

Article

Linking Leaf N:P Stoichiometry to Species Richness and Composition along a Slope Aspect Gradient in the Eastern Tibetan Meadows

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Abstract: As an important topographical factor, slope aspect has an essential influence on plant community structure and leaf traits. Leaf nitrogen (N) and phosphorus (P) stoichiometry is an important leaf trait indicating plant growth. However, it has rarely been studied how leaf N:P stoichiometry correlates with plant community structure along the slope aspect gradient. To understand the variation of leaf N:P stoichiometry and community structure, as well as their correlation with each other, the species composition and leaf N and P in Tibetan meadows were investigated across three slope aspects: the south-, west-, and north-facing slope aspects (i.e., SFS, WFS, and NFS). In our results, leaf N:P ratio was significantly lower on the NFS than on the SFS, indicating N and P limitation on the NFS and SFS, respectively. Richness of forb species and all species was higher on the NFS than on the SFS and was negatively correlated with leaf N concentration, whereas graminoid richness was not statistically different among the slope aspects and showed a negative correlation with leaf P concentration. Thus, our results provide evidence for the functional significance of leaf N:P stoichiometry for species composition along a natural environmental gradient. Our findings could provide applicable guidance in the refinement of grassland management and biodiversity conservation based on topography.

Keywords: topography; community assembly; species richness; leaf functional traits



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1. Introduction

Leaf nitrogen (N) and phosphorus (P) are the two most limiting elements of terrestrial vegetation relating to plant growth, development, and reproduction [1–3] because N is the key component of proteins that play pivotal roles in plant photosynthesis as enzymes, whereas P is critical to the formation of NADPH, ATP, and ribosomal RNA in the process of protein synthesis [4,5]. Furthermore, the critical leaf N:P ratio has been widely used to diagnose the type of nutrient limitations to plant productivity [6–8]. Leaf N and P concentration and allocation have been found to vary along environment gradients; although numerous studies have focused on their latitudinal and altitudinal patterns [9–16], it has rarely been studied how they change along the slope aspect gradient. Investigations on leaf N:P stoichiometry across slope aspects can provide applicable guidance in the refinement of grassland management and conservation based on topography at the local scale.

Leaf N and P availability also shows important functional significance for community composition [6]. In particular, relationships between plant N:P ratios and species richness are of particular interest in the context of biodiversity conservation and anthropogenic activities. Many studies have found the N:P ratio to be correlated with the richness and composition of species [17–19]. The coexistence of species was suggested to be possibly facilitated by P limitation, since the competition for P with lower mobility is weaker than the

competition for resources of high mobility in soil [17,20] and is facilitated by colimitation because differential nutrient limitations may reduce interspecific competition [21,22] but could also be weakened by the P limitation possibly resulting from P deficiency or nutrient imbalance [6] or the disproportionate increase in dominant clonal graminoids [23]. Hence, different correlations of species richness with plant N and P stoichiometry have been reported [17,18,24–26]. Moreover, a high leaf N:P ratio was expected to be associated with more graminoids and fewer forbs in vegetation [23]. However, most of these studies were indirectly demonstrated in experiments with nitrogen fertilization or deposition, and direct evidence is rare along natural environmental gradients. The slope aspect gradient significantly contributed to the heterogeneity of vegetation in mountain areas and thus provided an ideal platform to explore the relationships between leaf N/P stoichiometry and community structure.

Typically, south-facing slopes in the northern hemisphere (i.e., equator-facing slopes) are hot and dry, as the equator-facing orientation is associated with the strongest solar irradiation, whereas north-facing slopes (i.e., polar-facing slopes) are wet and cold, resulting from the lowest solar irradiations; western- or eastern-facing slopes are intermediate in terms of these aspects. Slope aspect substantially contributes to the heterogeneity of vegetation [27–32], possibly owing to the substantial microenvironmental changes, such as solar irradiance, soil moisture and temperature, and soil nutrients [33–36]. However, it is still not clear how vegetation heterogeneity, including species richness and composition, is associated with leaf N:P stoichiometry. Therefore, in the current study, based on a slope aspect gradient in the Tibetan meadow, we mainly aimed to explore the following questions: (1) How do leaf [N] and [P] and the N:P ratio vary in different slope aspects? (2) How do species richness and composition change with slope aspect? (3) How does leaf N:P stoichiometry correlate with species richness and composition along the slope aspect gradient?

2. Materials and Methods

2.1. Study Sites

Our study was conducted in an alpine meadow in the eastern part of the Tibetan Plateau in China. The Research Station of Alpine Meadow and Wetland Ecosystems of Lanzhou University has locations at two elevations: 2960 m and 3650 m (Figure 1A). Data were collected at these two sites: Hezuo (34°44' N, 102°53' E) and Maqu (33°39' N, 101°53' E), with the vegetation landscape shown in Figure 1B. We also recorded the precipitation and temperature of these two sites during the period of 1981–2017 according to geographical coordinates using the climate dataset provided by National Tibetan Plateau Data Center (<http://data.tpdc.ac.cn> (accessed on 10 May 2021)). The mean annual precipitation in Hezuo and Maqu was 570 mm and 690 mm, and the mean annual temperature was around 4 °C and 2 °C, respectively. The monthly mean precipitation and monthly mean, maximum, and minimum temperatures are shown in Figure 1C. Details about the study site can also be found in our previous publications [36,37].

2.2. Leaf N and P Concentration Measurements

In August of 2008, during the peak growing season, a 5 m × 5 m plot was established on each of the south-, west-, and north-facing slopes (i.e., SFS, WFS, and NFS) based on the shape of the hill and the ability to collect leaf samples at each site. At each plot, mature and healthy leaf samples were collected from 3–5 individuals of the dominant species. Across the six plots, 80 observations were collected in total, with 41 observations of 25 species in Hezuo and 39 observations of 20 species in Maqu. The measured species in each site, with their average leaf N and P content per unit of mass (hereafter leaf [N] and [P]), are shown in Table 1. All the species were simply classified into three plant functional groups (PFGs): graminoids (Poaceae and Cyperaceae), non-legume forbs (forbs), and legumes. However, in two plots, dwarf shrub was also found on the NFS.

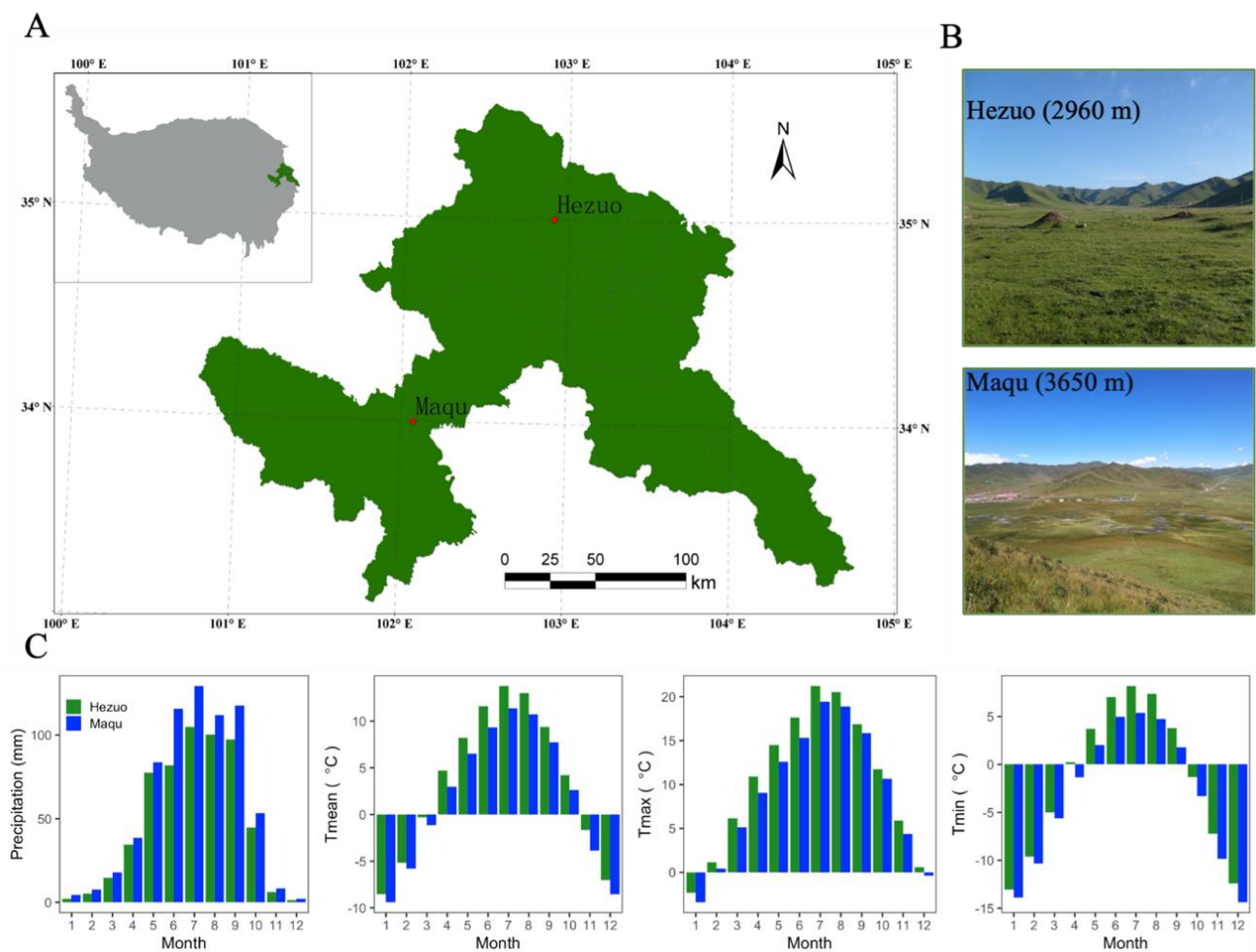


Figure 1. Site location in the Tibetan Plateau (Panel A), the vegetation landscape (Panel B), and key climate factors (Panel C) of the two study sites (Hezuo and Maqu). Tmean, Tmax, and Tmin represent the monthly mean, maximum, and minimum temperature, respectively.

After drying for 48 h at 70 °C, we ground the dry leaves to powder using a mortar. A total of 0.2 g of leaf powder was digested with H₂SO₄-H₂O₂. Digested solution was used to determine leaf [N] with a VAPODEST 40 programmable distillation system (Gerhardt, Germany), and leaf [P] by the vanadium-ammonium molybdate colorimetric method [38].

2.3. Species Composition Measurement

In each plot, we placed three 50 cm × 50 cm quadrates as replicates to survey the species by recording their names, coverage (%), and richness (i.e., the number of species) and then classified all the species into the four plant functional groups: graminoids, forbs, legumes, and shrubs (if any). The coverage was estimated visually, but significantly positive correlation of coverage and species richness confirmed the data reliability ($R^2 = 0.418$, $p < 0.001$).

2.4. Data Analysis

Firstly, the effects of slope aspect on leaf [N], [P], and N:P ratio were detected using a linear mixed model by treating “site” as the random factor (LMM) for the mixed samples, with species-level value as a replicate unit and one common species, *Anaphalis lacteal*, that occurred in each of the six plots. Correlations among leaf [N], [P], and N:P ratio were evaluated in each site using linear models. Comparison of the leaf N:P stoichiometry between different PFGs was also conducted using the LMM. Secondly, the effects of slope aspect on species richness and coverage and their correlations with leaf N:P stoichiometry (using plot-level means) were analyzed using LMM.

All the variables were log10-transformed. All analyses were performed with R version 4.0.3 (R Core Team, 2020) in RStudio version 1.3.1093 (RStudio Team, 2020).

Table 1. Mean value of leaf nitrogen (N) and phosphorus (P) concentrations of the 40 measured species. PFG represents plant functional group.

SPECIES	FAMILY	PFGs	Hezuo		Maqu	
			N (mg g ⁻¹)	P (mg g ⁻¹)	N (mg g ⁻¹)	P (mg g ⁻¹)
<i>Allium beesianum</i>	Amaryllidaceae	Forbs			16.69	1.43
<i>Allium condensatum</i>	Amaryllidaceae	Forbs			16.28	1.14
<i>Anaphalis hancockii</i>	Asteraceae	Forbs	17.86	1.28		
<i>Anaphalis lactea</i>	Asteraceae	Forbs	26.02	1.66	10.45	0.78
<i>Anemone trullifolia</i> var. <i>linearis</i>	Ranunculaceae	Forbs			13.16	1.04
<i>Aster tataricus</i>	Asteraceae	Forbs			11.02	0.78
<i>Astragalus membranaceus</i>	Fabaceae	Legumes	24.52	1.73	29.29	1.83
var. <i>membranaceus</i>						
<i>Bupleurum</i> sp	Apiaceae	Forbs			14.01	1.05
<i>Cyperaceae</i> sp	Cyperaceae	Graminoids	17.30	1.24		
<i>Daucus carota</i>	Apiaceae	Forbs			7.80	0.99
<i>Elephantopus scaber</i>	Asteraceae	Forbs	20.89	1.60		
<i>Fragaria ananassa</i>	Rosaceae	Forbs	13.33	1.65		
<i>Gentiana macrophylla</i>	Gentianaceae	Forbs	22.42	1.25		
<i>Gentianopsis barbata</i>	Gentianaceae	Forbs			14.10	1.25
<i>Gueldenstaedtia verna</i>	Fabaceae	Legumes	26.17	1.27	21.44	1.21
<i>Hamamelis mollis</i>	Hamamelidaceae	Shrubs	17.83	1.29		
<i>Kobresia humilis</i>	Cyperaceae	Graminoids	14.61	1.01		
<i>Lancea tibetica</i>	Mazaceae	Forbs	19.10	1.53		
<i>Leontopodium leontopodioides</i>	Asteraceae	Forbs			13.61	0.93
<i>Ligularia virgaurea</i>	Asteraceae	Forbs			11.69	1.10
<i>Medicago falcata</i>	Fabaceae	Legumes			4.36	1.05
<i>Medicago lupulina</i>	Fabaceae	Legumes	32.35	1.90		
<i>Nardostachys jatamansi</i>	Caprifoliaceae	Forbs			14.26	1.07
<i>Nardostachys jatamansi</i>	Caprifoliaceae	Forbs			8.15	0.88
<i>Nepeta cataria</i>	Lamiaceae	Forbs	25.12	1.65		
<i>Oxytropis</i> sp	Fabaceae	Legumes	36.79	2.00		
<i>Pedicularis szetschuanica</i>	Orobanchaceae	Forbs			13.38	1.94
<i>Plantago asiatica</i>	Plantaginaceae	Forbs	16.07	1.56		
<i>Polygonum macrophyllum</i>	Polygonaceae	Forbs			9.63	1.01
<i>Polygonum viviparum</i>	Polygonaceae	Forbs	25.53	1.59	15.41	1.83
<i>Potentilla anserina</i>	Rosaceae	Forbs	13.79	1.57		
<i>Potentilla bifurca</i>	Rosaceae	Forbs	17.76	1.25		
<i>Potentilla fragarioides</i>	Rosaceae	Forbs	12.92	1.03		
<i>Roegneria kamoji</i>	Poaceae	Graminoids	18.00	1.41		
<i>Saussurea graminea</i>	Asteraceae	Forbs			9.40	0.54
<i>Saussurea graminifolia</i>	Asteraceae	Forbs	15.92	1.39		
<i>Saussurea</i> sp	Asteraceae	Forbs	18.62	1.20	8.77	0.84
<i>Scirpus triquetus</i>	Cyperaceae	Graminoids	17.55	0.89		
<i>Stellera chamaejasme</i>	Thymelaeaceae	Forbs	36.87	2.31		
<i>Taraxacum</i> sp	Asteraceae	Forbs	33.27	1.85		

3. Results

3.1. Variations in Leaf [N], [P], and N:P Ratio across the Slope Aspects

The leaf [N], [P], and N:P ratios ranged from 10.09 to 42.96, 0.89 to 3.10, and 8.10 to 23.63 mg g⁻¹ in Hezuo and from 4.36 to 33.53, 0.536 to 2.33, and 4.14 to 21.21 mg g⁻¹ in Maqu, respectively. Overall, the leaf [N], [P], and N:P ratios were all significantly lower in Maqu, with higher elevations than in Hezuo (Figure 2A,C,E).

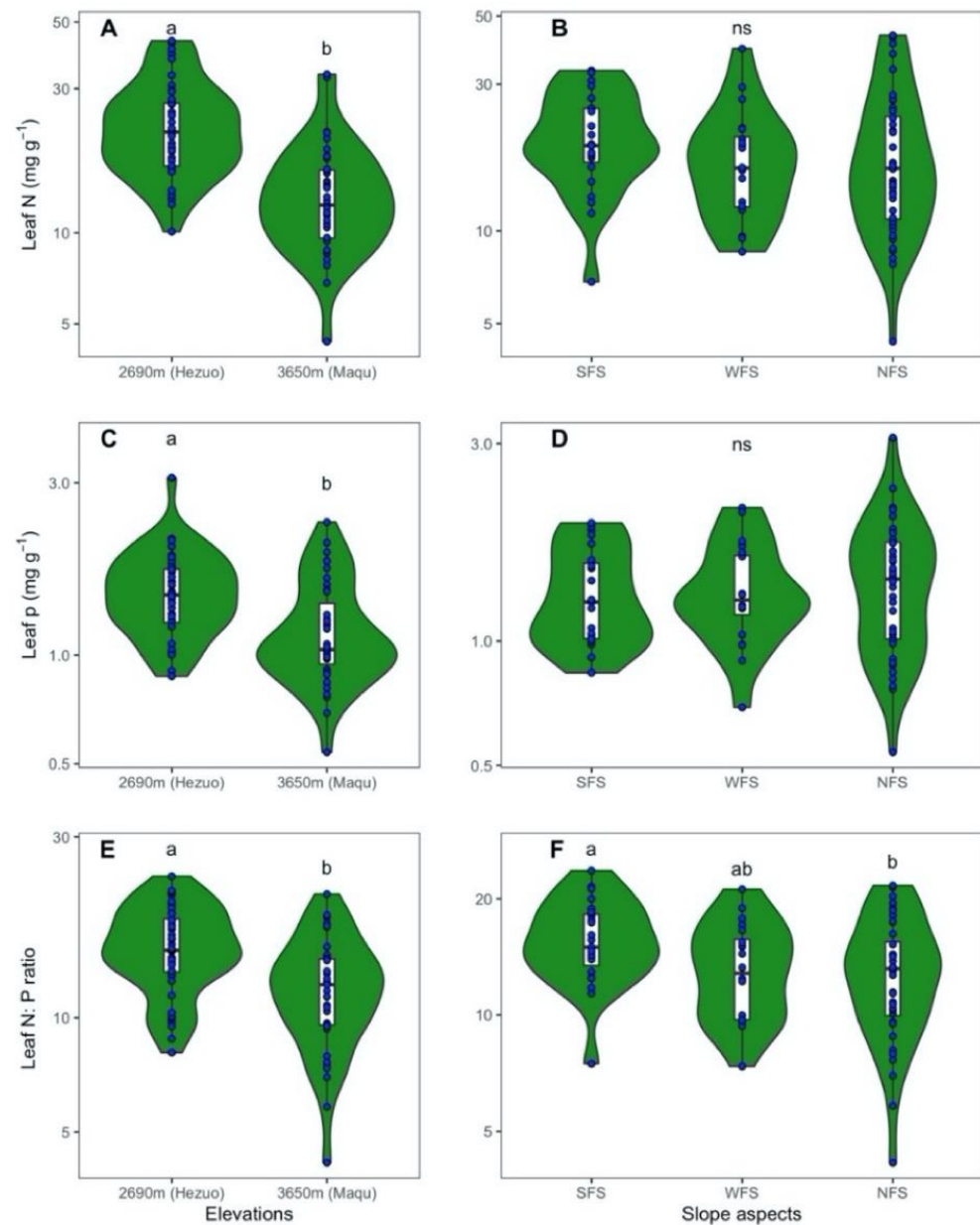


Figure 2. Comparisons of leaf [N] (A,B), [P] (C,D), and N:P ratio (E,F) between sites and among slope aspects. SFS, WFS, and NFS represent south-, west-, and north-facing slope aspects, respectively. Different letters represent significant differences at the level of $p < 0.05$. Variables are in log10 scale.

Although leaf [N] and [P] were not significantly different between slope aspects, leaf N:P ratio was significantly lower on the NFS than on the SFS for the mixed samples (Figure 2). The one common species, *Anaphalis lacteal*, showed the same patterns as those of the mixed samples (Figure S1). Moreover, significant correlations between leaf [N] and [P] and between the leaf N:P ratio and leaf [N] rather than [P] were found in each plot (Figure 3). In addition, legumes showed a significantly higher leaf [N] and [P] than forbs and graminoids and a higher leaf N:P ratio than forbs (Figure S2).

3.2. Correlations of Leaf Traits with Species Richness and Coverage

Significantly higher richness of all species and forbs and lower richness of legumes were found on the NFS than on the SFS and WFS (Figure 4A–D); however, the richness of graminoids and plant coverage for each PFG and for all species did not differ significantly among the slope aspects (Figure 4E–H).

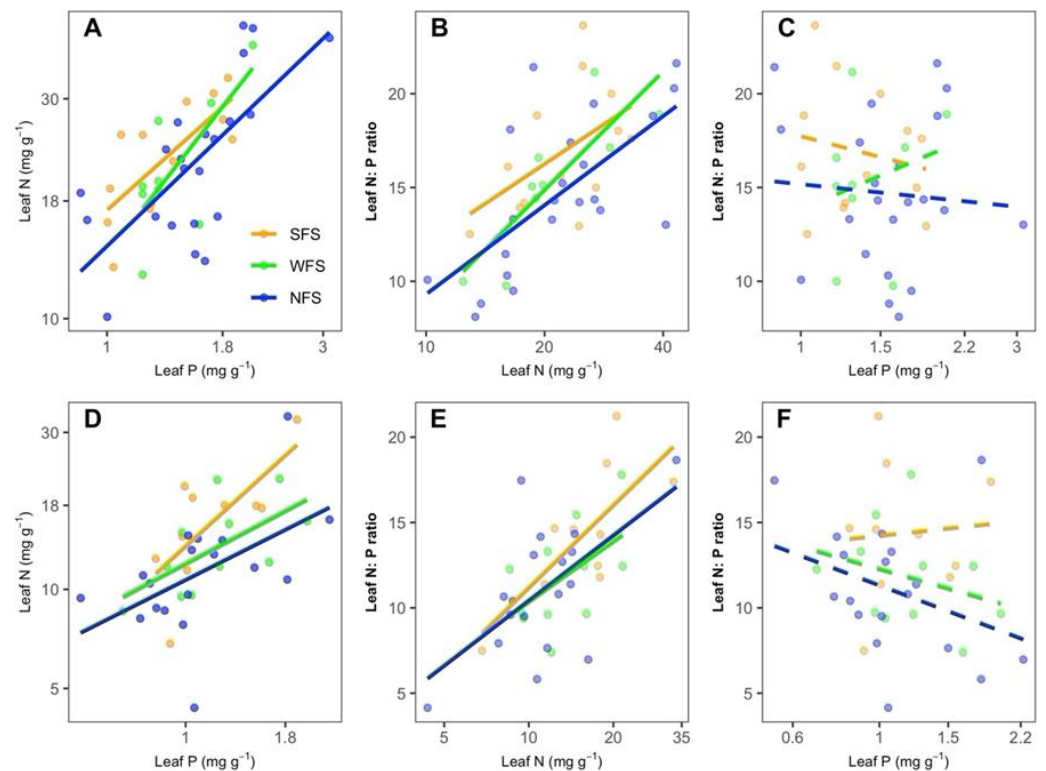


Figure 3. Linear regressions between leaf [N] and [P], between leaf [N] and leaf N:P ratio, and between leaf [P] and leaf N:P ratio in Hezuo (A–C) and Maqu (D–F). Solid and dashed lines indicate significant and non-significant regressions, respectively. SFS, WFS, and NFS represent south-, west-, and north-facing slope aspects, respectively. Variables are in log₁₀ scale.

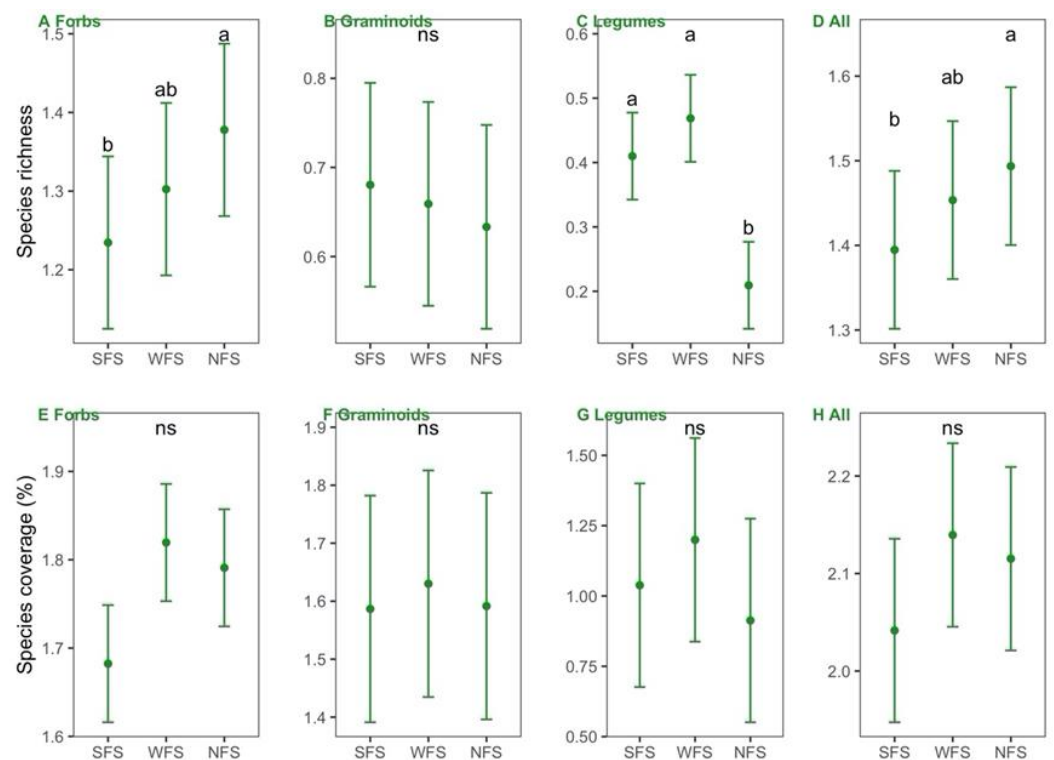


Figure 4. Comparisons of species richness (A–D) and coverage (E–H) for each plant functional group and the whole community among slope aspects. SFS, WFS, and NFS represent south-, west-, and north-facing slope aspects, respectively. Variables are log₁₀-transformed.

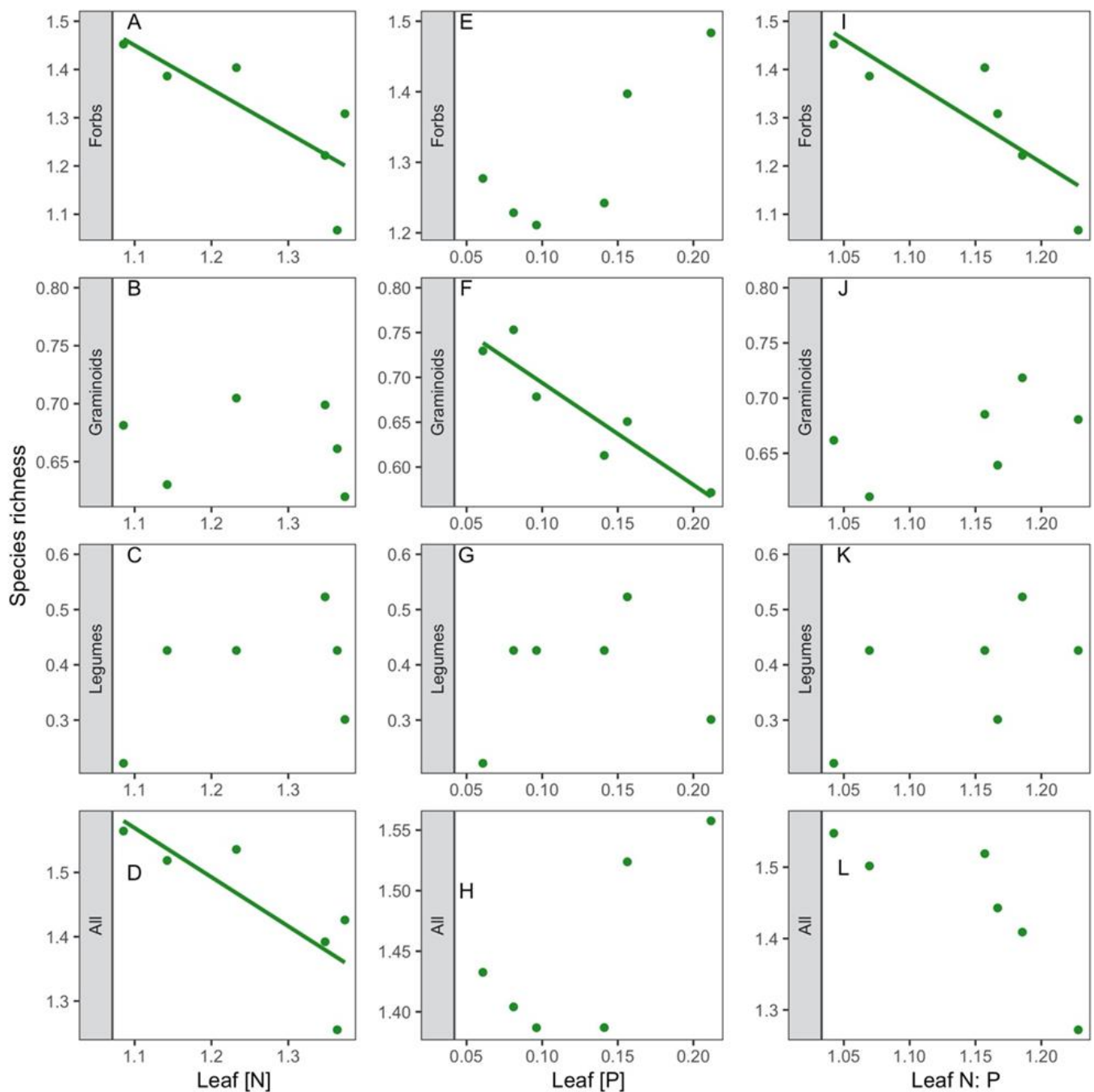


Figure 5. Correlations of species richness of each plant functional group and the whole community with leaf N concentration (A–D), with leaf P concentration (E–H), and with leaf N:P ratio (I–L). Variables are log10-transformed.

The correlations were found to be significantly negative between leaf [N] and richness of all species ($R^2 = 0.615$, $p = 0.047$) and forb species ($R^2 = 0.570$, $p = 0.061$), between leaf [P] and graminoid richness ($R^2 = 0.362$, $p = 0.093$), and between leaf N:P ratios and forb richness ($R^2 = 0.675$, $p = 0.032$) (Figure 5). On the other hand, legume coverage was positively correlated with leaf [N] ($R^2 = 0.809$, $p = 0.010$), and the coverage of graminoids and all species was negatively and positively correlated with leaf [P] and with marginal significance and significance, respectively ($R^2 = 0.051$ and 0.704 , $p = 0.103$ and 0.029 , respectively) (Figure 6).

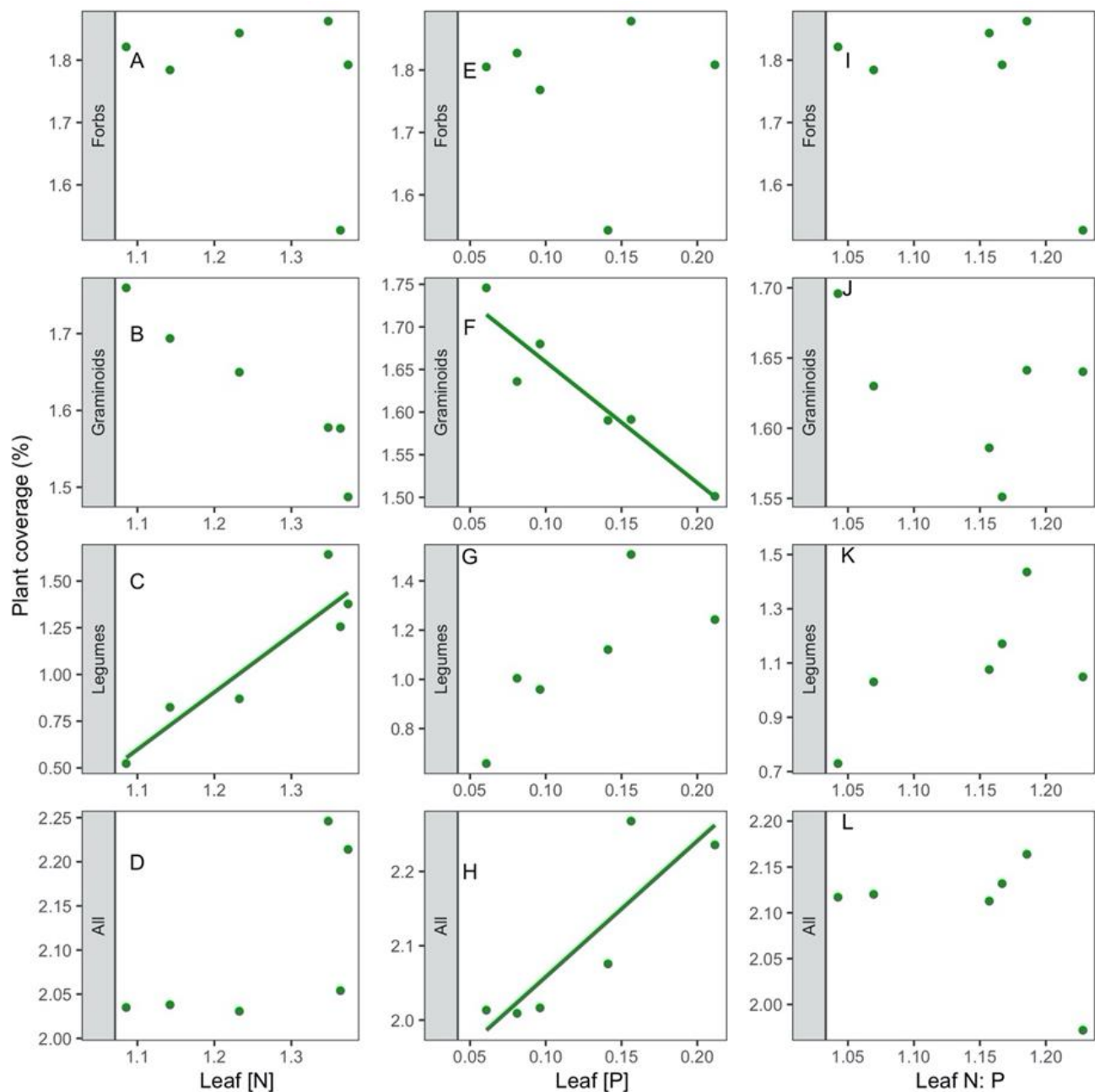


Figure 6. Correlations of species coverage of each plant functional group and the whole community with leaf N concentration (A–D), with leaf P concentration (E–H), and with leaf N:P ratio (I–L). Variables are log10-transformed.

4. Discussion

4.1. Variations in Leaf [N], [P], and N:P Ratio across Different Slope Aspects

Although leaf [N] and [P] did not differ significantly between slope aspects, we found a significantly lower N:P ratio on the NFS, with a mean of 11, and a higher N:P ratio on the SFS, with a mean of 16, which was consistent with a previous study reporting that the lowest N:P ratio occurred on the NFS out of the four slope aspects [39]. Tessier and Raynal [8] pointed out that plants were subject to N-, P-, and co-limitation when the plant N:P ratio was less than 14, higher than 16, and between 14 and 16, respectively. Therefore, our results indicate that plants on the NFS suffered N limitation. The tight correlation of leaf [N] with N:P ratio suggests that leaf N:P is determined by leaf [N] along the slope aspect gradient. A lower soil N availability reported in our previous studies [36]

was probably the reason for the lower leaf N:P ratio on the NFS, which supports the biogeochemical hypothesis suggesting that plant N and P are influenced by the availability of soil nutrients [9]. The lower soil N on the NFS was perhaps due to lower temperatures reducing the decomposition and mineralization of organic material.

In addition, the leaf [N], [P], and N:P ratio were lower in Maqu, which has a higher elevation, which is consistent with previous studies of elevational gradients [14,40], indicating an increase in N-limitation along altitudinal gradients.

4.2. Correlations of Leaf N:P Stoichiometry with Species Richness and Coverage across the Slope Aspects

Significantly higher species richness in each quadrat was found on the NFS than on the SFS, which was mainly caused by the variation in forb richness. These results are consistent with previous studies in which species richness was significantly lower on the SFS [31,41], with the possible mechanism of lower soil water content as the limiting factor.

Community species richness was negatively correlated with leaf [N], which is consistent with the negative effects of N-fertilization on species diversity [42–45]. Many N-fertilization experiments showed considerable species loss, with the underlying improved growth of dominating clonal graminoids excluding forbs through competition [45,46]. The possible mechanisms may be that N-fertilization led to a tendency of P limitation, but graminoids are often considered stress-tolerant species due to their low requirement for P and K [47]. Therefore, we found negative correlations of leaf [P] with graminoid richness and coverage because higher leaf [P] indicated the rapid growth of P-sensitive species. The significant negative correlations between leaf N:P ratio and forb richness provide direct evidence that on the natural environmental gradient, a higher N:P ratio is associated with fewer forbs and more graminoids, as hypothesized by Güsewell [6].

In addition, the higher legume richness on the SFS and the positive correlation of legume coverage with leaf [N] were consistent with the higher N:P ratio on the SFS due to their N-fixing functions.

5. Conclusions

In this study, we linked species composition and leaf N:P stoichiometry along a slope aspect gradient. Our results reveal different types of nutrition limitation and species compositions in different slope aspects and highlight the functional significance of leaf N:P stoichiometry in community composition along a slope aspect gradient. We found that leaf N:P ratio was significantly lower on the NFS than on the SFS and WFS, although leaf [N] and [P] were not statistically different between slope aspects, implying N limitation and P limitation of plant growth on the NFS and SFS, respectively. Higher richness and coverage of forbs were found on the NFS than on the SFS, whereas those of graminoids did not differ significantly between slope aspects. The variations in forb and graminoid richness were largely explained by leaf [N] and [P], respectively, with the possible mechanism of different N or P requirements for different PFGs. However, the mechanisms underlying the variations in leaf N:P stoichiometry and community composition across slope aspects are still not clear because we did not explore their correlations with environmental or soil factors.

Supplementary Materials: The following are available online at <https://www.mdpi.com/article/10.3390/d14040245/s1>, Figure S1: Comparisons of leaf [N] (A,B), [P] (C,D), and N:P ratio (E,F) between sites and among slope aspects, respectively, for the species *Anaphalis lacteal*, Figure S2: Comparisons of leaf [N] (Panel A), [P] (Panel B), and N:P ratio (Panel C) between different plant functional groups (PFGs).

Author Contributions: Conceptualization, X.L.; methodology, R.Z.; software, X.L.; formal analysis, X.L.; investigation, X.L.; data curation, Y.H., X.Z. and C.Q.; writing—original draft preparation, X.L.; writing—review and editing, Y.H.; visualization, X.L.; supervision, X.L.; project administration, X.L. and R.Z.; funding acquisition, X.L. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: The data presented in this study are available in article and Supplementary Materials.

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Conflicts of Interest: The authors declare no conflict of interest.

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