

# Precipitation and aridity index regulating spatial patterns of vegetation production and species diversity based on alpine grassland transect, Tibetan Plateau

Jian Sun <sup>Corresp.</sup> 1

<sup>1</sup> Institute of Geographical Sciences and Natural Resources Research

Corresponding Author: Jian Sun  
Email address: [sunjian@igsnr.ac.cn](mailto:sunjian@igsnr.ac.cn)

Although the relationship between the aboveground net primary production (ANPP) and species diversity (SR) have been widely reported, there is considerable disagreement about the fitting patterns of SR-ANPP, which has been variously described as 'positive', 'negative', 'unimodal', 'U-shaped' and so on. Not surprisingly, the effect-factors including precipitation, aridity index and geographic conditions (e.g., altitude, longitude and latitude) on ANPP and SR continue to interest researchers, especially the effects at high altitude regions. We investigated ANPP and SR from 113 sampled sites (399 plots) across alpine meadow and steppe in the Tibetan Plateau, which included Tibet, Qinghai and Sichuan province. The effects of various environmental factors (precipitation, temperature, aridity index, altitude, longitude, latitude and vegetation type on SR and ANPP) were explored. The results indicate that a unimodal pattern was confirmed between ANPP and SR in alpine steppe ( $R^2 = 0.45$ ,  $P < 0.0001$ ), alpine meadow ( $R^2 = 0.4$ ,  $P < 0.0001$ ), and all samples across alpine grassland ( $R^2 = 0.52$ ,  $P < 0.0001$ ). For the aboveground net primary production, the appropriate precipitation and aridity is 600mm and 42, respectively. Under the same moisture conditions, the maximum value of diversity is 0.75. Longitude ( $R^2 = 0.69$ ,  $P < 0.0001$ ) and altitude ( $R^2 = 0.48$ ,  $P < 0.0001$ ) have positive and negative effects on aboveground net primary production, and a similar relationship exists with diversity ( $R^2 = 0.44$ ,  $P < 0.0001$  and  $R^2 = 0.3$ ,  $P < 0.0001$ ). The same patterns of diversity and production responding to precipitation and the aridity index were evident in alpine steppe and meadow, and a unimodal pattern was confirmed between ANPP and SR in both locations.

1 **Precipitation and aridity index regulating spatial patterns of vegetation production and**  
2 **species diversity based on alpine grassland transect, Tibetan Plateau**

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4 **Running head:** Vegetation biomass and species diversity

5 Jian Sun

6 Synthesis Research Centre of Chinese Ecosystem Research Network, Key Laboratory of

7 Ecosystem Network Observation and Modelling, Institute of Geographic Sciences and Natural

8 Resources Research, Chinese Academy of Sciences, Beijing 100101, China

9

10 \* Corresponding to: sunjian@igsnr.ac.cn

11 Tel.: +86 18301068172

12

13 Address: Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of

14 Sciences (CAS), 11A, Datun Road, Chaoyang District, Beijing, 100101, China

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16 **The number of words in the Abstract: 218**

17 **The number of words in main body of the paper:2637**

18 **The number of references:23**

19 **The number of Tables: 1**

20 **The number of Figures:7**

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**31 Abstract**

32 Although the relationship between the aboveground net primary production (ANPP) and species  
33 diversity (SR) have been widely reported, there is considerable disagreement about the fitting  
34 patterns of SR–ANPP, which has been variously described as ‘positive’, ‘negative’, ‘unimodal’,  
35 ‘U-shaped’ and so on. Not surprisingly, the effect-factors including precipitation, aridity index and  
36 geographic conditions (e.g., altitude, longitude and latitude) on ANPP and SR continue to interest  
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38 sampled sites (399 plots) across alpine meadow and steppe in the Tibetan Plateau, which included  
39 Tibet, Qinghai and Sichuan province. The effects of various environmental factors (precipitation,  
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41 explored. The results indicate that a unimodal pattern was confirmed between ANPP and SR in  
42 alpine steppe ( $R^2=0.45$ ,  $P<0.0001$ ), alpine meadow ( $R^2=0.4$ ,  $P<0.0001$ ), and all samples across  
43 alpine grassland ( $R^2=0.52$ ,  $P<0.0001$ ). For the aboveground net primary production, the  
44 appropriate precipitation and aridity is 600mm and 42, respectively. Under the same moisture  
45 conditions, the maximum value of diversity is 0.75. Longitude ( $R^2=0.69$ ,  $P<0.0001$ ) and altitude  
46 ( $R^2=0.48$ ,  $P<0.0001$ ) have positive and negative effects on aboveground net primary production,  
47 and a similar relationship exists with diversity ( $R^2=0.44$ ,  $P<0.0001$  and  $R^2=0.3$ ,  $P<0.0001$ ). The  
48 same patterns of diversity and production responding to precipitation and the aridity index were  
49 evident in alpine steppe and meadow, and a unimodal pattern was confirmed between ANPP and  
50 SR in both locations.

51 **Keywords:** Precipitation, aridity index, aboveground net primary production, species diversity,  
52 Tibetan Plateau

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**54 INTRODUCTION**

55 Scientists have assessed the variation of grassland vegetation via remote sensing data, combined  
56 with field investigations, and explored the relationship between grassland and long-term  
57 environmental change (Roa-Fuentes *et al.*, 2012). Although NDVI (Normalized Different  
58 Vegetation Index) across the Tibetan Plateau shows increasing values due to global warming,  
59 different types of grasslands have different degrees of degradation, such as alpine meadow in

60 Nagqu. To some extent, grassland degradation means a decrease in grassland productivity and  
61 species richness, and although both net primary production and diversity play an important role in  
62 the ecosystem, the relationship between productivity and species diversity is not clear.

63 Classical theory holds that species-rich communities should be more productive. Although  
64 many hypotheses relate species diversity with productivity, including a linear positive relationship,  
65 there is insufficient evidence to support any one of them in different ecological habitats (Rusch *et al.*,  
66 1997). Previous studies have highlighted the positive relationship between plant diversity and  
67 aboveground net primary production (Odat *et al.*, 2010, Palmborg *et al.*, 2005, Sabais *et al.*, 2011),  
68 and some studies suggest that the effects of species diversity on biomass and resource-use are  
69 complementary (Dukes, 2002, Palmborg, Scherer-Lorenzen, Jumpponen, Carlsson, Huss-Danell  
70 and Hogberg, 2005). Moreover, previous research found that the difference among plant  
71 communities would impact the relationship between aboveground net primary production and  
72 species-richness (Odat *et al.*, 2004, Terheerdt *et al.*, 1991).

73 Many researchers have focused on the pattern of species richness, diversity, and productivity in  
74 grassland communities. In fact, control experiments could not indicate the effect on biomass by  
75 climate and diversity in the natural ecosystem {Bernhardt-Romermann, 2011 #10}. However,  
76 much less emphasis has been placed on the environmental factors affecting species diversity, and  
77 so, for the time being, it remains unclear whether the species diversity gradients respond to  
78 environmental factors (Houseman *et al.*, 2011). The objectives of this study are as follows: (a)  
79 What is the relationship between aboveground net primary production and diversity across the  
80 Tibetan Plateau? (b) What is the relationship between the environment and ANPP and SR? (c)  
81 What is the response difference between alpine meadow and alpine steppe to precipitation factors?

## 82 **METHODS**

### 83 **Study area**

84 The Tibetan Plateau (80°–105°E, 27°–37°N) in western China has an alpine climate with an  
85 annual mean temperature of 4°C, an annual mean precipitation of 400 mm, and the mean altitude  
86 is over 4000m. Annual mean precipitation increases gradually from the northwest to the southeast,  
87 and mainly falls in June-September, which is significant for the rainy season and dry season. The  
88 high mountain plateau climate results in a temperature decrease as altitude increases, and the total

89 area of the Tibetan Plateau is 2,400,000 km<sup>2</sup>. Fig.1 shows that the vegetation types are dominated  
90 by alpine meadow and alpine steppe in the east and northwest of the Tibetan Plateau. Resistance to  
91 cold and drought is a characteristic of the alpine steppe, but most species of alpine meadow in the  
92 region are perennial.

### 93 **Data collection and analysis**

94 In August 2015, 113 locations were selected in alpine meadow and steppe across the Tibetan  
95 Plateau (Supplementary file 1), including Qinghai, Tibet and Sichuan province (Field experiments  
96 were approved by the Institute of Geographic Sciences and Natural Resources Research, Chinese  
97 Academy of Sciences). For each location, three samples of 50cm × 50cm were randomly  
98 selected to investigate the height, cover percentage and number of species, the raw data for species  
99 diversity. The number of species in the samples was recorded, and the clipping method used to  
100 measure the aboveground net primary production. Three examples of aboveground net primary  
101 production were dried in an oven at 80°C and then weighed.

102 Simpson's diversity index is used to indicate the  $\alpha$  diversity of biodiversity, which focuses  
103 on the species number whining-habitat regional scale, and is calculated as (Vujnovic *et al.*, 2002):

$$104 \quad D = 1 - \sum p_i^2$$

105 Where  $p_i$  is the proportional abundance of the species ( $i$ ) in the community. It is the most  
106 suitable index because of its unbiased estimate (Morris *et al.*, 1979). The figures and table in this  
107 study were created with SPSS and R Core Team (R: A language and environment for statistical  
108 computing. The R Project for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.  
109 supplementary file 2).

## 110 **RESULTS**

### 111 **Variations of vegetation production and diversity in alpine steppe and meadow**

112 Fig.2 shows the results and range of aboveground net primary production and diversity in alpine  
113 meadow and alpine steppe. The mean value of ANPP in the alpine meadow is 143.15 g m<sup>-2</sup>, which  
114 is higher than the alpine steppe with a mean value of 55.81 g m<sup>-2</sup>. Otherwise, the range of both is  
115 similar; the domain of meadow is dispersed while that of steppe is mainly below 100 g m<sup>-2</sup>. There  
116 was a difference in the Simpson diversity index between alpine steppe and meadow, which is due  
117 to differing species-richness and species-evenness. As for the content of ANPP, the species

118 diversity of meadow is higher than that of the steppe. The median of both is 0.75 and 0.565,  
119 respectively, and the range of the second median is approximately 0.063.

120 Within each vegetation type, species diversity increased aboveground net primary production  
121 (Fig.3) and shows a curved relationship. Although the shape of the diversity-ANPP curves differed  
122 between meadow ( $y=0.51+0.0026x-(5.47E+006)x^2$ ,  $R^2=0.40$ ,  $P<0.0001$ ) and steppe  
123 ( $y=0.37+0.0053x-(1.72E+005)x^2$ ,  $R^2=0.45$ ,  $P<0.0001$ ), both vegetation types show similar  
124 unimodal lines with peaks at 250 g m<sup>-2</sup> and 160 g m<sup>-2</sup> of ANPP, respectively. In fact, the influence  
125 of diversity on ANPP was more sensitive in meadow than in steppe, but the correlation coefficient  
126 between ANPP and species diversity across the Tibetan Plateau is higher  
127 ( $y=0.42+0.0038x-(9.04E+006)x^2$ ,  $R^2=0.52$ ,  $P<0.0001$ ) than for each vegetation type, with peak  
128 values of 240 g m<sup>-2</sup> of ANPP and 0.75 of species diversity. In the low productivity sites, there was  
129 no effect of diversity on aboveground net primary production.

### 130 **Changes in vegetation production and species diversity along environmental gradients**

131 To test whether moisture was the crucial environmental factor that affects the  
132 productivity-diversity pattern in two vegetation types, we used partial correlation in SPSS to  
133 analyze the relationship among environment factors, as shown in Table 1. As a result, annual mean  
134 temperature has no significant effect on aboveground net primary production and diversity, except  
135 to show a significant negative relationship with aridity ( $R^2=-0.38$ ). In addition, latitude shows a  
136 positive effect on community production ( $R^2=0.42$ ) but not on species diversity. Hence latitude  
137 and temperature are excluded in the latter research. To summarize, longitude, precipitation and  
138 aridity performance have a positive affect while altitude shows a negative influence on  
139 aboveground net primary production and diversity.

140 Fig. 4 shows that the influence of precipitation and aridity on ANPP is similar, because aridity  
141 takes into account evaporation. For the alpine meadow, ANPP increases with moisture, and annual  
142 mean precipitation of 600mm is appropriate for the accumulation of organic matter with 250 g m<sup>-2</sup>  
143 ANPP based on the fitting line. Correspondingly, aridity with 48 is conducive to meadow growth  
144 across the Tibetan Plateau. On the other hand, most, though not all, of the ANPP sample values of  
145 is approximately 100 g m<sup>-2</sup>. For steppe, the suitable value of annual mean precipitation and aridity  
146 is approximately 310mm and 28, respectively – after which ANPP decreases as precipitation  
147 increases and aridity rises. As a consequence, the peak of ANPP is 120 g m<sup>-2</sup> in steppe. What this

148 means is that too much precipitation has no positive effect on aboveground net primary production,  
149 as a ratio of evaporation and precipitation. Nevertheless, the relationship between ANPP and  
150 precipitation is positive across the Tibetan Plateau. Within the range of 0-150  $\text{gm}^{-2}$ , the appropriate  
151 precipitation is 420mm, which is below the value of alpine meadow but above the alpine steppe.  
152 In terms of aridity, the feasible value is 42, which is close to the value of alpine meadow.

153 Alpine grassland biomass increased significantly with increasing longitude  
154 ( $y=82.62+0.18x+0.0004x^2$ ,  $R^2=0.69$ ,  $P<0.0001$ ), but decreased with increasing altitudes  
155 ( $y=4758.47-9.28x+0.12x^2$ ,  $R^2=0.48$ ,  $P<0.0001$ ) (Fig.5). Generally, this was true, from west to east,  
156 across the Tibetan Plateau. The alpine meadow biomass increased slightly with longitude at 150  
157  $\text{gm}^{-2}$  while it is almost invariant with ANPP at 200  $\text{gm}^{-2}$ . At the same time, increased alpine steppe  
158 biomass caused by longitude was significantly below 140  $\text{gm}^{-2}$ . As for the alpine grassland in the  
159 Tibetan Plateau, the positive relationship between ANPP and longitude was insignificant when the  
160 value was 100 of longitude. Different results of aboveground net primary production between  
161 alpine meadow and steppe is significant. The range of altitude in meadow and steppe is  
162 4700-3500m and 5000-3700m, respectively, and many samples were located in high altitude  
163 regions. It is worth noting that the ANPP of meadow is more than that of the steppe at the same  
164 altitude, especially under 3500m. The response of steppe to altitude was more sensitive than  
165 meadow.

166 The impact of moisture on diversity differs from ANPP, because the fitting correlation between  
167 precipitation and diversity is at the right of the unimodal fitting lines ( $y=221.43-232.20x+705.56x^2$ ,  
168  $R^2=0.36$ ,  $P<0.0001$ ) (Fig.6) – which is to say, precipitation and aridity have a significant positive  
169 impact on species diversity. Furthermore, species richness is more sensitive to high rainfall in  
170 alpine meadow regions than in the alpine steppe. As the annual mean precipitation increased from  
171 200mm to 400mm, species diversity increased from 0.25 to 0.75 in the steppe.

172 Fig.7 shows the relationship between longitude, altitude and diversity. Clearly, the former  
173 indicates a positive relationship ( $y=87.13-15.55x+36.40x^2$ ,  $R^2=0.44$ ,  $P<0.0001$ ) while the latter is  
174 negative ( $y=3557.26-4407.82x-5120.60x^2$ ,  $R^2=0.30$ ,  $P<0.0001$ ). Most samples in the steppe are  
175 distributed at 80°E-100°E, while sites of alpine meadow are located at 90°E-100°E, and the  
176 species diversity index changed from 0.50 to 0.75 on 100°E approximately.

## 177 **DISCUSSION**

### 178 **Size of vegetation production and species diversity**

179 ANPP and species diversity of meadow are both higher than those of the steppe, which shows a  
180 correlation with vegetation types. At a low diversity value, many studies suggest that increasing  
181 diversity is conducive to greater biomass production {Ram, 1989 #71}{Aarssen, 1997 #61}. In  
182 general, many results conclude that this from controlled experiments, such as standards of  
183 dominant species (Terheerdt, Bakker and Deleeuw, 1991). In fact, at the same level of  
184 aboveground net primary production, species richness of alpine meadow is more than that of  
185 alpine steppe, owing to the different characteristics of plant species. For grassland across the  
186 Tibetan Plateau, aboveground net primary production increased as the species richness increased  
187 with a curve line.

188 In addition, different ecological communities are an important factor in the relationship  
189 between biomass and diversity. In other words, different ecological system types have different  
190 vegetation types, which indicate that species composition determines the aboveground net primary  
191 production. What is worth noting is that species have not had a positive effect on biomass  
192 production, even though it is a common negative influence of production on diversity in mature  
193 natural systems because of competitive exclusion although not in the control of species diversity  
194 (Grace *et al.*, 2007). As the results of this study show, when diversity increases to 0.75, the  
195 aboveground net primary production shows a decreasing trend afterwards. Moreover, high  
196 production in a community is more likely to result from containing productive species but not all  
197 species (Aarssen, 1997).

### 198 **Environmental gradient patterns of vegetation production and species diversity**

199 For plants that are particular to biotic and resource conditions, classical niche theory holds that  
200 species richness is controlled by local environment factors (Gazol *et al.*, 2012). Aridity is soil  
201 moisture by another name, with an extremely significant positive correlation for precipitation by  
202 0.89 (Table 1). The influence of precipitation and aridity on aboveground net primary production  
203 and diversity is similar overall. The Tibetan Plateau was called “The third pole”, with a mean  
204 altitude of 4000 meter. Complex geologic conditions impacted the alpine steppe and the meadow,  
205 and both changed in a specific range. This area, which has high rainfall, has high evaporation,



206 which is distributed in meadow vegetation in the center of the Tibetan Plateau. Nevertheless,  
207 quantitative soil nutrients may limit the increase of aboveground net primary production even if  
208 the precipitation increases – although this is not true for species richness because of the ecological  
209 niche for moisture of various species. Because of drought-induced transformations in plant-soil  
210 resources, high plant species-richness was promoted (Bloor *et al.*, 2012). In the alpine grassland of  
211 the Tianshan mountains, rainfall in the early growing period and snowfall in winter play an  
212 important role on plant growth (Li *et al.*, 2015).

213 Form west to east across the Tibetan Plateau, the annual precipitation increased as the longitude  
214 from 80°E to 105°E. The relationship between longitude and aboveground primary net production,  
215 diversity shows in the horizontal variation. In the vertical variation, altitude response is negative  
216 for precipitation and temperature, and especially with annual precipitation. There is, however, a  
217 different pattern concerning the effect of environment factors on aboveground net primary  
218 production and diversity. Nevertheless, it is important to analyze the response to environmental  
219 factors. Plenty of aboveground net primary production could ensure the development of livestock,  
220 especially in winter when grassland resources are short. In recent years, with global temperatures  
221 increasing, the annual mean precipitation has also increased, and extreme climate events such as  
222 drought and rainfall influence vegetation. Normalized different vegetation index (NDVI) shows an  
223 increased tendency under climate change, and the suggestion that grassland across the Tibetan  
224 Plateau has degraded has been confirmed. On the other hand, species richness has an important  
225 role in the ecological system, not only because of the natural gene pool, but also to strengthen the  
226 region's capacity to adapt to the changing climate.

227 In addition, many factors should be explored through future research. Although the cornerstone  
228 ecological theory holds that the number of species control the nutrient availability in a community,  
229 there has been no effect of  $\text{NO}_3^-$  on distributive patterns of species diversity at the small scale  
230 (Anderson *et al.*, 2004). In terms of plant production, light became the control element with denser  
231 canopy (Eek *et al.*, 2001). Some studies have explored the various elements that effect production  
232 and species diversity such as invertebrate herbivores (Brady *et al.*, 2001, Buschmann *et al.*, 2005).  
233 Although grazing was another important factor on the variation of biomass and species diversity,  
234 grassland degradation would be caused by overgrazing over the long term (Zhao *et al.*, 2004).  
235 However, climate variables have less influence on biomass than biodiversity

236 (Bernhardt-Romermann *et al.*, 2011). Moreover, the influence of anthropogenic activity on  
237 diversity and the characteristics of the natural community are increasingly significant (Webster *et*  
238 *al.*, 2002).

## 239 CONCLUSIONS

240 The relationship between biomass and species richness is a topic of considerable interest to  
241 environmental scientists. There are several traditional assumptions about the relationship, but we  
242 cannot explore the internal mechanism of biomass and diversity by referring only to correlative  
243 patterns. To be sure, the relevance model changes with location, and the relationship between  
244 aboveground net primary production and species richness fits a unimodal model. Nevertheless, the  
245 variation range in the alpine steppe is smaller than in alpine meadow. Thus, the relationship  
246 between aboveground net primary production and species richness is non-linear: as species  
247 richness increased, aboveground net primary production of grassland increased to 250 g m<sup>-2</sup>, but  
248 then decreased after that. According to the aforementioned results, precipitation, aridity and  
249 longitude show a positive effect on aboveground net primary production and diversity while  
250 altitude indicates a negative effect on the whole. Clearly, the response of alpine meadow to  
251 environment factors is more sensitive than the response of alpine steppe.

## 252 ACKNOWLEDGMENTS

253 We appreciate all the people (Weipeng Li, Jianbo Wu, Xiaojing Qin, Tiancai Zhou, Hongwu Ran,  
254 Wei Jiao and Hong liu) who contributed their field work to the database. This work was funded by  
255 the National Natural Science Foundation of China (No. 41501057), West Light Foundation of The  
256 Chinese Academy of Sciences and the Open Fund of the Key Laboratory of Mountain Surface  
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**Table 1** The correlation coefficient of ANPP, diversity and environment factors.

Factors	ANPP	Diversity	Latitude	Longitude	Altitude	Precipitation	Temperature	Aridity
ANPP	1	0.64**	0.42**	0.75**	-0.70**	0.69**	-0.01	0.63**
Diversity		1	0.21	0.64**	-0.48**	0.69**	0.11	0.58**
Latitude			1	0.62**	-0.69**	0.13	-0.21	0.42
Longitude				1	-0.78**	0.82**	0.02	0.72**
Altitude					1	-0.49**	-0.21	-0.33**
Precipitation						1	0.05	0.89**
Temperature							1	-0.38**
Aridity								1

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365 **Figure captions**

366 **Fig. 1** Map of the Tibetan Plateau of China with locations of the 113 samples

367 **Fig. 2** Aboveground primary production and diversity differences between grasslands factor

368 **Fig. 3** Species diversity as a function of ANPP at vegetation type

369 **Fig. 4** The influence of precipitation and aridity on ANPP

370 **Fig. 5** The influence of longitude and altitude on ANPP

371 **Fig. 6** The influence of precipitation and aridity on diversity

372 **Fig.7** The influence of longitude and altitude on diversity

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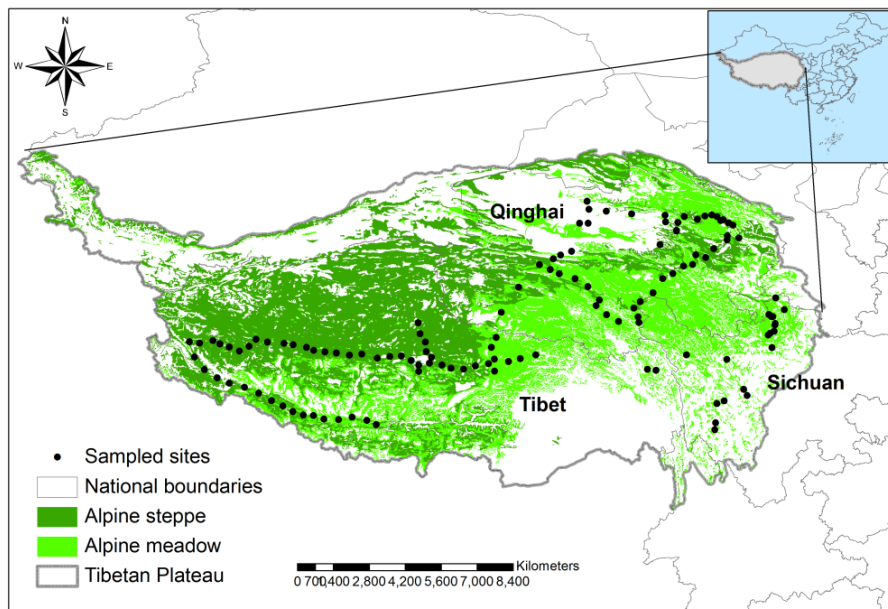
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**Fig. 1**

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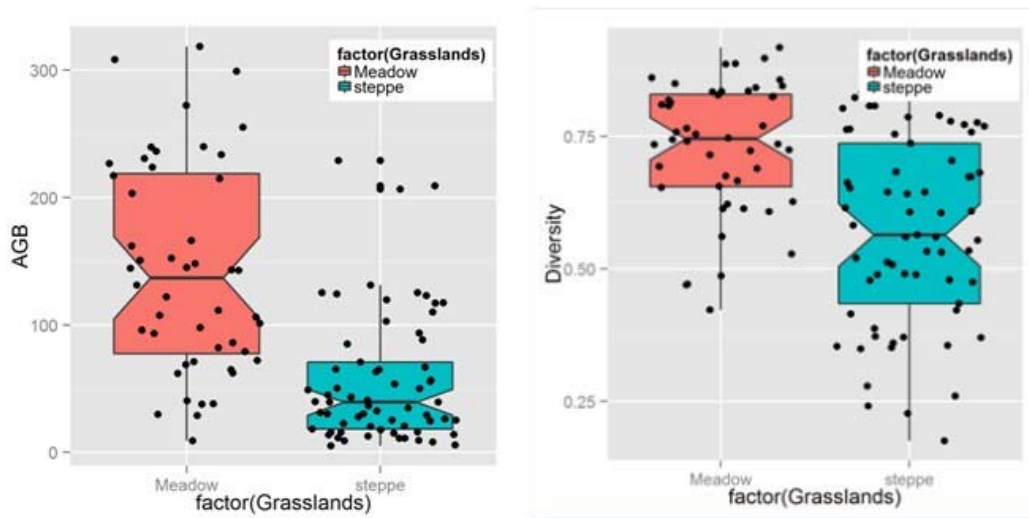
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Fig. 2

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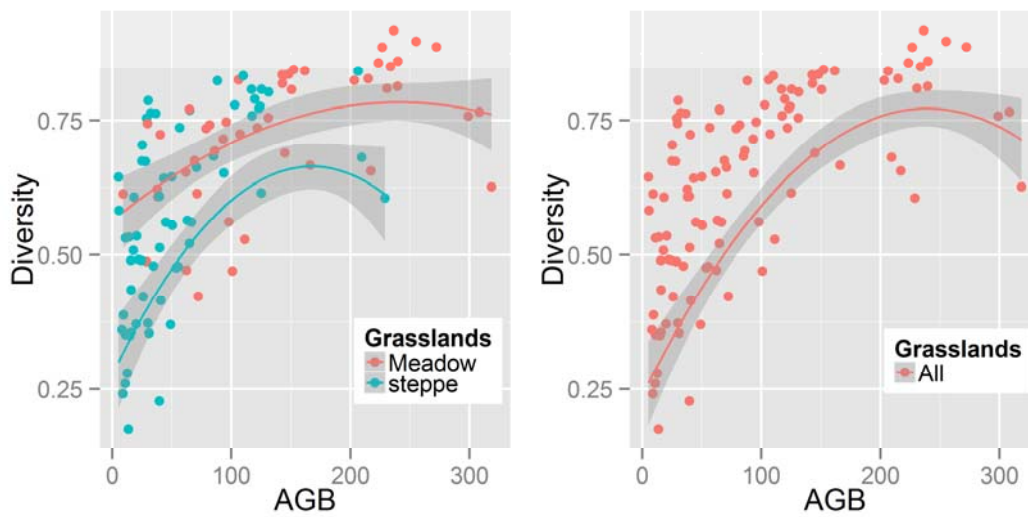
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Fig. 3

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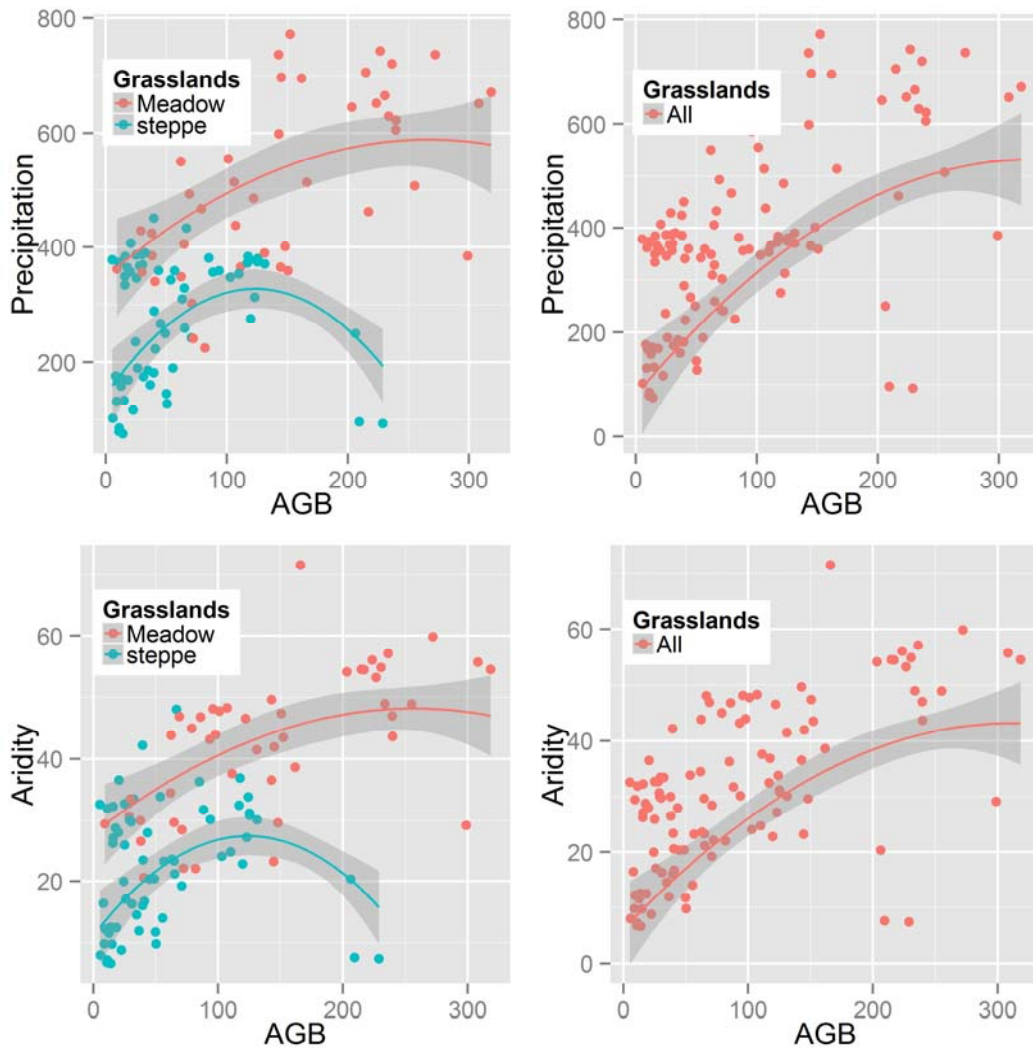
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Fig. 4

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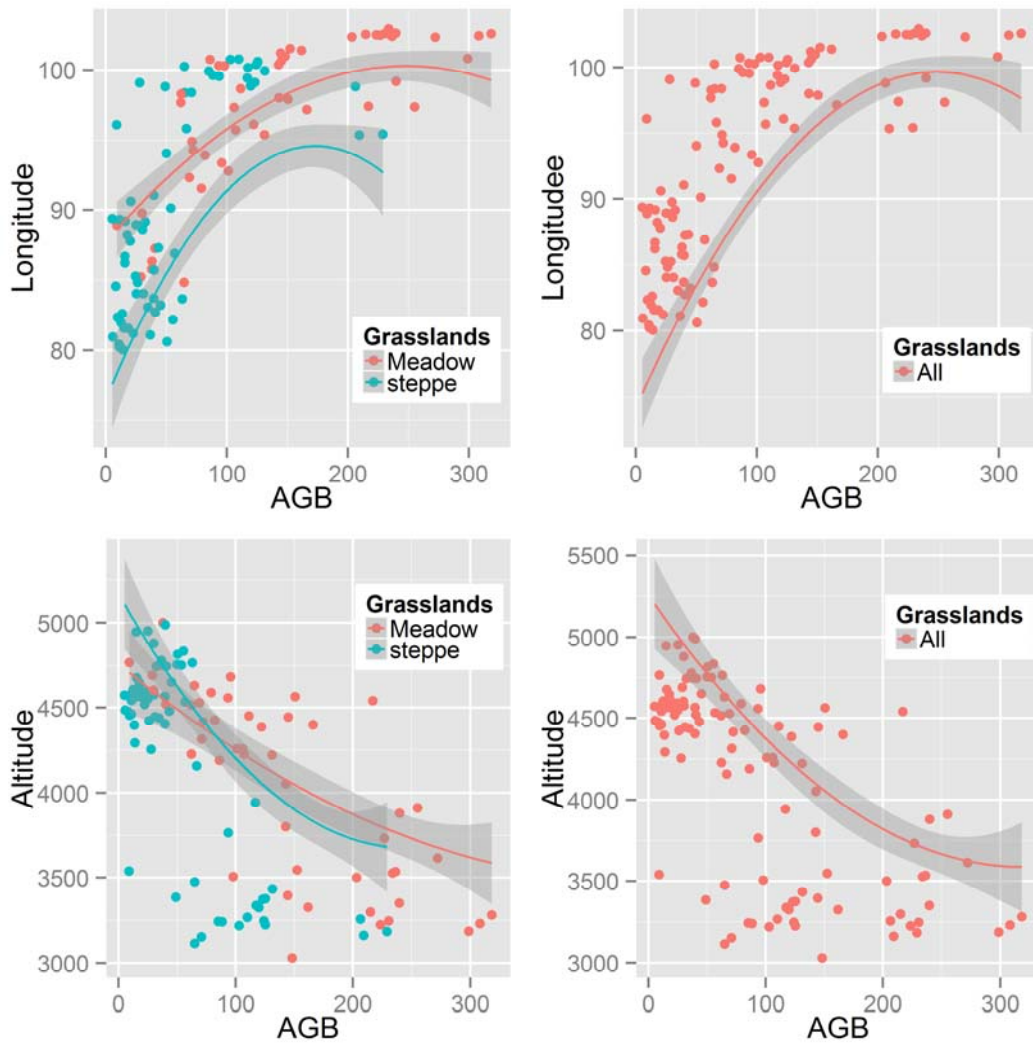
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Fig. 5

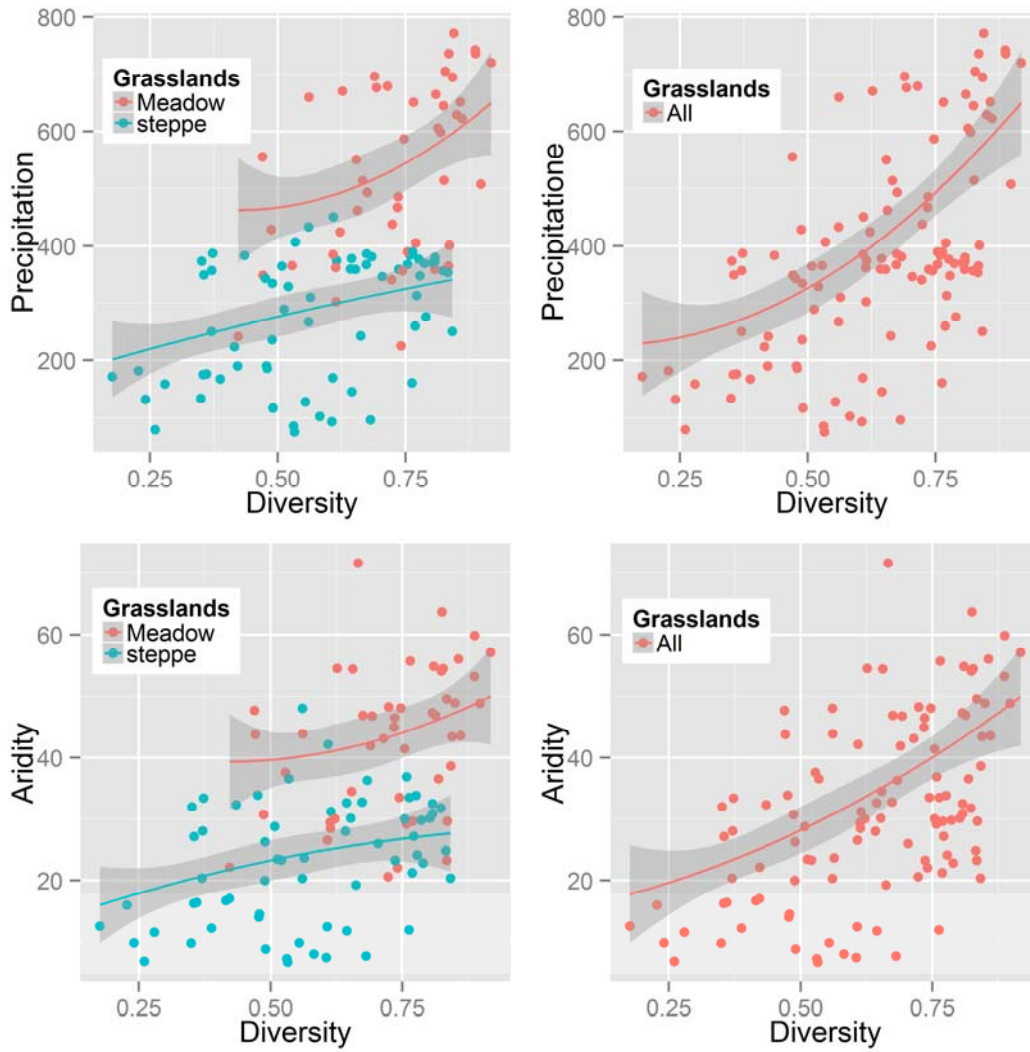


Fig. 6

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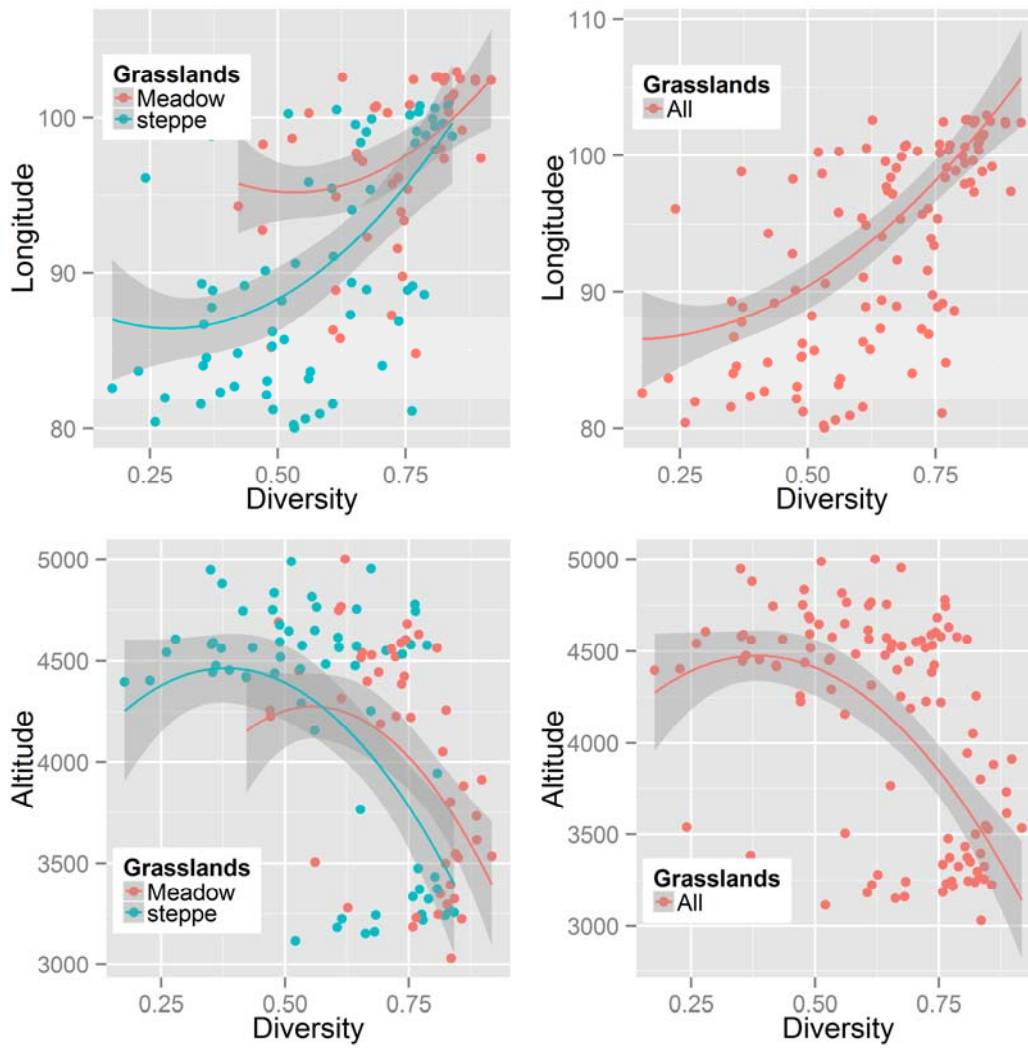


Fig.7

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