al., 2011; Sardans et al., 2016), and global scales

62   (Elser et al., 2000; Reich and Oleksyn, 2004). The leaf macroelements (carbon, nitrogen

63   and phosphorus) were widely explored to indicate nutrient limitation and its response

64   to environmental change (Elser et al., 2010). Investigating the interactions among leaf

65   stoichiometry and the environment along geographic gradients is ctritical to understand

66   the nutrient cycling process and the development of biogeochemical models.

67   Nowadays, it is increasingly rare to localize and work on extensive and natural

68   altitudinal gradient varying from low to high-altitude mountaintops (Nogués-Bravo et

69   al., 2008). A few studies have investigated the variations of leaf N and P at several

70   elevations (Soethe et al., 2008; van de Weg et al., 2009; Fisher et al., 2013; Zhao et al.,

71   2014); however, the scientists reported different altitudinal trends for leaf N and P. For

72   instance, Soethe et al. (2008) found that the foliar N and P concentrations of trees, herbs

73   and shrubs were largest at 1900 m than 2400 m and 3000 m in an Ecuadorian montane

74   forest. van de Weg et al. (2009) observed that the foliar P along an altitudinal transect

75   (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

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101   *Quercus monimotricha*). Consequently, the Tibetan Plateau can provide a more general

102   representation of the stoichiometry of various shrub types, which is an ideal site for

103   examining the altitudinal patterns and environmental variables influencing shrub

104   stoichiometry.

105   The objectives of this study were to (I) analyze the leaf C:N:P stoichiometric

106   patterns of various shrub types, and (II) clarify the significant factors affecting shrub

107   stoichiometry across an extensive altitudinal gradient. In this work, we measured the

108   leaf C, N and P concentrations of 48 shrub species on the Tibetan Plateau. The

109   geographic, climatic and soil data of sampling sites were recorded. Given that the

110   Tibetan Plateau encompasses a singular region of high spatial heterogeneity and

111   complex climatic conditions (Chen et al., 2013b) that may greatly affect shrub nutrient

112   accumulation, we hypothesized that (I) the overall leaf C:N:P variations would be

113   dominated by climate, and (II) the shrub leaf element contents would be different from

114   other terrestrial ecosystems. In addition, plant types and species can greatly affect the

115   leaf element concentrations (McGroddy et al., 2004). To reveal this effect, all shrubs

116   were classified into four ecosystem types that located in different vertical vegetation

117   belts (alpine, subalpine, montane and valley shrub), or three functional types based on

118   different leaf traits (evergreen broadleaf, evergreen conifer, and deciduous broadleaf

119   shrubs). Four dominant shrub species (*Rhododendron telmateium* – alpine, *Quercus*

120   *monimotricha* – subalpine, *Coriaria sinica* – montane, and *Bauhinia brachycarpa* –

121   valley) were also chosen to assess the leaf patterns at species level.

122

123   **2 Materials and Methods**

124   **2.1 Description of the study area**

125   Shrub is defined as a small or medium-sized woody plant, which is distinguished from

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126   a tree by its multiple stems and shorter height (below 5 m). Since shrub ecosystems are

127   mainly distributed in the southeastern margin of the plateau (Appendix B: Fig. B1), we

128   chose 108 mountainous sites of this region to examine the leaf stoichiometry of shrubs

129   that included alpine, subalpine and valley areas. Additionally, the 17 neighbouring

130   mountainous sites on the east of the Tibetan Plateau were selected to provide a

131   representation of low-altitude montane region. In these areas, shrub is one of the most

132   important growth forms. Evergreen broadleaf and deciduous broadleaf shrubs are the

133   primary functional types. The mean annual temperature (MAT) and mean annual

134   precipitation (MAP) vary from −4.67 to 22.16 ºC, and from 366.3 to 1696.3 mm,

135   respectively.

136   Fig. 1 shows the distribution of shrub ecosystem types and sample sites. These sites

137   contain extensive vertical zonation of shrubs, including alpine (3091−4685 m),

138   subalpine (2000−4078 m), montane (523−3342 m) and valley shrubs (600−2350 m)

139   (Appendix A: Table A1). The elevations of four ecosystem types are overlapping

140   because of the high spatial heterogeneity and diverse vegetation that adapted to

141   environments at different altitudes on the plateau. Alpine shrub is the main ecosystem

142   type located above the tree line, while subalpine shrub is distributed in the subalpine

143   coniferous forest zone (Appendix B: Figs. B2 and B3) (Worboys and Good, 2011).

144   Montane shrub exists in the evergreen and deciduous broadleaf forests, and valley shrub

145   occurs in the valley region.

146

2.2 Field sampling

148   During the growing seasons (from July to August) of 2011−2013, sample collection

149   was performed in 125 mountainous sites, with shrub coverage more than 30%. At each

150   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 ℃, 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.

166 Considering the mountainous areas exhibit various drought conditions (especially

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

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

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

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

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

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

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

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

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

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

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

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

179   (-2.0 to -1.5), moderate (-1.5 to -1.0) or mild (-1.0 to -0.5) (Vangelis et al. 2013).

180

181   **2.4 Element measurements**

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

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

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

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

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

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

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

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

190   correlations with leaf elements.

191

192   **2.5 Data analysis**

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

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

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

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

197   species level to control for pseudoreplication (Han et al., 2011). Because the leaf

198   element concentrations and ratios were highly skewed (Appendix B: Fig. B4), we

199   calculated their geometric means, standard deviations and coefficients of variation (CV)

200   to compare the differences of leaf C:N:P among different shrubs. Besides, the arithmetic

201   means of shrub leaf stoichiometry were also calculated to compare with prior studies

202   that only showed arithmetic means.

203   After all the leaf C:N:P values were $\log_{10}$-transformed to improve the data normality,

204   there was still no evidence for the test of homogeneity of variances. Therefore, we used

205   Kruskal-Wallis test (nonparametric) followed by pairwise comparisons to examine the

206   differences in leaf C:N:P among shrub types.

207   Partial correlation analysis allows one to distinguish the degree of the direct

208   correlation between geography (e.g., altitude) and leaf element, with the effect of other

209   controlling random variables removed (e.g., longitude and latitude). Linear and

210   nonlinear regressions were utilized to show the variation trends of leaf C:N:P along

211   climatic and soil gradients. Stepwise multiple regression (SMR) was applied to select

212   the most influential environmental factors (MAT, MAP, RDI, soil C, soil N and soil P),

213   and estimate their contributions to leaf stoichiometry.

214   To evaluate the relative effects of shrub type (ecosystem and functional types), soil

215   (soil C, N and P) and climate (MAT, MAP, RDI), partial general linear model (GLM)

216   analysis was applied. Partial GLM separates the total variance explained by different

217   factors into the independent effect of each factor and their interactive effects (Heikkinen

218   et al., 2005). The statistical analyses were conducted with SPSS v20 (SPSS Inc., USA),

219   Origin 8.0 (OriginLab Co., USA) and R 2.15.2.

220

221   **3 Results**

222   **3.1 Variations of leaf C, N, P and C:N:P ratios**

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

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

225   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.

226   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

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

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

229   477.6 mg g^{-1}, respectively, which were higher than those of montane and valley shrubs

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

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

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

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

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

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

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

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

238   to those in corresponding shrub ecosystem types.

239   The relative variability of leaf nutrients can be demonstrated by CV. Leaf P of all

240   samples had the greatest variation (37.0%), followed by N (30.4%) and C (6.3%). The

241   relative variability of leaf elements for each shrub type also showed the similar trends.

242

3.2 Altitudinal patterns of leaf stoichiometry

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

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

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

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

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

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

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

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

252

253   **3.3 Climatic influence on leaf stoichiometry**

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

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

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

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

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

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

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

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

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

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

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

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

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

267   greatly to adapt to different habitats.

268

269   **3.4 Soil influence on leaf stoichiometry**

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

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

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

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

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

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

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

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

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

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

280

281 **3.5 Relative effects of shrub type, soil and climate**

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

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

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

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

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

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

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

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

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

291

292 **4 Discussion**

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

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

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

296 on leaf elements have not yet been addressed. The statistical analysis proved that shrub

297 type explained the largest fraction of the leaf C:N:P variations, and the leaf element

298 levels differed from other terrestrial ecosystems. This work provides important

299 information on the specific leaf patterns of various shrub types and species over a large

300 altitudinal gradient.

301

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

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326 temperatures (Table 2) further suggested that the growth of shrubs at higher altitudes

327 are more limited by N. However, Han et al. (2005) reported that the 547 plant species

328 in China were strongly constrained by P, with mean leaf N:P (16.3) significantly higher

329 than those in global flora and shrubs in this work ($P < 0.05$, Table 3). It indicated that

330 the assessment of nutrient limitation at large scale could not reflect the pattern in

331 mountainous areas.

332 The CV patterns among leaf elements are consistent with the Stability of Limiting

333 Elements Hypothesis (Sterner and Elser, 2002). It is known that plant nutrient (e.g., C)

334 that required at a high concentration should show a small variation and lower sensitivity

335 to the environment. Leaf C was less variable than leaf N and P, suggesting leaf C had

336 stronger stoichiometric homeostasis. The CV value of shrub leaf C (6.3%) was smaller

337 than those of trees, herbs and shrubs (6.9%−28.0%) in other regions, whereas those of

338 shrub leaf N (30.4%) and P (37.0%) were within the range of other ecosystems (N:

339 11.0%−50.5%; P: 13.0%−44.0%) (Tibbets and Molles, 2005; He et al., 2006; Zheng

340 and Shangguan, 2007; Ladanai et al., 2010). Consequently, the high C accumulation

341 capacity of shrub is less sensitive to the complex climate conditions on the plateau.

342

343 **4.2 Relative influences of the environment and shrub type**

344 Precipitation, temperature and soil can affect leaf elements via changing element

345 allocation among plant organs, altering plant metabolism or influencing nutrient uptake

346 by roots (Ordoñez et al., 2009). In addition to MAP, MAT and soil nutrient, we first

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

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

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

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

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

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

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

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

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

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

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

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

359   the nutrient transportation of shrub.

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

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

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

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

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

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

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

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

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

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

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

371   dominant in leaf N that it may override any possible underlying temperature effect.

372   Soil nutrient was the most significant environmental factor for leaf P, C:P and N:P.

373   Appendix B: Fig. B6 also exhibits the closest relationship between soil P and leaf P (P

374   < 0.001). It was known that P mainly originates from the soil via rock weathering

375   (Walbridge et al., 1991). Moreover, all the soil C:P ratios were less than 200 (implies

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376 net mineralization in soil), confirming the soil may provide sufficient soluble P (Bui

377 and Henderson, 2013).

378   Climate, soil nutrient and vegetation type can together influence plant mineral

379 biogeography in complex ways, while significant collinearities among these factors

380 may potentially obscure their true impacts (Han et al., 2011). Here we used partial GLM

381 regressions to separate the total variance into the independent effect of each factor and

382 their interactive effects (Heikkinen et al., 2005). We found that the independent effect

383 (t) of shrub type was the largest contributor to explain the leaf element variations (Fig.

384 3). For climate, however, the result disagreed with our hypothesis (I) that the leaf C:N:P

385 variations would be dominated by climate. The independent effect of climate (c) was

386 small, and climate mainly affected the leaf C:N:P via its interactive effects on shrub

387 type (ct) or among the three factors (cst). Combined with SMR analysis (Table 2), this

388 finding suggests that climate-induced (e.g., temperature and drought) changes of shrub

389 distribution may affect the leaf nutrient contents. Soil nutrient (s) accounted for large

390 parts of the variations in leaf P and C:P ratio, which was ascribed to the coupled

391 relationships between soil P and plant P (Walbridge et al., 1991).

392

393 **4.3 Large heterogeneity in leaf C:N:P patterns among various shrubs**

394 To our knowledge, the leaf C:N:P patterns among different shrub types and species have

395 not been sufficiently evaluated before. Our analysis suggests the leaf element contents

396 and their responds to environments were highly heterogeneous among shrub types and

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

398 capacities and physiological adaptation to environments governed the leaf nutrient

399 variations.

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

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

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

403   Valley shrub possessed the greatest leaf N and high leaf P, especially at altitude of about

404   1500 m. This result could be explained as follows: (I) larger nutrient deposition in the

405   valleys may result from accumulated sediment, nutrient leaching, or runoff from higher

406   elevations (average MAP reaches up to 882.1 mm); (II) the functional type in valley

407   was mostly short-lived, fast-growing deciduous broadleaf shrub (e.g., *Bauhinia*

408   *brachycarpa*, Table 1), which exhibited faster litter decomposition and nutrient

409   resorption abilities than long-lived, slow-growing evergreen types (Güsewell and

410   Koerselman, 2002; Diehl et al., 2003); and (III) the MAT values of valley sites were

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

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

413   Hypothesis (Aerts and Chapin, 1999). It should be also noted that the alpine shrub

414   exhibited higher leaf N and P than subalpine and montane shrubs located in low-altitude

415   regions ($P < 0.001$). This result agreed with the Temperature-Plant Physiological

416   Hypothesis (Weih and Karlsson, 2001; Zhang et al., 2017). In high-altitude area, the

417   growing season was short, and accompanied by lower temperature. Hence, shrubs

418   might increase their nutrient absorption to compensate for lower enzyme efficiency and

419   metabolic rate.

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

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

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

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

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

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

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

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

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

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

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

431   leaf nutrient acquisition abilities.

432   The leaf traits of shrub ecosystem, functional types and species with respect to four

433   environmental variables differed from each other (Appendix A: Tables A4−A6).

434   Specifically, the leaf N and P contents of montane, evergreen conifer shrubs and

435   *Rhododendron telmateium* were not correlated with climate or soil, whereas those of

436   evergreen broadleaf, deciduous broadleaf and *Bauhinia brachycarpa* exhibited positive

437   relationships with soil or RDI. It revealed that the diverse shrubs showed great

438   heterogeneity in their responses to water status and soil nutrients. Interestingly, the leaf

439   N of evergreen broadleaf shrub had the closest correlation with soil N ($P < 0.01$).

440   Meanwhile, the evergreen broadleaf shrub was largely limited by N (mean leaf N:P =

441   11.5) (Table 1), suggesting the growth of this N-limiting shrub may be highly sensitive

442   to soil N contents.

443

444   **5 Conclusions**

445   This work was the first field investigation of the leaf C:N:P stoichiometry of different

446   shrub types along an extensive altitudinal range, providing important data for future

447   research on global C, N and P cycling. Results highlight that different shrub leaf C:N:P

448   contents and ratios emerged compared to other terrestrial ecosystems, and the leaf

449   C:N:P variations were primarily explained by shrub type. This phenomenon is likely

450   due to the large heterogeneity in nutrient uptake and physiological adaptation to

451 extreme environments across various shrubs on the plateau. However, the underlying

452 physiological mechanisms of specific shrub type or species require further examination.

453 Our findings also indicated that the drought severity was the key climatic factor

454 correlated with leaf N and P, which should be integrated into future biogeochemical

455 models of element cycling. We should pay attention to the N shortage problem to

456 improve the growth of shrubs. Global changes in vegetation distribution, temperature

457 and drought severity will strongly affect the spatial patterns of shrub nutrient pools and

458 ecosystem functioning.

459

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

461

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

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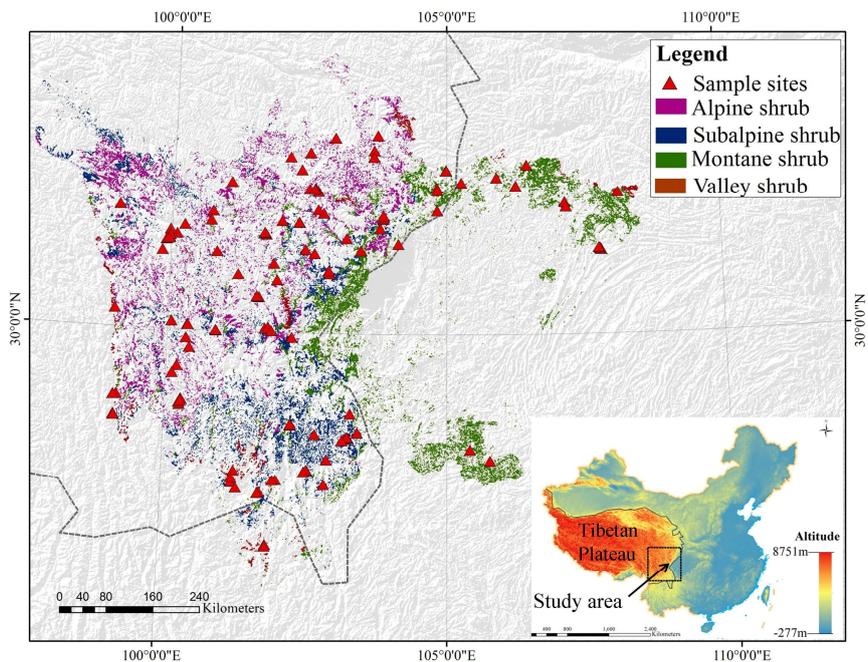
Figure 1. Locations of the southeastern Tibetan Plateau and 125 sample sites in mountainous areas. The purple, blue, green, and brown areas stand for the distribution of alpine, subalpine, montane and valley shrub types, respectively.

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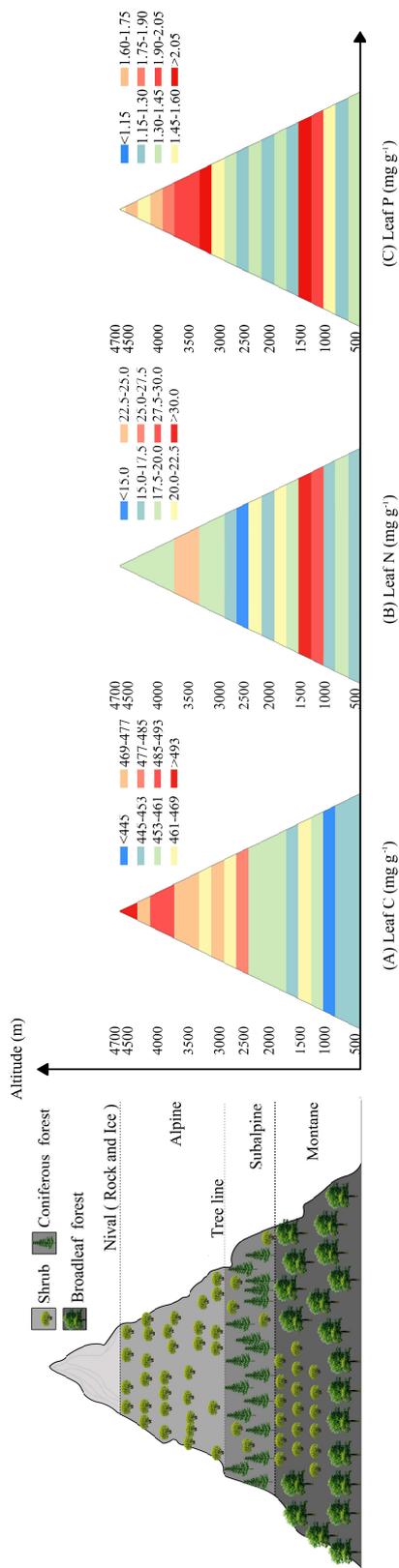
Figure 2. Vertical distribution of leaf C, N and P contents of mountainous shrubs on the Tibetan Plateau. Alpine shrub occurs at relatively higher altitude (3091−4685 m, above tree line), followed by subalpine shrub (2000−4078 m, coniferous forest zone), montane shrub (523−3342 m, broadleaf forest zone)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

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(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

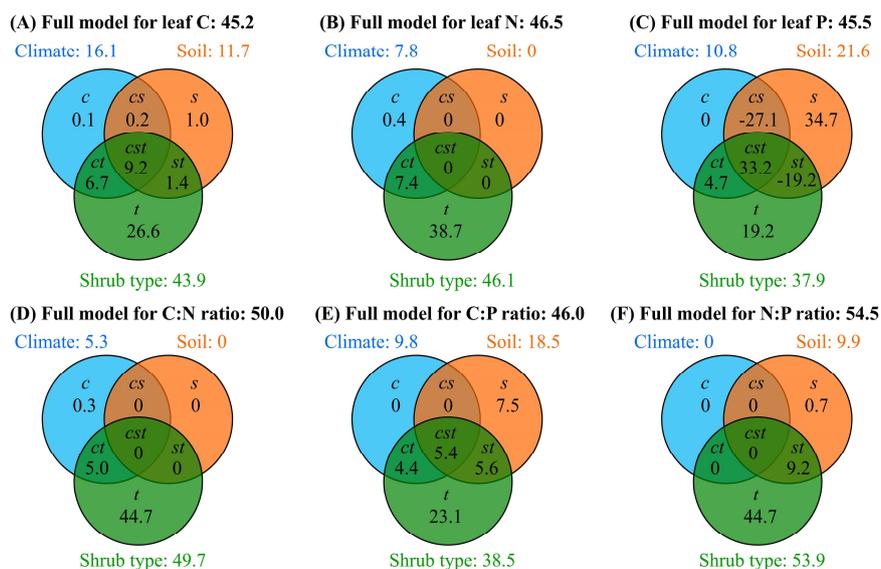|		
c 0.3	*cs* 0	*s* 0
ct 5.0	*cst* 0	*st* 0
	t 44.7	

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).

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%)

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

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

695　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

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

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

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

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

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

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

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712   **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

713   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

714   * 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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716 **Appendix A: Additional tables**

717 **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 (°C)	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
Cotinus coggygria	600~2011	373.5~1435.7	2.59~15.31	−1.64~−0.43	16.9~60.8	1.37~4.19	0.51~0.73

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

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

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

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

722 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

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

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

725 Leaf element concentrations and ratios were log_{10}-transformed before analysis.

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

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

728 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	–	–	–

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

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

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

732 concentrations and ratios were log_{10}-transformed before analysis.

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

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

735 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	–	–	–

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

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

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

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

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

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

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

746 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	–	–	–	–	–	–	–	–	–

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

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

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

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

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

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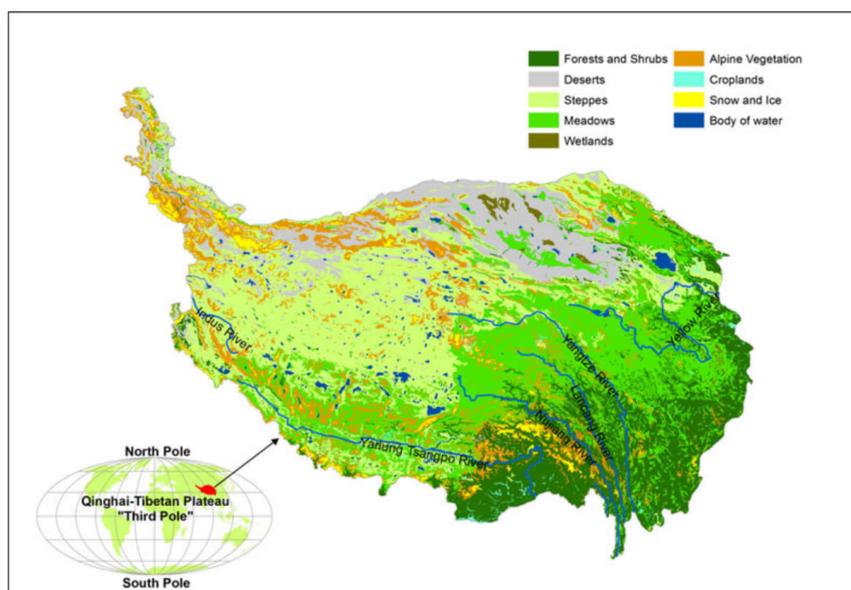
Figure B1. Distribution of vegetation types on the Tibetan Plateau, which is regarded as the "third pole" of the Earth. The complex climate conditions cause a diverse vegetation pattern, resulting in the local plant communities highly sensitive to global climate change. The southeastern margin of the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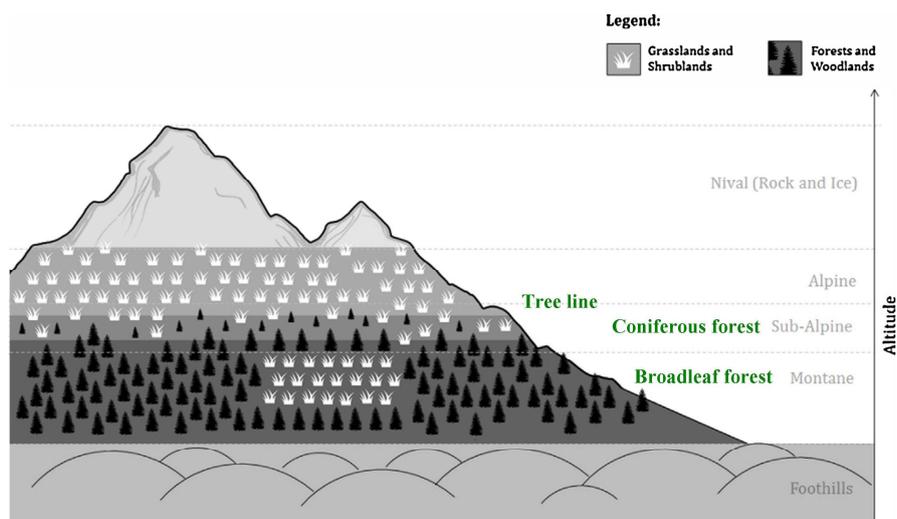
Figure B2. Diagram illustrating the delineation of montane, subalpine, alpine, and nival altitudinal belts relative to the location of shrubland and grassland ecosystems. Various shrub species are able to live in these altitudinal belts at the life form limit for shrubs, and could not be found in the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

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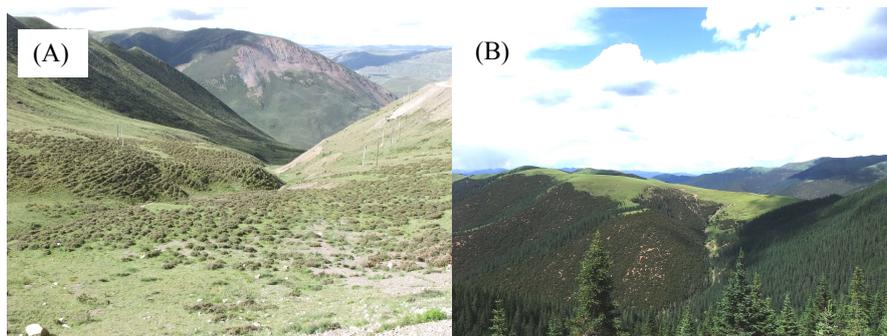
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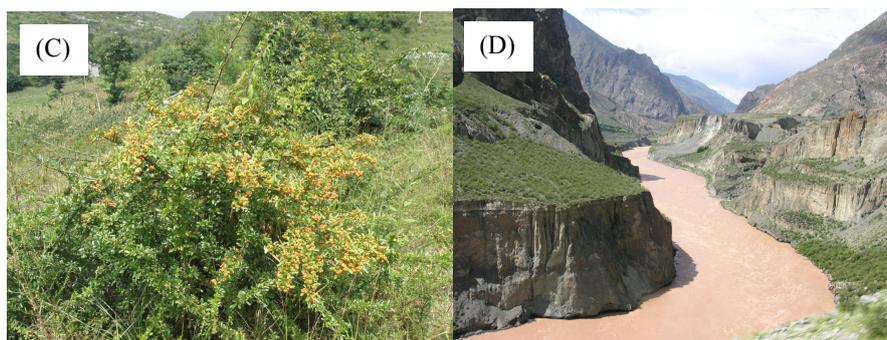
784 **Figure B3.** Representative photos of (A) alpine, (B) subalpine, (C) montane, and (D)

785 valley shrubs on the Tibetan Plateau.

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Geometric mean = 468.9
Median = 467.6
SD = 29.8
SV = 6.3%
Skewness = -0.66

Geometric mean = 18.6
Median = 18.2
SD = 5.9
SV = 30.4%
Skewness = 0.85

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Geometric mean = 1.50
Median = 1.44
SD = 0.59
SV = 37.0%
Skewness = 1.05
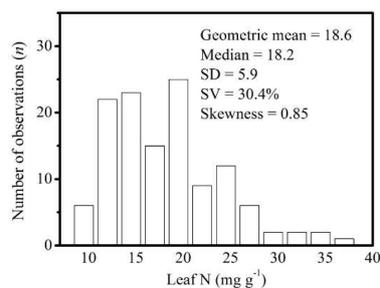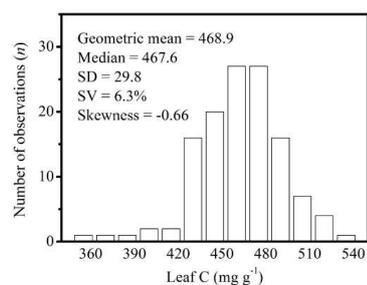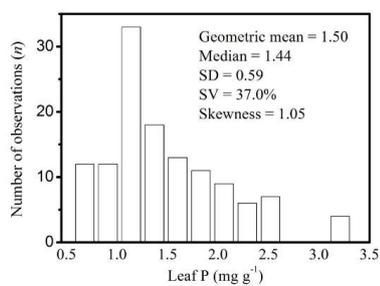
798 **Figure B4.** Distribution of leaf C, N and P concentrations of all shrubs on the Tibetan
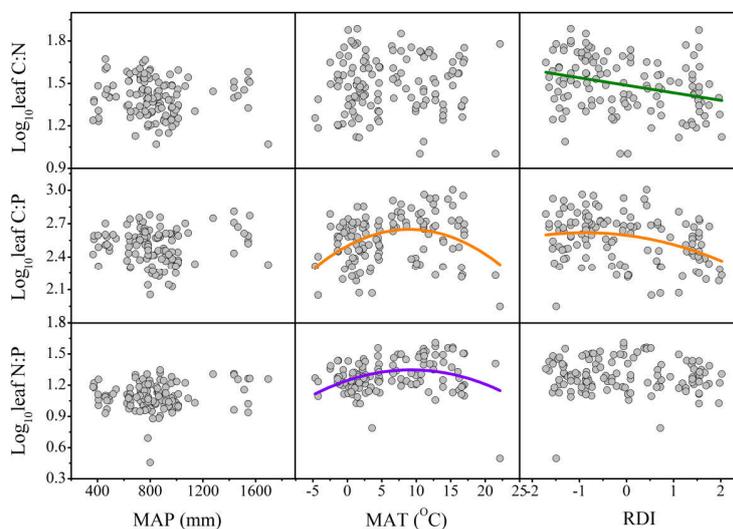
799 Plateau.

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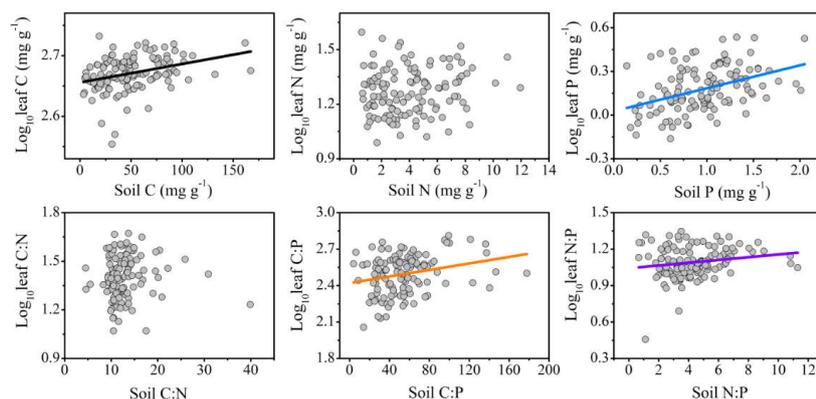
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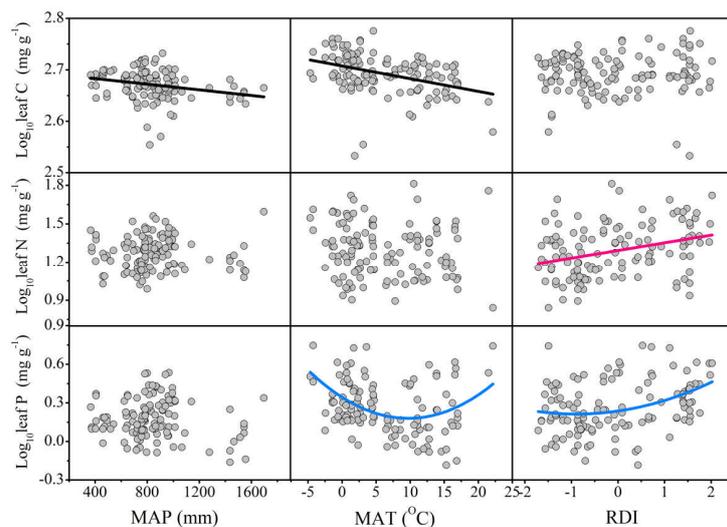
Figure B5. Variation trends of leaf C:N:P stoichiometry as a function of climatic factors.

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.

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837   **Appendix C: Additional methods**

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

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

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

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

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

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

844    $$\text{RDI}_\alpha{}^{(i)} = \frac{\sum_{j=1}^{12} P_{ij}}{\sum_{j=1}^{12} PET_{ij}}, \; i = 1(1)N \text{ and } j = 1(1)12 \tag{1}$$

845   where P_{ij} and PET_{ij} are the precipitation and potential evapotranspiration of the j-th

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

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

848   (Thornthwaite, 1948).

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

850   computed based on the following equation:

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

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

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

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

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

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