Effects of Soil Physico-Chemical Properties on Plant Species Composition and Diversity Along an Elevation Gradient Over Alpine Grassland on the Qinghai-Tibetan Plateau, China

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Research Article

Abstract

Background and aims Alpine grassland on the Qinghai-Tibetan Plateau (QTP) is sensitive and fragile, and it is subject to serious degradation. It is essential to determine the effects of soil parameters on plant species to explain grassland degradation.

Methods We classified plant communities into six types based on hierarchical clustering. Then we analyzed the effects of soil physico-chemical properties on plant species composition and diversity by canonical ordination and spatial regression from an elevation perspective.

Results Elevation class had significant effects on soil moisture content, soil pH, and soil available nitrogen content. The primary soil parameter affecting plant species composition and diversity in alpine grassland was soil available nitrogen content. The effect of soil available nitrogen content on plant species richness varied at different elevations. For Gramineae plants (G), plant species richness declined with the increase in soil available nitrogen content at low elevation, but rose at middle elevation. Soil available nitrogen content had a more significant limiting effect on species richness at high elevation.

Conclusion Analyzing the relationship between plant species and soil physico-chemical properties increases our understanding of grassland degradation, and will improve grassland restoration programs and responses to climate change.

1. Introduction

The Qinghai-Tibetan Plateau (QTP) is called "Asia's water tower" because it is the headwaters of Asia's major rivers, on which approximately 40% of the world population depends (Kuang and Jiao, 2016). The QTP is an important ecological barrier in China and even Asia. Alpine grassland is the main ecosystem on the QTP (Liu et al., 2018), accounting for more than half of the total plateau area. It has important ecological and socio-economic roles, such as storing carbon, altering biodiversity by evolving grass species that shape grassland environments (Gieselman et al., 2013), and impacting livestock by producing forage (Harris, 2010). Alpine grassland on the QTP is one of main pastoral areas in China and provides important grazing grounds for livestock. Furthermore, the QTP is highly sensitive to global climate change (Xu et al., 2008; Yao et al., 2012), and the warming rate on the QTP has been almost twice that of general global warming over recent decades (Kuang and Jiao, 2016). This means that the alpine grassland ecosystem on the QTP is sensitive and fragile (Guo et al., 2018).

Alpine grassland on the QTP has suffered from severe degradation due to climate change and human activities in recent decades (An et al., 2017; Harris 2010). Furthermore, alpine grassland degradation has led to a decline in grassland productivity, a decrease in biodiversity, and environmental deterioration (An et al., 2017). It has caused fragmentation of grassland coverage, a decrease in the proportion of edible herbage, a reduction in soil fertility, and soil erosion (Li et al., 2013). The alpine grassland ecosystem is under threat and grassland degradation has attracted substantial national attention.

There have been many studies on grassland degradation, and technological restoration solutions and measures have been proposed. Some researchers have investigated grassland degradation and restoration from the view point of plant community, including grass coverage (Zhang et al., 2014), grassland net primary production (Chen et al., 2014), and grassland yield (Cai et al., 2015). Some studies have investigated environmental issues, such as topographic parameters (Li et al., 2018) and soil condition (Harris, 2010), and a series of studies have analyzed the relationship between plant community and environmental parameters. Based on species dominance, some studies have investigated the effect of environmental factors on species diversity patterns among different plant community types (Jiang et al., 2016). In addition, natural gradient studies have been conducted to explore the mechanisms of species character changes. For instance, the relationships between the physico-chemical parameters of soil and plant species have been analyzed in terms of geological structure and lithology (Do Carmo and Jacobi 2016; Hanaka et al., 2019). Topography plays a crucial role in grassland degradation because it affects the distribution of moisture and energy (Li et al., 2018). The QTP has complex topographic features with contiguous mountains and hills. However, there have been few studies on how the relationships between plant species and soil parameters along the elevation gradient affect grassland degradation on the QTP.

This study focused on the relationship between species composition/diversity and soil parameters. We explored the effect of soil physico-chemical properties on plant species along an elevation gradient to provide information that could be used to improve the restoration of damaged grassland ecosystems and responses to climate change. The specific objectives were to (1) clarify significant differences in soil parameters at different elevations; (2) determine which soil parameters affect species composition and diversity, and (3) elucidate the effects of key soil parameters on species diversity at different elevations.

2. Materials And Methods

2.1. Description of the study area

The study area is located in the southeastern part of the QTP (83°47⊠~104° 31⊠ E, 25° 24⊠~36° 24⊠ N) (Fig. 1), and includes Naqu, Jiali, Changdu, Basu, and Baqing Counties in the Tibetan autonomous prefecture, Qumalai, Zhiduo, Zaduo, and Nangqian Counties in Qinghai Province, and Ruoergai, Aba, Ganzi, and Hongyuan Counties in Sichuan Province. It covers an area of 747,729 km^2 and accounts for nearly 30% of the QTP. The elevation ranges from 1,200 m to 5,754 m above sea level, with geographical characteristics of mountains and valley plains. The study area is in the temperate semi-arid monsoon climate zone, the mean annual temperature ranges from − 9.4°C to 14.7°C, and the multi-year average precipitation is from 175 mm to 1,280 mm. The vegetation types are mainly alpine meadow and alpine steppe, followed by temperate meadow, temperate steppe, and sparse grass. The soil types are mainly felt soil, meadow soil, and dark felt soil, followed by permafrost soil, brown cold calcium soil, and swamp soil.

2.2. Sampling design

The grassland community was sampled during the growing season between July and August, 2017 and 2018. We selected 112 field sites with representative alpine meadow. They contained natural vegetation and were homogeneous sites within the study area (Fig. 1). Each site covered an area of 900 m^2 (30 m × 30 m). We established five 1 m × 1 m quadrats, which were placed at the four corners and at the center of the site. Within each quadrat, we measured the cover, height, and density of every vascular plant species, and we recorded latitude, longitude, elevation, and topographic slope using a handheld global positioning system (GPS) device. Five soil samples were collected at a depth of 0–20 cm in each quadrat.

2.3. Data collection and analysis

2.3.1. Vegetation data collection

We recorded the coverage of all plants as the fractional vegetation cover, and the species names and abundance of each vascular plant species. The height of each species was evaluated by randomly measuring five individual plants. We also recorded the coverage and frequency of each species in each quadrat. The nomenclature follows Flora of China (foc.iplant.cn). The importance values (IVs) of the species were calculated as follows:

$$p_i = \left(\frac{C_i}{\sum_i^S C_i} + \frac{H_i}{\sum_i^S H_i} + \frac{F_i}{\sum_i^S F_i}\right)/3 \times 100 \ (1)$$

where C_i is the coverage of species i; H_i is the height of species i; and F_i is the frequency of species i.

We used α diversity and β diversity to describe species diversity. The α diversity indices used were the species richness index (R), the Shannon-Wiener index (H'), and Pielou's evenness index (J). For β diversity, Sørenson's similarity index (C$_s$) was used as a similarity coefficient based on presence-absence species data and represented diversity among communities (Stirling and Wilsey, 2001). The diversity indices were calculated as follows:

R = S (2)

$$H' = -\sum_{i=1}^{s}\left(p_i ln p_i\right)$$

3

$$J = -\sum_{i=1}^{s}\left(p_i ln p_i\right)/lnS$$

4

C$_s$ = 2t / (a + b) (5)

where S is the number of species in the plot; i is species i; p$_i$ is the importance value (IVs) of species i; t is the number of species shared by two communities or plots; a and b represent the total number of species in two communities or plots, respectively.

2.3.2. Soil physico-chemistry analysis

Soil samples were collected at a depth of 0–20 cm from the surface in each field quadrat. A total of five soil samples were collected from each quadrat and the soil parameters were the average of the five samples. The soil samples were air-dried and sieved, and the soil moisture content and soil bulk density were determined by the oven drying method according to Thomasson (2010). Soil pH was measured using a pH meter and a 1:1 water/soil suspension, and soil total carbon content and soil total nitrogen content were measured using the flash dynamic combustion method and a gas chromatographic separation and thermal conductivity detection system (vario EL cube Elementar, Germany), respectively (Feng et al., 2017). Soil organic carbon content was determined by the dichromate oxidation method and soil available nitrogen content was measured by the alkali-hydrolysis reduction diffusion method (Bao, 2000). Soil available phosphorus content was extracted using the ammonium bicarbonate method and soil available potassium content was extracted using the acetamide extraction method (Zhang et al., 2018).

2.3.3. Climate and topography data

The climate parameters were calculated by using the ANUSPLIN software package (version 4.4) and the weather and elevation data (Xu and Hutchinson, 2013). The temperature and precipitation data were derived from the national weather stations data for 1982–2015 (freely available at the web site: http://cdc.cma.gov.cn). The elevation data was derived from digital elevation models at a 1 km resolution and were obtained by resampling the data from CGIAR-CSI (freely available at the web site: http://srtm.csi.cgiar.org).

2.4. Statistical analysis

We used the vegan and cluster packages in R version 3.5.0 to analyze species composition and diversity in the different communities. The plant communities were classified by hierarchical clustering using Ward's method and the Bray-Curtis distance. Then, the optimal number of clusters was selected by the cluster package. We used non-metric multidimensional scaling (NMDS) analysis to show the species cluster characteristics of the different plant communities.

Statistical analyses of soil parameters were performed using SPSS Statistics software (version 20). One-way analysis of variance (ANOVA) was used to compare significant differences among the soil physico-chemical properties of the different plant communities. A paired significance analysis was undertaken using the Scheffe test when the variation was significant ($p < 0.05$). The correlations between species diversity (species richness, Shannon-Wiener index, and evenness) and soil physico-chemical properties were calculated using Pearson's correlation coefficient by the function cor and psych package in R version 3.5.0. Stepwise multiple linear regression was used to screen the variables affecting species richness. The vegan package in R version 3.5.0 was used to perform a canonical correspondence analysis to further confirm the relationships between species data and soil parameters in the different plant communities. A Mantel test (999 permutations) was used to test the significance of the

relationships and the linear model (LM) was used to explore the significant relationship between species richness and its primary factor.

3. Results

3.1. Changes in plant species composition and diversity along the elevation gradient

There were 369 herbaceous plant species belonging to 174 genera and 49 families. Families with larger IVs (> 1) included Cyperaceae, Gramineae, Rosaceae, Compositae, Ranunculaceae, Polygonaceae, Leguminosae, Gentianaceae, Scrophulariaceae, Euphorbiaceae, Labiaceae, Primulaceae, and Umbelliferae in descending order. The plant communities were classified into six clusters by the cluster analysis, which was based on Bray-Curtis distance matrices (Supplementary Fig. 1). After combining the cluster results with ecological background information and other related studies (Antony et al., 2015; Zhang et al., 2018), the classifications were as follows: *Kobresia pygmaea* (Kp), *Kobresia pygmaea* + miscellaneous plants (KpM); *Kobresia setchwanensis* (Ks), *Carex moorcroftii* (Cm), miscellaneous plants (M); and Gramineae plants (G). The dominant species in the different plant communities were characterized by their IVs (Table 1).

Table 1

The dominance of species selected by IVs across six plant community types

Plant community types	Species names	Family	IV
Kp	*Kobresia pygmaea*	Cyperaceae	9.472
	Carex moorcroftii	Cyperaceae	3.750
	Potentilla saundersiana	Rosaceae	2.984
	Leontopodium leontopodioides	Compositae	1.823
	Stipa capillata	Gramineae	1.150
	Astragalus propinquus	Leguminosae	1.062
	Kobresia tibetica	Cyperaceae	0.833
	Kobresia setschwanensis	Cyperaceae	0.817
	Poa crymophila	Gramineae	0.780
	Taraxacum mongolicum	Compositae	0.738
	Anaphalis sinica	Compositae	0.728
	Oxytropis alpina	Leguminosae	0.702
	Polygonum macrophyllum	Polygonaceae	0.656
	Potentilla anserina	Rosaceae	0.584
	Aster himalaicus	Compositae	0.544
KpM	*Kobresia pygmaea*	Cyperaceae	3.090
	Potentilla saundersiana	Rosaceae	1.524
	Carex moorcroftii	Cyperaceae	1.022
	Leontopodium leontopodioides	Compositae	0.936
	Salix cupularis	Salicaceae	0.638
	Polygonum viviparum	Polygonaceae	0.522
Ks	*Kobresia setschwanensis*	Cyperaceae	1.607
	Potentilla saundersiana	Rosaceae	0.817
	Kobresia pygmaea	Cyperaceae	0.676
	Carex moorcroftii	Cyperaceae	0.572

Notes: Kp, *Kobresia pygmaea*; KpM, *Kobresia pygmaea* + Miscellaneous plants; Ks, *Kobresia setchwanensis*; Cm, *Carex moorcroftii*; M, Miscellaneous plants; G, Gramineae plants.

Plant community types	Species names	Family	IV
	Elymus nutans	Gramineae	0.503
Cm	*Carex moorcroftii*	Cyperaceae	2.292
	Kobresia pygmaea	Cyperaceae	1.302
	Potentilla saundersiana	Rosaceae	0.780
	Polygonum viviparum	Polygonaceae	0.686
	Kobresia setschwanensis	Cyperaceae	0.660
	Leontopodium leontopodioides	Compositae	0.570
	Potentilla anserina	Rosaceae	0.542
M	*Kobresia pygmaea*	Cyperaceae	1.813
	Carex moorcroftii	Cyperaceae	1.624
	Kobresia setschwanensis	Cyperaceae	1.589
	Potentilla saundersiana	Rosaceae	1.299
	Leontopodium leontopodioides	Compositae	0.768
	Polygonum viviparum	Polygonaceae	0.670
	Kobresia tibetica	Cyperaceae	0.657
G	*Elymus nutans*	Gramineae	0.762
	Poa crymophila	Gramineae	0.530

Notes: Kp, *Kobresia pygmaea*; KpM, *Kobresia pygmaea* + Miscellaneous plants; Ks, *Kobresia setchwanensis*; Cm, *Carex moorcroftii*; M, Miscellaneous plants; G, Gramineae plants.

The relative proportions of the families in six plant communities were distinct (Fig. 2). Kp, KpM, Cm, and M were dominated by the Cyperaceae; the Cyperaceae and Compositae proportions were similar for Ks; and Gramineae (22.66%) was predominant in G. The NMDS plot (Fig. 2) shows the species composition characteristics of the different plant communities along coordinate 1 and coordinate 2 of an elevation gradient (I: low elevation, II: middle elevation, III: high elevation). The species composition profile of Kp at high elevation was different from the other elevation classes (Fig. 2a). The species composition profiles at low and middle elevations for all community types except Ks tended to group together (Fig. 2c). The Cyperaceae proportions rose in all the community types other than Ks and G with increasing elevation gradient. For Kp and KpM, the Compositae proportions decreased as elevation increased, but the Compositae proportion in Cm obviously increased with an average growth rate of 30.44% (Fig. 2d). For M, the Gramineae proportion decreased as elevation increased and reached a minimum of 6.78% at high elevation (Fig. 2e).

The species diversity characteristics (species richness, Shannon-Wiener index, and Pielou's evenness index) showed a certain regularity along the elevation gradient (Table 2). The species richness of the overall communities showed an obviously decreasing trend as the elevation rose, and followed the order of low elevation (35.24) > middle elevation (29.45) > high elevation (22.24) (Fig. 3a). The species richness for Kp and KpM dropped gradually as elevation increased, and species richness for Cm and M rose at first and then decreased as elevation increased (Fig. 3b). The Shannon-Wiener index for the overall communities showed a downward trend as elevation increased and the Pielou's evenness index reached a maximum at middle elevation. Sørenson's similarity indices differed among elevation classes for different community types (Supplementary Table 1). The highest similarity index was between KpM and Ks with a value of 0.75, followed by the index between KpM and G (0.73).

Table 2
Characteristics of species diversity at different elevation classes

Diversity characteristics	Plant community type	Low elevation	Middle elevation	High elevation
Richness index	Kp	28.56 ± 4.83	25.50 ± 3.85	20.93 ± 3.32
	KpM	29.25 ± 5.56	26.00 ± 4.43	25.29 ± 10.72
	Ks	45.25 ± 8.20	34.25 ± 2.50	——
	Cm	32.20 ± 5.45	34.50 ± 4.65	24.50 ± 2.38
	M	35.78 ± 5.73	35.83 ± 5.22	20.80 ± 5.26
	G	40.50 ± 9.61	38.50 ± 9.95	——
Shannon-Wiener index	Kp	2.87 ± 0.34	2.71 ± 0.38	2.52 ± 0.21
	KpM	2.72 ± 0.16	2.74 ± 0.19	2.69 ± 0.36
	Ks	3.34 ± 0.31	3.09 ± 0.13	——
	Cm	2.97 ± 0.35	3.03 ± 0.31	2.75 ± 0.15
	M	3.03 ± 0.39	3.04 ± 0.57	2.53 ± 0.35
	G	3.24 ± 0.36	3.24 ± 0.27	——
Pielou's evenness index	Kp	0.87 ± 0.03	0.85 ± 0.04	0.83 ± 0.04
	KpM	0.81 ± 0.03	0.85 ± 0.03	0.85 ± 0.03
	Ks	0.88 ± 0.04	0.88 ± 0.02	——
	Cm	0.86 ± 0.02	0.86 ± 0.02	0.86 ± 0.03
	M	0.85 ± 0.04	0.87 ± 0.03	0.84 ± 0.05
	G	0.88 ± 0.04	0.89 ± 0.02	——

Notes: Kp, *Kobresia pygmaea*; KpM, *Kobresia pygmaea* + Miscellaneous plants; Ks, *Kobresia setchwanensis*; Cm, *Carex moorcroftii*; M, Miscellaneous plants; G, Gramineae plants.

3.2. Soil physical and chemical properties along the elevation gradient

Elevation had a significant impact ($p < 0.05$) on soil physico-chemical properties, such as soil moisture content, soil pH, and soil available nitrogen content, in all the plant communities (Table 3). However, the soil physico-chemical properties were not significantly influenced ($p < 0.05$) by plant community type at the same elevation class. Soil moisture content for Kp was significantly greater by 1.8 times at high elevation compared to the low and middle elevations. Soil pH significantly varied ($p < 0.05$) along the

elevation gradient for Kp in the order high elevation (5.53) < low elevation (5.89) < middle elevation (6.67). Soil available nitrogen content increased significantly (p < 0.05) from middle elevation to high elevation for KpM and Cm, and was 9.4 and 4.7 times greater at high elevation than at middle elevation for KpM and Cm, respectively. A significant (p < 0.05) increase in soil available nitrogen content for Kp was observed at high elevation, with an average of 485.27 mg kg^{-1} at high elevation, 56.98 mg kg^{-1} at low elevation, and 43.67 mg kg^{-1} at middle elevation. Soil available nitrogen content was significantly greater (p < 0.05) by six times at high elevation compared to low elevation for M (Fig. 4).

Table 3
Soil physico-chemical properties as influenced significantly by elevation for different plant communities

Plant community type	Soil physico-chemical property	Low elevation	Middle elevation	High elevation
Kp	SMC	24.79 ± 7.95a	22.38 ± 7.15a	62.41 ± 15.71b
	SpH	5.89 ± 0.53a	6.67 ± 0.64b	5.53 ± 0.26a
	SAN	56.98 ± 15.95a	43.57 ± 16.06a	485.27 ± 89.21b
KpM	SAN	43.11 ± 12.36a	45.44 ± 12.36a	474.32 ± 82.15b
Cm	SAN	57.87 ± 4.49a	61.82 ± 12.50a	354.43 ± 121.43b
M	SAN	59.11 ± 28.69a	47.74 ± 15.55a	417.04 ± 129.27b
Analyses of variance (p values)				
Variable	Elevation class	Community type	Elevation × Community	
SMC	p ⩽0.01	0.196	p ⩽0.05	
SpH	p ⩽0.05	0.27	0.059	
SAN	p ⩽0.001	0.788	0.469	

Notes: Kp, *Kobresia pygmaea*; KpM, *Kobresia pygmaea* + Miscellaneous plants; Cm, *Carex moorcroftii*; M, Miscellaneous plants; SMC, soil moisture content; SpH, soil pH; SAN, soil available nitrogen content.

3.3. Soil physico-chemical properties effects on plant species composition and diversity

Figure 5 shows the Pearson's correlations between species diversity and soil physico-chemical properties. Species richness was significantly negatively correlated with soil available nitrogen content (r = -0.41, p <

0.01), soil bulk density (r = -0.29, p < 0.01), and soil moisture content (r = -0.19, p < 0.05). Species richness was significantly positive correlated with the Shannon-Wiener index (r = 0.96, p < 0.01), and with species evenness (r = 0.58, p < 0.01). Therefore, species richness was chosen as the species variable. A stepwise multiple linear regression was used to determine the effect of plant species richness on the explanatory variables, such as soil physico-chemical properties and community types (Type1: Kp, *Kobresia pygmaea*; Type2: Cm, *Carex moorcroftii*; Type3: Ks, *Kobresia setchwanensis*; Type4: KpM, *Kobresia pygmaea* + Miscellaneous plants; Type5: M, Miscellaneous plants) (Table 4). The ANOVA analysis indicated that soil available nitrogen content, Type 2, and soil pH had significant impacts (p < 0.01) on species richness. Soil available nitrogen content contributed the most (46.1%) to the variance in species richness explained by the regression model (R^2 = 0.35), followed by Type 2 (23.5%), soil pH (14.1%), community type 5 (9.9%), and soil bulk density (6.3%).

Table 4
Results of a stepwise multiple linear regrassion of species richness against explanatory variables

Variable	Estimate (standard error)	ANOVA		Relative importance
		F-value	Pr(꞉ F)	
SAN	0.65	22.32	***	46.1%
Type 2	0.17	18.81	***	23.5%
SpH	-0.40	16.25	***	14.0%
Type 5	-0.36	14.47	***	10.0%
SBD	-0.49	12.10	***	6.3%

Notes: SAN, soil available nitrogen content; Type, plant community type (Type1: Kp, *Kobresia pygmaea*; Type2: Cm, *Carex moorcroftii*; Type3: Ks, *Kobresia setchwanensis*; Type4: KpM, *Kobresia pygmaea* + Miscellaneous plants; Type5: M, Miscellaneous plants); SpH, soil pH; SBD, soil bulk density.

The CCA results indicated that soil available nitrogen content and soil moisture content were the most influential factors among the soil variables because they drove changes in the composition and diversity of plant species. Plant species composition and diversity followed the first two axes of the ordination with soil variables (Fig. 6). The overall Mantel significance test was significant (F = 2.411, p < 0.001), and the significance test was also significant for the first axis (F = 7.107, p < 0.001) and the second axis (F = 2.555, p < 0.001). The first axis accounted for 42.11% of the total variation with an eigenvalue of 0.4261 and the second axis accounted for 15.14% with an eigenvalue of 0.1532. Soil available nitrogen content was strongly negatively correlated (-0.94) and soil bulk density was negatively correlated (-0.39) with the first axis. Soil moisture content had a strong negative correlation with the second axis (−0.76) and soil pH was positively correlated with the second axis (0.60).

3.4. Influence of soil available nitrogen content on species richness along the elevation gradient

The overall elevation class results showed that there was a significant relationship between species richness and soil available nitrogen content. Furthermore, the relationships between species richness and soil available nitrogen content varied among the elevation classes (Fig. 7). The variations between species richness and soil available nitrogen content for the different communities at the low and middle elevations had similar trends, except for G. Species richness had a significant negative relationship with soil available nitrogen content for M at the low elevation (R^2 = 0.54, p = 0.01). A similar trend was observed for M at the middle elevation (R^2 = 0.80, p = 0.04). Increased species richness was associated with increasing soil available nitrogen content for Kp at middle elevation (R^2 = 0.29, p = 0.04), but species richness had no significant correlation with soil available nitrogen content for all communities at high elevation.

4. Discussion

4.1. Effects of soil available nitrogen content on species composition and diversity along the elevation gradient

Many studies have demonstrated that elevation is a decisive factor influencing the distribution pattern of plant species because it leads to variations in hydrothermal conditions (Antony et al., 2015; Tesfaye et al., 2016). Our study showed that the species richness of the plant communities declined as elevation increased (Fig. 3a), but for the same plant community type, the species diversity values for the different elevation classes were not significantly different (Table 2). Species richness was affected by soil available nitrogen content to different extents at the different elevations (Fig. 7). Plant growth in an alpine meadow ecosystem is strongly limited by available nitrogen (Jiang et al., 2017). The conversion of soil available nitrogen is impeded due to the extreme climate conditions in alpine regions (Xu et al., 2011). Elevation is a restrictive factor for soil available nitrogen content. It influences the soil available nitrogen conversion because the hydrothermal conditions vary at different elevations. The partial correlation coefficient between plant species richness and soil available nitrogen content was insignificant on the overall elevation, and there was a decrease in species richness of 0.916 with every 100 mg kg^{-1} increase in soil available nitrogen content. For different elevations, the relationships between species richness and soil available nitrogen content shown by the partial correlation regression tended to decrease insignificantly (Supplementary Fig. 2).

Our study eliminated the redundancy effects of each factor by using stepwise multiple linear regression. The results showed that soil available nitrogen content explained the most variance (46.1%) in the regression model for species richness against the explanatory variables. The LM analysis, which controlled the elevation variable (Fig. 7), showed that Cm species richness significantly increased (1.14 ± 0.73 (mg kg^{-1})$^{-1}$) and the species richness of Ks significantly decreased (-0.47 ± 0.23 (mg kg^{-1})$^{-1}$) with increasing soil available nitrogen content at low elevation. The species richness value for G had the highest intercept (2.13 ± 1.57 (mg kg^{-1})$^{-1}$) at middle elevation. Furthermore, species richness decreased for all plant communities (Kp, KpM, Cm, M) appearing at high elevation, but this was not obvious (Fig. 8).

Figure 8 Intercepts for species richness response to soil available nitrogen content by the different plant communities along the elevation gradient. Error bars indicate standard errors

4.2. Effects of climate factors on species richness and soil available nitrogen

The climate of the study area located in the southeast of the QTP is clearly warming and the rates of the temperature rise have been found to increase with increasing elevation (Kuang and Jiao, 2016; Song et al., 2014). The precipitation on the QTP is generally increasing, but annual precipitation in the study area shows an insignificant downward trend. The variation in precipitation does not have a uniform spatial distribution and the changes in precipitation are not as pronounced as the changes in temperature (Kuang and Jiao, 2016). It is widely acknowledged that climate factors are the main drivers of species richness patterns because they influence the effects of temperature on rates of species evolution or interactions between organisms (Kubota et al., 2015). Some studies have found that climate warming enhances the mineralization of soil organic matter, which contains most of the soil nitrogen (Kahmen et al., 2006; Manning et al., 2008). This mineralization leads to soil nutrient enrichment and the available nitrogen in soil increases (Klein et al., 2004). The multiple regression analysis of soil available nitrogen content against its influential factors indicated that temperature ranked next to elevation among the environmental factors at 8.4% (Supplementary Table 2). The increase in temperature will accelerate the decomposition of nitrogen in soil organic matter, which will affect soil available nitrogen content.

4.3. Implications for alpine grassland management

Analyzing the effects of soil physico-chemical properties on plant species composition and diversity within different plant communities along an elevation gradient provides guidance that could be used to improve the grassland management of different community types. The results can be used to improve grassland restoration programs and the construction of alpine grassland (Li et al., 2018). The different effects of soil variables on plant species composition and the diversity of different plant community types help explain species distribution patterns and the formation of communities. The resource utilization modes used by different plant species vary among community types. They depend on the characteristic differences among the niches utilized by the dominant species (Thakur and Wright, 2017). Nitrogen is the main limiting element on plant growth in alpine grassland ecosystems (Gao et al., 2013; Jiang et al., 2017), especially for Cyperaceae plants. Soil available nitrogen content increased along axis 1 from right to left, and KpM was mainly distributed across a spatial area with a high soil available nitrogen content (Fig. 6). Soil available phosphorus content positively impacts species richness in Cm, in which the addition of phosphorus fertilizer promotes plant community growth. Climate warming causes plants to migrate from lower to higher altitudes, and it can also directly reduce plant diversity by replacing dominant and native species that have been disappeared due to habitat loss (Niu et al., 2019; Steinbauer et al., 2018). The result that nitrogen enrichment caused by soil warming reduces the loss of plant species diversity provides a theoretical foundation for scientific fertilization (Xu et al., 2011). The rebuilding of artificial grassland can be regarded as an effective approach for restoring degraded

grassland by regulating community structure and improving grassland productivity in alpine grassland (Wu et al., 2010).

5. Conclusion

In this study, we divided plant communities into six types based on species importance values and analyzed how plant species composition/diversity was influenced by soil parameters along an elevation gradient. The results showed that elevation was the main background factor affecting species richness. Species richness decreased as elevation increased for all plant communities, but the trend was not significant among community types. Soil available nitrogen content was the most important factor driving the changes in plant species composition and diversity among the soil parameters. Our results further indicated that the effect of soil available nitrogen content on plant species richness was influenced by elevation, and that the limiting effect of soil available nitrogen content was more obvious at high elevation. Furthermore, climate warming accelerated the decomposition of soil organic nitrogen and temperature was the most important environmental factor after elevation. Therefore, nitrogen mineralization caused by climate warming exacerbated the decline in species richness at high elevation. The findings of this study can be used to refine grassland management measures and improve the restoration and construction of alpine grassland.

Declarations

Conflicts of interest

The authors declare that they have no known conflicts of interest.

Availability of data and material

Not applicable.

Code availability

Not applicable.

Authors' contributions

W. Han, L. Chen designed the study, analyzed the data and wrote the manuscript. X. Su, G. Liu modified article structure. D. Liu organized and analyzed the data. T. Jin, S. Shi, T. Li participated in the field survey. All the authors contributed discussion to improve the manuscript.

Ethics approval

Not applicable.

Consent to participate

All authors consent to participate.

Consent for publication

All authors consent for publication.

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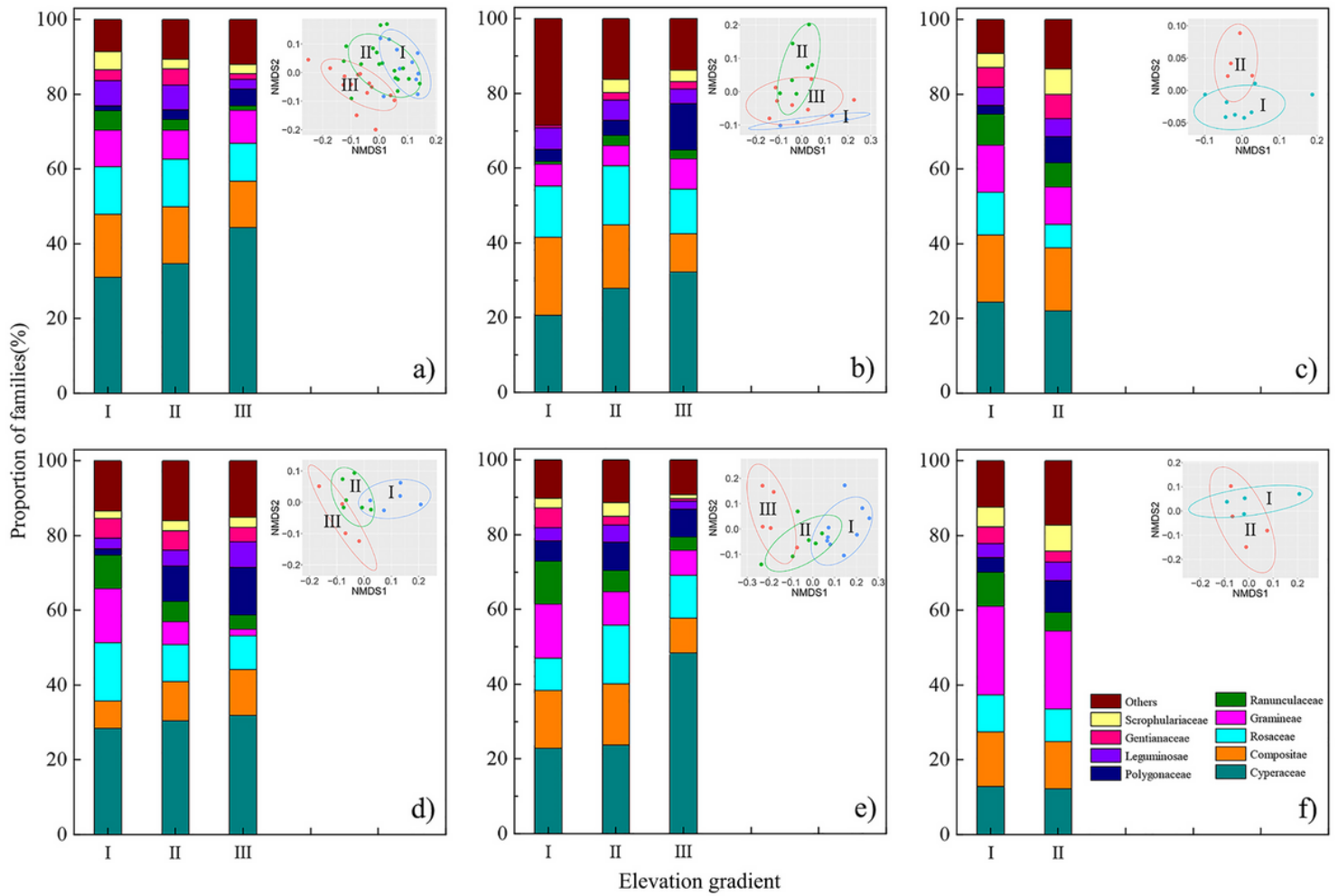
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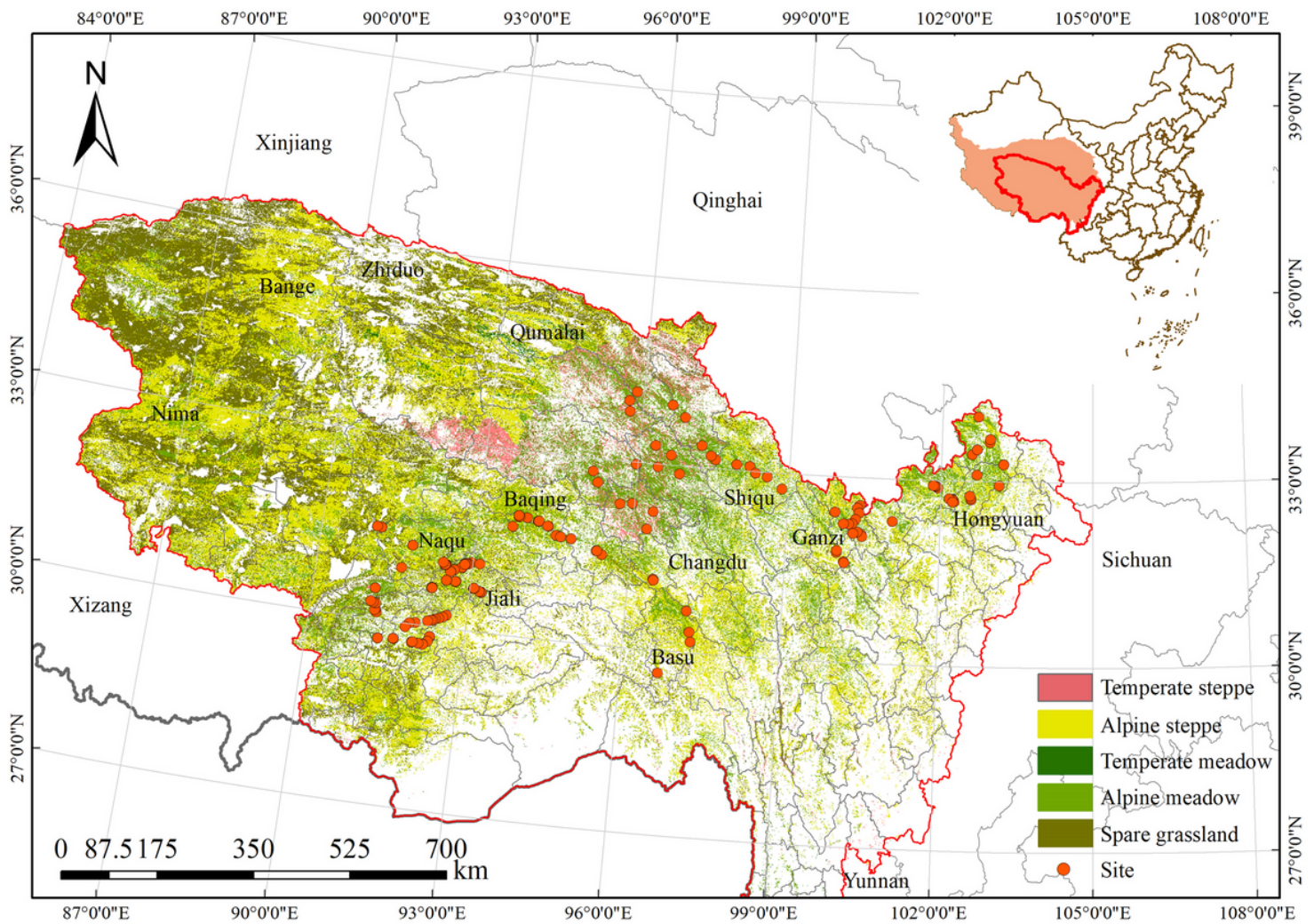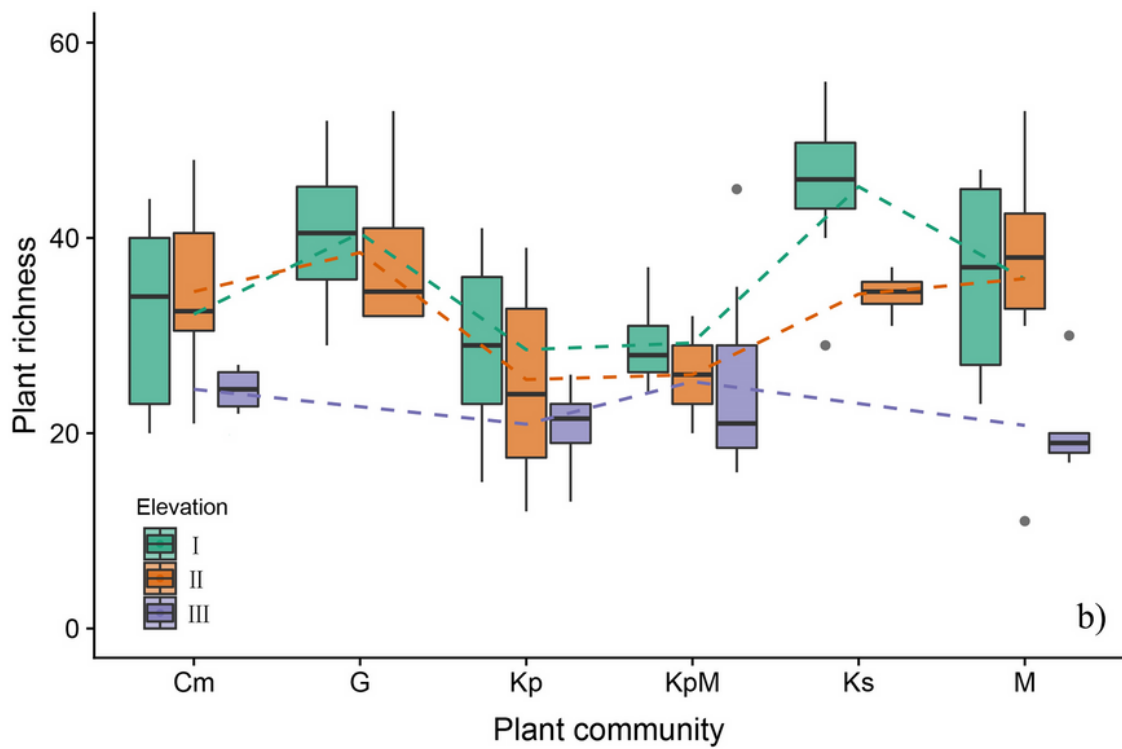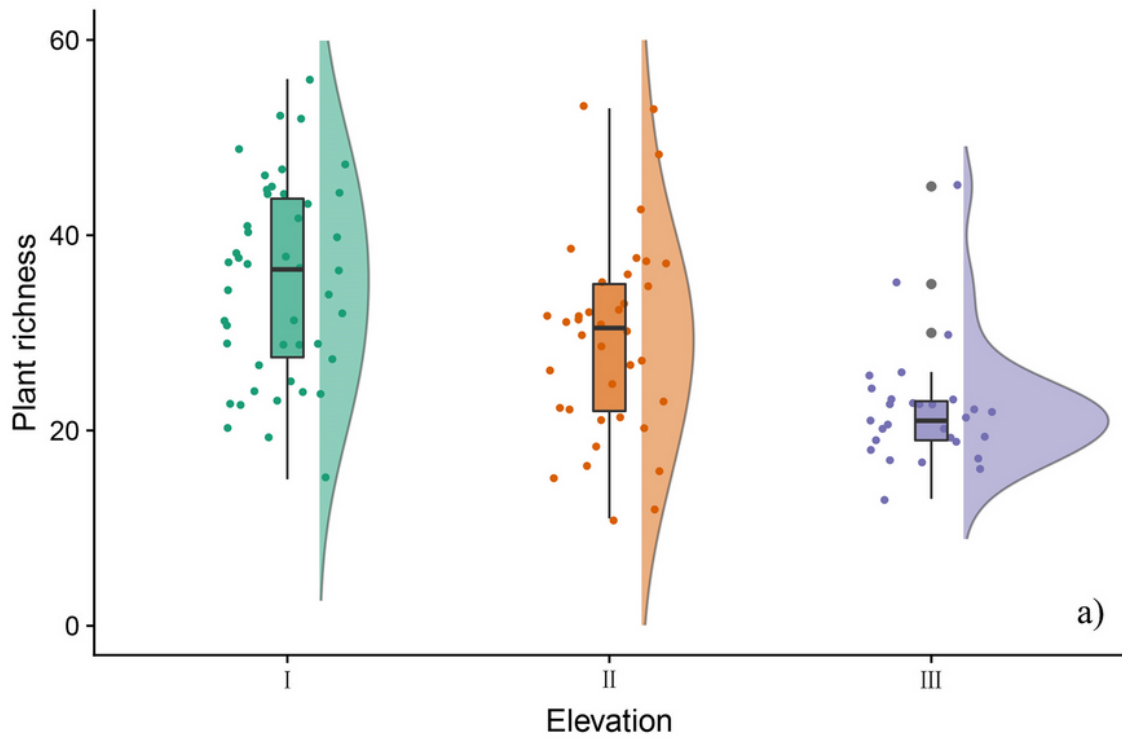
Figures

Figure 1

Location of the study area.

Figure 2

Composition of the plant communities along an elevation gradient for six plant communities and non-metric multidimensional scaling analysis (NMDS) of plant composition based on the Bray-Curtis distance. Kp: Kobresia pygmaea (a), KpM: Kobresia pygmaea + Miscellaneous plants (b), Ks: Kobresia setchwanensis (c), Cm: Carex moorcroftii (d), M: Miscellaneous plants (e), G: Gramineae plants (f)
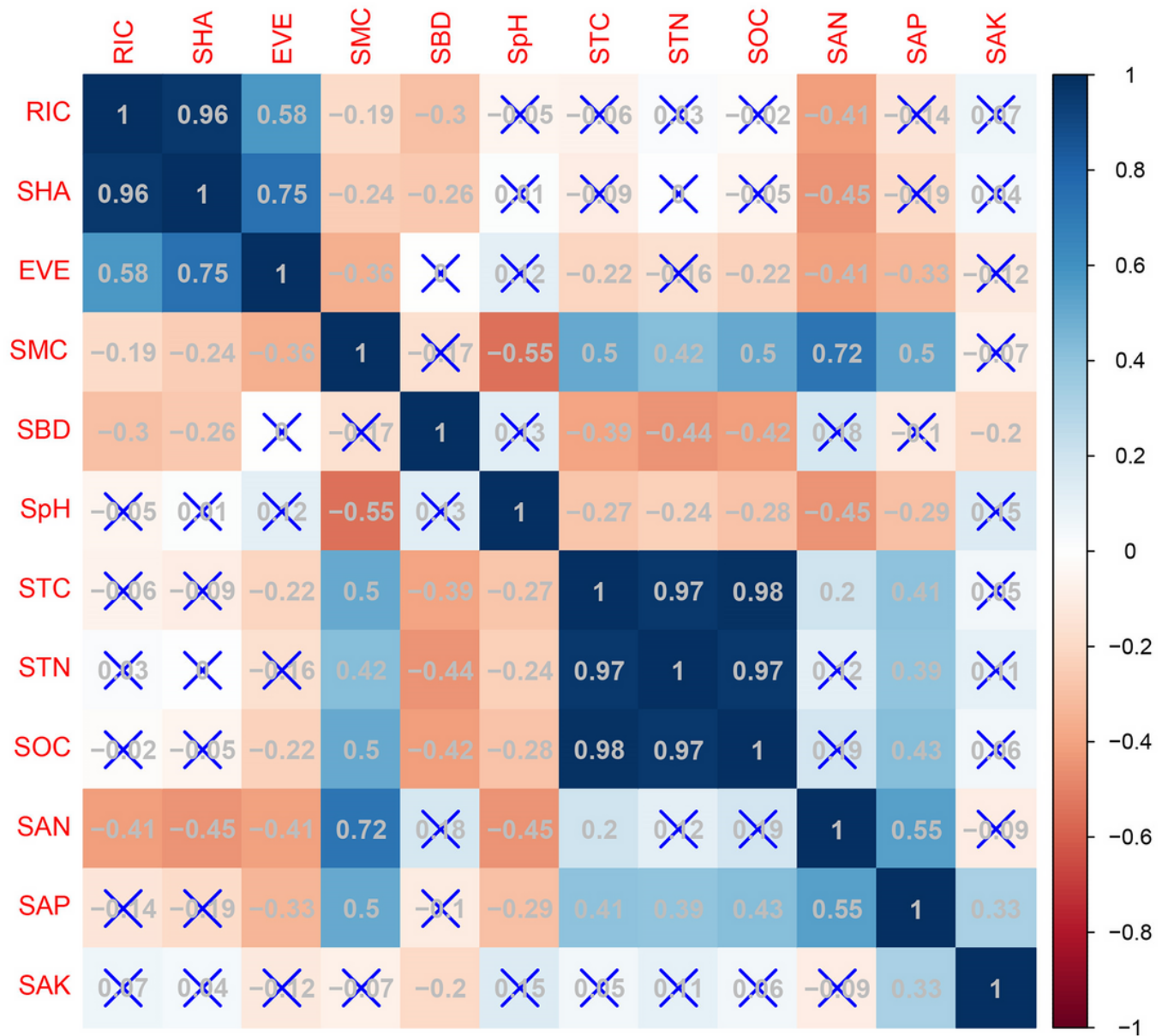
Figure 3

Box (a) and raincloud plots (b) of plant richness along the elevation gradient
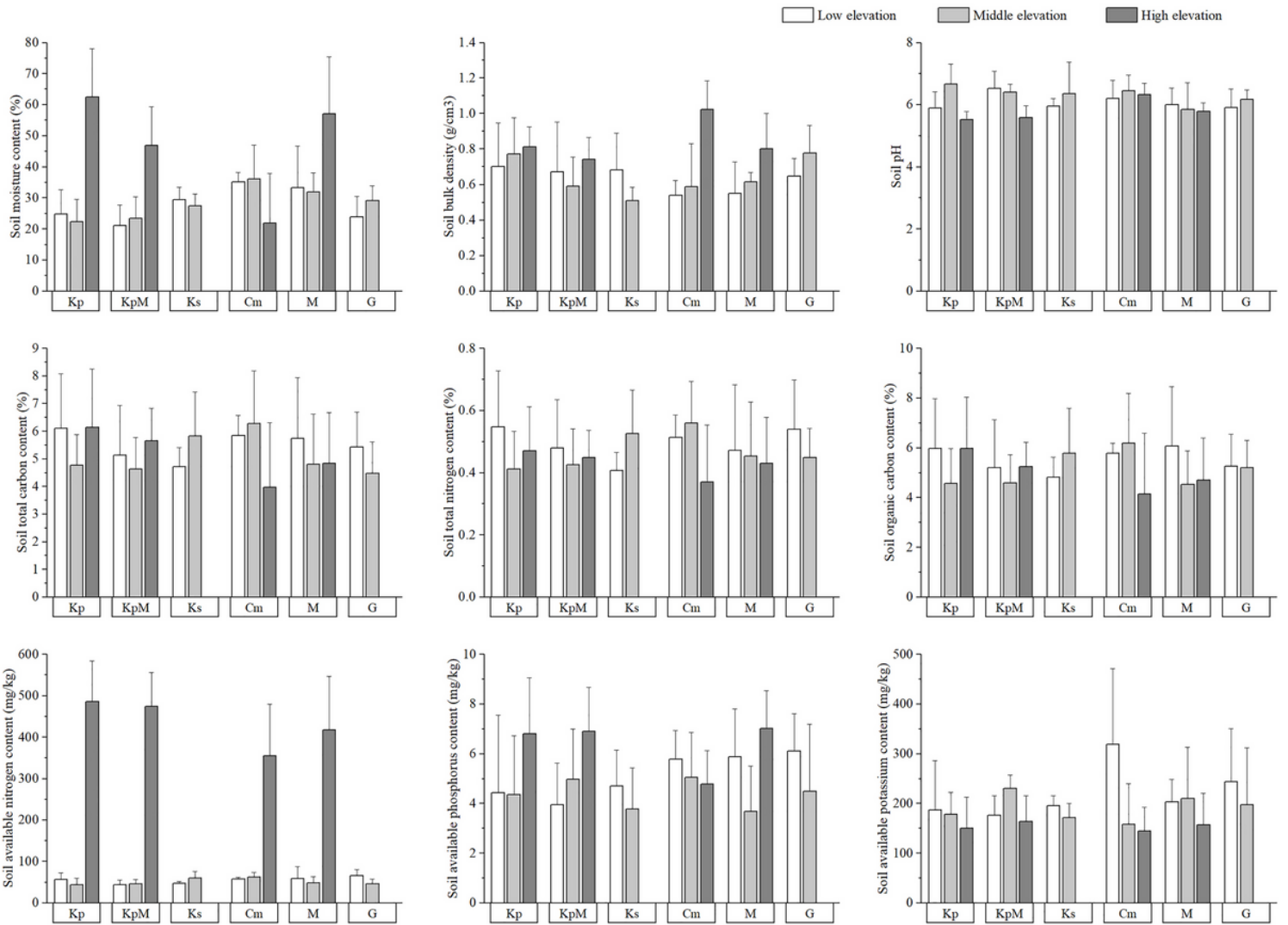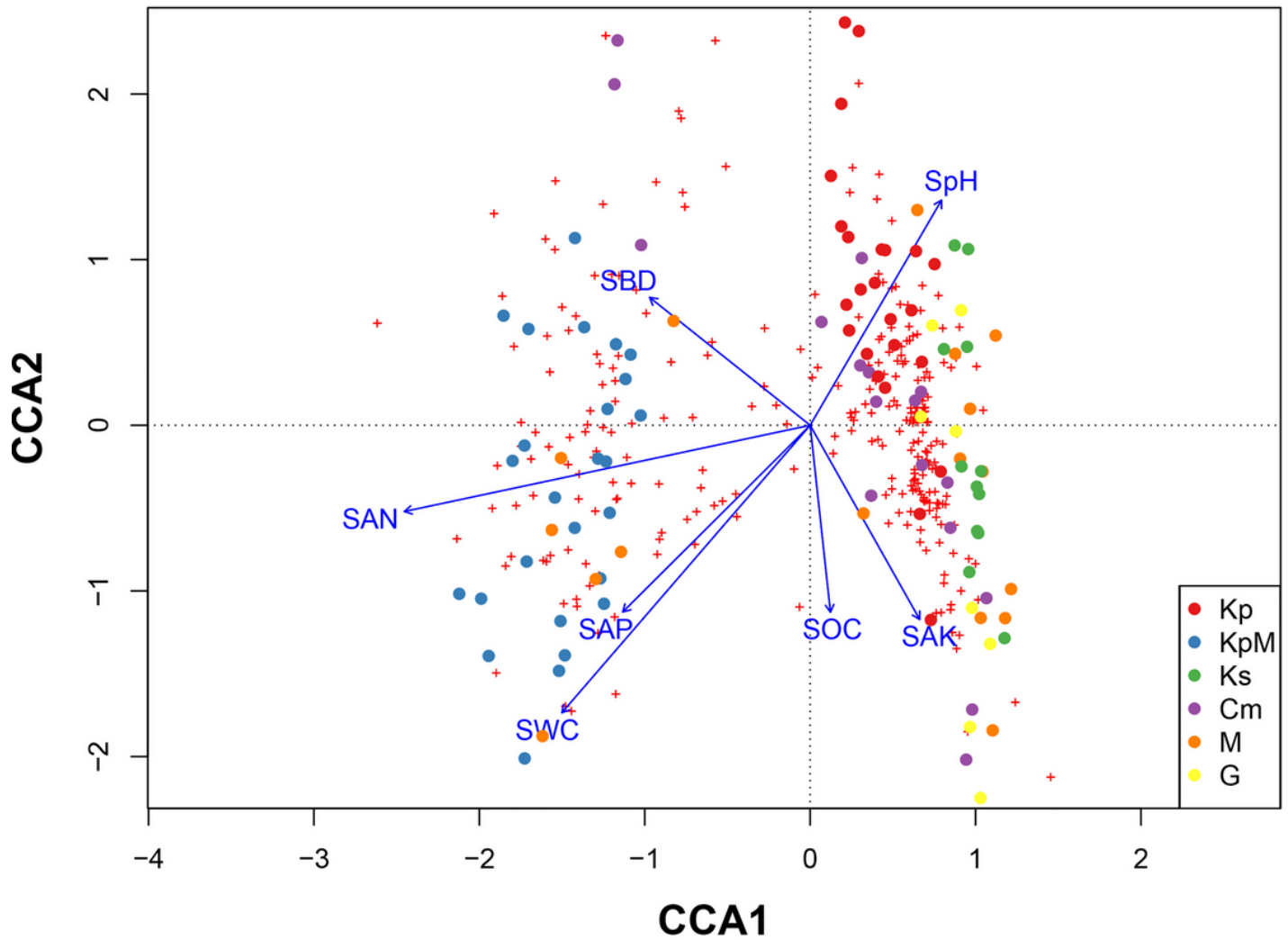
Figure 4

Influence of elevation on the soil physico-chemical properties of the different plant communities. Kp: Kobresia pygmaea, KpM: Kobresia pygmaea + Miscellaneous plants, Ks: Kobresia setchwanensis, Cm: Carex moorcroftii, M: Miscellaneous plants, G: Gramineae plants

Figure 5

Pearson's correlations between species diversity and soil variables. (RIC: species richness, SHA: Shannon-Wiener index, EVE: species evenness, SMC: soil moisture content, SBD: soil bulk density, SpH: soil pH, STC: soil total carbon content, STN: soil total nitrogen content, SOC: soil organic carbon content, SAN: soil available nitrogen content, SAP: soil available phosphorus content, SAK: soil available potassium content)

Figure 6

Canonical correspondence analysis showing the relationships between species and soil variables across different plant communities. Kp: Kobresia pygmaea, KpM: Kobresia pygmaea + Miscellaneous plants, Ks: Kobresia setchwanensis, Cm: Carex moorcroftii, M: Miscellaneous plants, G: Gramineae plants, SMC: soil moisture content, SBD: soil bulk density, SpH: soil pH, STC: soil total carbon content, STN: soil total nitrogen content, SOC: soil organic carbon content, SAN: soil available nitrogen content, SAP: soil available phosphorus content, SAK: soil available potassium content
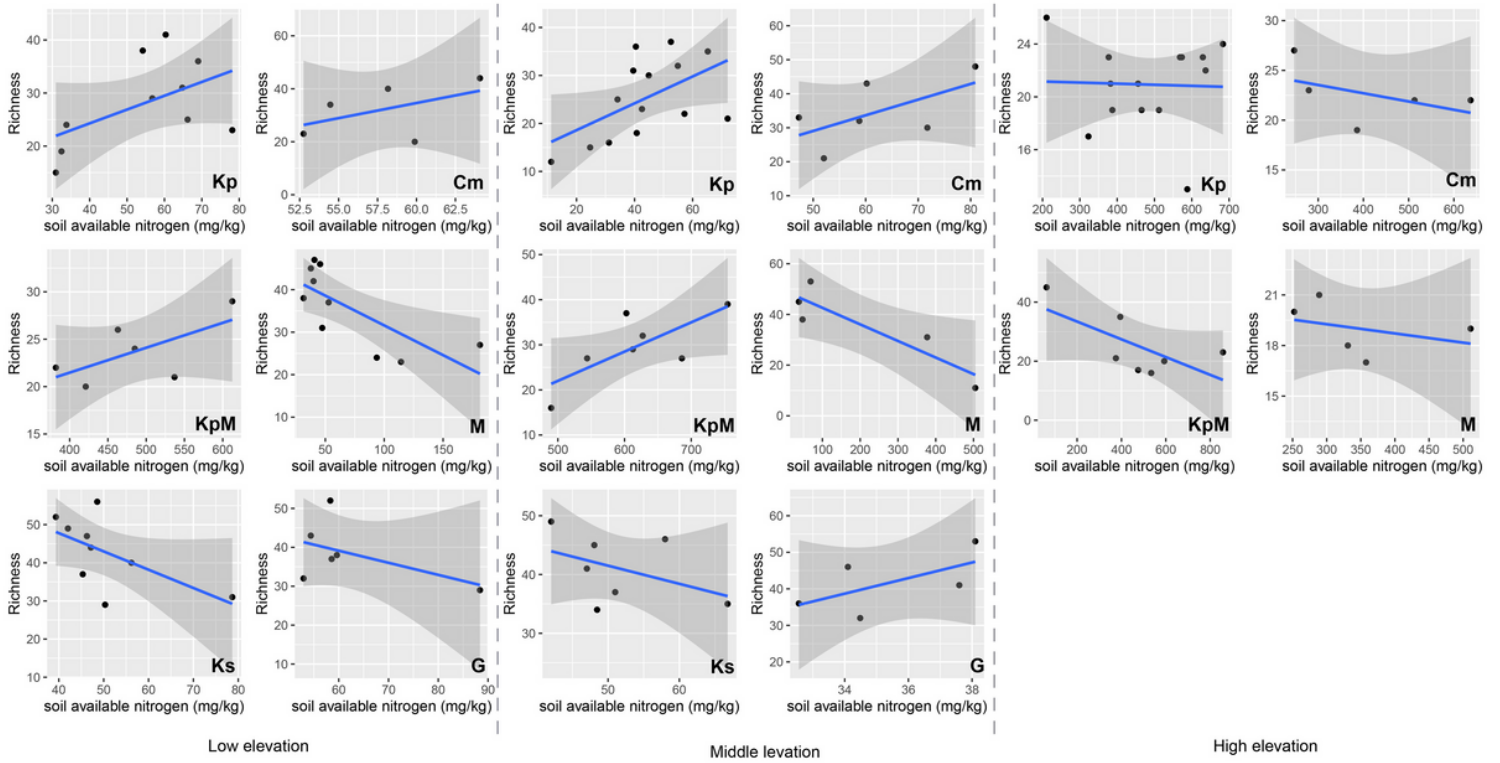
Figure 7

Relationships between plant species richness and soil available nitrogen content for the different communities along the elevation gradient
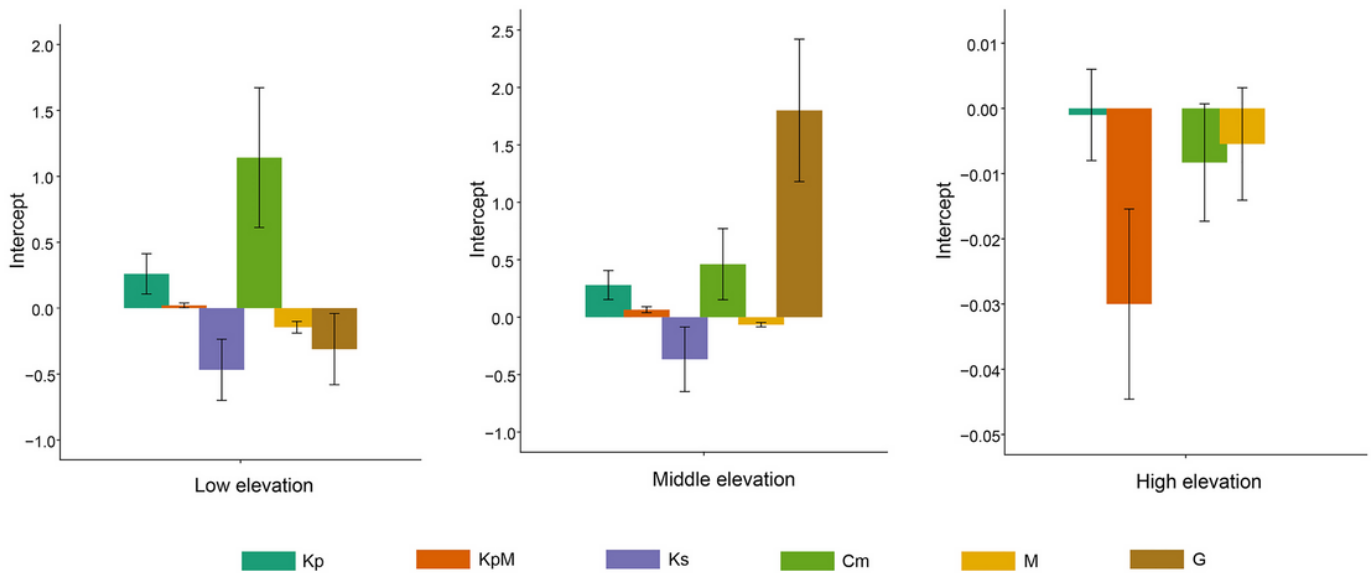

Figure 8

Intercepts for species richness response to soil available nitrogen content by the different plant communities along the elevation gradient. Error bars indicate standard errors

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