

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

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 **critical** 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

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

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 °C, 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

147 **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 \times 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 °C, 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 $0.1^\circ \times 0.1^\circ$ 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

201 element concentrations and ratios were highly skewed (Appendix B: Fig. B4), we
202 calculated their geometric means, standard deviations and **coefficients of variation (CV)**
203 to compare the differences of leaf C:N:P among different shrubs. Besides, the arithmetic
204 means of shrub leaf stoichiometry were also calculated to compare with prior studies
205 that only showed arithmetic means.

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

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

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

223

224 **3 Results**

225 **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
228 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.
229 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
230 P, 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

301 type explained the largest fraction of the leaf C:N:P variations, and the leaf element
302 levels differed from other terrestrial ecosystems. This work provides important
303 information on the specific leaf patterns of various shrub types and species over a large
304 altitudinal gradient.

305

306 **4.1 Different leaf C:N:P levels of shrubs on the plateau**

307 The leaf C, N and P of shrubs on the Tibetan Plateau confirmed our hypothesis (II) that
308 they were different from those at regional, national and global levels (Table 3),
309 suggesting mountainous shrubs had different ways in allocating nutrients. The
310 arithmetic means of shrub leaf C and C:N were 7.3%–47.5% greater than those of other
311 regional and global flora ($P < 0.05$), whereas the mean leaf N and N:P were 10.2%–75.8%
312 lower ($P < 0.05$, except herbaceous species in central England) (Thompson et al., 1997;
313 Elser et al., 2000; Campo and Dirzo, 2003; Reich and Oleksyn, 2004; Han et al., 2005;
314 Tibbets and Molles, 2005; He et al., 2006; Townsend et al., 2007; Zheng and Shangguan,
315 2007; Chen et al., 2013a). The arithmetic mean of shrub leaf P (1.60 mg g^{-1}) were within
316 the range of those reported in other regions ($0.82\text{--}2.70 \text{ mg g}^{-1}$). In this study, the
317 altitudes (523–4685 m) were much wider and higher than those investigated in other
318 terrestrial ecosystems (Soethe et al., 2008; van de Weg et al., 2009; Fisher et al., 2013).
319 Two classical hypotheses may account for this phenomenon. On the one hand, based
320 on the plant physiological acclimation mechanism, it is likely that more non-structural
321 C (e.g., starch, low molecular weight sugars and storage lipid) may accumulate in leaf
322 (e.g., alpine shrub) to balance the osmotic pressure of cells and resist freezing (Hoch et
323 al., 2002; Hoch and Körner, 2012). On the other hand, according to the Biogeochemical
324 Hypothesis, low temperatures in these areas could limit soil microbe activity (Reich
325 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 Shanguan, 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 $^{\circ}\text{C}$ to 22.16 $^{\circ}\text{C}$) 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.

376 Soil nutrient was the most significant environmental factor for leaf P, C:P and N:P.
377 Appendix B: Fig. B6 also exhibits the closest relationship between soil P and leaf P (P
378 < 0.001). It was known that P mainly originates from the soil via rock weathering
379 (Walbridge et al., 1991). Moreover, all the soil C:P ratios were less than 200 (implies
380 net mineralization in soil), confirming the soil may provide sufficient soluble P (Bui
381 and Henderson, 2013).

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

396

397 **4.3 Large heterogeneity in leaf C:N:P patterns among various shrubs**

398 To our knowledge, the leaf C:N:P patterns among different shrub types and species have
399 not been sufficiently evaluated before. Our analysis suggests the leaf element contents
400 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
406 with 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 coggygia*), which belonged to short-lived, fast-
427 growing deciduous broadleaf functional type. These valley species exhibited faster
428 litter 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

451 probably also formed mycorrhizal fungal structures to enhance its survival and growth
452 under stressed environments. *Rhododendron telmateium* may access unavailable
453 organic N and P via the enzymatic degradation of soil organic polymers by mycorrhizal
454 fungi (Näsholm and Persson, 2001), resulting in higher leaf N and P contents compared
455 to *Coriaria sinica*. In addition, the valley shrub *Bauhinia brachycarpa* in our study
456 exhibited relatively high leaf N and P levels (although insignificant), despite its low soil
457 total nutrients relative to alpine and subalpine shrub species (Appendix A: Table A1).
458 This leguminous species possibly interacts symbiotically with soil microorganisms to
459 form fungal assemblages or nitrogen-fixing root nodules, improving its nutrient
460 acquisition in infertile soil. It has been verified that a high level of AMF diversity
461 occurred in the rhizosphere of another dominant valley shrub species (*Bauhinia faberi*)
462 on the Tibetan Plateau (Chen et al., 2016).

463 The leaf traits of shrub ecosystem, functional types and species with respect to four
464 environmental variables differed from each other (Appendix A: Tables A4–A6).
465 Specifically, the leaf N and P contents of montane, evergreen conifer shrubs and
466 *Rhododendron telmateium* were not correlated with climate or soil, whereas those of
467 evergreen broadleaf, deciduous broadleaf and *Bauhinia brachycarpa* exhibited positive
468 relationships with soil or RDI. It revealed that the diverse shrubs showed great
469 heterogeneity in their responses to water status and soil nutrients. Interestingly, the leaf
470 N of evergreen broadleaf shrub had the closest correlation with soil N ($P < 0.01$).
471 Meanwhile, the evergreen broadleaf shrub was largely limited by N (mean leaf N:P =
472 11.5) (Table 1), suggesting the growth of this N-limited shrub may be highly sensitive
473 to soil N contents.

474

475

476 **5 Conclusions**

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

491

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

493

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

495

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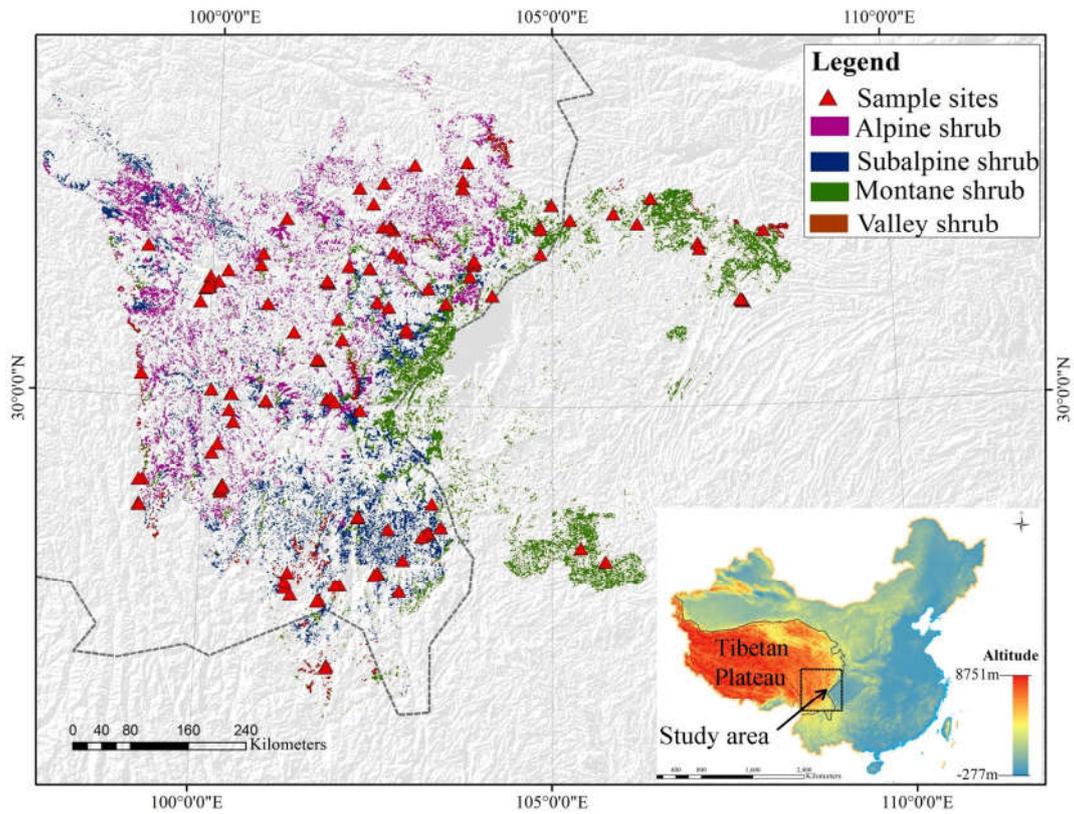
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702 **Figure 1.** Locations of the southeastern Tibetan Plateau and 125 sample sites in
 703 mountainous areas. The purple, blue, green, and brown areas stand for the distribution
 704 of alpine, subalpine, montane and valley shrub types, respectively.

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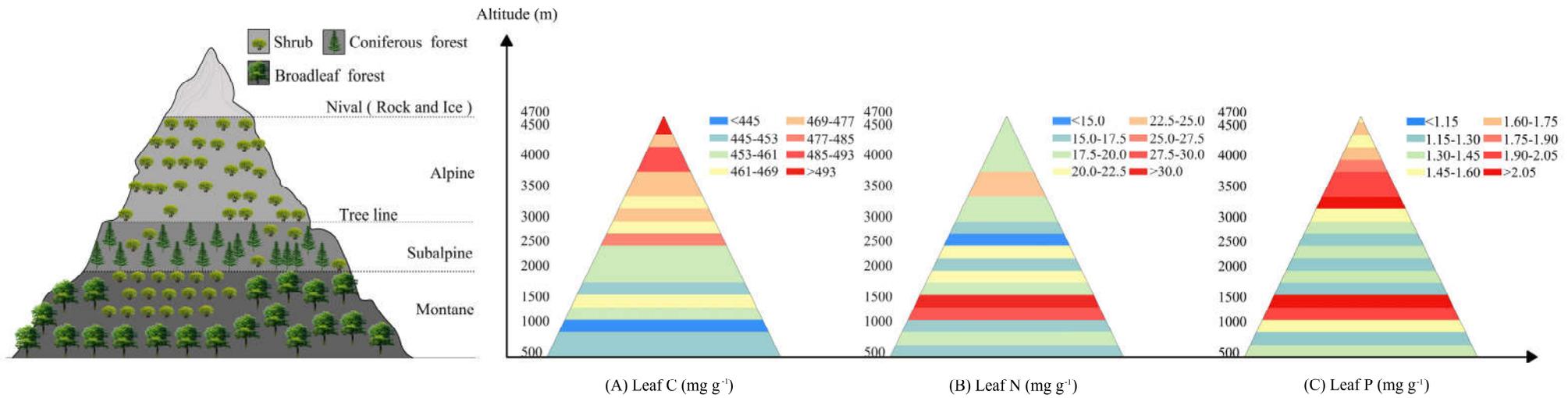
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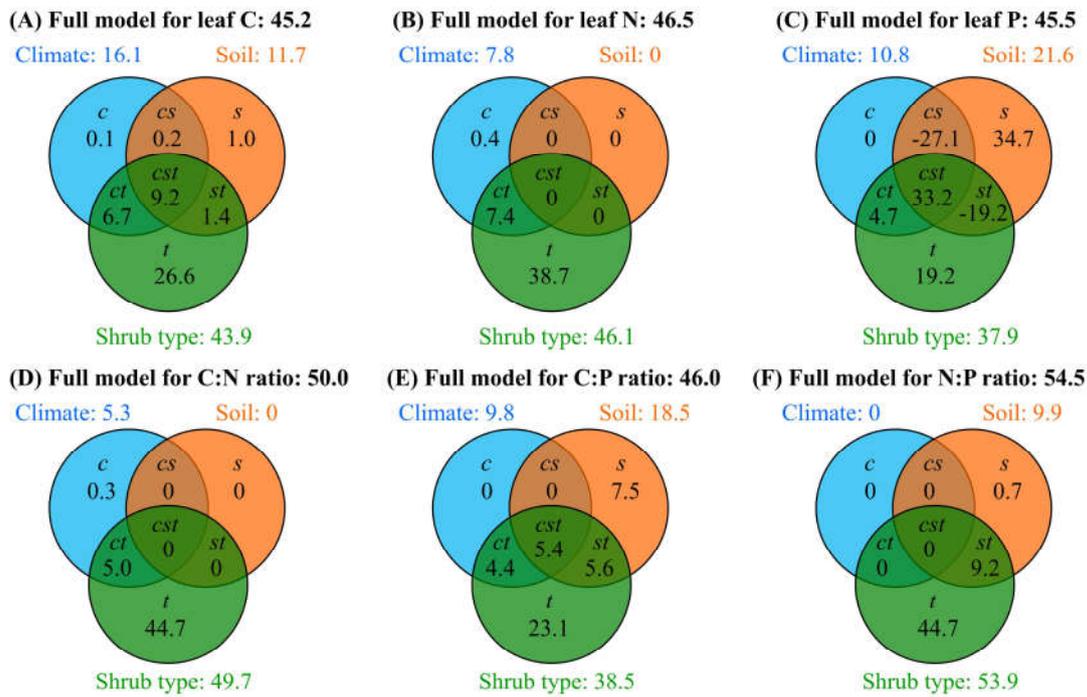


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717 **Figure 2.** Vertical distribution of leaf C, N and P contents of mountainous shrubs on the Tibetan Plateau. Alpine shrub occurs at relatively higher
 718 altitude (3091–4685 m, above tree line), followed by subalpine shrub (2000–4078 m, coniferous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

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723 **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 log₁₀-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).

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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.

		<i>n</i>	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	<i>Rhododendron telmateium</i>	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%)
	<i>Quercus monimotricha</i>	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%)
	<i>Coriaria sinica</i>	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%)
	<i>Bauhinia brachycarpa</i>	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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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.

765

766 **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 (°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							
<i>Rhododendron telmateium</i>	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
<i>Quercus monimotricha</i>	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
<i>Coriaria sinica</i>	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
<i>Bauhinia brachycarpa</i>	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						
<i>Rhododendron telmateium</i> vs <i>Quercus monimotricha</i>	$P = 0.081$	$P > 0.05$	$P = 0.435$	$P = 1.000$	$P > 0.05$	$P = 1.000$
<i>Rhododendron telmateium</i> vs <i>Coriaria sinica</i>	$P < 0.001$	$P > 0.05$	$P < 0.01$	$P = 1.000$	$P > 0.05$	$P < 0.01$
<i>Rhododendron telmateium</i> vs <i>Bauhinia brachycarpa</i>	$P < 0.05$	$P > 0.05$	$P = 1.000$	$P = 0.061$	$P > 0.05$	$P < 0.05$
<i>Quercus monimotricha</i> vs <i>Coriaria sinica</i>	$P = 0.880$	$P > 0.05$	$P = 1.000$	$P = 0.366$	$P > 0.05$	$P < 0.05$
<i>Quercus monimotricha</i> vs <i>Bauhinia brachycarpa</i>	$P = 1.000$	$P > 0.05$	$P = 1.000$	$P < 0.05$	$P > 0.05$	$P = 0.076$
<i>Coriaria sinica</i> vs <i>Bauhinia brachycarpa</i>	$P = 1.000$	$P > 0.05$	$P = 0.841$	$P = 0.784$	$P > 0.05$	$P = 1.000$

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 log₁₀-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 log₁₀-transformed before analysis.

783 **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 log₁₀-transformed before analysis.

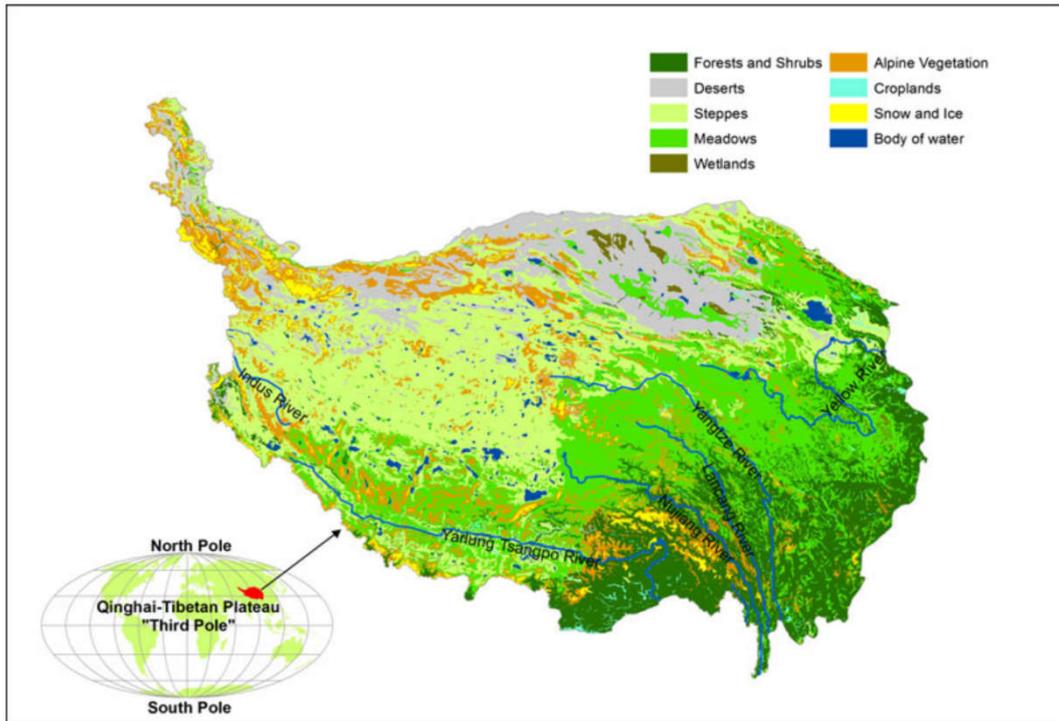
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794 **Table A6.** Model summary for the stepwise multiple regression (SMR) of leaf element
 795 concentrations of dominant shrub species on the climatic and soil variables (MAT, MAP,
 796 RDI, soil element and ratio).

Leaf element	Adj. R^2 Full mode	Partial regression coefficient				Contribution of predictor (%)				
		MAT	MAP	RDI	Soil	MAT	MAP	RDI	Soil	
<i>Rhododendron telmateium</i>										
C	–	–	–	–	–	–	–	–	–	–
N	–	–	–	–	–	–	–	–	–	–
P	–	–	–	–	–	–	–	–	–	–
C:N	–	–	–	–	–	–	–	–	–	–
C:P	–	–	–	–	–	–	–	–	–	–
N:P	0.162	–	–	–	0.013*	–	–	–	–	100
<i>Quercus monimotricha</i>										
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
<i>Coriaria sinica</i>										
C	0.885	–	–	0.015**	–	–	–	100	–	–
N	–	–	–	–	–	–	–	–	–	–
P	–	–	–	–	–	–	–	–	–	–
C:N	–	–	–	–	–	–	–	–	–	–
C:P	0.611	–	<0.001*	–	–	–	100	–	–	–
N:P	–	–	–	–	–	–	–	–	–	–
<i>Bauhinia brachycarpa</i>										
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.

802 **Appendix B: Additional figures**



803

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

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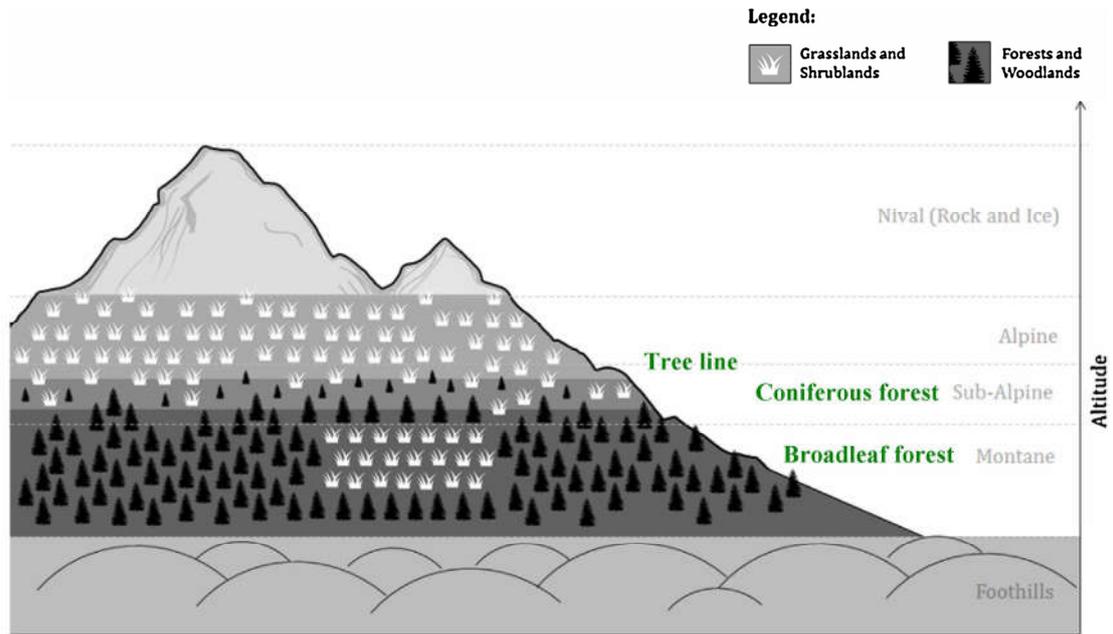
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818 **Figure B2.** Diagram illustrating the delineation of montane, subalpine, alpine, and nival
 819 altitudinal belts relative to the location of shrubland and grassland ecosystems. Various
 820 shrub species are able to live in these altitudinal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

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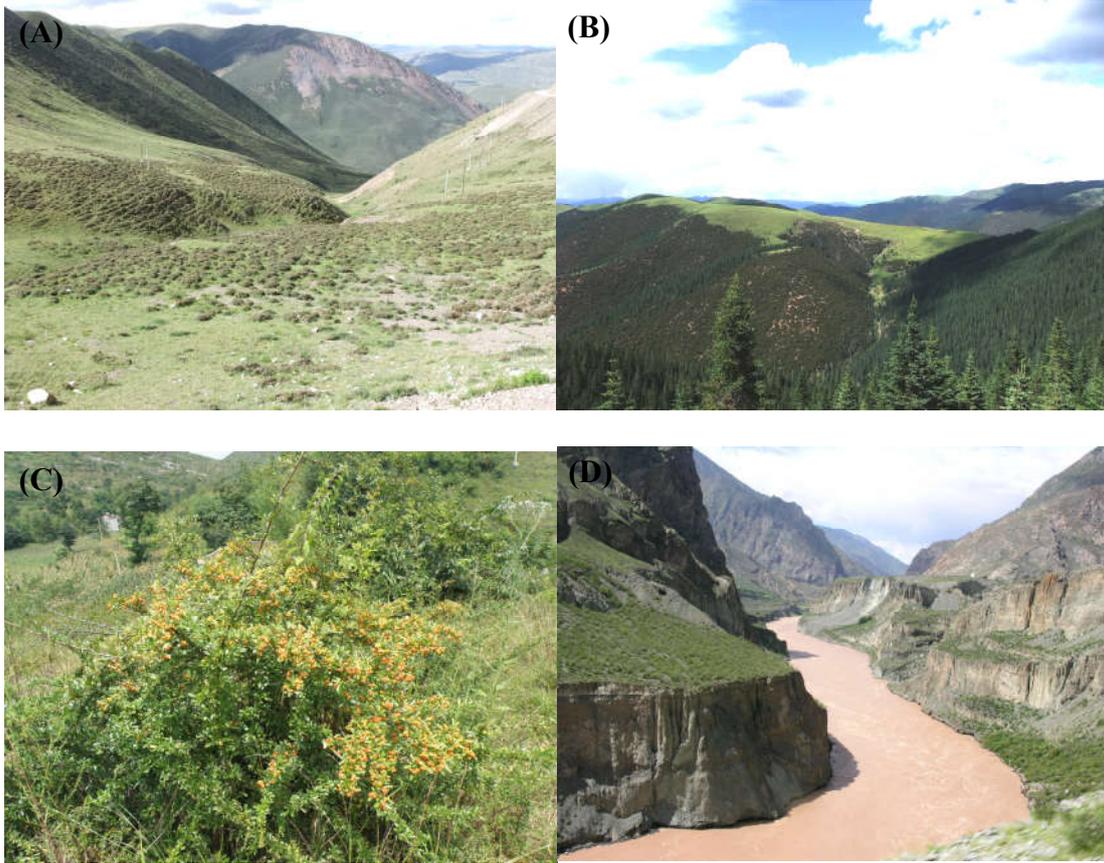
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834 **Figure B3.** Representative photos of (A) alpine, (B) subalpine, (C) montane, and (D)

835 valley shrubs on the Tibetan Plateau.

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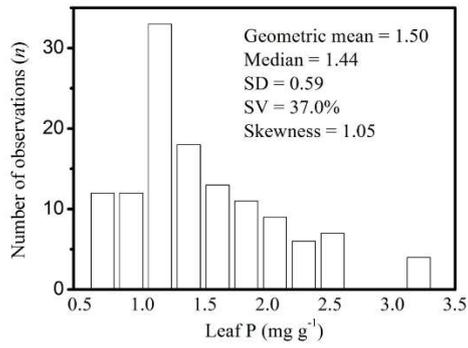
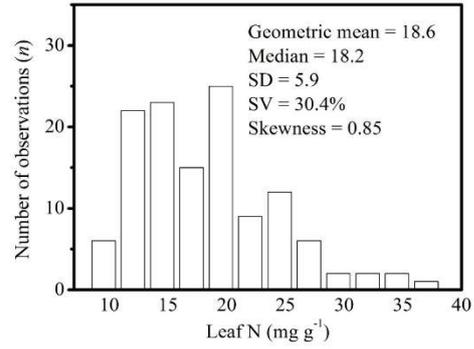
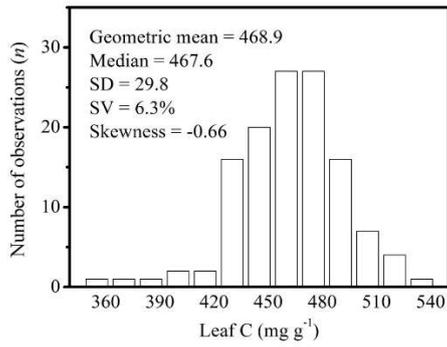
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848 **Figure B4.** Distribution of leaf C, N and P concentrations of all shrubs on the Tibetan
 849 Plateau.

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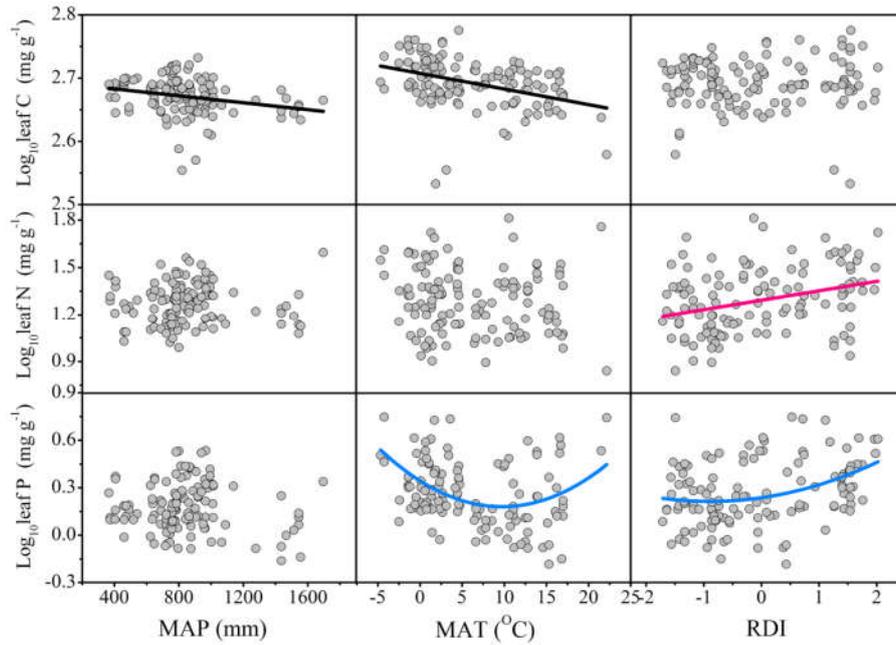
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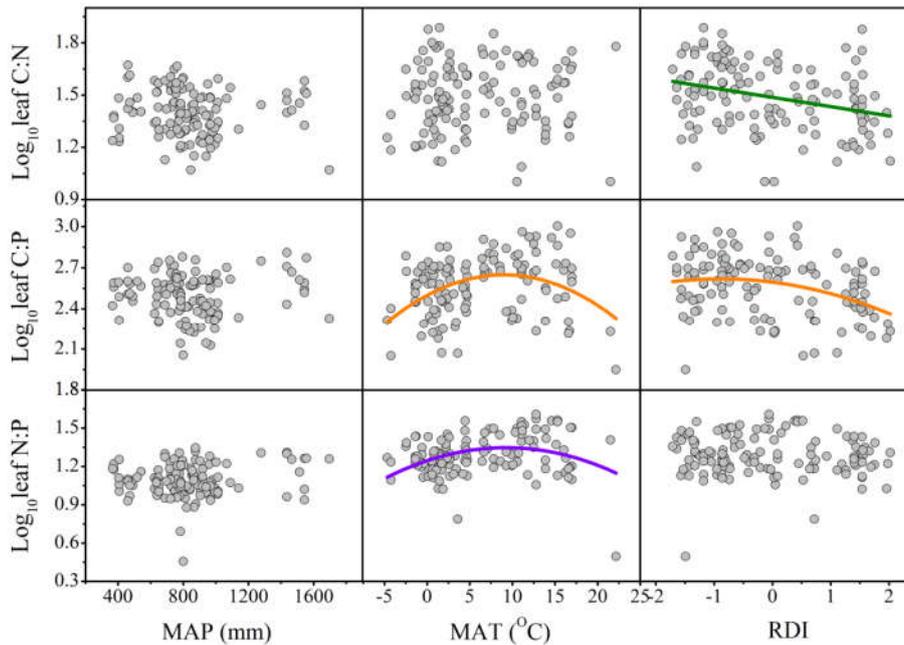
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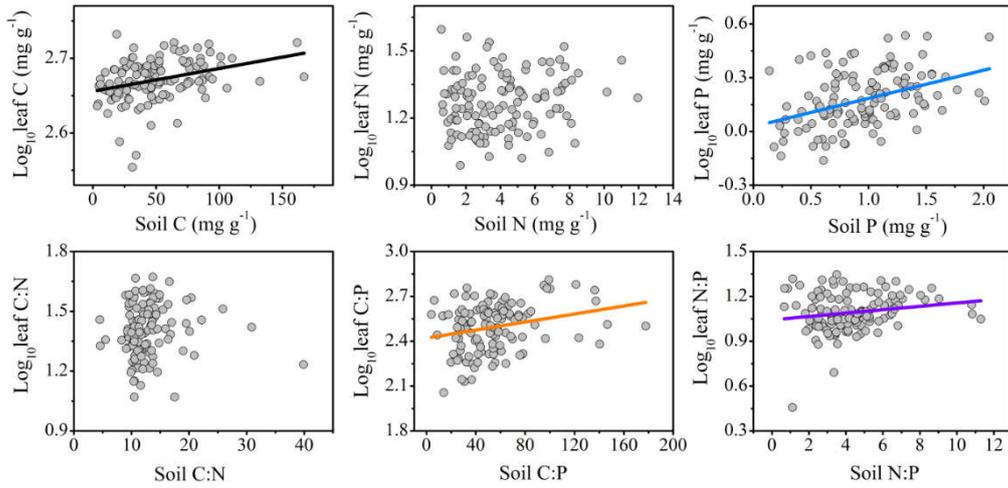
863 **Figure B5.** Variation trends of leaf C:N:P stoichiometry as a function of climatic factors.

864 Data points indicate every observation of shrub stoichiometry within the sampling sites

865 ($n = 125$). Lines are plotted if regressions were significant at $P < 0.05$. Leaf element

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

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869 **Figure B6.** Variation trends of leaf C:N:P stoichiometry as a function of soil C:N:P.

870 Data points indicate every observation of shrub stoichiometry within the sampling sites

871 ($n = 125$). Lines are plotted if regressions were significant at $P < 0.05$. Leaf element

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

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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_α) is usually calculated for
893 the *i*-th year in a time basis of 12 consecutive months as follows:

$$894 \text{RDI}_\alpha^{(i)} = \frac{\sum_{j=1}^{12} P_{ij}}{\sum_{j=1}^{12} \text{PET}_{ij}}, i = 1(1)N \text{ and } j = 1(1)12 \quad (1)$$

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:

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

902 where $\gamma^{(i)}$ is the $\ln(\text{RDI}_\alpha^{(i)})$, $\bar{\gamma}$ is the arithmetic mean and σ_γ is the standard
903 deviation of $\ln(\text{RDI}_\alpha)$. The RDI_α 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.

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