Soil Nutrient and Vegetation Diversity Patterns of Alpine Wetlands on the Qinghai-Tibetan Plateau

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Abstract: To predict the consequences of environmental change on the biodiversity of alpine wetlands, it is necessary to understand the relationship between soil properties and vegetation biodiversity. In this study, we investigated spatial patterns of aboveground vegetation biomass, cover, species diversity, and their relationships with soil properties in the alpine wetlands of the Gannan Tibetan Autonomous Prefecture of on the Qinghai-Tibetan Plateau, China. Furthermore, the relative contribution of soil properties to vegetation biomass, cover, and species diversity were compared using principal component analysis and multiple regression analysis. Generally, the relationship between plant biomass, coverage, diversity, and soil nutrients was linear or unimodal. Soil pH, bulk density and organic carbon were also significantly correlated to plant diversity. The soil attributes differed in their relative contribution to changes in plant productivity and diversity. pH had the highest contribution to vegetation biomass and species richness, while total nitrogen was the highest contributor to vegetation cover and nitrogen–phosphorus ratio (N:P) was the highest contributor to diversity. Both vegetation productivity and diversity were closely related to soil properties, and soil pH and the N:P ratio play particularly important roles in wetland vegetation biomass, cover, and diversity.

Keywords: plant species diversity; plant biomass; vegetation cover; soil nutrients; Qinghai-Tibetan Plateau; alpine wetlands; nitrogen; phosphorus

1. Introduction

Plant diversity can characterize plant community structure and habitat diversity to a great extent [1]. Spatial changes in plant diversity are significantly influenced by environmental factors, including climate change, soil properties, and herbivory [2–4], while plant community development is dependent largely on the availability of soil nutrients [5]. Despite decades of research, the relationship between wetland plant diversity and nutrient availability is still a research focus for ecologists [6]. Changes in species composition, loss of overall plant diversity, conversion of a unique flora to one dominated by a few common species, and replacement of native species by exotics have been reported in connection with nutrient enrichment in several types of wetlands [7]. Generally, wetland plant species richness either decreases as nutrient availability increases beyond a certain threshold [7], or exhibits higher “inflation” at a medium level of nutrients. There are complex relationships among plant species richness, productivity, and nutrient supply. For relatively undisturbed environments, wetlands with moderate productivity and standing crops frequently show higher plant richness and lower nutrient availability [7,8]. Many studies have shown that soil nutrients limit plant productivity and diversity in wetlands and other ecosystems [7,9–11].

Besides soil nutrients, soil pH, soil organic carbon (SOC), and soil bulk density (SBD) have also been found to be important drivers of plant species diversity. Generally, low pH leads to low species richness [12–14]. High SOC can impose positive feedback on vegetation species richness and productivity by increasing soil water-holding capacity and...
sustaining soil fertility [15], thereby increasing soil microbial community diversity and activity [16,17]. SBD is also considered to be one of the factors that influences vegetation species diversity in wetland ecosystems; it affects soil porosity, aeration, available water capacity and nutrients, and activity of soil microorganisms, and is negatively correlated with plant species richness [18].

Numerous studies have been conducted on soil nutrients and plant diversity. However, the relationships between nutrient enrichment, productivity, and species richness in wetlands are not always consistent, and there is little experimental data available for alpine wetlands on the Qinghai-Tibetan Plateau (QTP) to determine how plant species diversity varies with soil nutrients.

Alpine wetlands are currently among the ecosystems most impacted by the pressures of environmental change because of their ecological sensitivity and fragility in high latitude and high altitude environments [19]. Recently, water shortages and overgrazing have resulted in changes in plant community composition and diversity, and serious degradation of alpine wetlands [19–21]. The QTP, known as the “Roof of the World,” is a region in which alpine wetlands dominate the landscape [22]. The alpine wetlands of the QTP are key biomes key biomes with globally important communities of alpine flora and fauna. The Gannan Tibetan Autonomous Prefecture of (GTAP) is located in the northeast of the QTP and is the main water source conservation area in the upper reaches of the Yellow River. Recently, soil moisture and nutrients in this region have decreased noticeably, resulting in changes in plant community structure and composition, loss of many alpine plant species, and depletion in vegetation cover and diversity [21,23]. Understanding the interactions among resource availability, species richness, and productivity is fundamental to the management and preservation of biodiversity [24,25]. In this study, we attempted to gain a better insight into the interactions between vegetation productivity, biodiversity, and soil nutrients in QTP wetlands. We focused on: (1) identifying the spatial patterns of plant biomass, cover, species diversity, and soil nutrients of alpine wetlands on the QTP; (2) determining the relationship between plant biomass, cover, species diversity, and soil nutrients; and (3) determining the relative contribution of soil nutrients to explain vegetation biomass, cover, and species diversity compared with SBD, pH, and total SOC.

2. Materials and Methods

2.1. Study Site

This study was carried out in 13 wetlands in the GTAP (33°06′–35°34′ N, 100°45′–104°45′ E), southwest Gansu province, China, in the water conservation and recharge area of the Yellow River and the Yangtze River. The average altitude of the GTAP is approximately 2960 m, ranging from 1200 to 4800 m, and the mean annual temperature is 1.7 °C. The mean annual precipitation is 404–610 mm, mainly distributed during the short, cool summer, and the mean annual evaporation is 1214.5–2004.0 mm [26]. The vegetation is that of a typical alpine wet meadow, dominated by Blysmus sinocompressus, Kobresia tibetica, Kobresia kansuensis, Poa pratensis, Potentilla anserina, and Elymus nutans.

2.2. Plant Species Diversity Index Measurements

From June to August 2016–2018, 13 wetlands were investigated (Figure 1). In each wetland, we randomly selected three to twelve 30 m × 30 m plots. At least three plots were selected per square kilometer, and each wetland had a minimum of three plots. Three 1 m × 1 m quadrats were tossed with a steel quadrat frame within each of the three plots. The quadrats were used to determine species presence, abundance, and vegetation cover. Four species diversity indices, Patrick index (R_0) [27], Shannon index (H) [28], Pielou index (J) [29], and Simpson index (D) [30] were chosen to calculate species diversity using the following formulas, respectively. Furthermore, importance value index (IV) [31] was used to determine the dominant species:

\[ R_0 = SH = - \sum P_i \ln P_i = \frac{H}{\ln S} \]
\[ D = 1 - \sum P_i^2 \]
\[ IV = \frac{N_i}{N} \]

where \( P_i \) is the percentage frequency of species i, \( N \) is the total number of species, \( N_i \) is the number of occurrences of species i, and \( IV \) is the importance value of species i.
where $P_i$ is the proportion of individuals found in the $i$th species, $S$ is the number of species, $N_i$ is the number of individuals of species $i$, and $N$ is the number of all individuals in the community; $C_r$ is relative cover, $D_r$ is relative density, and $F_r$ is relative frequency.

Figure 1. Sampling sites in wetlands of Gannan Tibetan Autonomous Prefecture.

2.3. Soil and Plant Sampling and Analysis

All plants were clipped at the soil surface in each quadrat, and the standing aboveground biomass of vascular plants at peak biomass during the growing season were used to measure productivity. The dry mass of the plant material was determined after drying at 70 °C to a constant weight. Soil samples were also collected randomly from each quadrat after the plant communities had been characterized. Three cores (3.6 cm in diameter × 0–15 cm in depth) were collected in each quadrat and pooled to generate a mixed sample in each quadrat. Both plant and soil samples were ground through a 2 mm sieve to remove coarse debris and stones before laboratory analysis.

Fresh soil samples were air-dried to measure the soil bulk density. Soil pH was measured in a 1:2.5 soil-KCl suspension using a pH meter (PH400, Spectrum, Aurora, IL USA) with a glass electrode. Soil organic carbon was determined using the potassium dichromate oxidation method [32]. Soil total nitrogen (TN) and total phosphorus (TP) were determined using the methods of Page et al. [33], and soil total potassium (TK) was determined using an inductive coupled plasma emission spectrometer (iCAP6300, Thermo Fisher, Waltham, MA, USA).

2.4. Data Analysis

The dependence of vegetation biomass, cover, and species diversity indices on soil TN, TP, TK, and N:P ratio was analyzed using second-order polynomial regression, to fit linear and unimodal relationships. Species diversity indices were square root-transformed, and vegetation biomass, cover, soil TN, TP, TK, and N:P ratios were log-transformed. Spearman correlation was employed to assess the relationship between soil factors, plant biomass, cover, and diversity.

Principal component analysis (PCA) was carried out to explore the effect of soil nutrients on vegetation biomass, cover, and species diversity. The Kaiser–Meyer–Olkin (KMO) measure and Bartlett’s test of sphericity were used to assess the usefulness and adequacy of PCA (Budaev 2010). The Spearman correlation coefficient ($r$) was used to
test the relationship between the vegetation biomass, cover, and species diversity, and the soil attributes. Prior to analysis, data on soil attributes, except pH, were log-transformed (log(x + 1)). A covariance matrix (Σ) of the soil attributes was calculated. According to the order of eigenvalues, the first m principal components that contribute to more than 80% of the cumulative rate were selected. Regression analysis was carried out between vegetation biomass, cover, species diversity, and first m principal components. Then, the regression equations between soil properties and vegetation biomass, cover, and species diversity were obtained by replacing the principal components with soil attributes. The contribution of soil properties was determined based on their coefficients. This process was performed using the SPSS v22.

3. Results

3.1. Plant Composition

A total of 1702 records from 186 vascular plant species were sampled from 13 alpine wetlands. Blysmus sinocompressus (IV = 47.1%), Kobresia tibetica (IV = 32.6%), Poa pratensis (IV = 31.2%), Kobresia pygmaea, (IV = 26.5%), Potentilla anserina (IV = 18.0%) and Elymus nutans (IV = 17.9%) were the dominant species in the south of the GTAP, other species importance values were not more than 7.4%. Blysmus sinocompressus (IV = 31.8%), Elymus nutans (IV = 26.3%), Kobresia pygmaea (IV = 20.6%) and Poa pratensis (IV = 17.4%) were the dominant species in the north of the GTAP, and other 121 species importance values were not more than 8.5%. Lakes dominated by Potamogeton pectinatus (IV = 37.9%), Myriophyllum spicatum (IV = 33.4%), Blysmus sinocompressus (IV = 22.7%), Halerpestes cymbalaria (IV = 22.4%), Hydrilla verticillata (IV = 14.5%) were distributed in the middle of the GTAP.

3.2. Spatial Patterns of Vegetation Biomass and Species Diversity

The aboveground plant biomass and cover in the alpine wetland of the GTAP varied greatly according to spatial dimensions, ranging from 390.7 to 1130.7 g dry weight m-2 (Figure 2a) and from 35 to 100%, respectively (Figure 2b). There was substantial spatial variation in plant species diversity, as shown by the 3D models, with the R0 ranging from 1.7 to 11.7 (Figure 2c), H ranging from 0.02 to 2.16 (Figure 2d), J ranging from 0.02 to 0.95 (Figure 2e), and D ranging from 0.04 to 0.85 (Figure 2f). Generally, there were linear distribution patterns for the vegetation biomass, cover, and species diversity indices based on the altitudinal dimension. Aboveground biomass (F = 11.48, p = 0.001) increased with altitude, while R0 (F = 12.72, p < 0.001) and H (F = 10.86, p = 0.001) decreased with altitude. The peak values for plant biomass and species diversity were observed at elevations of 3400–3500 m and 3000–3200 m in the northeastern region and 3500–3600 m in the northwestern region of the GTAP.

3.3. Nutrient Concentrations and N:P Ratios in Surface Soils

In the GTAP wetlands, Total nitrogen, Total phosphorus, and Total potassium ranged from 2.03 to 17.8, 0.24 to 1.36, and 6.21 to 24.15 g kg⁻¹, respectively, and the N:P ratios ranged from 4.2 to 23.2. There were linear distribution patterns for TP, TK, and N:P ratios, but not TN, based on longitudinal, latitudinal, and altitudinal dimensions (Figure 3a–d). Both TP and TK increased with longitude and latitude and decreased with altitude, with an opposite trend for the N:P ratio.
Figure 2. Three-dimensional distribution patterns of vegetation biomass, cover, and species diversity indices: (a) Plant aboveground biomass; (b) Patrick index ($R_0$); (c) Vegetation cover; (d) Shannon index ($H$); (e) Pielou index ($J$); (f) Simpson index ($D$).

Figure 3. Three-dimensional distribution patterns of soil nutrient concentrations and N:P ratios: (a) soil total nitrogen (TN); (b) soil total phosphorus (TP); (c) soil total potassium (TK); (d) soil N:P ratio (N:P).
3.4. Relationships between Vegetation Biomass, Cover, Species Diversity, and Nutrient Availability

Soil nutrients were significantly related to vegetation diversity ($p < 0.01$). $R_0$ ($r = 0.376$, $p < 0.01$), $H$ ($r = 0.236$, $p < 0.01$), and vegetation cover ($r = -0.231$, $p < 0.01$) were significantly related to the soil TN (Figure 4a–f), and the relationships were fitted to both linear and unimodal distribution models. Generally, $R_0$ and $H$ increased with soil TN, whereas plant cover decreased with soil TN. Aboveground biomass ($r = -0.106$, $p < 0.05$), $R_0$ ($r = 0.469$, $p < 0.01$), and $H$ ($r = 0.371$, $p < 0.01$) were significantly related to soil TP (Figure 5a–f), and Aboveground biomass ($r = -0.160$, $p < 0.01$), $R_0$ ($r = 0.392$, $p < 0.01$), and $H$ ($r = 0.392$, $p < 0.01$) were significantly related to soil TK (Figure 6a–f). Aboveground biomass was only fitted to a binomial equation with soil TP, while $R_0$, vegetation cover, and $H$ were fitted to both linear and unimodal models with soil TP and TK. Both $R_0$ and $H$ increased with soil TP and TK, whereas cover decreased with soil TP and TK. Aboveground biomass ($r = 0.137$, $p < 0.01$), $R_0$ ($r = -0.249$, $p < 0.01$), $H$ ($r = -0.279$, $p < 0.01$), and $D$ ($r = -0.164$, $p < 0.01$) were significantly related to the soil N:P ratio (Figure 7a–f). The relationships between aboveground biomass, $R_0$, $H$, $J$, and N:P ratios were fitted to both linear and unimodal models, but $D$ and N:P ratios were only fitted to a unimodal model. Aboveground biomass increased with N:P ratio, while $R_0$, $H$, and $J$ decreased with N:P ratio.

![Figure 4. Plant aboveground biomass, species diversity in relation to soil total nitrogen (TN) (log scale): (a) plant aboveground biomass; (b) Patrick index ($R_0$); (c) vegetation cover; (d) Shannon index ($H$); (e) Pielou index ($J$); (f) Simpson index ($D$). Relationships were modeled with second-order polynomial regression; F values and significance levels are indicated within each graph for the linear ($x$) and binomial ($x^2$) terms. Regression lines are shown if significant. Aboveground biomass and cover were log-transformed, species diversity index $R_0$, $H$, $J$, and $D$ were square root-transformed for the regression calculations. “ns”: the regression equation was not significantly correlated at $p < 0.05$, “*”: the regression equation was significantly correlated at $p < 0.05$, “**: the regression equation was significantly correlated at $p < 0.01$.](image-url)
Figure 5. Plant aboveground biomass, species diversity in relation to soil total phosphorus (TP) (log scale): (a) plant aboveground biomass; (b) Patrick index ($R_0$); (c) vegetation cover; (d) Shannon index ($H$); (e) Pielou index ($J$); (f) Simpson index ($D$). Relationships were modeled with second-order polynomial regression; F values and significance levels are indicated within each graph for the linear ($x$) and binomial ($x^2$) terms. Regression lines are shown if significant. Aboveground biomass and cover were log-transformed, species diversity index $R_0$, $H$, $J$, and $D$ were square root-transformed for the regression calculations. "ns": the regression equation was not significantly correlated at $p < 0.05$, "*": the regression equation was significantly correlated at $p < 0.05$, "**": the regression equation was significantly correlated at $p < 0.01$.

Figure 6. Plant aboveground biomass, species diversity in relation to soil total potassium (TK) (log scale): (a) plant aboveground biomass; (b) Patrick index ($R_0$); (c) vegetation cover; (d) Shannon index ($H$); (e) Pielou index ($J$); (f) Simpson index ($D$). Relationships were modeled with second-order polynomial regression; F values and significance levels are indicated within each graph for the linear ($x$) and binomial ($x^2$) terms. Regression lines are shown if significant. Aboveground biomass and cover were log-transformed, species diversity index $R_0$, $H$, $J$, and $D$ were square root-transformed for the regression calculations. "ns": the regression equation was not significantly correlated at $p < 0.05$, "*": the regression equation was not significantly correlated at $p < 0.05$, **": the regression equation was significantly correlated at $p < 0.01$. **"**: the regression equation was significantly correlated at $p < 0.01$. **"**: the regression equation was significantly correlated at $p < 0.01$. **"**: the regression equation was significantly correlated at $p < 0.01$. **"**: the regression equation was significantly correlated at $p < 0.01$. **"**: the regression equation was significantly correlated at $p < 0.01$.
Figure 7. Plant aboveground biomass, species diversity in relation to the soil N:P ratio (log scale). (a) Plant aboveground biomass; (b) Patrick index (R_0); (c) vegetation cover; (d) Shannon index (H); (e) Pielou index (J); (f) Simpson index (D). Relationships were modeled with second-order polynomial regression; F values and significance levels are indicated within each graph for the linear (x) and binomial (x^2) terms. Regression lines are shown if significant. Aboveground biomass and cover were log-transformed, species diversity index R_0, H, J and D were square root-transformed for the regression calculations. “ns”: the regression equation was not significantly correlated at p < 0.05, “*”: the regression equation was significantly correlated at p < 0.05, “**: the regression equation was significantly correlated at p < 0.01.

3.5. Relationships between Vegetation Biomass, Cover, Species Diversity, and Soil Attributes

First, we found that soil properties had a large effect on plant diversity and productivity by correlation analysis (Table 1). In addition to soil nutrients, SOC, pH, and SBD were significantly related to plant biomass, cover, and diversity.

Table 1. Correlations between plant biomass, cover, diversity, and soil parameters.

| Variables                  | Aboveground Biomass | Vegetation Cover | R_0   | H         | J         | D         |
|----------------------------|---------------------|------------------|-------|-----------|-----------|-----------|
| Total nitrogen             | 0.006               | −0.231 **        | 0.376 ** | 0.236 **  | −0.056    | 0.105     |
| Total phosphorus           | −0.090              | −0.246 **        | 0.469 ** | 0.371 **  | −0.007    | 0.188 **  |
| Total potassium            | −0.160 **           | −0.209 **        | 0.392 ** | 0.285 **  | −0.064    | 0.101     |
| N:P                       | 0.137 *             | 0.013            | −0.249 ** | −0.279 ** | −0.064    | −0.164 ** |
| Soil organic carbon        | 0.198 **            | 0.186 **         | −0.189 ** | −0.132 *  | 0.087     | −0.052    |
| pH                        | −0.269 **           | 0.025            | −0.040  | −0.012    | −0.027    | 0.016     |
| soil bulk density          | −0.121 *            | −0.199 **        | 0.471 ** | 0.348 **  | −0.034    | 0.161 **  |

Note: ** Correlation is significant at the 0.01 level (2-tailed). * Correlation is significant at the 0.05 level (2-tailed).

PCA and a principal component regression algorithm were used to evaluate the significance of soil attributes in vegetation biomass, cover, and species diversity. Most of the analyzed variables were interdependent and correlated significantly. The KMO measure of sampling adequacy (0.634) and Bartlett’s test of sphericity (p < 0.001) indicated
the usefulness of PCA, with the first two axes explaining 60.17% and 20.34% of the total variation, respectively (Figure 8). The first PCA axis scores were significantly related to vegetation biomass (r = −0.149, p = 0.009), cover (r = −0.214, p < 0.001), \(R_0\) (r = 0.415, p < 0.001), \(H\) (r = 0.328, p < 0.001), and \(D\) (r = 0.161, p = 0.005). The second PCA axis scores were highly correlated with vegetation biomass (r = 0.161, p = 0.005), cover (r = −0.150, p = 0.009), and \(R_0\) (r = 0.187, p = 0.001). The third PCA axis scores were highly correlated with biomass (r = −0.114, p = 0.048), \(R_0\) (r = −0.174, p = 0.002), and \(H\) (r = −0.164, p = 0.004). There were no significant correlations between PC1 scores (r = −0.024, p = 0.674), PC2 scores (r = −0.065, p = 0.258), PC3 scores (r = −0.049, p = 0.391), and the variable \(J\), indicating that \(J\) was independent of soil attributes.

![Figure 8. Principal Components Analysis (PCA) of the soil attribute variables (factor loadings of the variables).](image)

The original soil attribute variables were substituted into the principal component regression algorithms, and the relationships between vegetation biomass, cover, species diversity, and soil attributes are given as follows:

\[
\begin{align*}
\hat{y}_{\text{biomass}} &= -16.99[pH] + 10.11[SBD] + 11.33[TOC] + 12.11[TN] - 1.72[TP] - 6.46[TK] + 15.59[N:P] \\
\hat{y}_{\text{coverage}} &= 1.13[pH] - 0.18[SBD] - 0.22[TOC] - 2.39[TN] - 1.20[TP] - 0.62[TK] - 1.01[N:P] \\
\hat{y}_{R_0} &= -0.38[pH] + 0.28[SBD] + 0.04[TOC] + 0.21[TN] + 0.35[TP] + 0.26[TK] - 0.32[N:P] \\
\hat{y}_{H} &= -0.055[pH] + 0.036[SBD] + 0.008[TOC] - 0.011[TN] + 0.046[TP] + 0.038[TK] - 0.090[N:P]
\end{align*}
\]

Based on the coefficients of the independent variables, the contribution of the soil attributes to the vegetation biomass was \(pH > N:P > TN > SOC > SBD > TK > TP\); the
contribution to vegetation cover was TN > TP > pH > N:P > TK > SOC > SBD; the contribution to species richness \( R_0 \) was pH > TP > N:P > SBD > TK > TN > SOC; and the contribution to the Shannon index (H) was N:P > pH > TP > TK > SBD > TN > SOC. The principal component regression results showed that there were no significant linear relationships between J, D, and the three principal components.

4. Discussion

Biodiversity is one of the major issues in plant ecology [4,34]. Previous studies have indicated that plant species diversity decreases with increasing latitude and altitude, although it can exhibit “inflation” at mid-level altitudes. In our study, \( R_0 \) and H decreased with altitude, but we did not detect changes along latitudinal gradients in the GTAP wetlands. Many studies have shown that environmental factors, such as water, nutrients, and human disturbance, are more important than geographical factors in the distribution pattern of plants [4,35].

Similar distribution patterns were observed in total phosphorus and total potassium in the GTAP wetlands. Both TP and TK increased with longitude and latitude and decreased with altitude, while the N:P ratio showed contrasting results. The soil N:P ratio decreased with increasing latitude [36], and soil N:P was lower at high altitudes [37], with spatial patterns being primarily regulated by climate factors. However, there was no significant relationship between total nitrogen and geographical distribution. This is consistent with a study on soil nutrient distribution in the Gannan Plateau by Chen et al. [38]. This may be partly due to the greater spatial heterogeneity in TN compared to TP and TK [39,40].

Soil nutrient availability is one of the most important factors influencing vegetation productivity. In our study, the relationship between vegetation biomass, cover, and soil nutrients was linear or unimodal. Generally, a unimodal relationship is visible with an increase in nutrient supply, which is considered to be the driver of primary production [41]. Previous studies [42,43] supported these findings by obtaining similar results for different types of ecosystems. Many studies have sought to identify the nutrients that limit vegetation productivity and cover in wetlands and other systems [44–46]. In our study, there were no strong interdependences between plant biomass and soil TN, which is supported by Bi et al. [47]. The relationship between soil TN and vegetation biomass was equivocal. Several studies have suggested that soil TN increases with increasing vegetation biomass and cover [48–50], whereas others have reported no or a negative relationship between them [42,47,51,52]. There was no significant relationship between vegetation cover and soil N:P ratio in our study, which was supported by a previous study that reported that soil N:P ratios showed no trends with increasing canopy [53]. Some studies have, however, indicated that spatial patterns of soil N:P ratios display a strong resemblance to those of vegetation cover [54].

There were significant linear and unimodal relationships between \( R_0 \), H, and soil nutrients in the wetlands of the GTAP. Both \( R_0 \) and H are positively correlated with nutrient enrichment up to a certain threshold value, beyond which it declines [7]. In our study, \( R_0 \) and H were positively correlated with soil TN, TP, and TK, whereas they were negatively correlated with the N:P ratio. These results are consistent with those of other studies of the QTP [55–57]. In the GTAP wetlands, J and D were unimodal with soil N:P ratio and were not correlated with soil nutrients. This indicated that, compared with J and D, \( R_0 \) and H were more sensitive to soil nutrient changes. The soil N:P ratio was significantly related to both plant production and species diversity indices. Thus, the soil N:P ratio seemed more indicative of a potential plant response to nutrient availability than the absolute content of N or P [7,58,59].

Plant biomass, cover, and species diversity in wetlands are not solely related to nutrient availability. The hydrological regime and microtopography often play more important roles than nutrients, especially for undisturbed sites [7,60]. However, soil nutrients, soil pH, SOC, and SBD are all considered to be important factors affecting the species composition of plant communities [61–66]. In the GTAP wetlands, soil factors have a significant influence
on plant diversity and productivity. Spearman correlation analysis showed that SOC was positively correlated with vegetation biomass and cover, but negatively correlated with species diversity. Generally, a high organic content in the soil should have a positive effect on plant communities because of the resources from decomposing plants [67]. However, in the GTAP wetlands, soil has a higher C:N ratio and is expected to decompose slower owing to the lack of available N sources for nutrient-starved microbes, resulting in lower plant species diversity [68]. Soil pH was significantly negatively related to biomass and not significantly related to species diversity in the GTAP wetlands. This is supported by previous studies in other ecosystems [12, 69]. In our study, SBD was negatively related to biomass and cover and positively related to species diversity. The SBD was negatively correlated with soil moisture. Higher availability of soil moisture should increase plant biomass because it allows for greater growth potential [70]. Higher SBD means higher root content, which should decrease plant diversity owing to competition between plant species [71, 72].

The contributions of the various soil attributes to changes in plant productivity and diversity differed. For plant biomass, the contribution of soil pH, N:P ratio, and TN was greater, while that of TP was lesser. Soil pH was negatively correlated with aboveground biomass, which is consistent with the findings of Bhandari and Zhang [73]. Cheng Jun et al. [74] found that soil pH was negatively correlated with the mean annual temperature. At warmer temperatures, where plant inputs are greater than losses owing to decomposition, the SOC density can increase [75] and release more H+ ions into the soil solution [76]. In our study, both single factor regression and Spearman correlation analysis showed that there was no relationship between soil TN and aboveground plant mass. However, there was a significant positive correlation in the multiple regression analysis. This indicated that soil TN could promote plant biomass because of its indirect effects on other influencing factors. For example, in a study by Robertson and Groffman [77], increasing TN caused a relatively low C:N ratio, so the microbes had no trouble obtaining N, mineralization dominated over immobilization, and plant-available N increased in soil. In our study, the contribution of soil TN, TP, pH, and N:P ratio to vegetation cover was relatively high, and that of soil TK, SOC, and SBD was less. Among them, the N:P ratio was not significantly correlated with vegetation cover in the correlation analysis. However, its contribution to vegetation cover was higher in the multiple regression analysis. This indicated that the N:P ratio affected vegetation cover by confounding effects with other soil attributes. For example, the N:P ratio was significantly inversely related to soil pH (Figure 5), indicating the effect of pH on the chemical form (and thus, availability) of N and P in soil [78]; thus, N:P indirectly reduced vegetation cover. Generally, the contributions of soil attributes to the vegetation diversity indices R₀ and H were similar. The contributions of pH, TP, and N:P were higher, SBD and TK were in the middle, and TN and SOC were the lowest. Low P availability has sometimes been considered a prerequisite for high species richness [12]. Soil pH, as the “master soil variable,” influences soil biological, chemical, and physical properties and processes that affect plant growth [79]. The availability of soil nutrients to plants is determined by soil pH [80]. Accordingly, soil pH often affects plant community composition and species richness because plants differ in their requirements for available nutrients as well as tolerance of soil acidity or alkalinity [81]. The soil N:P ratio plays an important role in both plant biomass and cover, and species diversity. It can serve as an indicator of N saturation, which in turn indicates the availability of soil nutrient elements during plant growth and is used to determine the threshold of nutrient restriction [78, 82, 83]. In summary, N:P stoichiometry plays a key role in the structure and function of ecosystems [84, 85]. Compared with other soil attributes, soil SOC contributed relatively less to vegetation cover and species diversity in our study. Usually, high soil SOC storage can result in positive feedback on species richness and productivity by increasing soil water-holding capacity and sustaining soil fertility. This may be due to the rich organic matter in the peatland soil of the QTP, which weakens the effect of organic carbon on plant cover and species diversity.
In summary, we discovered that plant biomass was positively correlated with SOC and N:P ratio, whereas it was negatively correlated with soil pH, TK, and SBD. Vegetation cover was positively correlated with SOC, but negatively correlated with SBD, TN, TP, and TK. Plant richness ($R_0$) and the Shannon index ($H$) were positively correlated with soil TN, TP, TK, and SBD, and negatively correlated with the N:P ratio and SOC. The Simpson index ($D$) was positively correlated with TP and SBD, but negatively correlated with the N:P ratio. The contribution of the soil properties to explain the variation of plant biomass, cover, and diversity in GTAP wetlands differed. Overall, the pH and N:P ratio of soils played important roles in vegetation biomass, cover, and diversity in alpine wetlands. In this study, wetland hydrological conditions, microtopography, and soil microbial activity were not investigated and analyzed. This may magnify the contribution of soil properties to changes in plant biomass, cover and diversity to a certain extent. Hence, more research should be conducted on this topic to examine these relationships holistically for alpine wetland restoration and sustainable development.

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