J Arid Land (2026) 18(5): 868–885
doi: 10.1016/j.jaridl.2026.05.008; CSTR: 32276.14.JAL.20250098

Grassland biomass production and plant species diversity in response to nitrogen and phosphorus addition in central and southwestern Tajikistan

Mekhrovar OKHONNIYOZOV[1,2,3,4], FAN Lianlian[1*], MA Xuexi[1], Sino YUSUPOV[4], Hikmat HISORIEV[1,4], Abdullo MADAMINOV[4], Fakher ABBAS[1], TAO Ye[1], LI Yaoming[1,2,3]

[1] China-Tajikistan Belt and Road Joint Laboratory on Biodiversity Conservation and Sustainable Use, Xinjiang Institute of Ecology Geography, Chinese Academy of Sciences, Urumqi, 830011, China;
[2] Research Center for Ecology and Environment of Central Asia, Dushanbe 734063, Tajikistan;
[3] University of Chinese Academy of Sciences, Beijing 100049, China;
[4] Institute of Botany, Plant Physiology and Genetics, National Academy of Science of Tajikistan, Dushanbe 734017, Tajikistan

Abstract: Nitrogen (N) and phosphorus (P) are essential nutrients regulating plant growth, yet their long-term impacts on grassland ecosystems in Tajikistan remain poorly understood. This study conducted a five-year (2018–2022) field experiment across four grassland sites (Tabakqi, Balkhi, Luchob, and Ziddi) along an elevation gradient in central and southwestern Tajikistan to explore the effects of varying N (0, 30, and 90 kg N/(hm^2•a)) and P (0 and 30 kg P/(hm^2•a)) additions on aboveground biomass (AGB) and plant species diversity. Nutrient addition significantly increased AGB across all sites. Compared with the control (without N or P addition), AGB increased by 20%–80% under moderate N treatment (adding 30 kg N/(hm^2•a)) and by up to 190%–200% under high N and P addition treatment (adding 90 kg N/(hm^2•a) and 30 kg P/(hm^2•a)). In 2022, AGB at the low-elevation site (Tabakqi) increased from 494 g/m^2 under the control to 650 g/m^2 under high N and P treatment, while at the high-elevation site (Ziddi), it rose from 552 to 1614 g/m^2. In contrast, biodiversity responses were elevation-dependent: species richness declined at mid-elevation grassland sites (Balkhi and Luchob) but showed little change at low-elevation (Tabakqi) and high-elevation (Ziddi) sites. Shannon-Wiener index, Simpson's dominance index, and Pielou's equitability index also varied, reflecting complex interactions among nutrient addition, precipitation, and temperature. The structural equation model (SEM) confirmed that nutrient addition directly enhance AGB but generally suppress plant species diversity, while precipitation promotes AGB, and temperature effects are inconsistent across sites. Overall, our findings demonstrate that nutrient enrichment can increase productivity but reduce biodiversity, with responses strongly mediated by elevation and climate. These results provide the first long-term experimental evidence from Tajikistan's grasslands and underscore the need to balance productivity gains with biodiversity conservation in sustainable grassland management.

Keywords: aboveground biomass (AGB); plant species diversity; species richness; nutrient addition; structural equation model (SEM); Tajikistan

Citation: Mekhrovar OKHONNIYOZOV, FAN Lianlian, MA Xuexi, Sino YUSUPOV, Hikmat HISORIEV, Abdullo MADAMINOV, Fakher ABBAS, TAO Ye, LI Yaoming. 2026. Grassland biomass production and plant species diversity in response to nitrogen and phosphorus addition in central and southwestern Tajikistan. Journal of Arid Land, 18(5): 868–885. https://doi.org/10.1016/j.jaridl.2026.05.008; https://cstr.cn/32276.14.JAL.20250098

*Corresponding author: FAN Lianlian (E-mail: flianlian@ms.xjb.ac.cn)
Received 2025-03-11; revised 2025-10-30; accepted 2025-11-06

1 Introduction

Nitrogen (N) and phosphorus (P) are the fundamental drivers that have the most significant impact on grassland productivity (Fay et al., 2003; Chen et al., 2020; Guo et al., 2022). While N addition typically stimulates aboveground net primary productivity, it can also shift species composition, promote nitrophilous taxa, and reduce overall diversity (Isbell et al., 2013; Avolio et al., 2014). Excessive N inputs from fertilizers and atmospheric deposition further promote soil acidification and accelerate species losses (Stevens et al., 2006; Clark et al., 2017). In contrast, P addition can enhance productivity in P-limited ecosystems; however, its effects on diversity are inconsistent and often depend on interactions with N availability (Tang et al., 2017; Gao et al., 2021). Thus, while the productivity benefits associated with nutrient enrichment are well documented, the mechanisms underlying biodiversity responses remain less clear.

P limitation is common in low-productivity or historically grazed systems, where long-term nutrient removal and soil weathering can deplete available P pools. Under such conditions, fertilization typically favors species capable of efficiently exploiting added P, such as fast-growing grasses with high root phosphatase activity, while disadvantaging forbs and legumes that rely on mycorrhizal symbioses for P uptake (Olde Venterink, 2011; Ceulemans et al., 2013). Consequently, community structure shifts toward dominance by a few competitive grass species, leading to reduced functional and taxonomic diversity. In semi-savanna grasslands, where water limitation interacts with nutrient availability, this process can be exacerbated further: fertilization promotes grass expansion, suppresses less competitive species, and increases community homogenization despite an increase in total biomass (Kupari, 2024). These patterns suggest that nutrient enrichment, especially in P-limited and water-constrained ecosystems, may enhance productivity at the expense of biodiversity. Understanding these trade-offs is crucial for identifying the mechanisms by which nutrient management and climate change jointly shape grassland stability and functioning.

Central Asia harbors diverse ecosystems ranging from steppes and deserts to alpine meadows, providing critical habitats for global biodiversity (De Beurs et al., 2018). Tajikistan, dominated by the Pamir, Alay, and Hissar ranges, supports highly heterogeneous environments and numerous endemic species (Batsaikhan and Dabrowski, 2017). Southwestern Tajikistan's semi-savanna grasslands represent transitional ecosystems mediated by nutrient constraints, climate change, and land-use pressures. Compared with Eurasian and North American grasslands, these systems experience harsher climatic fluctuations, lower precipitation, and a greater degradation history, rendering them particularly sensitive to fertilization (Geng et al., 2025). However, despite their ecological significance, minimal systematic experimental research has been conducted to evaluate the mechanisms by which nutrient enrichment and climate interact to influence productivity and biodiversity in Tajikistan's grasslands. Long-term overgrazing and nutrient depletion have degraded these grasslands, reducing forage quality and productivity (Muminjanov, 2008; Han et al., 2016). Fertilizer use has increased in recent years (Madaminov, 2000); however, excessive application risks soil acidification, greenhouse gas emissions, and biodiversity declines (Chen et al., 2020; Malghani et al., 2020). Further, whether grasslands at specific elevations respond consistently to N and P enrichment, or how climatic factors modulate these responses, remains unclear.

To address this knowledge gap, this study conducted a five-year field experiment with *in situ* N and P addition at four grassland sites of central and southwestern Tajikistan: Tabakqi, Balkhi, Luchob, and Ziddi. The experiment examined the response of grassland aboveground biomass (AGB) and plant species diversity to nutrient addition, while climatic factors such as precipitation and temperature were also considered. This study aims to assess the impact of N and P addition on AGB and plant species diversity and determine whether the AGB and plant species diversity of specific grassland types exhibit site-specific responses to nutrient enrichment, while also considering climatic factors.

2 Materials and methods

2.1 Experiment site

The experiment was conducted in central and southwestern Tajikistan, a region with a continental climate and strong elevation gradients. Four grassland sites were selected: Tabakqi, Balkhi, Luchob, and Ziddi, where Tabakqi is a low-elevation site, Balkhi and Luchob are mid-elevation sites, and Ziddi is a high-elevation site. Tabakqi, Balkhi, and Luchob are semi-savanna grasslands, whereas Ziddi is a mountain meadow. Vegetation coverage ranges from 50% to 70% at Tabakqi and Balkhi, from 80% to 90% at Luchob, and from 90% to 100% at Ziddi. The growing season is short, encompassing March to June at low-to-mid elevation sites and June to August at the high-elevation site. The soil types differ across sites, ranging from nutrient-poor Calcisols at Tabakqi to nutrient-rich Nitisols at Luchob (Table 1). Details of precipitation and temperature variations at the four sites during 2018–2022 are shown in Figures S1 and S2.

Table 1 Brief description of the four grassland sites in central and southwestern Tajikistan

Parameter	Tabakqi	Balkhi	Luchob	Ziddi
Latitude	37°51′33″N	38°14′03″N	38°39′55″N	39°02′11″N
Longitude	68°57′34″E	69°17′01″E	68°39′23″E	68°49′22″E
Elevation (m)	650	1100	1250	2000
Slope (°)	19	29	23	24
MAT (°C)	17.5	17.3	13	6.3
MAP (mm)	252	447	1017	667
SOC (g/kg)	8.2	17.3	28.65	29.79
TN (g/kg)	0.74	1.57	2.85	2.6
TP (g/kg)	0.6	0.79	0.88	0.63
Soil pH	8.04	7.96	7.63	8.41
Dominant species	*Aegilops triuncialis* L., *Poa bulbosa* L., and *Strigosella turkestanica* (Litv.) Botsch.	*Aegilops triuncialis* L. and *Cynodon dactylon* (L.) Pers.	*Hordeum bulbosum* L., *Bothriochloa ischaemum* (L.) Keng, *Avena trichophylla* K.Koch, and *Cynodon dactylon* (L.) Pers.	*Prangos pabularia* Lindl. and *Geranium collinum* Stephan ex Willd.

Note: MAT, mean annual temperature; MAP, mean annual precipitation; SOC, soil organic carbon; TN, total nitrogen; TP, total phosphorus.

2.2 Experimental design

This study was conducted from February 2018 to December 2022. The four distinct grassland sites were selected for their diverse elevation gradients, soil compositions, and climate conditions, allowing an examination of biodiversity responses to nutrient enrichment. Historical botanical studies and ecological assessments supported their selection because of their vulnerability to climate change and anthropogenic pressures. To prevent grazing disturbance, we established 20 m×15 m fenced areas at each site (Fig. S3). Within each fenced area, four experimental blocks were constructed, each divided into five 3 m×3 m split plots with 1-m spacings between them. According to previous studies in this region (Safarov, 2003; Madaminov et al., 2012) and combined with a pre-treatment analysis for soil nutrient content (Table 1), we randomly assigned five subplots the following nutrient addition treatments: CK (the control without N or P addition), N30 (adding 30 kg N/(hm^2·a)), P30 (adding 30 kg P/(hm^2·a)), N30P30 (adding 30 kg N/(hm^2·a)) and 30 kg P/(hm^2·a)), and N90P30 (adding 90 kg N/(hm^2·a) and 30 kg P/(hm^2·a)). Previous experimental studies in this region have shown that urea and ammonium dihydrogen phosphate are the most commonly used fertilizers. Moreover, they also have significant effects on plant growth (Ovchinnikov and Sidorenko, 1977; Sinkovsky and Madaminov, 1989; Madaminov, 2000). Therefore, based on the snowmelt timing for each grassland site, granular fertilizers containing N (urea; $CO(NH_2)_2$) and P (ammonium dihydrogen phosphate; $(NH_4)H_2PO_4$) were evenly applied before the snow totally melted (mid-February at Tabakqi, early March at Balkhi, late March to early April at Luchob, and late May at Ziddi). Stainless steel sheets were inserted into each plot to minimize water infiltration between treatment subplots. These sheets were embedded 40 cm into the soil and extended 10 cm above ground to prevent lateral water movement and nutrient leaching.

2.3 Community measurement and sample collection

Within each subplot, a 1 m×1 m quadrat was placed at the center for vegetation sampling. Sampling was conducted during peak biomass periods (April at Tabakqi, May at Balkhi, May to June at Luchob, and July at Ziddi). Several randomly selected plants were measured for the canopy height of each species using a ruler. The abundance of each plant species was determined through manual counts, a meticulous process that involved identifying and tallying every individual within the sampling plots. Afterward, all live aboveground tissues from each plant species were harvested by clipping, returned to the laboratory, and oven-dried at 65.0°C until attaining constant weight. No grazing, mowing, or other management was permitted within the fenced areas. The total calculated biomass of the plants was used as an estimate of AGB (g/m^2). Species richness represents the number of species within each quadrat. The Simpson's dominance index (Simpson index) was calculated using Equation 1 (Simpson, 1949). The Shannon-Wiener index (Shannon index) was determined using Equation 2 (Niu et al., 2018). The Margalef's richness index (Margalef index) was derived from Equation 3 (Margalef, 1958). The Pielou's equitability index (Pielou index) was calculated using Equation 4 (Smith and Wilson, 1996).

$$C = 1 - \sum P_i^2 , \quad (1)$$

$$H = -\sum P_i \ln P_i , \quad (2)$$

$$D_{ma} = (S-1) / \ln N , \quad (3)$$

$$E_{pi} = H / \ln S , \quad (4)$$

where C indicates the Simpson index; P_i represents the proportion of individuals belonging to a particular species within a given quadrat; H indicates the Shannon index, which quantifies species diversity by incorporating both richness and equitability in the community; D_{ma} indicates the Margalef index; S denotes the total number of species observed within that quadrat; N refers to the total number of individual plants recorded across all species in the quadrat; and E_{pi} indicates the Pielou index.

2.4 Statistical analysis

Statistical analyses were conducted using SPSS 24.0 software, Microsoft Excel 365, and Origin Pro 2021. Two-way analysis of variance (ANOVA) was performed to assess the effects of nutrient addition on AGB, species richness, and plant species diversity. The level of statistical significance was set at P=0.050. Based on the regression results, we performed a structural equation model (SEM) to examine how precipitation, temperature, and nutrient addition affect AGB through plant species diversity. The SEM analyses were performed using AMOS 19.00. Microsoft Excel 365 and Origin Pro 2021 were used to generate all figures.

3 Results

3.1 Impact of nutrient addition on AGB and species richness across four grassland sites

Nutrient addition and year significantly influenced AGB across all four grassland sites (Fig. 1; Table 2). At low- and mid-elevation grassland sites (Tabakqi, Balkhi, and Luchob), the interaction of nutrient addition and year also significantly influenced AGB; however, this significant effect was not observed at the high-elevation grassland site (Ziddi; P>0.050). The application of N, P, and their combination led to an increasing trend in AGB across almost all grassland sites over the consecutive five years (Fig. 1). Compared with the CK, AGB increased by 20%–80% under N30 and by up to 190%–200% under N90P30. The AGB values at Luchob and Ziddi sites were slightly higher than those at Tabakqi and Balkhi sites. Regarding interannual variations, the AGB in 2020 was marginally lower compared with other years across four grassland sites (Fig. 1a and c). In 2022, AGB at the low-elevation site (Tabakqi) increased from 494 g/m^2 under the CK to 650 g/m^2 under N90P30, while at the high-elevation site (Ziddi), it rose from 552 to 1614 g/m^2.

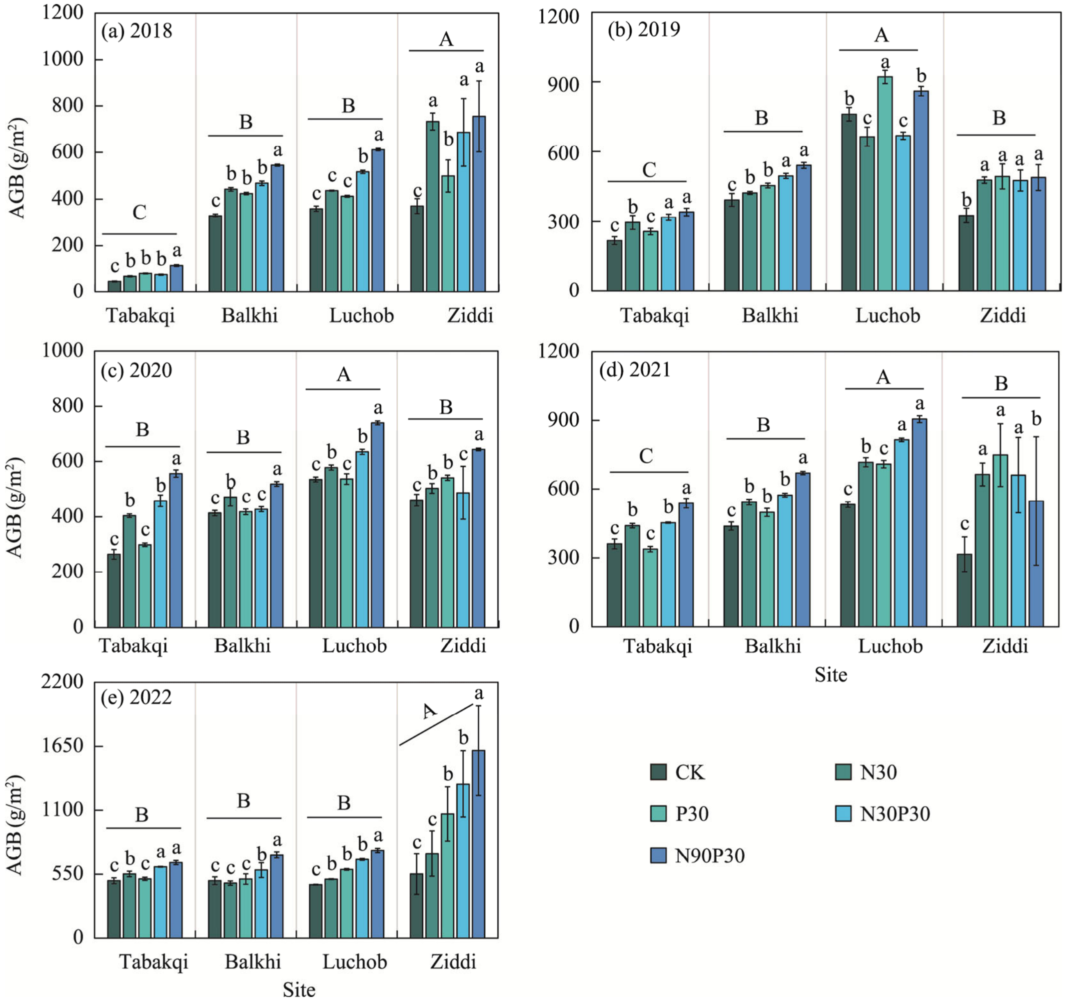

Fig. 1 Variations in aboveground biomass (AGB) under various nutrient addition treatments at the four grassland sites in 2018 (a), 2019 (b), 2020 (c), 2021 (d), and 2022 (e). In each panel, groups labeled with the identical capital letters above them do not exhibit significant differences at a significance level of *P*<0.050 level according to Duncan's test. Among each set of five error bars, error bars with distinct letters exhibit significant differences with *P*<0.050 level according to Duncan's test. Error bar represents the standard error of the mean. CK indicates the control (without nitrogen (N) and phosphorus (P) addition), N30 indicates adding 30 kg N/(hm^2•a), P30 indicates adding 30 kg P/(hm^2•a), N30P30 indicates adding 30 kg N/(hm^2•a) and 30 kg P/(hm^2•a), and N90P30 indicates adding 90 kg N/(hm^2•a) and 30 kg P/(hm^2•a).

Table 2 Effects of treatment, year, and their interactions on the aboveground biomass (AGB) at the four grassland sites during 2018–2022

Source	Tabakqi		Balkhi		Luchob		Ziddi	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Year	725.68	0.000	32.05	0.000	292.24	0.000	12.62	0.000
Treatment	95.47	0.000	50.80	0.000	167.48	0.000	5.26	0.000
Year×Treatment	6.75	0.000	2.59	0.000	20.73	0.000	1.52	0.120

Note: *F*-statistic is the core measure in analysis of variance (ANOVA) used to determine whether group differences are significant. A larger *F*-value and a *P*-value less than 0.050indicate a significant effect on AGB.

The effect of nutrient addition on species richness exhibited station-specific characteristics (Fig. 2). N and P addition significantly influenced the species richness of Balkhi and Luchob grasslands, while Tabakqi and Ziddi sites showed no significant response to nutrient addition (Fig. 2; Table 3). In terms of interannual variations, species richness differed significantly across years at Balkhi, Luchob, and Ziddi sites, with the exception of Tabakqi. Overall, the average species richness values ranged between 7 and 24 among the four grassland sites.

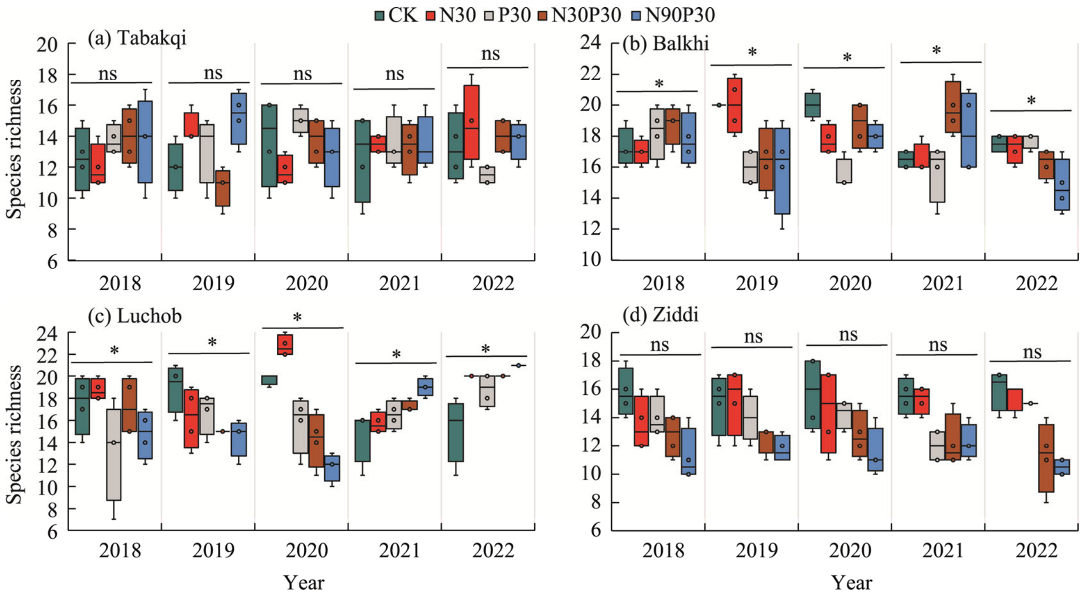

Fig. 2 Impact of nutrient addition treatments on species richness at Tabakqi (a), Balkhi (b), Luchob (c), and Ziddi (d) during 2018–2022. * indicates that there are significant differences between treatments at $P<0.050$; ns indicates that the observed differences are not statistically significant among treatments. The upper and lower boundaries of the box represent the 25th and 75th percentiles, respectively. The line in the box indicates the median. The upper and lower whiskers represent the maximum and minimum values within 1.5 times the interquartile range from the 25th and 75th percentiles, respectively. Dots represent individual replicate values for each treatment; overlapping points may appear as a single dot when replicate values are identical or very similar.

Table 3 Effects of treatment, year, and their interactions on species richness at the four grassland sites during 2018–2022

Source	Tabakqi		Balkhi		Luchob		Ziddi	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Year	0.10	0.980	4.43	0.000	5.57	0.000	20.89	0.000
Treatment	0.76	0.560	2.46	0.050	6.65	0.000	0.14	0.970
Year×Treatment	2.06	0.020	4.48	0.000	7.69	0.000	0.97	0.490

3.2 Relationships among AGB, plant species diversity, and climatic factors

The correlation analysis revealed distinct relationships among AGB, species diversity indices, and climatic factors (precipitation and temperature). Species richness exhibited a moderate positive correlation with precipitation (correlation coefficient r=0.29) and the Margalef index (r=0.31), indicating that higher precipitation may enhance species diversity in specific grassland ecosystems. However, precipitation showed a negative correlation with the Shannon index (r= –0.27), Simpson index (r= –0.10), and Pielou index (r= –0.45), suggesting that increased precipitation might reduce species evenness and dominance (Fig. S4).

Temperature demonstrated strong positive correlations with the Shannon index (r=0.87), Simpson index (r=0.85), and Pielou index (r=0.62), implying that higher temperatures contribute to increased species diversity and equitability. Additionally, AGB showed a weak positive correlation with precipitation (r=0.25), but no significant relationship with temperature, indicating that AGB accumulation is influenced primarily by water availability rather than thermal conditions. In addition, the correlation matrix highlighted site-specific variations in biodiversity responses to environmental factors. The Shannon index and Simpson index exhibited the strongest correlation (r=0.95), confirming their close relationship in quantifying species dominance and richness (Fig. S4). These findings emphasize the importance of climate–nutrient interactions in shaping biodiversity patterns across Tajikistan's semi-savannah and mountain meadow ecosystems.

3.3 Impact of nutrient addition on plant species diversity across four grassland sites

At the Tabakqi grassland site, treatment, year, and their interaction significantly influenced the Simpson, Shannon, and Pielou indices (P<0.050), but not the Margalef index (P>0.050; Table S1). During the first growing season, nutrient addition caused transient increases for the Simpson, Shannon, and Pielou indices, followed by subsequent declines (Fig. 3a–c). In 2019, the Simpson and Pielou indices increased under N30, while the Shannon index increased under both N30 and P30 (Fig. 3d–f). In 2020, the Simpson and Shannon indices were higher under P30 but declined under other treatments (Fig. 3g and h), and the Pielou index decreased across all treatments (Fig. 3i). In 2021, all three indices increased under N30, P30, and N30P30 but declined under the high-dose N90P30 treatment (Fig. 3j–l). By 2022, the Simpson index was enhanced under N30, and the Shannon index increased under N30 and N90P30 (Fig. 3m and n), whereas the Pielou index declined under all treatments compared with the CK (Fig. 3o).

At the Balkhi grassland site, treatment, year, and their interaction significantly affected all species diversity indices (P<0.050). Overall, the Simpson index declined under nutrient addition treatments in 2018, 2020, and 2021, but increased in 2019 under N30, P30, and N90P30 (Fig. 3a–j). The Shannon index showed contrasting trends: it was higher under P30 but lower under other treatments in 2018, increased under N30, P30, and N90P30 but decreased under N30P30 in 2019, and declined consistently across all treatments from 2020 to 2022 (Fig. 3b and n). The Pielou index generally decreased throughout the study period, except in 2019, when P30 and N90P30 increased the index values relative to the CK (Fig. 3c and o).

At the Luchob grassland site, treatment, year, and their interaction also significantly influenced all species diversity indices. The Simpson index increased under P30 in 2018, 2019, 2020, and 2022, but decreased under all treatments in 2021 (Fig. 3a and m). The Shannon index increased significantly under N30 and P30 during the first two years, remained higher under all treatments (except N90P30) in 2021, and then declined across treatments in 2022 (Fig. 3b and n). The Pielou index increased under P30 and N30P30 in 2018, decreased under N90P30 in 2019, and declined under all treatments in 2020 and 2021, before rising again under N30 and P30 in 2022 (Fig. 3k and o).

At the Ziddi grassland site, only year significantly affected species diversity indices (P<0.050), with no significant effects of treatment or their interaction (Table S1). The Simpson index decreased under nutrient addition treatments in 2018 and 2019, increased slightly under N30 and P30 in 2020, declined again under N30 in 2021, and then increased in 2022. The Shannon index showed a similar pattern (Fig. 3a and j). The Pielou index decreased under all treatments during the first three years, rebounded in 2021 under most treatments except for N30, and increased only under N30 in 2022; however, these changes were not statistically significant (Fig. 3c and o).

3.4 Relationship between AGB and plant species diversity

The relationships between total AGB and plant species diversity indices varied across grassland sites and treatments (Fig. 4). At the Tabakqi grassland site, AGB was positively correlated with the Simpson index (P<0.050; Fig. 4a) and negatively correlated with with the Margalef index (P<0.050; Fig. 4i). No significant relationships were identified between AGB and the Shannon index (Fig. 4e). The Pielou index was generally unrelated to AGB, except for a positive association under N90P30 (P<0.050; Fig. 4m). At the Balkhi grassland site, AGB–species diversity relationships were more variable. AGB showed positive correlations with the Margalef index under certain treatments (e.g., N30P30; P<0.050), but negative correlations under P30 and N90P30 (P<0.050; Fig. 4j). The Pielou index decreased with AGB under N30 (P<0.050; Fig. 4n), whereas

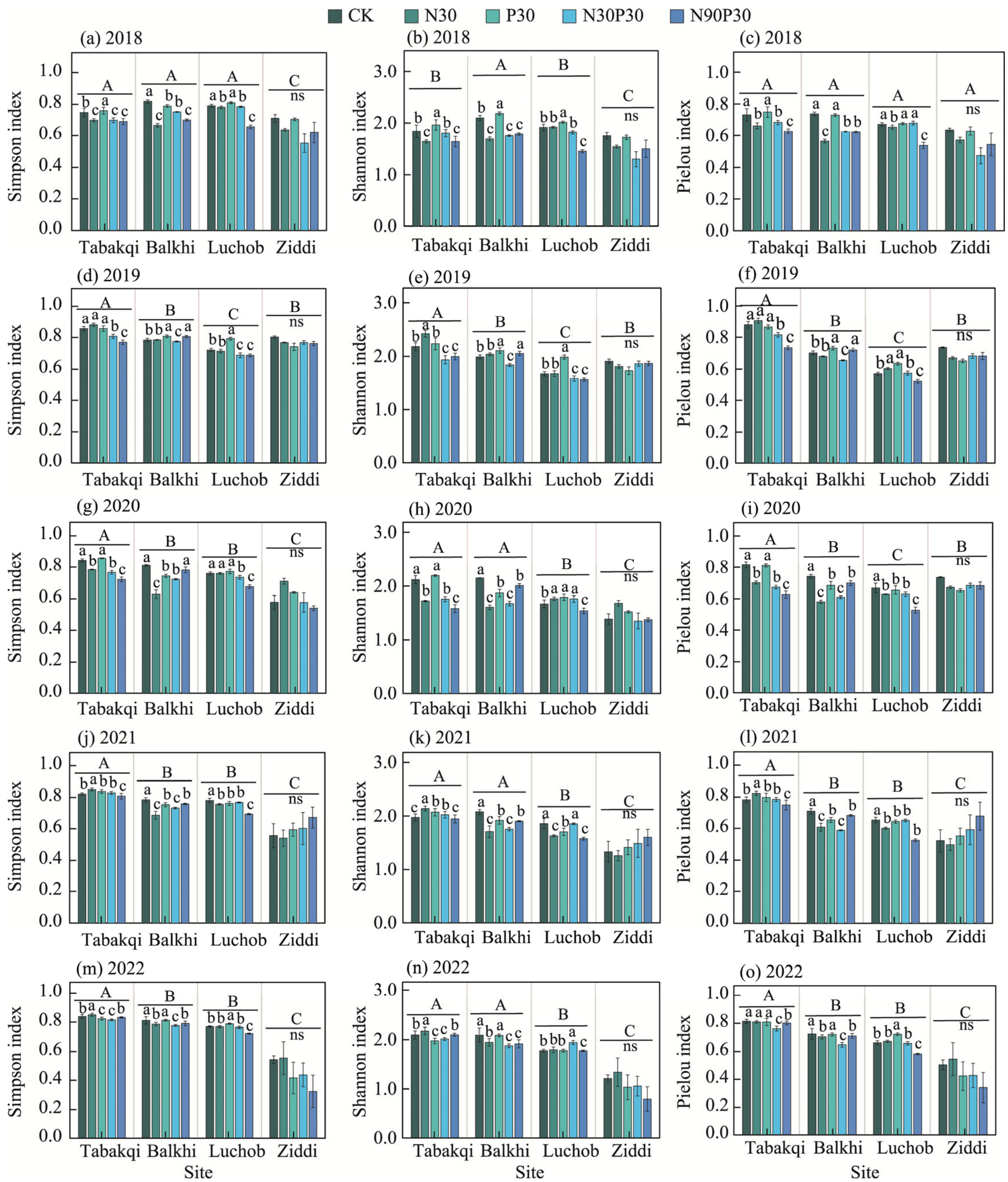

Fig. 3 Variations in the Simpson index (a, d, g, j, and m), Shannon index (b, e, h, k, and n), and Pielou index (c, f, i, l, and o) under various nutrient addition treatments at the four grassland sites from 2018 to 2022. In each panel, groups labeled with the identical capital letters above them do not exhibit significant differences at a significance level of $P<0.050$. Different lowercase letters above the error bars represent significant differences ($P<0.050$) among nutrient enrichment treatments; ns means that differences are not significant. Error bar represents the standard error of the mean. Simpson index, Simpson's dominance index; Shannon index, Shannon-Wiene index; Pielou index, Pielou's equitability index.

the Simpson and Shannon indices were not significantly related to AGB in majority of cases (Fig. 4b and f). At the Luchob grassland site, AGB exhibited contrasting correlations with the Simpson index: negative under CK and N30, but positive under N90P30 ($P<0.050$; Fig. 4c). The Shannon index was negatively correlated with AGB under N30 ($P<0.050$; Fig. 4g), while other treatments showed no relationships. The Margalef index was positively associated with AGB only under

N90P30 (P<0.050; Fig. 4k). The Pielou index was negatively related to AGB under CK and N30 (P<0.050; Fig. 4o) but unaffected under other treatments. At the Ziddi grassland site, AGB showed consistent negative correlations with the Simpson index, Shannon index, and Pielou index across nutrient addition treatments of N30, P30, N30P30, and N90P30 (P<0.050; Fig. 4d, h, and p). No significant association was observed between AGB and the Margalef index (P<0.050; Fig. 4l).

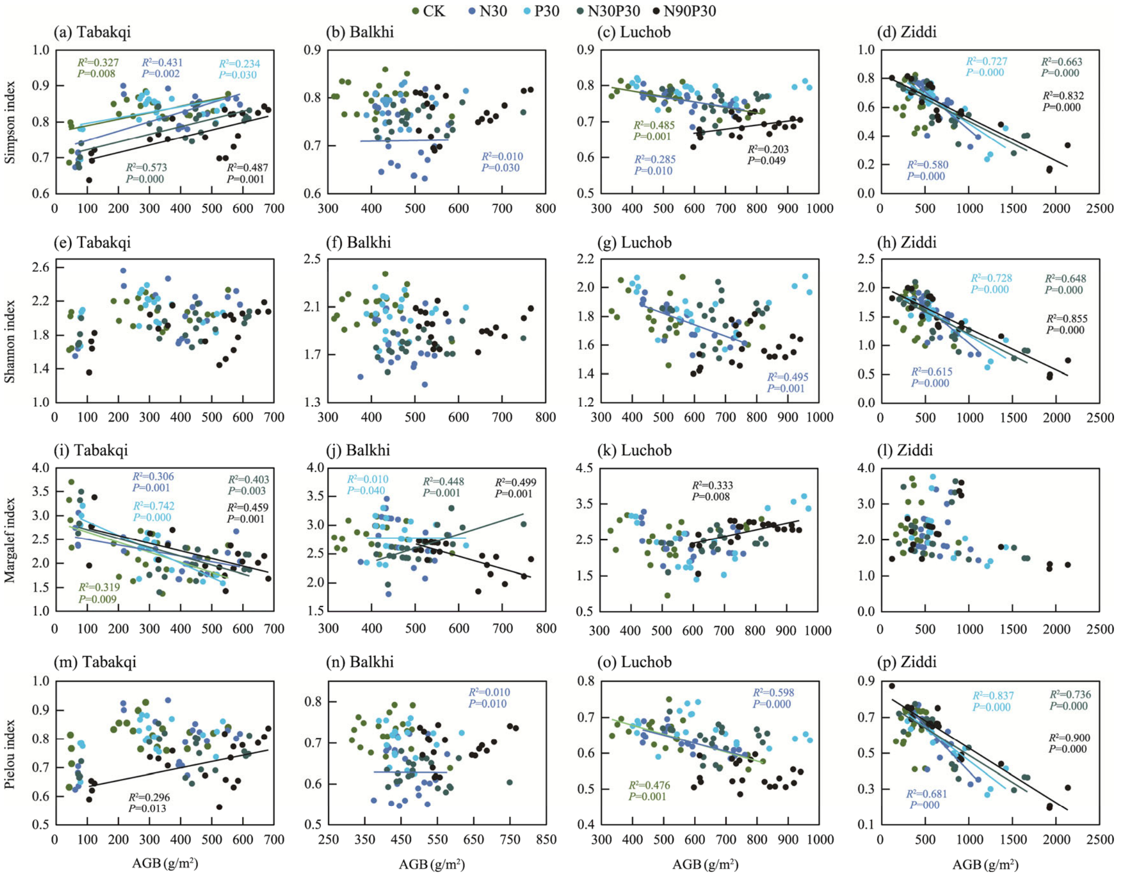

Fig. 4 Relationships of AGB with the Simpson index (a–d), Shannon index (e–h), Margalef index (i–l), and Pielou index (m–p) at Tabakqi, Balkhi, Luchob, and Ziddi sites. Margalef index, Margalef's richness index. Only fitted curves with significant correlations (P<0.050) are shown.

3.5 Impact of precipitation, temperature, and nutrient addition on AGB and plant species diversity

The SEM analysis revealed that nutrient addition significantly enhanced AGB at all four grassland sites through direct positive effects (P<0.001; Fig. 5). In contrast with AGB, nutrient addition negatively influenced almost all species diversity metrics. This effect was particularly pronounced at Tabakqi and Luchob grassland sites, where the Pielou index declined significantly following fertilization (Fig. 5a and c). Overall, precipitation had a positive direct effect on biomass accumulation, but a statistically significant impact was only observed at the Balkhi grassland site (Fig. 5b). Dissimilar to precipitation and nutrient addition, temperature exhibited both positive and negative effects on AGB. Specifically, temperature showed a significant positive influence on AGB at the Tabakqi grassland site, while demonstrating a significant adverse effect at Balkhi and Ziddi grassland sites (Fig. 5b and d). Species richness significantly positively influenced AGB at Luchob and Ziddi grassland sites (P<0.050). In addition to direct effects, AGB was also indirectly influenced by temperature, nutrient addition, and precipitation via their impacts on plant species diversity.

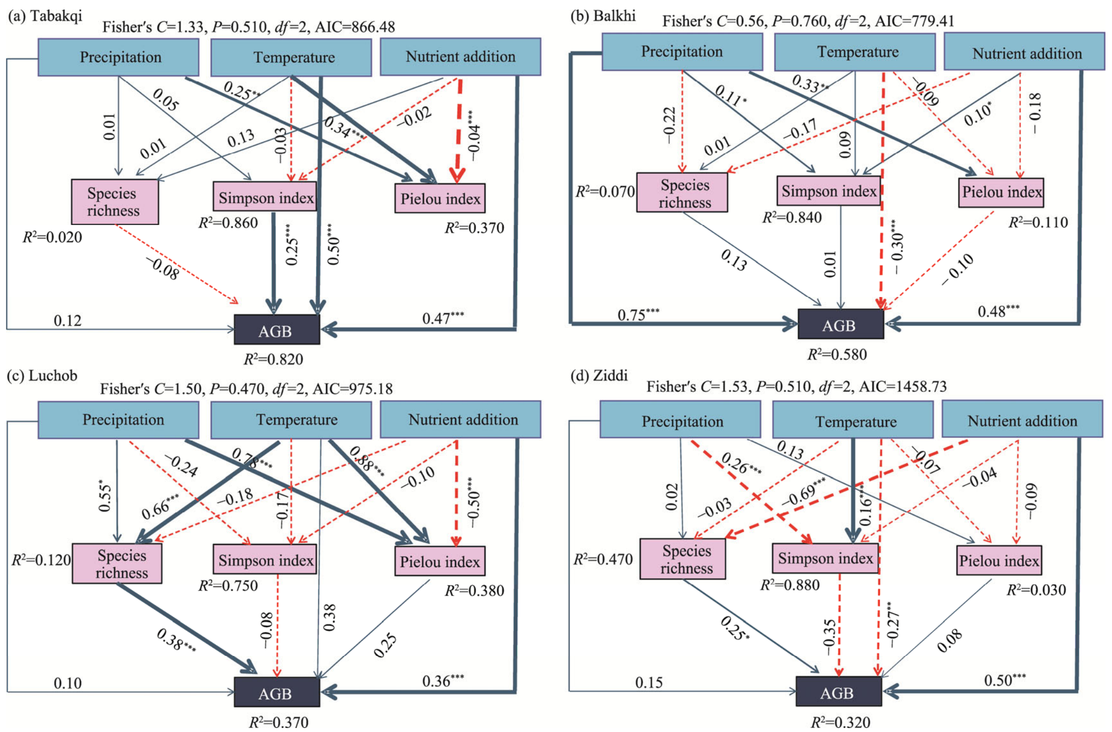

Fig. 5 Structural equation model (SEM) for the effect of climatic factors and nutrient addition on AGB and plant species diversity at Tabakqi (a), Balkhi (b), Luchob (c), and Ziddi (d) sites. *df*, degrees of freedom; AIC, Akaike Information Criterion. Blue bold arrows represent significant positive pathway; red dashed bold arrows represent significant negative pathway; and thin arrows represent non-significant pathways. The values beside the arrows indicate standardized path coefficients; the proportion of variance explained (R^2) appears alongside the response variable in the model. In Fisher's *C* test, the *P*-value evaluates the overall goodness-of-fit of the SEM, where $P>0.050$ indicates that the model fits the data well (i.e., no significant difference between observed and expected relationships). In regression analysis of the SEM, *, **, and *** indicate statistically significant effects at $P<0.050$, $P<0.010$, and $P<0.001$ levels, respectively.

4 Discussion

4.1 Impact of nutrient addition and climatic factors on AGB and species richness

This study showed that nutrient addition, particularly N, substantially increase AGB in Tajikistan's grasslands. This pattern reflects the well-documented role of N as the primary limiting nutrient in many terrestrial ecosystems, where it directly supports photosynthetic activity and leaf area expansion (Li et al., 2017; Zhao et al., 2019). P has a weaker effect on AGB, but its influence becomes more apparent in combination with N, suggesting that P uptake and utilization are mainly dependent on sufficient N availability. In addition, this observation explains why combined N–P treatments could yield the strongest productivity gains (Fay et al., 2015). At higher elevations, where soils are typically less fertile, this interaction can be especially evident, pointing to N-driven constraints on biomass accumulation.

Climatic conditions further modulate these responses. An increase in precipitation enhances nutrient mobility in soils and facilitates seedling establishment, in turn promoting plant growth and recruitment (Fan et al., 2021). However, greater water availability also intensifies competitive exclusion, as fast-growing, moisture-adapted species are able to outcompete less competitive taxa. This mechanism likely underlies why higher precipitation is positively associated with species richness but negatively related to evenness and community stability indices. Such shifts reflect a reduction in niche diversity, where resource enrichment favors dominant species and reduces overall community balance (Tilman et al., 1997; Du et al., 2025). Temperature plays a contrasting role. Temperature does not strongly affect biomass production, supporting the idea that productivity in semi-arid grasslands is more constrained by water than thermal inputs (Yao et al., 2022). Instead, warmer conditions shape biodiversity patterns by influencing physiological processes, phenological timing, and thermal niche partitioning (Körner, 2007; Miao et al., 2025). Higher temperatures promote greater species diversity and evenness, likely because species with different thermal tolerances could coexist through staggered growth and reproductive strategies, highlighting that climate impacts on biodiversity extend beyond biomass production, operating through mechanisms of metabolic adaptation and seasonal resource use.

In combination, these findings emphasize that nutrient availability and climatic factors interact in complex ways to regulate productivity and biodiversity. While N is the key driver of biomass increases, precipitation and temperature determine how plant communities are structured and maintained. These results suggest that the resilience of Tajikistan's semi-savannah and mountain meadow ecosystems depends on nutrient inputs and the balance of climatic drivers that shape competition, recruitment, and coexistence.

4.2 Ecological reactions of plant species diversity to nutrient addition

Numerous studies have shown that N deposition can reduce species richness and community diversity, even at relatively low input levels (Chiarucci and Maccherini, 2007; Seabloom et al., 2021). In this experiment, the effects of N addition, P addition, and their interactions on plant species diversity varied across grassland sites and time, reflecting both the sensitivity of plant communities to nutrient availability and the influence of local environmental conditions.

At the low-elevation site (Tabakqi), species diversity initially increased after nutrient enrichment, suggesting that moderate nutrient addition can stimulate the coexistence of multiple species. However, plant species diversity declined in later years, indicating that sustained fertilization will lead to nutrient saturation and the dominance of a few competitive taxa. This temporal shift is consistent with the theory that enrichment first alleviates resource limitation but eventually promotes competitive exclusion, resulting in homogenized communities (Xu et al., 2012).

At the mid-elevation site (Balkhi), plant species diversity consistently declined following fertilization. This outcome likely reflects strong dominance by nitrophilic and fast-growing species that monopolize light and soil resources, thus displacing less competitive taxa. Such resource asymmetry, particularly in light capture, is a well-documented mechanism by which nutrient enrichment accelerates biodiversity loss (Bobbink et al., 2010; Ma et al., 2020).

The mid-elevation grassland site (Luchob) exhibited a threshold-dependent response. Plant species diversity increased only under moderate N and P addition, suggesting that balanced nutrient availability promotes coexistence by supporting complementary resource use among species. In contrast, high nutrient inputs shift community composition toward dominance by a few taxa, reducing overall diversity (Seabloom et al., 2015; Palpurina et al., 2018). These contrasting outcomes highlight that the biodiversity consequences of fertilization depend not only on the quantity but also on the ratio of nutrients supplied.

At the high-elevation site (Ziddi), species richness declined steadily over the study period, but fertilization treatments had minimal effect, suggesting that non-nutrient factors, such as climate change, grazing pressure, and soil physical constraints, play a stronger role in shaping community dynamics than nutrient addition. For example, fluctuations in precipitation and temperature likely influence competitive hierarchies and recruitment success, while grazing masks fertilization effects by altering soil nutrient availability and plant regeneration patterns (Cheng et al., 2022; Han et al., 2023). In addition, edaphic limitations such as soil texture and water retention may have constrained nutrient uptake, dampening the influence of enrichment on plant species diversity (Wankmüller et al., 2024).

These findings underscore the complex interactions between nutrient availability, species dynamics, and environmental variability, reinforcing the need to consider both biotic and abiotic influences when assessing grassland biodiversity responses to fertilization.

4.3 Impact of nutrient addition on the relationship between AGB and plant species diversity

The relationship between plant biomass and biodiversity remains a central ecological question, particularly in grasslands that support local livestock production (Fayiah et al., 2019). Previous studies have reported a wide range of patterns, including positive, negative, or nonlinear biomass–diversity relationships (Zhang et al., 2022; Ye et al., 2023). In this study, this relationship was not uniform across grassland sites but instead varied depending on nutrient levels, dominant species dynamics, and environmental conditions.

At the low-elevation site (Tabakqi), greater AGB was associated with stronger species dominance, suggesting that nutrient enrichment favors competitive species capable of rapid growth. However, the link with species richness was weak, implying that while AGB increases, it does not translate into higher species richness. This pattern is consistent with the idea that nutrient addition stimulates dominant taxa while only marginally influencing the total number of species present (Harpole et al., 2016; Midolo et al., 2019).

The mid-elevation site (Balkhi) showed a clearer trade-off between AGB and plant species diversity. As AGB accumulates, community evenness declines, reflecting reduced opportunities for coexistence when nitrophilic species monopolize resources. Light limitation appears to be a central mechanism here: taller, fast-growing species shaded competitors, leading to uneven resource distribution and reduced diversity (Bobbink et al., 2010; Ma et al., 2020).

At the mid-elevation site (Luchob), the relationship between AGB and plant species diversity was more variable. Moderate nutrient addition treatments promoted coexistence, while higher nutrient inputs encouraged dominance. This suggests a threshold response, where low to intermediate nutrient supply can sustain complementary resource use among species, but excessive enrichment can intensify competition and reduce diversity (Palpurina et al., 2018).

In contrast, the high-elevation site (Ziddi) exhibited a predominantly negative biomass–diversity relationship. At this site, increases in AGB are strongly associated with declines in species richness and community evenness. This effect appears to be driven by the dominance of *Prangos pabularia* Lindl., which proliferates under fertilization and occupies more space and resources, suppressing the growth of subordinate species. Similar to other studies (Li et al., 2017; Koerner et al., 2018), this indicates that intense competition for light and nutrients by dominant species can destabilize community diversity. The negative association was most evident in years of highest AGB, suggesting that interannual variability in climatic factors could further amplify competitive asymmetries.

Collectively, these findings underscore that the biomass–diversity relationship in Tajikistan's grasslands is markedly context-dependent. At lower to intermediate levels of nutrient enrichment, increases in biomass do not invariably suppress species diversity and, in certain cases, may even promote coexistence through niche differentiation and resource partitioning. Conversely, sustained or excessive nutrient inputs exacerbate competitive asymmetries, fostering the dominance of a limited number of taxa, thus diminishing both species richness and community evenness. This pattern reinforces the broader ecological principle that biodiversity conservation within fertilized grassland ecosystems necessitates a careful balance between productivity enhancement and management interventions aimed at mitigating competitive exclusion by dominant species.

4.4 Relationship among climatic factors, AGB, and plant species diversity

This study's findings indicate that nutrient addition can reduce species diversity, primarily by decreasing species richness, particularly at the high-elevation site (Ziddi), where long-term fertilization promoted competitive exclusion. This pattern is consistent with global evidence showing that nutrient inputs favor fast-growing dominant species at the expense of less competitive taxa, ultimately simplifying community structure (Liu et al., 2025; Zhang et al., 2025a). In contrast, at the Luchob grassland site, species diversity responded positively to precipitation and temperature, highlighting the central role of climate in supporting species recruitment and persistence in resource-limited environments (Van Oijen et al., 2018).

Community evenness and dominance emerge as key drivers of diversity dynamics across all sites. Increases in dominance reduces evenness, particularly under fertilization, where a few species captured disproportionate amounts of resources, reflecting a common pathway by which nutrient enrichment alters community composition via strengthening competitive hierarchies and shifting ecosystem balance toward a smaller subset of taxa (Kitikidou et al., 2024).

AGB is shaped by both biodiversity and environmental conditions, though their relative influence differs among grasslands. At Tabakqi and Luchob grassland sites, greater species richness and dominance were positively associated with AGB, supporting the biodiversity–productivity hypothesis, which posits that more diverse communities make more efficient use of resources (Wang et al., 2024). In contrast, at Balkhi and Ziddi grassland sites, AGB was more strongly regulated by abiotic factors than by biodiversity, indicating that under harsher climatic conditions, environmental constraints override the benefits of species diversity (Mekhrovar et al., 2024; Spohn et al., 2025).

Nutrient enrichment itself is a major driver of productivity, especially at Ziddi and Balkhi grassland sites, where fertilization substantially boosts biomass accumulation. These gains reflect the enhanced resource availability provided by added nutrients (Wilcots et al., 2025). However, increases in species dominance sometimes reduced productivity, suggesting that strong competitive asymmetries can limit overall resource-use efficiency (Zhang et al., 2025b).

Temperature effects on biomass are highly context-dependent. At Tabakqi and Luchob grassland sites, warmer conditions enhance productivity by lengthening the growing season and supporting higher metabolic activity. Conversely, at the Ziddi grassland site, higher temperatures suppresses AGB, likely because of heat stress and moisture loss that limits both nutrient uptake and physiological performance (Yao et al., 2022; Liu et al., 2025). These findings illustrate that while warming can stimulate growth in some grasslands, it can reduce productivity in more arid or high-elevation ecosystems where heat intensifies water limitations.

Overall, the findings demonstrate that grassland productivity emerges from the complex interaction of biodiversity, nutrient enrichment, and climate change. While fertilization generally stimulates AGB, it often compromises species richness and community evenness. Climatic drivers, particularly precipitation and temperature, further regulate these outcomes by either intensifying or mitigating the effects of added nutrients. Recognizing these coupled influences is crucial for anticipating ecosystem responses to global change and for guiding sustainable management of Tajikistan's grasslands. In this context, management approaches that carefully balance nutrient inputs with biodiversity conservation will be vital to maintaining both ecological stability and long-term productivity.

5 Conclusions

The five-year *in situ* study revealed that N and P enrichment significantly increase AGB across the four grassland sites in central and southwestern Tajikistan, with N identified as the primary limiting nutrient. N addition increased AGB, while P addition alone contributed little but substantially amplified productivity when combined with N addition. These results indicated that P utilization is strongly dependent on sufficient N availability, and that N–P interactions are particularly important at higher elevations where soil fertility is lower. Climatic factors modulated these fertilization responses. Precipitation enhanced nutrient mobility and seedling establishment, driving stronger biomass accumulation and higher species richness, but simultaneously promoted competitive exclusion that reduced community evenness. Temperature, by contrast, had little effect on AGB but exerted strong control over biodiversity patterns by regulating phenology, thermal niche partitioning, and coexistence among species with differing tolerances. Thus, water availability remained the dominant regulator of productivity in semi-arid grasslands, while temperature primarily influenced community composition. Our findings highlighted that long-term fertilization enhances productivity but may undermine biodiversity through competitive dominance. A sustainable management strategy for Tajikistan's grasslands should therefore prioritize moderate N addition, apply N and P together at nutrient-poor high-elevation sites, and carefully adjust fertilization intensity according to precipitation conditions. Such a context-dependent approach can improve forage yields while maintaining biodiversity and ecosystem resilience under ongoing climate change.

Conflict of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This study was supported by the National Key Research and Development Program of China (2025YFE0103800, 2023YFE0102600) and the Xinjiang Talent Development Fund (XJRC-2025-KJ-PY-KJLJ-090). We express our gratitude to all the personnel at the Research Center for Ecology and Environment of Central Asia (Dushanbe subcenter) for their exceptional and efficient support.

Author contributions

Conceptualization: LI Yaoming, FAN Lianlian; Data curation: Mekhrovar OKHONNIYOZOV, Sino YUSUPOV, MA Xuexi; Formal analysis: Mekhrovar OKHONNIYOZOV, FAN Lianlian; Funding acquisition: LI Yaoming, FAN Lianlian; Methodology: Hikmat HISORIEV, Abdullo MADAMINOV; Resources: Mekhrovar OKHONNIYOZOV, LI Yaoming, FAN Lianlian; Software: Mekhrovar OKHONNIYOZOV, FAN Lianlian, Fakher ABBAS; Validation: LI Yaoming, TAO Ye, Abdullo MADAMINOV; Visualization: Mekhrovar OKHONNIYOZOV; Writing - original draft: Mekhrovar OKHONNIYOZOV, FAN Lianlian; Writing - review and editing: Mekhrovar OKHONNIYOZOV, FAN Lianlian, LI Yaoming. All authors approved the manuscript.

References

Avolio M L, Koerner S E, La Pierre K J, et al. 2014. Changes in plant community composition, not diversity, during a decade of nitrogen and phosphorus additions drive above-ground productivity in a tallgrass prairie. Journal of Ecology, 102(6): 1649–1660.

Batsaikhan U, Dabrowski M. 2017. Central Asia—twenty-five years after the breakup of the USSR. Russian Journal of Economics, 3(3): 296–320.

Bobbink R, Hicks K, Galloway J, et al. 2010. Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. Ecological Applications, 20(1): 30–59.

Ceulemans T, Merckx R, Hens M, et al. 2013. Plant species loss from European semi-natural grasslands following nutrient enrichment—is it nitrogen or is it phosphorus? Global Ecology and Biogeography, 22(1): 73–82.

Chen Z F, Xiong P F, Zhou J J, et al. 2020. Grassland productivity and diversity changes in responses to N and P addition depend primarily on tall clonal and annual species in semiarid Loess Plateau. Ecological Engineering, 145: 105727, doi: 10.1016/j.ecoleng.2020.105727.

Cheng Z, Zhao J X, Sun J, et al. 2022. Determining the role of richness and evenness in alpine grassland productivity across climatic and edaphic gradients. Oecologia, 200(3): 491–502.

Chiarucci A, Maccherini S. 2007. Long-term effects of climate and phosphorus fertilisation on serpentine vegetation. Plant and Soil, 293(1–2): 133–144.

Clark C M, Bell M D, Boyd J W, et al. 2017. Nitrogen-induced terrestrial eutrophication: cascading effects and impacts on ecosystem services. Ecosphere, 8(7): e01877, doi: 10.1002/ecs2.1877.

De Beurs K M, Henebry G M, Owsley B C, et al. 2018. Large scale climate oscillation impacts on temperature, precipitation and land surface phenology in Central Asia. Environmental Research Letters, 13(6): 065018, doi: 10.1088/1748-9326/aac4d0.

Du E, De Vries W, Collalti A, et al. 2025. Climate warming alters nutrient cycling and its constraint on CO_2 fertilization in Global Forests. Current Climate Change Reports, 11(1): 3, doi: 10.1007/s40641-025-00201-6.

Fan L L, Mekrovar O, Li Y M, et al. 2021. Effect of nutrient addition on the productivity and species richness of grassland along with an elevational gradient in Tajikistan. Frontiers in Plant Science, 12: 765077, doi: 10.3389/fpls.2021.765077.

Fay P A, Carlisle J D, Knapp A K, et al. 2003. Productivity responses to altered rainfall patterns in a C_4-dominated grassland. Oecologia, 137: 245–251.

Fay P A, Prober S M, Harpole W S, et al. 2015. Grassland productivity limited by multiple nutrients. Nature Plants, 1(7): 15080, doi: 10.1038/nplants.2015.80.

Fayiah M, Dong S K, Li Y, et al. 2019. The relationships between plant diversity, plant cover, plant biomass and soil fertility vary with grassland type on Qinghai-Tibetan Plateau. Agriculture, Ecosystems and Environment, 286: 106659, doi: 10.1016/j.agee.2019.106659.

Gao L M, Su J, Chen C, et al. 2021. Increases in forage legume biomass as a response to nitrogen input depend on temperature, soil characters and planting system: a meta-analysis. Grass and Forage Science, 76(2): 309–319.

Geng Y X, Hisoriev H, Wang G Y, et al. 2025. Time-lag of seasonal effects of extreme climate events on grassland productivity across an altitudinal gradient in Tajikistan. Plants, 14(8): 1266, doi: 10.3390/plants14081266.

Guo N, Xie M Y, Fang Z, et al. 2022. Divergent responses of plant biomass and diversity to short-term nitrogen and phosphorus addition in three types of steppe in Inner Mongolia, China. Ecological Processes, 11(1): 32, doi: 10.1186/s13717-022-00376-y.

Han Q F, Luo G P, Li C F, et al. 2016. Simulated grazing effects on carbon emission in Central Asia. Agricultural and Forest Meteorology, 216: 203–214.

Han X, Ochoa-Hueso R, Ding Y, et al. 2023. Grazing intensity by sheep affects spatial diversity in botanical composition of Inner Mongolian grassland. Agriculture, Ecosystems and Environment, 378: 109311, doi: 10.1016/j.agee.2023.109311.

Harpole W S, Sullivan L L, Lind E M, et al. 2016. Addition of multiple limiting resources reduces grassland diversity. Nature, 537(7618): 93–96.

Isbell F, Reich P B, Tilman D, et al. 2013. Nutrient enrichment, biodiversity loss, and consequent declines in ecosystem productivity. Proceedings of the National Academy of Sciences, 110(29): 11911–11916.

Kitikidou K, Milios E, Stampoulidis A, et al. 2024. Using biodiversity indices effectively: considerations for forest management. Ecologies, 5(1): 42–51.

Koerner S E, Smith M D, Burkepile D E, et al. 2018. Change in dominance determines herbivore effects on plant biodiversity. Nature Ecology and Evolution, 2(12): 1925–1932.

Körner C. 2007. Climatic treelines: conventions, global patterns, causes. Erdkunde, 61(4): 316–324.

Kupari S. 2024. Impacts of fertilization on forest ecosystem services and biodiversity. MSc Thesis. Jyväskylä: University of Jyväskylä.

Li W, Cao W X, Wang J L, et al. 2017. Effects of grazing regime on vegetation structure, productivity, soil quality, carbon and nitrogen storage of alpine meadow on the Qinghai-Tibetan Plateau. Ecological Engineering, 98: 123–133.

Liu Y Z, Zhang M L, Zhao Y Y, et al. 2025. Effect of environmental factors on grassland biodiversity and biomass in the Zhangye Region. Agronomy, 15(2): 476, doi: 10.3390/agronomy15020476.

Ma F F, Song B, Quan Q, et al. 2020. Light competition and biodiversity loss cause saturation response of aboveground net primary productivity to nitrogen enrichment. Journal of Geophysical Research: Biogeosciences, 125(3): e2019JG005556, doi: 10.1029/2019JG005556.

Madaminov A A. 2000. Changing structures and productivity of different types of grassland under anthropogenic influence in Tajikistan. EuroMAB-Symposium: Changing Agriculture and Landscape: Ecology, Management and Biodiversity Decline in Anthropogenous Mountain Grassland. Vienna: Austrian Academy of Science.

Madaminov A A, Saidov M, Yusupov S Y. 2012. Influence of climate and anthropogenic factors on pasture productivity in Tajikistan. In: Ecological Problems and Rational Use of Natural Resources. Proceedings of the Republican Scientific Conference. Dushanbe: Tajik National University, 195–199. (in Russian)

Malghani S, Yoo G Y, Giesemann A, et al. 2020. Combined application of organic manure with urea does not alter the dominant biochemical pathway producing N_2O from urea treated soil. Biology and Fertility of Soils, 56: 331–343.

Margalef R. 1958. Information theory in ecology. General Systems, 3: 36–71.

Mekhrovar O, Li Y M, Abdullo M, et al. 2024. Nutrient addition alters plant community productivity but not the species diversity of a mountain meadow in Tajikistan. Frontiers in Plant Science, 14: 1235388, doi: 10.3389/fpls.2023.1235388.

Miao Z G, Chen J, Wang C L, et al. 2025. Global dynamics of grassland FVC and LST and spatial distribution of their correlation (2001–2022). Plants, 14(3): 439, doi: 10.3390/plants14030439.

Midolo G, Alkemade R, Schipper A M, et al. 2019. Impacts of nitrogen addition on plant species richness and abundance: A global meta-analysis. Global Ecology and Biogeography, 28(3): 398–413.

Muminjanov H. 2008. State of plant genetic resources for food and agriculture (PGRFA) in the Republic of Tajikistan. Country Report, 55. [2025-02-10]. http://www.fao.org/pgrfa-gpa-archive/tjk/Tajikistan2.pdf. (in Russian)

Niu D C, Yuan X B, Cease A J, et al. 2018. The impact of nitrogen enrichment on grassland ecosystem stability depends on nitrogen addition level. Science of The Total Environment, 618: 1529–1538.

Olde Venterink H. 2011. Does phosphorus limitation promote species-rich plant communities? Plant and Soil, 345: 1–9.

Ovchinnikov P N, Sidorenko G T. 1977. Pastures and Hayfields of Tajikistan. Dushanbe: Donish. (in Russian)

Palpurina S, Chytrý M, Hölzel N, et al. 2018. The type of nutrient limitation affects the plant species richness-productivity relationship: Evidence from dry grasslands across Eurasia. Journal of Ecology, 106(2): 692–703.

Safarov N. 2003. National strategy and action plan on preservation and rational use of Biodiversity. National Center for Biodiversity and Biosafety of the Republic of Tajikistan. Dushanbe, Tajikistan. (in Russian)

Seabloom E W, Borer E T, Buckley Y M, et al. 2015. Plant species' origin predicts dominance and response to nutrient enrichment and herbivores in global grasslands. Nature Communications, 6: 7710, doi: 10.1038/ncomms8710.

Seabloom E W, Adler P B, Alberti J, et al. 2021. Increasing effects of chronic nutrient enrichment on plant diversity loss and ecosystem productivity over time. Ecology, 102(2): e03218, doi: 10.1002/ecy.3218.

Simpson E H. 1949. Measurement of diversity. Nature, 163(4148): 688, doi: 10.1038/163688a0.

Sinkovsky L P, Madaminov A A. 1989. The Pastures of Low-grass Semi-savannahs of Central Asia (The Biological and Ecological Bases of Their Use and Improvement). Dushanbe: Donish. (in Russian)

Smith B, Wilson J B. 1996. A consumer's guide to evenness indices. Oikos, 76(1): 70–82.

Spohn M, Bagchi S, Bakker J D, et al. 2025. Interactive and unimodal relationships between plant biomass, abiotic factors, and plant diversity in global grasslands. Communications Biology, 8(1): 97, doi: 10.1038/s42003-025-07518-w.

Stevens C J, Dise N B, Gowing D J, et al. 2006. Loss of forb diversity in relation to nitrogen deposition in the UK: regional trends and potential controls. Global Change Biology, 12(10): 1823–1833.

Tang Z S, Deng L, An H, et al. 2017. The effect of nitrogen addition on community structure and productivity in grasslands: a meta-analysis. Ecological Engineering, 99: 31–38.

Tilman D, Knops J, Wedin D, et al. 1997. The influence of functional diversity and composition on ecosystem processes. Science, 277(5330): 1300–1302.

Van Oijen M, Bellocchi G, Höglind M. 2018. Effects of climate change on grassland biodiversity and productivity: The need for a diversity of models. Agronomy, 8(2): 14, doi: 10.3390/agronomy8020014.

Wang X Y, Zhu J, Pan P P. 2024. Spatiotemporal dynamics of grassland aboveground biomass in northern China and the alpine region: Impacts of climate change and human activities. PLoS ONE, 19(12): e0315329, doi: 10.1371/journal.pone.0315329.

Wankmüller F J P, Delval L, Lehmann P, et al. 2024. Global influence of soil texture on ecosystem water limitation. Nature, 635: 631–638.

Wilcots M E, Schroeder K M, Henning J A, et al. 2025. Alleviation of nutrient co-limitation increases grassland biomass production, but not carbon storage. Ecosystems, 28(1): 11, doi: 10.1007/s10021-024-00956-3.

Xu Z W, Wan S Q, Ren H Y, et al. 2012. Effects of water and nitrogen addition on species turnover in temperate grasslands in northern China. PLoS ONE, 7(6): e39762, doi: 10.1371/journal.pone.0039762.

Yao Z Y, Xin Y, Yang L, et al. 2022. Precipitation and temperature regulate species diversity, plant coverage and aboveground biomass through opposing mechanisms in large-scale grasslands. Frontiers in Plant Science, 13: 999636, doi: 10.3389/fpls.2022.999636.

Ye R H, Yu W Y, Yang D, et al. 2023. Effects of precipitation and grazing on the diversity and productivity of desert steppe. Land Degradation and Development, 34(9): 2622–2635.

Zhang F W, Du W, Song C G, et al. 2025a. Long-term multi-nutrient enrichment enhances aboveground biomass without compromising ecosystem temporal stability in a Tibetan alpine meadow. Agriculture, Ecosystems and Environment, 394: 109917, doi: 10.1016/j.agee.2025.109917.

Zhang L J, Du H, Yang Z Q, et al. 2022. Topography and soil properties determine biomass and productivity indirectly via community structural and species diversity in Karst Forest, Southwest China. Sustainability, 14(13): 7644, doi: 10.3390/su14137644.

Zhang P F, Seabloom E W, Foo J, et al. 2025b. Dominant species predict plant richness and biomass in global grasslands. Nature Ecology and Evolution, 9: 924–936.

Zhao Y N, Yang B, Li M X, et al. 2019. Community composition, structure and productivity in response to nitrogen and phosphorus additions in a temperate meadow. Science of The Total Environment, 654: 863–871.

Appendix

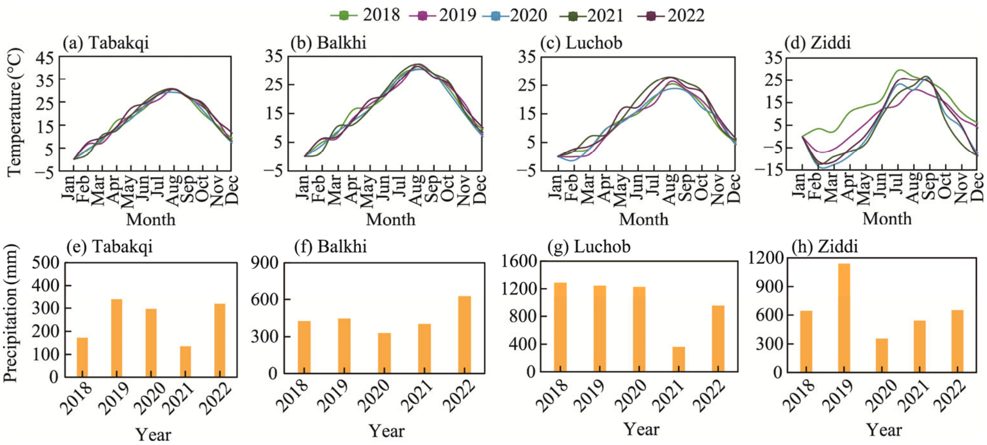

Fig. S1 Monthly temperature and annual precipitation at Tabakqi (a and e), Balkhi (b and f), Luchob (c and g), and Ziddi (d and h) sites during 2018–2022

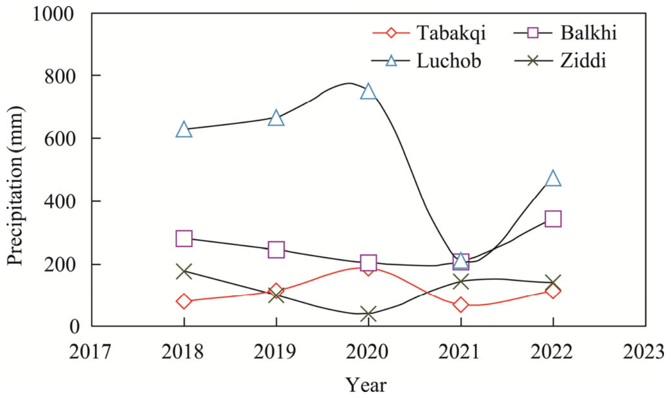

Fig. S2 Growing season precipitation at Tabakqi (February–April), Balkhi (February–May), Luchob (March–June), and Ziddi (May–August) sites from 2018 to 2022

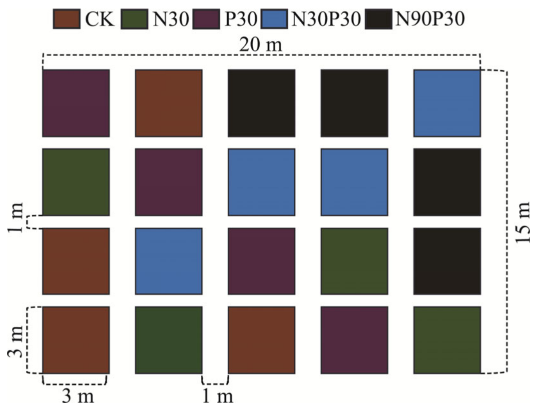

Fig. S3 Experimental design in this study. CK indicates the control (without nitrogen (N) and phosphorus (P) addition); N30 indicates adding 30 kg N/(hm^2•a), P30 indicates adding 30 kg P/(hm^2•a), N30P30 indicates adding 30 kg N/(hm^2•a) and 30 kg P/(hm^2•a), and N90P30 indicates adding 90 kg N/(hm^2•a) and 30 kg P/(hm^2•a).

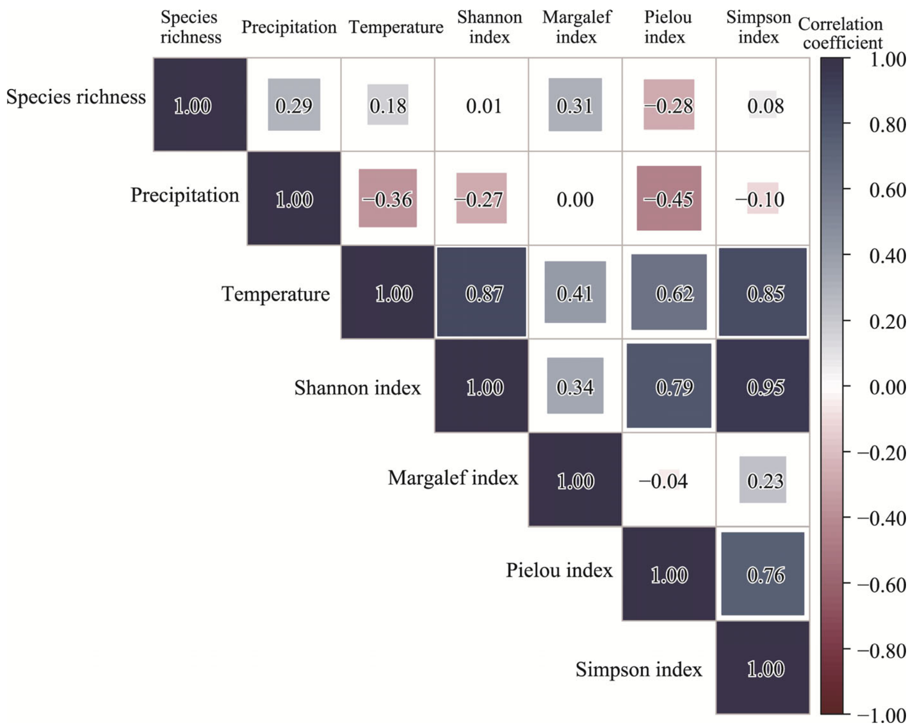

Fig. S4 Pearson correlation matrix of aboveground biomass (AGB) with species diversity indices and climatic factors across four grassland sites. Larger and darker squares represent larger absolute correlation coefficients. Shannon index, Shannon-Wiener index; Simpson index, Simpson's dominance index; Margalef index, Margalef's richness index; Pielou index, Pielou's equitability index.

Table S1 Summary of the linear mixed-effect model relating fixed factors (year and treatment) for the species diversity indices at the four grassland sites during 2018–2022

Site	Source	Simpson index		Shannon index		Margalef index		Pielou index	
		f	*P*	*f*	*P*	*f*	*P*	*f*	*P*
Tabakqi	Year	68.58	0.000	23.56	0.000	27.17	0.000	48.01	0.000
	Treatment	20.48	0.000	9.77	0.000	0.49	0.746	23.92	0.000
	Year×Treatment	4.31	0.000	4.64	0.000	2.24	0.010	4.24	0.000
Balkhi	Year	25.82	0.000	7.04	0.000	6.39	0.000	14.42	0.000
	Treatment	38.69	0.000	30.49	0.000	7.33	0.000	45.04	0.000
	Year×Treatment	7.53	0.000	4.21	0.000	4.89	0.000	5.00	0.000
Luchob	Year	20.03	0.000	8.69	0.000	8.88	0.000	24.78	0.000
	Treatment	83.57	0.000	24.59	0.000	3.09	0.021	66.55	0.000
	Year×Treatment	6.40	0.000	6.64	0.000	7.96	0.000	2.33	0.008
Ziddi	Year	18.68	0.000	18.00	0.000	96.79	0.000	15.18	0.000
	Treatment	1.11	0.359	0.66	0.623	0.72	0.583	0.66	0.619
	Year×Treatment	1.27	0.242	1.27	0.239	0.92	0.554	1.20	0.292

Note: Shannon index, Shannon-Wiener index; Simpson index, Simpson's dominance index; Margalef index, Margalef's richness index; Pielou index, Pielou's equitability index.