Research Topics

Vegetation-based degradation and restoration on the alpine grasslands of the Tibetan plateau

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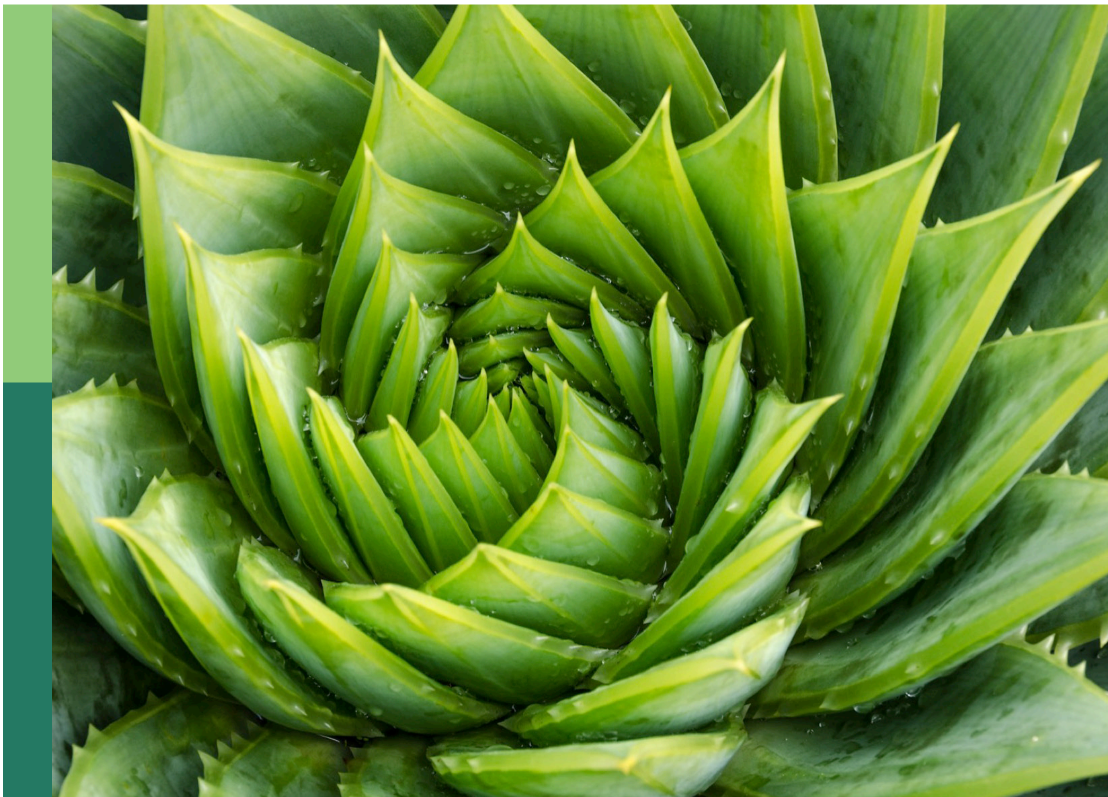

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Vegetation-based degradation and restoration on the alpine grasslands of the Tibetan plateau

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Editorial: Vegetation-based degradation and restoration on the alpine grasslands of the Tibetan plateau

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vegetation classification, disturbance, land degradation, climate change, plant-soil interactions

Editorial on the Research Topic
Vegetation-based degradation and restoration on the alpine grasslands of the Tibetan plateau

The Tibetan Plateau is the world's highest and largest plateau, often referred to as 'the roof of the world' due to its high elevation and extensive mountain systems, which host hotspots of endemic biodiversity. It is also known as the "third pole" because of its cold environment, and the "Asian water tower" owing to its rich river systems. This unique physical and geographical environment supports a variety of alpine ecosystems, predominantly classified as alpine grasslands (Figure 1). These grasslands cover approximately 50-70% of the Tibetan plateau's total land area (Wu et al., 2021; Zhang et al., 2022). Such a range in estimates arises from varying definitions of grassland according to different authorities and scientists, particularly concerning the inclusion of cropland, desert, or shrublands. Most of these rangelands feature a fragile, tundra-like environment that is difficult to restore once degraded (Niu et al., 2019) due to the slow soil formation processes, low nutrient availability, limited seed recruitment, and the short growing season (Li et al., 2023; Niu et al., 2023a). The main natural grassland types on the Tibetan plateau include alpine deserts, alpine steppes, alpine meadows, alpine swamps, and the transitional types between them varying along the precipitation gradient. The alpine grasslands continue to experience severe degradation due to multiple factors (Liu et al., 2018; Niu et al., 2023b), primarily anthropogenic disturbances (e.g. overgrazing, road construction), as well as natural environmental changes (e.g. climate change, rodent outbreak). As a result, its degradation presents a major global environmental threat given the importance of Tibetan grasslands to biodiversity, ecosystem complexity, and provision of ecosystem services. This Research Topic tried to explore the current state of vegetation-based alpine grassland degradation, the causes of this degradation and possible solutions to restore and re-establish the local plant communities.

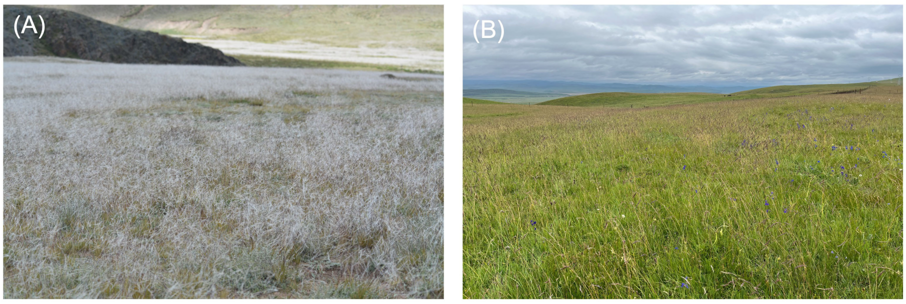

FIGURE 1
Two main undegraded grassland types of alpine steppe dominated by *Stipa* spp. **(A)** and alpine meadow dominated by tall grasses with *Kobresia* spp. underneath **(B)** on the Tibetan plateau. Alpine grasslands offer numerous material and non-material benefits to humans. These include a variety of ecosystem services such as water supply and regulation, air quality improvement, carbon sequestration, erosion control, and various cultural services, among others. Photos by YN.

Current state and the causes of Tibetan grassland degradation

Grassland degradation is widespread in many low- to middle-income countries and regions, threatening the livelihoods of hundreds of millions of people, as well as the wildlife and livestock they rely on. One notable hotspot of severe vegetation and soil degradation (Hua et al., 2023) is the Tibetan plateau (Bardgett et al., 2021), the largest grassland area on the Eurasian continent. This region includes the Three-River Headwater area, which supplies water to over a billion people. The causes of Tibetan grassland degradation, whether due to anthropogenic disturbances or climate change (Wu et al., 2021), are still under debate, hindering our understanding of the current drivers and the attribution of degradation. For example, Qiqige et al. demonstrated how climate, not grazing, affects soil microbial diversity through changes in vegetation and abiotic factors across the Eurasian steppe. Over the past four decades, the large increase in livestock numbers has been considered by many scientists to be the major cause of alpine grassland degradation on the Tibetan plateau, which has led to massive degradation and soil erosion of the alpine ecosystems (Niu et al., 2019), regardless of the livestock species, grazing regime, or grassland type. Stocking rates on these alpine grasslands have significantly increased in recent years, with overstocking rates in the range of 27–529% in various regions (Niu et al., 2019). The plateau's annual temperature rose by 0.34–0.44°C per decade, nearly twice the global average increase of 0.19°C per decade (Meng et al., 2023). Coupled with this significant regional warming, the Tibetan grasslands have faced greater impacts. Additionally, other natural and anthropogenic disturbances including road construction such as the Qinghai-Tibet Highway (Tan et al.), mining (Yang et al.), earthquakes (Zuo et al.), and rodent outbreak (Xu et al.) have also significant effects on plant species distribution, diversity and community structure on the grasslands. So far, we do not have a complete and reliable picture of Tibetan grassland degradation. Xu et al. employed the TSMK-FVC method using Landsat imagery to assess the effects of terrain and climate on vegetation, facilitating large-scale degradation investigations. The estimates of degradation vary for the Tibetan grasslands. The most frequently quoted value is between 30-50% of grasslands on the Tibetan plateau are degraded (Liu et al., 2018; Miehe et al., 2019) with impaired ability to conserve biodiversity and deliver ecosystem services including primary production and key functions such as regulation of hydrology, soil carbon storage and efficient nutrient cycling. For examples, Wu et al. found the significant changes in plant community dynamics and dominant species along the alpine wetland degradation of Qinghai Lake.

Restoring Tibetan grasslands

Halting and reversing Tibetan grassland degradation is a major challenge in meeting the targets of the UN Decade on Ecosystem Restoration and the 30 by 30 restoration goals of the Kunming-Montreal Global Biodiversity Framework. The restoration must lie first by designing research projects that diagnose the ecological problem and degree of degradation and the key turning points (Li et al.) for different ecosystems, then link the identified problem to the underlying processes or critical components that have been affected (Palmer and Stewart, 2020), finally focus on what can be done to improve restoration outcomes. Wang et al. evaluated the effects of various current restoration measures on short-term grassland restoration. Chen et al. found that improved grazing management can restore *Chnatherum inebrians*-type degraded grassland. Central to scientific advances is the recognition that restoration efforts must focus on re-establishing ecological processes and the strong interactions among different trophic levels. Li et al. also shown the key role of microbes in restoring alpine desertified grasslands. However, Tibetan restoration efforts are at risk of failing without fundamental knowledge about the reproductive capacity of plant species during degradation, especially the clonal propagation in this cold region. Li et al. shown the correlation between bud diversity and community composition in different degraded alpine grasslands. Furthermore, the restoration process should not focus solely on improving a single function, such as production (Wang et al.), but on enhancing multifunctionality, including biodiversity. Shu et al. demonstrated that mixed and diverse shrub-grass planting enhances both biodiversity and ecosystem stability.

Facing the strong need for promoting ecosystem restoration that sustainably achieves socio-economic-natural benefits on Tibetan plateau, scientific research plays a vital role in developing and refining dynamic restoration strategies that are efficient, cost-effective, suitable for such sensitive ecosystems, ensuring the long-term sustainability and resilience of restored areas. Importantly, nature conservation and preventing Tibetan grassland degradation should have priority over restoration.

Author contributions

YN: Conceptualization, Investigation, Methodology, Supervision, Validation, Writing – original draft, Writing – review & editing. YB: Conceptualization, Funding acquisition, Investigation, Methodology, Validation, Writing – review & editing. SR: Conceptualization, Investigation, Methodology, Validation, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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More management is needed to improve the effectiveness of artificial grassland in vegetation and soil restoration on the three-river headwaters region of China

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Establishing an artificial grassland is a common measure employed to restore heavily degraded alpine grasslands for regional sustainability. The Three-River Headwaters Region in China has significant areas of black-soil-type grassland which is typified by heavy degradation; nearly 35% of the grassland regions in the Three-River Headwaters Region has degraded into this type. There are different plant community types of black-soil-type grasslands, however, it is not clear which restoration measures should be adopted for different kinds of black-soil-type grasslands. Here, we investigate the plant community characteristics and soil physicochemical properties of artificial grasslands, two types of black-soil-type grasslands, and native undegraded grassland in the Three-River Headwaters Region, then analyzed the direct and indirect interactions between the plant and soil properties by partial least squares path models (PLS-PM). Our results revealed that establishing artificial grassland significantly increased aboveground biomass and plant community coverage, and also decreased plant species richness and diversity and soil water content, soil organic carbon and total nitrogen in the 0-10 cm soil layer as compared with black-soil-type grasslands. Plant community diversity had a positive effect on plant community productivity, soil nutrient, and soil water content in native undegraded grassland. These results suggest that more management interventions are needed after establishing an artificial grassland, such as reducing dominant species in two types of black-soil-type grasslands, water regulation in the *A. frigida*-dominated meadow, diversifying plant species (i.e., Gramineae and sedges), and fertilizer addition.

KEYWORDS

degraded alpine grassland, artificial grassland, plant-soil interaction, restoration management, partial least squares path models

1 Introduction

The Three-River Headwaters Region is located in the hinterland of the Qinghai-Tibetan Plateau, which is the source region of the Yangtze River, the Yellow River, and the Lancang (Mekong) River, known as "Asia's water tower" (Mao et al., 2016). It is important for the ecological security of China and the countries surrounding the Qinghai-Tibetan Plateau (Shao et al., 2017). The alpine grassland biome is the main ecosystem of this area, which provides important ecosystem functions and services, such as climatic regulation (Liu et al., 2018; Dai et al., 2021), biodiversity conservation (Dong et al., 2020), soil erosion prevention (Wang et al., 2016) and habitat for both grazing livestock and wildlife (Liu et al., 2017; Lu et al., 2017; Liu et al., 2021), as well as the carbon sequestration (Feng et al., 2010; Chen X. et al., 2021). However, the Three-River Headwaters Region has experienced grassland degradation because of its fragile ecosystem, climate, and human influence (Guo et al., 2019; Wu et al., 2021). Nearly 35% of the grassland area has been heavily degraded into black-soil-type grassland, which is typified by bare land with no plants in the cold season and covered with forbs or poisonous plants in the warm season (Ma et al., 2002; Shang and Long, 2007; Dong et al., 2018). This has reduced plant coverage, species biodiversity, soil nutrient availability (Wen et al., 2013; Peng et al., 2018), and regional ecosystem stability (Dong et al., 2020; Yang and Sun, 2021). Furthermore, grassland degradation has an increasingly negative impact on regional security and social sustainability (Harris, 2010).

The restoration of the black-soil-type grassland is of vital importance and has received considerable study e.g., Wu et al., 2010; Dong et al., 2013; Wen et al., 2018). Approaches such as fencing enclosures (Chen X. et al., 2021; Du and Gao, 2021), application of fertilizers (Luo et al., 2017), or seeding (Shang et al., 2008) were conducted to restore degraded grasslands. However, none of these measures had significant positive effects on black-soil-type grasslands, which indicated that favorable natural restoration approaches were difficult for its rehabilitation (Shang and Long, 2007). One recent attempt to overcome this issue employed establishing Elymus nutans artificial grassland in black-soil-type grasslands (Feng et al., 2010; Wen et al., 2018). Some researches revealed that artificial grassland could be used as an effective restoration approach to improve productivity and regulate community and soil properties in black-soil-type degraded grasslands (Wu et al., 2010; Gao et al., 2019).

Many studies have analyzed the restoration effect of artificial grasslands by examining the effects on soil nutrients or vegetation characteristics at distinct intervals after the recovery work [e.g., 4-year, 6-year or 9-year (Wu et al., 2010; Gao et al., 2019)], and those results suggested an artificial grassland in black-soil-type grasslands requires a long-term for recovery (~ 16-18 years). However, there are different types of plant communities in black-soil-type grassland (Dong et al., 2010), but few studies have focused on the effect of rebuilding artificial grasslands as compared with different kinds of black-soil-type grasslands or healthy grasslands. It's yet unclear whether the targeted restoration measures should be adopted in different kinds of black-soil-type grasslands. Furthermore, many studies have reported correlations between soil properties, such as soil moisture or nutrients, with alpine grassland properties, such as grassland aboveground biomass or biodiversity (Li et al., 2014; Fayiah et al., 2019; Faucon, 2020; Li et al., 2020; Xiao et al., 2022). Yet, little is known about the direct and indirect interaction between plant community characteristics and soil physicochemical properties, which is required for efficient and sustainable restoration practice in a degraded grassland ecosystem (e.g., ameliorate soil properties favoring autochthonous species) (Shen et al., 2015; Maiti and Ghosh, 2020; Peng et al., 2020).

Here, we investigate plant community characteristics and soil physicochemical properties in artificial *Elymus nutans* grasslands, two types of black-soil-type grasslands, and healthy *Kobresia* grassland. Our objectives are: (i) examine the differences in soil characteristics and plant communities among these grassland types, (ii) understand which targeted restoration measures (if any) should be adopted for different types of black-soil-type grasslands. The results of this study may help guide future grassland restoration programs in the Three-River Headwaters Region or other regions that face similar issues.

2 Materials and methods

2.1 Study sites

The study area (31°45′N-39°19′N, 89°27′E-103°04′E) is located in the source region of the Yangtze River, the Yellow River, and the Lancang (Mekong) River (Figure 1). The altitude ranges from 2610 to 6950 m, with an average elevation of 4500m and many high mountains peaks. The site has a typical plateau continental climate with annual mean temperature ranges from -5.38 to 4.14°C, annual precipitation ranges from 262.2 to 772.8mm and annual evaporation rate ranges from 730 to1700 mm (Yi et al., 2012; Cao and Pan, 2014). The typical vegetation of the region are alpine meadows dominated by sedges and Gramineae, such as *Kobresia pygmaea*, *Kobresia capillifolia* and *Poa annua*. The soil is defined as alpine meadow in the Chinese Soil Classification System (Shi et al., 2006).

2.2 Field sampling design

Field sampling was conducted from July through August in 2019 and 2020 at the peak of the growing season to minimize differences due to the time of year. The sites were chosen to represent true replications of *K.pygmea*-dominated meadows (KM), *P.anserina*-dominated meadows (PM), *E.nutans*-dominated grasslands (EG), and *A.frigida*-dominated meadows (AM). KM represents healthy grassland, PM and AM are two kinds of black-soil-type grasslands, and EG is the artificial grassland (Table 1). We established six sites for each kind of grassland. At each site, a 10m×10m plot was randomly chosen. Within each plot, three 0.5m×0.5m quadrats were placed to survey vegetation and soil. In total, 72 quadrats (24 sites × 3 quadrats) were sampled, and the geographical coordinates were also recorded for each plot. Black-soil-type grasslands tend to

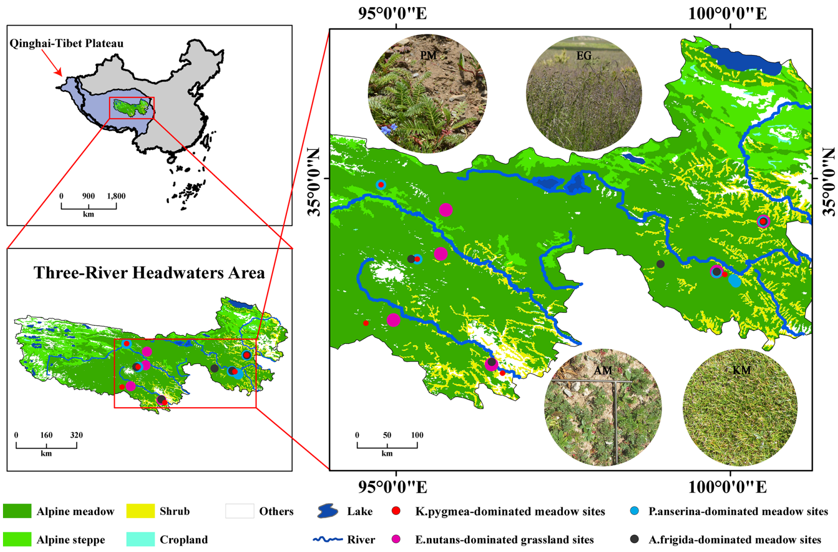

FIGURE 1
The distribution of vegetation types and sampling sites on the Three-River Headwaters Region. The vegetation map is based on a 1:1,000,000 scale vegetation distribution map of China (http://westdc.westgis.ac.cn). EG, *E.nutans*-dominated grassland; PM, *P.anserina*-dominated meadow; AM, *A.frigida*-dominated meadow; KM, *K.pygmea*-dominated meadow. Some sampling points are located relatively close to each other, resulting in overlapping symbols on the map.

occur near artificial grasslands, therefore, sometimes these sampling sites would be set up in the same area.

2.3 Plant community survey

We investigated plant community characteristics, including species identity, height, coverage, abundance and aboveground biomass of each species in each quadrat. Plant coverage was represented by the ratio of the shady area of a specific species to the total area of a quadrat. The plant species were clipped and then put into an envelope for each quadrat. We determined the aboveground biomass for every quadrat by weighing the plants after drying at 65°C to a constant weight. We calculated the Gleason index (G), Shannon-Wiener index (H′), Simpson index (D) and Pielou index (J) to characterize the richness, diversity and evenness of plant community:

$$Pi=(RC+RA+RH)/3 \tag{1}$$

$$G=S/InA \tag{2}$$

$$H'=-\sum PiInPi \tag{3}$$

$$D=1-\sum Pi^2 \tag{4}$$

$$J=H'/InS \tag{5}$$

where Pi is the important value of the species in the plant community site, RC is the relative coverage, RA is the relative abundance, and RH is the relative height. S is the sum of the species in the site and A is the area of the site.

2.4 Soil physicochemical properties’ measurement

We collected topsoil (0-5 cm) and subsoil (5-10 cm) samples from the plot after the plant community survey. Oven-drying was

TABLE 1 Characteristics of sampling sites in the Three-River Headwaters Region.

	Grassland type	Abbreviation	Altitude(m)	Main plant species
Healthy grassland	*K.pygmea*-dominated meadow	KM	4318	*Kobresia pygmaea, Poa annua, Carex alatauensis, Carex myosuroides*
Black-soil-type grasslands	*P.anserina*-dominated meadow	PM	4208	*Potentilla anserina, Knorringia sibirica, Lagotis brachystachya, Microula sikkimensis*
	A.frigida-dominated meadow	AM	4118	*Artemisia frigida, Ajuga lupulina, Elsholtzia densa*
Artificial grassland	*E.nutans*-dominated grassland	EG	4130	*Elymus nutans, Poa annua*

used to measure soil bulk density (BD) and soil water content (SW) through drying the soil sample of the steel cutting rings. Soil pH and electrical conductivity (EC) were measured from a soil water ratio of 1:2.5 with a pH meter and conductivity meter. Soil organic carbon (SOC) was determined using the dichromate oxidation method. Total nitrogen (TN) was analyzed by the Kjeldahl method. Total potassium (TK) and total phosphorus (TP) were measured by flame photometer and molybdenum antimony resistance colorimetry after wet digestion with H_2SO_4 and $HCLO_4$. The soil particle size composition was measured by the laser scattering particle size distribution analyzer, and we classified soil as clay, silt and sand by international particle size standards.

2.5 Analysis of the plant-soil interaction

The Shapiro-Wilk normality test and Bartlett's test of homogeneity were performed to check for normality and equal variance among groups. The plant community characteristics of four groups were non-normal data and all showed variance heterogeneity. Thus, we compared the vegetation parameters between four groups with the Mann-Whitney U test by using the wilcox.test function in R. Spearman correlation coefficients were used to characterize the relationship between the soil properties and the plant community. To screen the important soil properties that influenced the plant community, we performed the random forest model with R-package "linkET".

We constructed a partial least squares path models (PLS-PM) that provide a comprehensive view of a system by modeling multiple relationships between its components to better integrate the interaction among plant community characteristics and soil physicochemical properties. In the PLS-PM framework, a latent variable is viewed as a concept and is linked to a set of measurements. Our latent variables included soil physical properties, soil nutrient content, plant characteristics, and plant diversity. We identified these latent variables by choosing the important soil properties based on the results of the random forest model, for example, soil nutrients including SOC and TN. PLS-PM was performed using the "plspm" R-package. All statistical analyses were conducted using R version 4.1.2 unless noted otherwise.

3 Results

3.1 Vegetation parameters in different plant community grasslands

The four kinds of plant community grasslands showed different plant community characteristics (Figure 2). The coverage and Gleason index were significantly higher in KM as compared with

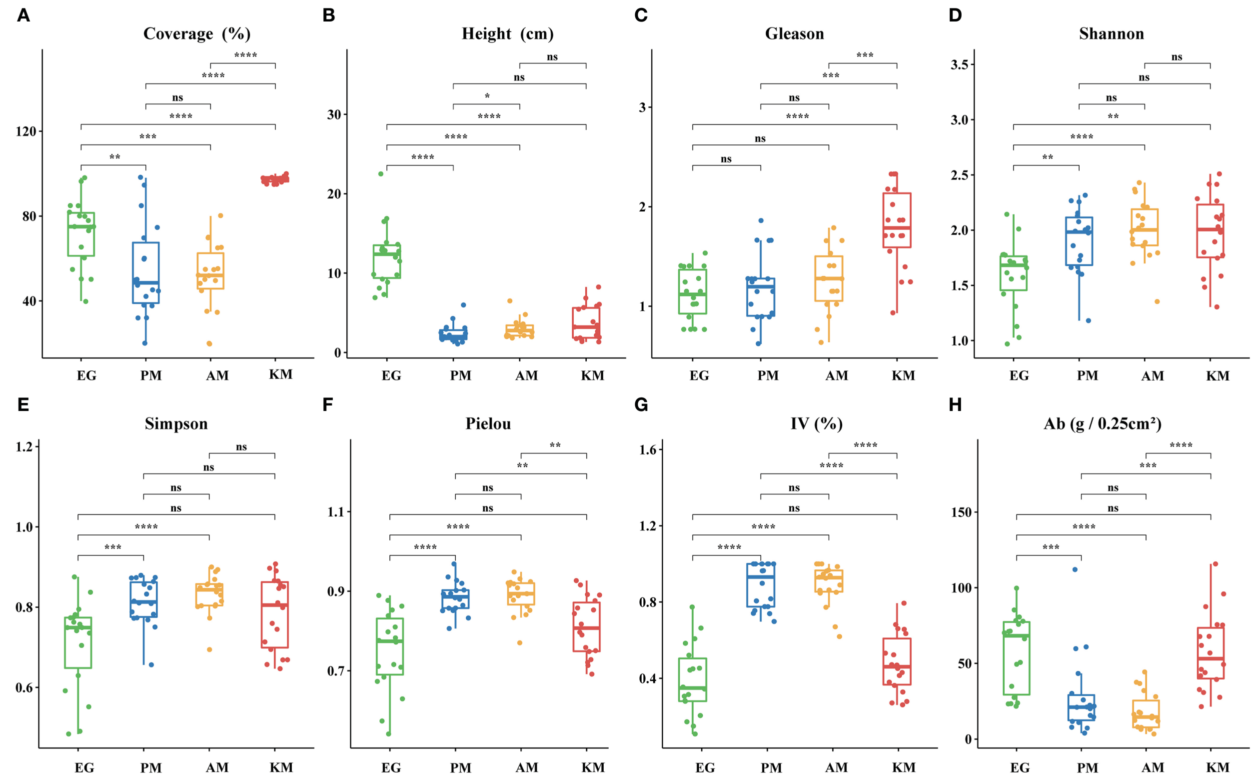

FIGURE 2
Boxplot of vegetation parameters. **(A)** Coverage of plant community; **(B)** Height of plant community; **(C)** Gleason index; **(D)** Shannon-Wiener index; **(E)** Simpson index; **(F)** Pielou index; **(G)** Important value of forbs; **(H)** Aboveground biomass. Significant *P* values were shown in boxplot. * means adjusted *P* values ≤ 0.05, ** means adjusted *P* values ≤ 0.01, *** means adjusted *P* values ≤ 0.001 and **** means *P* ≤ 0.0001, if not indicated, means adjusted *P* values > 0.05. EG, *E.nutans*-dominated grassland; PM, *P.anserina*-dominated meadow; AM, *A.frigida*-dominated meadow; KM, *K.pygmea*-dominated meadow.

the other three kinds of plant community grasslands ($P \le 0.001$, Figures 2A, C), while PM and AM exhibited no significant differences (Figures 2A, C). The average height of EG was the highest ($P \le 0.0001$, Figure 2B), but there were no significant differences in the other three groups. The important value of forbs and Pielou evenness index in PM and AM were higher than that in EG and KM ($P \le 0.0001$, Figure 2G). Conversely, the aboveground biomass of EG and KM was significantly greater than PM and AM (Figure 2H). The plant diversity index (Shannon-Wiener and Simpson) was similar among PM, AM, and KM, and the lowest diversity index was recorded in EG (Figures 2D, E). In addition, the Pielou index of PM and AM was significantly higher than KM and EG ($P \le 0.01$, Figure 2F).

3.2 Soil physicochemical properties in different plant community grasslands

The soil water content, soil organic carbon and total nitrogen of EG and AM was less on average compared with the other two kinds of grasslands, especially the surface layer soil (0-5cm) of KM (Figures 3A, H, I). Correspondingly, KM had the lowest soil bulk

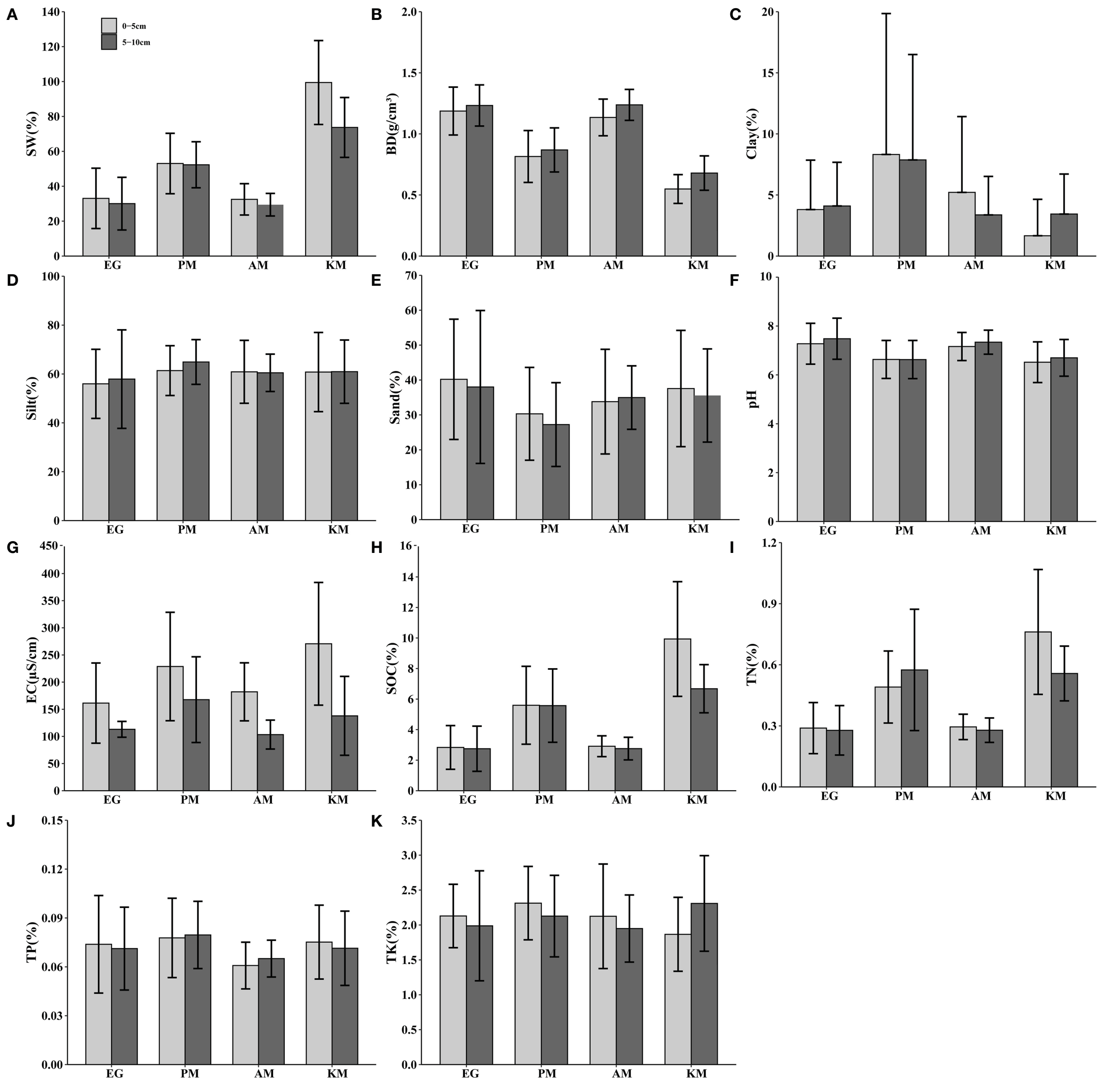

FIGURE 3
Soil physicochemical properties of plant communities in different alpine grasslands. Error bars indicate standard error. **(A)** SW(%), soil water content; **(B)** BD(g/cm^3), bulk density; **(C)** Clay(%), clay percentage; **(D)** Silt(%), silt percentage; **(E)** Sand(%),sand percentage; **(F)** pH, Potential of Hydrogen; **(G)** EC (μS/cm), Electrical Conductivity; **(H)** SOC(%), Soil Organic Carbon; **(I)** TN(%), Total Nitrogen; **(J)** TP(%), Total Phosphorous; **(K)** TK(%), Total Potassium; EG, *E.nutans*-dominated grassland; PM, *P.anserina*-dominated meadow; AM, *A.frigida*-dominated meadow; KM, *K.pygmea*-dominated meadow.

density (0.55g/cm^3 in 0-5cm soil layer, 0.68g/cm^3 in 5-10cm soil layer), and PM followed (Figure 3B). In addition, silt content in four kinds of alpine grassland was the highest, followed by sand and clay content (Figures 3C–E). The differences in silt content among these alpine grasslands were marginal, but the clay content in PM was significantly higher than the other three kinds of grasslands (Figures 3C, D). Soil pH in EG (7.28 in 0-5cm soil layer, 7.48 in 5-10cm soil layer) and AM (7.16 in 0-5cm soil layer, 7.33 in 5-10cm soil layer) was higher than in KM and PM, whereas the electrical conductivity in EG and AM was lower than KM and PM (Figures 3F, G). The electrical conductivity of the 0-5cm soil layers was higher than the 5-10cm soil layers among all kinds of grassland (Figure 3G). Total phosphorous was lowest in AM but showed no differences in the other three kinds of grassland (Figure 3J). Furthermore, total potassium of the 0-5cm soil layers in KM (0.075%) was significantly higher than the 5-10cm soil layers, but it was opposed to the other three kinds of grassland (Figure 3K).

3.3 Plant-soil interaction

The important value of forbs was positively correlated with SOC, TN, and TP in the 0-5cm and 5-10cm soil layers but was negatively correlated with pH, TK, and sand percentage in the 0-5cm and 5-10cm soil layers in KM. This was more pronounced in the surface soil layer of 0-5 cm (Figure 4D), but was only positively correlated with EC in the 5-10cm soil layer of EG (Figure 4A). Aboveground biomass was negatively correlated with TN, SOC, TP, and SW in the 0-10cm soil layer and positively correlated with pH, and BD in the 0-10cm soil layer of EG (Figure 4A); No soil physicochemical properties were significantly correlated with the aboveground biomass of PM (Figure 4B). In addition, BD of the 0-5cm soil layer was negatively correlated with the coverage, richness, and diversity of plant community but was positively correlated with important value of forbs, aboveground biomass, and the Pielou index for AM (Figure 4C). Furthermore, the relationship between

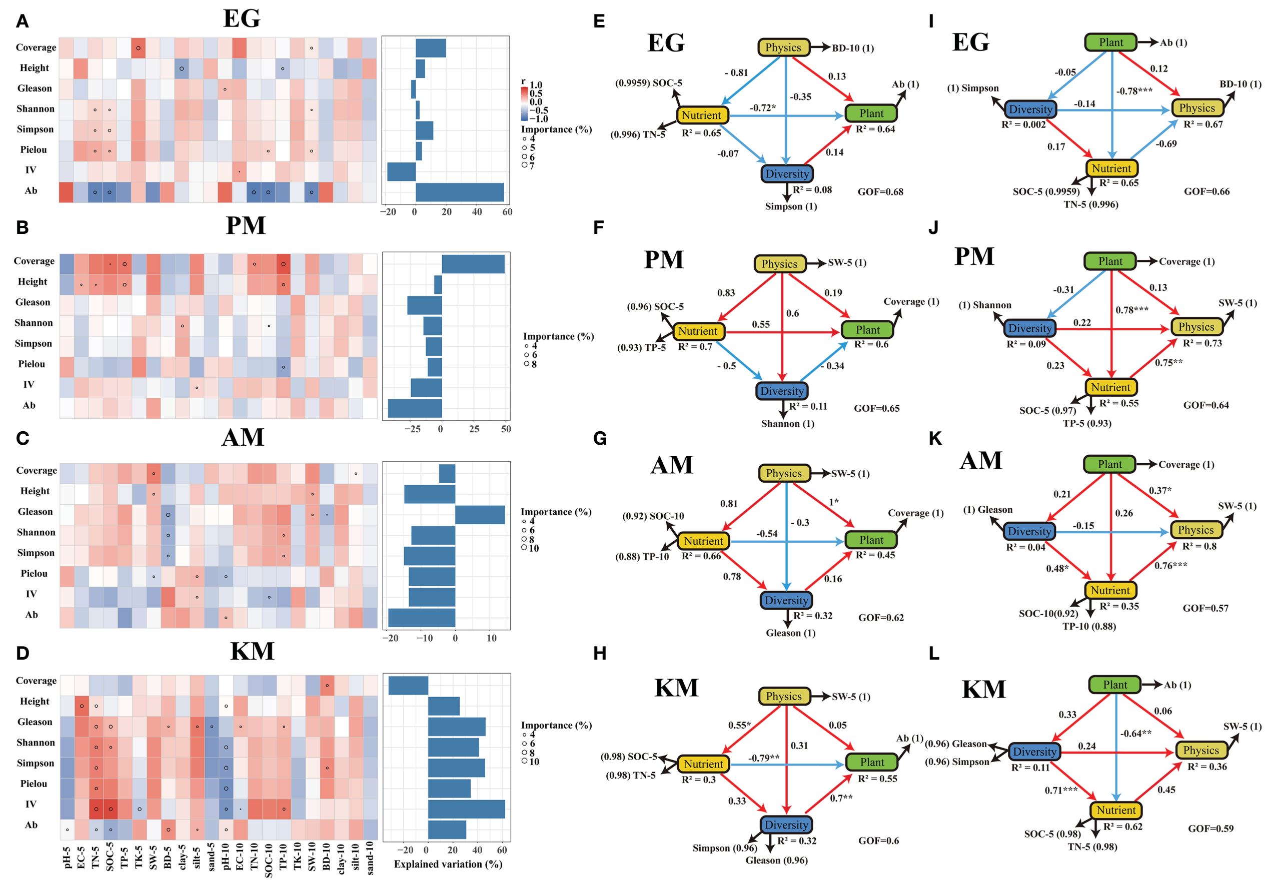

FIGURE 4
The correlations and interactions between plant communities and soil physicochemical properties. **(A–D)** Contributions of soil properties to the vegetation parameters based on correlation and a random forest model. The circle size represents the importance of the variables (percentage of increase of mean square error calculated via random forest model). Colors represent Spearman correlations. Diagrams **(E–L)** of partial least squares path models (PLS-PM) describing the interactions among the soil physicochemical properties and plant community characteristics. Each box represents a latent variable, the manifest variables are the indexes beside the latent variables, and the value in the brackets represent the loading values. Arrows connecting latent variables indicate inner model paths, with blue and red indicating negative and positive effects, respectively. R^2 denotes the proportion of variance explained. * means adjusted P values $\leq$ 0.05, ** means adjusted P values 175 $\leq$ 0.01, *** means adjusted P values $\leq$ 0.001.

plant community characteristics and physicochemical properties was tighter in KM than the other three kinds of grassland, especially plant diversity and soil nutrient availability.

PLS-PM seems to explained a majority of the soil nutrient variability in EG and KM (R^2 = 0.65 and 0.62 resp., Figures 4E, L) and the physical properties (SW at 0-5cm soil layer) were well explained in PM and AM (R-square =0.73 and 0.8 resp., Figures 4J, K). There was a significant direct negative interaction between soil nutrients and aboveground biomass of plant communities in EG and KM (Figures 4E, H, I, L), meanwhile, the effect of plant diversity on plant community aboveground biomass was significantly positive (path coefficient = 0.7, *P* values ≤ 0.01, Figure 4H) in KM but had only a marginal positive effect (path coefficient = 0.14, Figure 4E) in EG. In addition, the effect of plant community coverage on soil nutrient availability were both positive in PM and AM (path coefficient = 0.78 and 0.26 resp., Figures 4J, K), and the effect of soil nutrients on plant community coverage was negative in AM (path coefficient = -0.54, Figure 4G) but positive in PM (path coefficient = 0.55, Figure 4G). Moreover, the direct effects of plant community diversity on soil nutrients were positive among four types of plant community grasslands (path coefficient = 0.17, 0.23, 0.48 and 0.71 resp., Figures 4I–L), in which the effect was highly significant (P values ≤ 0.001, Figure 4L) in the KM and marginal in EG (Figure 4I). However, the direct effects of soil nutrients on plant community diversity were negative in EG and PM (path coefficient = -0.07 and -0.5 resp., Figures 4E, F) but positive in AM and KM (path coefficient = 0.78 and 0.33 resp., Figures 4G, H).

The interactions between soil physical properties and plant community characteristics were significant in AM (path coefficient = 1 and 0.37 resp., *P* values ≤ 0.05, Figures 4G, K) but marginal among EG, PM, and KM (path coefficient<0.2, Figures 4E–L). However, the direct interactions between soil physical properties and plant community diversity were both negative in EG (path coefficient = -0.35 and -0.14 resp., Figures 4E, I) and AM (path coefficient = -0.3 and -0.15 resp., Figures 4G, K) but positive in PM (path coefficient = 0.6 and 0.22 resp., Figures 4F, J) and KM (path coefficient = 0.31 and 0.24 resp., Figures 4H, L). In addition, certain soil physical properties (SW at 0-5cm soil layer) had an indirect effect (path coefficient = -0.41 and 0.64 resp., Table 2) on plant community diversity through the effect on soil nutrients in PM and AM. Moreover, there was an indirect positive effect of plant community diversity on the physical properties of soil through the beneficial effect of soil nutrients in PM, AM and KM (path coefficient = 0.18,0.7 and 0.32 resp., Table 2). In general, the effect of plant on soil was greater than the effect of soil on plant in EG, PM and KM and the plant-soil interaction was significant greater in the healthy *Kobresia* meadow than the artificial *Elymus* nutans grassland and the two types of black-soil-type grasslands (Figure 4).

4 Discussion

The establishment of artificial grasslands is a common practice to restore vegetation and soil in many extremely degraded grasslands in alpine areas (Li et al., 2013). Our investigation in the Three-River Headwaters Region demonstrated that artificial grassland increased aboveground biomass but decreased plant species richness and diversity, which is consistent with previous studies on artificial grasslands of alpine grassland ecosystem (Shang et al., 2008; Feng et al., 2010; Wu et al., 2010). This may be attributed to the fact that *Elymus nutans* have greater competitive ability and increase in abundance than forbs. On one hand, the *Elymus nutans* is taller than other native species and produces shading effects, which may limit the growth of short species because of their advantage for light (Wu et al., 2010; Peng et al., 2023). On other hand, the *Elymus nutans* generally have deeper roots than other plant species, which may have enabled the plant community to acquire more water and thus increase primary production (Liu et al., 2018).

TABLE 2 Direct and indirect path effects of latent variables based on partial least squares path modeling (PLS-PM).

	EG		PM		AM		KM	
Path	Direct	Indirect	Direct	Indirect	Direct	Indirect	Direct	Indirect
Physics -> Nutrient	-0.81	0	0.83	0	0.81	0	0.55	0
Nutrient -> Physics	-0.69	0	0.75	0	0.76	0	0.45	0
Physics -> Diversity	-0.35	0.06	0.6	-0.41	-0.3	0.64	0.31	0.18
Diversity -> Physics	-0.14	-0.12	0.22	0.18	-0.15	0.37	0.24	0.32
Nutrient -> Diversity	-0.07	0	-0.5	0	0.78	0	0.33	0
Diversity -> Nutrient	0.17	0	0.23	0	0.48	0	0.71	0
Nutrient -> Plant	-0.72	-0.01	0.55	0.17	-0.54	0.13	-0.79	0.23
Plant -> Nutrient	-0.78	-0.01	0.78	-0.07	0.26	0.1	-0.64	0.24
Diversity -> Plant	0.14	0	-0.34	0	0.16	0	0.7	0
Plant -> Diversity	-0.05	0	-0.31	0	0.21	0	0.33	0
Plant -> Nutrient	-0.78	-0.01	0.78	-0.07	0.26	0.1	-0.64	0.24
Nutrient -> Plant	-0.72	-0.01	0.55	0.17	-0.54	0.13	-0.79	0.23

We also found that the establishment of artificial grassland did not improve the soil water, soil organic carbon, or total nitrogen, which suggests a lower water-holding capacity and increased loss of soil nutrients. This is inconsistent with the findings of Wu et al. (2010), who reported that soil nutrient properties all significantly increased in artificial grassland. However, Dong et al. (2012) reported that the establishment of artificial grassland did not restore soil quality or nutrient stocks in the headwaters of the Yellow River. And different grassland types may respond differently to a given restoration measure. Previous studies reported that there was a reoccurrence of black-soil-type grasslands in artificial grassland projects (Zhang et al., 2018), which suggests that the soil quality of artificial grassland struggles to maintain the sustainable growth of *Elymus nutans*. Most of the artificial grassland is seriously lacking in scientific management after establishment (Shang et al., 2018; Dong et al., 2020). Our study indicated that the soil water and nutrient content of artificial grasslands are much worse than that of natural meadows (Figure 3). Therefore, protective measures should be taken to alleviate soil erosion and the loss of soil nutrients after the establishment of artificial grassland. Mulching the non-woven materials in the artificial grassland may significantly boost seed germination rate and reduce soil erosion (Li et al., 2019; Chen B. J. et al., 2021). Further studies are required to explore the soil quality resilience of the artificial grassland across the restoration time.

We found that the restoration efficiency of artificial grasslands is significantly different compared with the two kinds of black-soil-type grasslands. The soil nutrient and soil water content in the *P.anserina*-dominated meadow were significantly higher than *E.nutans*-dominated grassland and *A.frigida*-dominated meadow (Figure 3), implying the restoration efficiency of the artificial grassland in *P.anserina*-dominated meadow was lower than the *A.frigida*-dominated meadow. This result may reflect plant community could steer grassland vegetation via the effect of soil (Peng et al., 2020; Heinen et al., 2020; Xu et al., 2022). For instance, *Potentilla anserina* in *P.anserina*-dominated meadow is the perennial stoloniferous clonal plant that has a strong reproductive capacity at the low tropic level (Saikkonen et al., 1998). Due to its fast-growing creeping stem (Li, 2004), the coverage of the *P.anserina*-dominated meadow is higher in general, which is beneficial to soil water conservation. In addition, the development of the root system of *Potentilla anserina* (Kang, 2007) indicates that the soil organic matter content is relatively high. However, *Artemisia frigida* in the *A.frigida*-dominated meadow adapts to soil with low nutrients (Yan et al., 2016) and also has strong allelopathy (Li et al., 2011). The allelochemicals of *A.frigida* may be produced in leaves and roots, from which they can be released into the soil to inhibit the germination and growth of other plant species (Mutlu et al., 2009). Furthermore, we found that the negative effect (path coefficient = -0.54) of soil nutrient on plant community coverage was larger than the positive effect (path coefficient = 0.26) of plant community coverage on soil nutrient in the *A.frigida*-dominated meadow (Figures 4G, K). It suggested that the plant species might have a high efficiency of nutrient utilization in low nutrient soil (Figures 3H, I) and contribute little to fertile soil which may be due to their allelochemicals. This implied that *A.frigida* and other weeds should be eradicated, and fertilizer addition should be considered when restoring the *A.frigida*-dominated meadow. More knowledge is required on the plant growth patterns in different kinds of black-soil-type grasslands and the plant-soil interactions of these grasslands.

5 Conclusions

The establishment of artificial grassland improved vegetation productivity and plant community coverage when compared to two kinds of black-soil-type grasslands. However, restoration could not fully achieve the recovery of plant community diversity, soil nutrient content, or soil water content, even though the soil nutrient content and water were lower than in *P.anserina*-dominated meadows. In general, artificial grasslands did not restore the two types of black-soil-type grasslands to the level seen for native undegraded grassland. This could indicate that management interventions such as fertilizer addition should be implemented after establishing the artificial grassland. In addition, our results show that the soil nutrient content in the *P.anserina*-dominated meadows was higher compared with *A.frigida*-dominated meadows. We hypothesize that the dominant species in the *A.frigida*-dominated meadows has strong allelopathy which could inhibit the growth of plant species and lead to nutrient-poor soil. Moreover, soil water content had a significant positive influence on plant community and soil nutrient content in the *A.frigida*-dominated meadows. Consequently, the forbs should be reduced, and water and fertilizer should be added during the restoration of *A.frigida*-dominated meadows. Furthermore, plant community diversity had a positive effect on plant community productivity, soil nutrient content, and soil water in native undegraded grassland, which indicated that plant diversity was beneficial for the stability of the plant community. Therefore, more plant species such as Gramineae and sedges should be planted in artificial grasslands. Our findings may be used in the restoration of *P.anserina*-dominated meadows and *A.frigida*-dominated meadows and in the management of artificial grasslands.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

NW, MD, and HZ contributed to conception and design of the study. NW, JW, MD, HZ organized the database and performed the statistical analysis. NW wrote the first draft the manuscript. NW, JW, MD, HZ, SL, LL and YZ reviewed and revised the manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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Ecosystem multifunctionality and soil microbial communities in response to ecological restoration in an alpine degraded grassland

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Linkages between microbial communities and multiple ecosystem functions are context-dependent. However, the impacts of different restoration measures on microbial communities and ecosystem functioning remain unclear. Here, a 14-year long-term experiment was conducted using three restoration modes: planting mixed grasses (MG), planting shrub with *Salix cupularis* alone (SA), and planting shrub with *Salix cupularis* plus planting mixed grasses (SG), with an extremely degraded grassland serving as the control (CK). Our objective was to investigate how ecosystem multifunctionality and microbial communities (diversity, composition, and co-occurrence networks) respond to different restoration modes. Our results indicated that most of individual functions (i.e., soil nutrient contents, enzyme activities, and microbial biomass) in the SG treatment were significantly higher than in the CK treatment, and even higher than MG and SA treatments. Compared with the CK treatment, treatments MG, SA, and SG significantly increased the multifunctionality index on average by 0.57, 0.23 and 0.76, respectively. Random forest modeling showed that the alpha-diversity and composition of bacterial communities, rather than fungal communities, drove the ecosystem multifunctionality. Moreover, we found that both the MG and SG treatments significantly improved bacterial network stability, which exhibited stronger correlations with ecosystem multifunctionality compared to fungal network stability. In summary, this study demonstrates that planting shrub and grasses altogether is a promising restoration mode that can enhance ecosystem multifunctionality and improve microbial diversity and stability in the alpine degraded grassland.

KEYWORDS

ecological restoration, multifunctionality, biodiversity, microbial stability, alpine grassland

1 Introduction

Ecological restoration has been widely implemented as an effective strategy to address the loss of biodiversity and ecosystem functions and services (Huang et al., 2019; Strassburg et al., 2020). Previous studies have reported on the influence of ecological restoration on individual ecosystem functions (Yang et al., 2019; Bai et al., 2020), while the benefits of ecological restoration can be more effective when multiple ecosystem functions are comprehensively considered (Tian et al., 2022). Ecosystem multifunctionality (EMF), as a reliable index to summarize the complex and interactive processes of ecosystems, has been increasingly applied to evaluate the influence of human activities and climate change on the multiple functions of ecosystems (Hector & Bagchi, 2007; Garland et al., 2021). Understanding the effects and fundamental mechanisms of ecological restoration on ecosystem multifunctionality can help predict the responses of ecosystems to long-term ecological restoration and therefore facilitate the implementation of large-scale restoration projects.

Soil microbiota constitutes a significant portion of the earth's biodiversity and plays a crucial role in various ecosystem functions and services, including organic matter decomposition, nutrient cycling, soil aggregate stabilization, and plant productivity (Saleem et al., 2019). The diversity and composition of microbial communities are highly sensitive to anthropogenic disturbances and environmental changes, such as climate change, land use change, and restoration (Farrell et al., 2020; Rillig et al., 2019). Ecological restoration can have substantial effects on soil microbial communities, often leading to consequences for ecosystem functions and services. Furthermore, the response of microbial communities in terms of diversity and composition varies depending on the restoration modes enployed(Bizuti et al., 2022; Lu et al., 2022). Given the significance of soil microbial community diversity and composition in relation to EMF, they should be considered when examining the mechanisms underlying the response of degraded grassland ecosystems to ecological restoration.

Microbial communities exhibit structured interactions, forming complex ecological network through processes such as competition, facilitation, and inhibition (Hirano & Takemoto, 2019). In recent years, the stability of soil microbial network has garnered increasing attention due to its potential implications for ecosystem functions (Karimi et al., 2017). Co-occurrence network analysis, a mathematical modeling approach, has been utilized to understand the stability of microbial communities and how it evolves in response to natural and anthropogenic perturbations (Barberán et al., 2012). Network topological properties, such as modularity and cohesion indices, have been successfully employed to estimate microbial network stability (de Vries et al., 2018). While numerous studies have demonstrated that environmental changes can alter soil microbial network stability and subsequently impact ecosystem functions (Ye et al., 2021; Yuan et al., 2021), only a limited number ofstudies have investigated the response of microbial network stability to ecological restoration and its relationship with EMF.

The alpine grasslands in the northwest Sichuan, located at the eastern margin of the Tibetan Plateau, play a crucial role in protecting water resources and ecological security (Zhou and Peng, 2021). However, due to human disturbances and climate changes, the degradation of grassland in this area increased by 307.7% during the 34 years from 1966 to 2000, with an average annual degradation area increased by 816.0 hm^2 (Ma et al., 2020). In response to this, the Chinese government had implemented ecological restoration measures in an attempt to reverse the decline in ecosystem functions and services (Gou et al., 2019; Liu et al., 2022). However, there is limited information available regarding the effectiveness of different restoration modes in this unique area. Therefore, this study aims to explore how different restoration modes may influence ecosystem functions and soil microbial communities in the alpine degraded grasslands on the eastern margin of the Tibetan Plateau. Three restoration modes are considered: planting mixed grasses (MG), planting shrub with *Salix cupularis* alone (SA), and planting shrub with *Salix cupularis* in combination with grasses (SG). The specific objectives of this study are: 1) to investigate changes in EMF after a 14-year restoration treatment, 2) to examine the influence of different restoration modes on microbial communities, and (3) to identify the driving mechanism of the relationship between microbial communities and EMF.

2 Materials and methods

2.1 Study site and experimental design

The study area is located in the Restoration Demonstration region of degraded grassland in Hongyuan County (33° 1' N and 102° 37' E), China, at the eastern margin of the Tibetan Plateau (Supplementary Figure S1). The average elevation of this region is over 3400 m. The mean annual precipitation in this region is 791.95 mm, with approximately 60–75% occurring from May to September. The mean annual temperature is 1.1°C, and the mean temperatures are -10.3°C and 10.9°C for the coldest and warmest months, respectively. The soil is classified as cambic arenosol (FAO, 2006), which is sandy in texture, loose in structure and low in nutrients. The characteristics of the restoration demonstration region are gently undulating moving, semi-moving, and semi-fixed dunes. The dominant vegetation species in the recovery area are mainly *Salix cupularis*, *Carex peaeclara*, *Kobresia pygmaea*, *Artemisia wellbyi*, and *Heracleum souliei*. Since 2007, different restoration modes had been started to restore degraded grassland. The restoration actions included 1) planting mixed grasses (MG), 2) planting shrub with *Salix cupularis* alone (SA), and 3) planting shrub with *Salix cupularis* plus grasses (SG). After 14 years, these restoration modes have been successfully established in the restored area. Further details on dominant plant communities can be found in Table 1.

In this study, our main purpose was to assess the performance of the three restoration modes after 14 years of successful establishment. From October to April in the study area, freezing and ice-induced erosion may inhibit plant growth and alter the physical, chemical, and biological properties of the habitat, likely leading to habitat homogenization. These changes may not reflect the real effects of restoration modes on ecosystem functions and

TABLE 1 Basic information of dominant plant communities under different restoration modes.

Restoration modes	Mean slope (°)	*Salix Cupularis*		Coverage (%)	Dominant species
		Mean height (m)	Mean canopy (m)		
CK	< 5			4.2 ± 1.9	*Cyperus stoloniferus*
MG	< 5			94.3 ± 0.8	*Carex praeclara Nelmes,* *Tibetia himalaica,* *KobresiasetchwanensisHand.–Mazz,* *Potentilla anserina*
SA	< 5	1.52	1.97×1.84	6.6 ± 1.4	*Lancea tibetica,* *Leymus secalinus,* *Salix cupularis*
SG	< 5	1.64	1.98×1.91	81.4 ± 8.9	*Euphrasia regelii subsp. Kangtienensis,* *Salix cupularis,* *Anaphalis lactea,* *Peucedanum praeruptorum,* *Potentilla discolor,* *Elymus nutans*

CK, extremely degraded grassland; MG, planting mixed grasses; SA, planting shrub with Salix cupularis alone (SA); SG, planting shrub with Salix cupularis plus mixed grasses.

microbial communities. We collected soil and plant samples in August 2021, because the effects of different restoration modes may be more apparent in the summer season due to enhanced growth of plant and microorganisms, higher temperature, and more stable weather conditions. For each treatment, four 25 m × 25 m plots were selected as the replicates. For the CK and MG plots, four 1 m × 1 m quadrats were randomly performed to survey herbaceous plants. For the SA and SG plots, three 10 m × 10 m subplots were randomly selected to investigate shrub height and canopy, while four 1 m × 1 m quadrats were selected for bare land between two adjacent shrubs to explore herbaceous features in each subplot. At each plot, four 1 m × 1 m quadrats at least 10 m apart from each other were selected. Above-ground plant and litter biomass in the quadrat were determined by cutting the herbs close to the ground and placing them in hard envelopes for ongoing drying at 65°C for 72 h. We randomly sampled 1 kg of soil from the top 0-20 cm in each plot using a soil auger of 5 cm diameter, and then pooled and thoroughly mixed it to produce a composite soil sample. After transporting these samples to the laboratory on ice, one-tenth of each soil sample was stored at -80°C for the soil microbial community analysis. Two-tenths of each soil sample was stored at 4°C for testing soil microbial biomass carbon and nitrogen and enzyme activities. The remaining soil was air-dried and sieved for pH, organic matter, and soil nutrients analysis.

2.2 Soil analysis

Soil properties were analyzed as previously described by Carter & Gregorich (2008). Soil pH was determined by a glass electrode with a soil-to-water ratio of 1:2.5 (weight/volume) (Mettler Toledo MP220, Mettler-Toledo, Switzerland). Soil organic matter (SOM) content was analyzed using the $K_2Cr_2O_7$ oxidation method. Soil total nitrogen (TN) content was measured using a flow injection autoanalyzer (AutoAnalyzer 3, Bran+ Luebbe, Germany). Soil total phosphorus (TP) content was analyzed calorimetrically using the H_2SO_4-$HClO_4$ method. Microbial biomass carbon (MBC) and nitrogen (MBN) were measured by the chloroform fumigation-extraction method (Brookes et al., 1985). Dissolved organic carbon (DOC) and total nitrogen (DTN) were measured by TOC/TN analyzer (Elementer Analysensysteme, Germany). Additionally, we analyzed the potential activities of five soil extracellular enzymes, including β-glucosidase (BG), β-D-cellubiosidase (CBH), N-acetyl-β-glucosaminidase (NAG), leucine amino peptidase (LAP), and acid phosphatase (ACP) (Supplementary Table S1). All enzymes were quantified using commercial enzyme kits following the manufacturer's protocol (Solarbio Science and Technology Co., Ltd., Beijing, China).

2.3 Ecosystem multifunctionality

The multifunctionality includes multiple ecosystem functions such as plant biomass, nutrient cycling, soil fertility and SOM decomposition (Delgado-Baquerizo et al., 2020; Guo et al., 2021). To obtain a quantitative ecosystem multifunctionality index for each plot, we used two independent multifunctionality approaches: (1) the averaging multifunctionality index and (2) the multidimensional multifunctionality index (Delgado-Baquerizo et al., 2020). Before analyses, we averaged the standardized scores (a common scale ranging from 0 to 1) of all individual ecosystem functions (Byrnes et al., 2014). The averaging approach takes the mean value across all standardized functions as a multifunctional index for each plot (Maestre et al., 2012). The multidimensional approach is calculated based on a principal coordinates analysis (PCoA) by using the data of each ecosystem-related function (Manning et al., 2018). The multifunctionality index is calculated by summing up all site-scores of the PCoA after weighting the axes by their eigenvalues. A notable benefit of the multidimensional approach is the avoidance of potential collinearity issues among multiple measured functions (Chen et al., 2022). Here both the averaging and multidimensional indices of ecosystem multifunctionality were highly correlated ($r = 0.98$, $P < 0.001$). Thus, we present results using the multidimensional calculation of ecosystem multifunctionality.

2.4 DNA extraction and Illumina MiSeq sequencing

For each sample, total DNA was extracted from 0.5 g soil using the PowerSoil® DNA Isolation Kit (MoBio Laboratories Inc. Carlsbad, CA, USA) following the manufacturer's instructions. The concentration and quality of DNA were measured by Nanodrop 2000 (Thermo Scientific, Wilmington, DE, USA). Before performing PCR amplification, the DNA sample was diluted to 10 ng/μL. The 16S rRNA V4–V5 regions were sequenced for bacterial communities with the primer pair 515F (5'-GTGCCAGCMGCCGCGGTAA-3') and 909R (5'-CCCCGYCAATTCMTTTRAGT-3'). Fungal communities were assessed by using the ITS1 region of the rRNA operon with the primer pair ITS4 (5'- TCCTCCGCTTATTGATATGC-3') and gITS7F (5'-GTGARTCATCGARTCTTTG-3'). Sequencing was conducted on an Illumina MiSeq2500 platform by Novogene (Beijing, China).

2.5 Statistical analysis

Statistical analyses were conducted using the R statistical software (R version 4.0.2, R Core Team, Vienna, Austria). Unless otherwise stated, statistical significance was set at $P < 0.05$. Differences in the plant above-ground biomass, litter biomass, soil properties, microbial α-diversity indices, and parameters of microbial co-occurrence networks were tested using one-way analyses of variance (ANOVA) followed by Tukey's honestly significant difference (HSD) test. Normality and homogeneity of the distribution of residuals were verified and log-transformations performed when necessary. Linear regression analysis was used to evaluate the relationships between EMF and microbial variables. Principal coordinate analysis (PCoA) and permutational multivariate analysis of variance (PERMANOVA; based on Bray-Curtis distance) were used to determine significant differences in microbial communities at the various restoration modes. Metastat analysis was used to detect significant differences among treatments in term of bacteria and fungi at the phylum level. Redundancy analysis (RDA) was performed with a Monte Carlo permutation test (999 permutation) to identify soil properties that influence the microbial community structure. We performed random forest analysis to evaluate important predictors of ecosystem multifunctionality among bacterial Shannon and fungal Shannon diversity indices, bacterial richness (Chao1 index), fungal richness (Chao1 index), bacterial composition, and fungal composition. The composition of microbial communities was estimated based on Bray–Curtis distances between samples. All predictors and response variables were standardized before analyses using the Z-core to interpret parameter estimates on a comparable scale. Random forest analysis was performed using the "randomForest" package, with the significance of the model and each predictor evaluated using the "rfPermute" packages.

The co-occurrence network was constructed using the "microeco" package based on the spearman correlation matrix (Liu et al., 2021). Only the relative abundance of OTU > 0.01% was adopted in the analyses. The random matrix theory (RMT) was achieved to identify 0.79 and 0.80 as the thresholds for bacterial and fungal networks, respectively. Here, the P -value cutoff for statistical significance was set to 0.01. Microbial network modularity index of each sample was implemented using the subgraph function of the "microeco" package. Visualization of the microbial co-occurrence network was obtained using the interactive platform "Gephi".

3 Results

3.1 Effects of restoration on ecosystem functioning

Long-term restoration had a positive effect on ecosystem functions (Table 2). Restoration modes had a significant effect on Plant AGB, SOM, TN, AN, DOC and DON, MBC and MBN, NAG, and ACP ($P < 0.05$), but had no significant effect on TP, AP, and CBH ($P > 0.05$). Treatment SG significantly increased litter biomass and BG on average by 484.9 and 585.3, respectively, relative to the CK ($P < 0.05$). Treatments MG and SA significantly decreased soil pH ($P < 0.05$). Compared with the CK treatment, treatments MG, SA, and SG significantly increased the multifunctionality index on average by 0.57, 0.23 and 0.76, respectively ($P < 0.05$).

3.2 Effects of restoration on the diversity and composition of microbial communities

The Shannon index of bacteria was higher in the SG treatment than in the CK, MG, and SA treatments. The Chao1 index of bacteria was significantly higher in the SG than the CK treatment ($P < 0.05$) (Figure 1). The Chao1 index of fungi in the MG and SG treatments were higher than in the CK treatment; SA was lower than in CK; and there were no significant differences between MG, SA and SG.

Soil bacterial communities under different restoration modes were primarily comprised of members of the phyla Proteobacteria, Actinobacteria, Acidobacteria, Chloroflexi, and Firmicutes (Figure 2A). Treatments MG, SA and SG significantly decreased the relative abundance of Chloroflexi on average by 3.8%, 2.9% and 4.1% relative to the CK treatment, respectively ($P < 0.05$).Compared with the CK, the MG significantly increased the relative abundance of Acidobacteria by 4.36%, but significantly decreased the relative abundance of Actinobacteria, Gemmatimonadetes and Thaumarchaeota by 8.2%, 1.2%, and 8.2%, respectively ($P < 0.05$). The SG significantly increased the relative abundance of Proteobacteria, Acidobacteria, and Verrucomicrobia by 10.2%, 6.4%, and 2.4%, respectively ($P < 0.05$). Ascomycota (~79%) and Basidiomycota (~19%) were the major fungal phyla (Figure 2B). At the phylum level, the fungal community compositions remained relatively stable among different treatments.

TABLE 2 Effects of different restoration modes on soil basic properties and ecosystem functions.

Variables	CK	MG	SA	SG
AGB (g m^{-2})	9.4 ± 10.2 b	275.7 ± 63.0 a	32.6 ± 19.2 b	201.8 ± 39.6 a
Litter biomass (g m^{-2})	0.6 ± 0.4 b	54.3 ± 25.2 b	328.8 ± 218.2 ab	485.5 ± 239.4 a
pH	6.81 ± 0.08 a	6.33 ± 0.07 b	6.27 ± 0.18 b	6.68 ± 0.04 a
SOM (g kg^{-1})	3.53 ± 1.34 b	9.11 ± 1.64 a	5.84 ± 2.17 ab	9.29 ± 2.29 a
TN (g kg^{-1})	0.11 ± 0.02 b	0.35 ± 0.01 a	0.17 ± 0.02 b	0.39 ± 0.08 a
TP (g kg^{-1})	0.16 ± 0.00 a	0.17 ± 0.00 a	0.17 ± 0.01 a	0.18 ± 0.01 a
AN (mg kg^{-1})	10.32 ± 7.43 b	79.54 ± 9.19 a	29.39 ± 1.04 b	62.62 ± 15.07 a
AP (mg kg^{-1})	9.86 ± 1.87 a	8.85 ± 0.44 a	9.85 ± 2.52 a	11.64 ± 3.01 a
DOC (mg kg^{-1})	51.9 ± 0.9 c	82.7 ± 4.9 b	67.3 ± 3.5 bc	106.4 ± 15.4 a
DTN (mg kg^{-1})	14.9 ± 0.8 b	24.9 ± 2.5 a	16.3 ± 1.2 b	32.2 ± 6.8 a
MBC (mg kg^{-1})	171.1 ± 36.7 b	237.0 ± 10.2 a	205.0 ± 18.8 ab	238.3 ± 22.0 a
MBN (mg kg^{-1})	23.8 ± 4.2 b	51.4 ± 6.3 a	30.8 ± 5.3 b	48.3 ± 7.6 a
BG (nmol g^{-1} h^{-1})	196.8 ± 56.4 b	381.6 ± 73.8 b	365.1 ± 86.6 b	682.1 ± 198.8 a
CBH (nmol g^{-1} h^{-1})	63.5 ± 18.6 a	88.8 ± 30.7 a	97.5 ± 47.8 a	100.3 ± 11.8 a
NAG (nmol g^{-1} h^{-1})	74.6 ± 38.9 b	209.5 ± 44.1 a	121.3 ± 50.2 ab	232.2 ± 80.7 a
LAP (nmol g^{-1} h^{-1})	31.2 ± 13.1 a	34.7 ± 6.1 a	28.4 ± 18.2 a	31.7 ± 7.4 a
ACP (nmol g^{-1} h^{-1})	96.9 ± 25.4 b	663.0 ± 155.1 a	250.9 ± 26.4 b	722.8 ± 119.8 a
Multifunctionality (Zcore)	0.004 ± 0.003 c	0.578 ± 0.121 a	0.233 ± 0.041 b	0.768 ± 0.152 a

Values are mean ± standard deviation (n = 4). Values followed by different letters in superscript are significantly different among treatments ($P < 0.05$). CK: extremely degraded grassland. MG: planting mixed grasses. SA: planting shrub with Salix cupularis alone (SA). SG: planting shrub with Salix cupularis plus mixed grasses. AGB, above-ground biomass; SOM, soil organic matter; TN, total nitrogen; TP, total phosphorus; AN, available nitrogen; AP, available phosphorus; DOC, dissolved organic carbon; DTN, dissolved total nitrogen; MBC, microbial biomass carbon; MBN, microbial biomass nitrogen; BG, β-1,4-glucosidase; CBH, β-D-cellobiosidase; NAG, β-1,4-N-Acetyl-glucosaminidase; LAP, leucine aminopeptidase; ACP, acid phosphatase.

The PCoA analyses demonstrated restoration altered the overall patterns of both bacterial and fungal communities (Figures 2C, D). The PERMANOVA test showed significant differences between treatments. For bacteria, samples from MG, SA and SG clustered separately from CK samples. For fungi, MG samples clustered separately from CK ones. RDA analyses indicated the the first two components explained 50.9% and 50.7% of the total variability for bacterial and fungal community structure, respectively (Supplementary Figure S2). Soil pH, SOM, TN and DTN were the important soil properties controlling the bacterial community structure ($P < 0.05$). Moreover, SOM contents significantly correlated with the fungal communities ($P < 0.01$) (Supplementary Table S2).

3.3 Contribution of the diversity and composition of microbes to EMF

Random forest analysis indicated that bacterial composition and fungal composition controlled EMF rather than the richness and diversity of bacteria and fungi (Figure 3). The EMF index was significantly positively associated with the Chao1 index of bacteria ($P < 0.05$). Plant above-ground biomass and AN were positively associated with the Chao1 index of bacteria and fungi ($P < 0.05$). Acidobacteria was positively correlated with multifunctionality index, SOM, TN, AN, DOC, DTN, MBC, MBN, BG, CBH, NAG, ACP, and AGB ($P < 0.05$). Proteobacteria was significantly positively correlated with BG, CBH and litter biomass, but negatively correlated with pH ($P < 0.05$). Ascomycota was positively correlated with SOM, AN, NAG, ACP and AGB ($P < 0.05$) (Figure 4).

3.4 Effects of restoration on microbial co-occurrence network

The co-occurrence network of bacterial and fungal communities is shown in Figures 5A, B. Compared with the CK treatment, the MG, SA, and SG treatments increased the modularity of bacterial network. This indicates that bacterial communities in restoration treatments were more compartmentalized than in degraded treatments (Figure 5C). Treatments MG, SA, and SG increased the ratio of negative to positive cohesion of bacterial network relative to the CK (Figure 5D). Restoration modes had no significant effect on the fungal network stability ($P > 0.05$). Correlation analysis showed that the EMF index was positively correlated with the modularity ($R^2 = 0.57$, $P < 0.001$) and the ratio of negative cohesion to positive cohesion ($R^2 = 0.60$, $P < 0.001$) of bacteria network (Figures 5E, F). The modularity and the ratio of negative cohesion to positive cohesion of bacterial network were

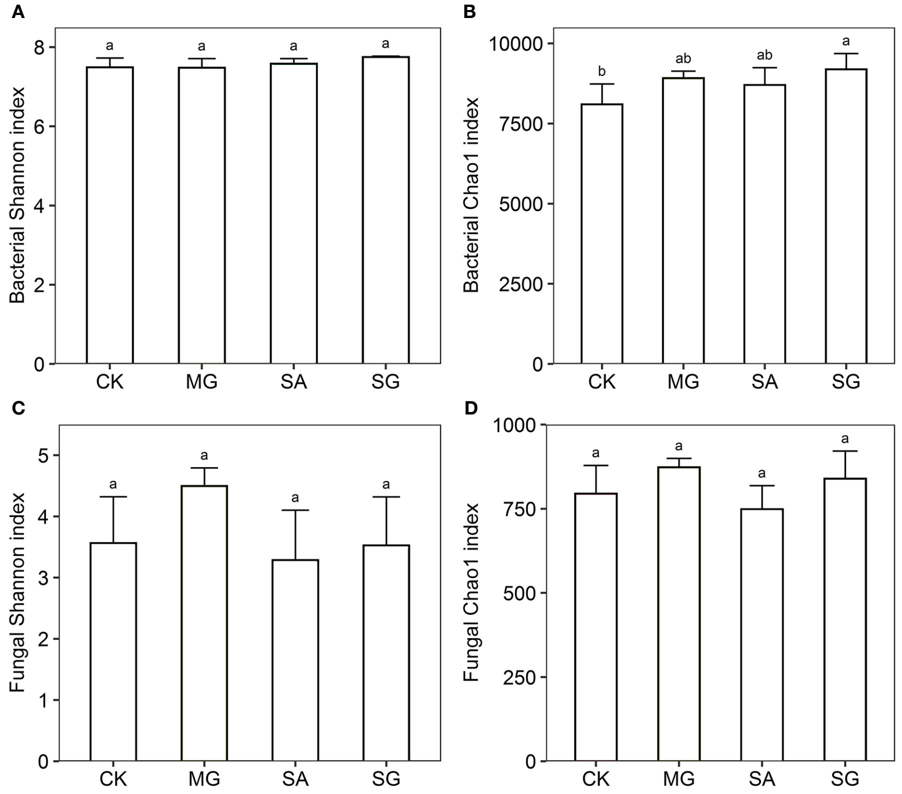

FIGURE 1
Responses of alpha diversity of bacterial and fungal communities to different restoration modes. **(A)** bacterial Shannon index, **(B)** bacterial Chao1 index, **(C)** fungal Shannon index, **(D)** fungal Chao1 index. CK: extremely degraded grassland. MG: planting mixed grasses. SA: planting shrub with *Salix cupularis* alone (SA). SG: planting shrub with *Salix cupularis* plus mixed grasses. Different lowercase letters indicate significant differences among treatments ($P < 0.05$).

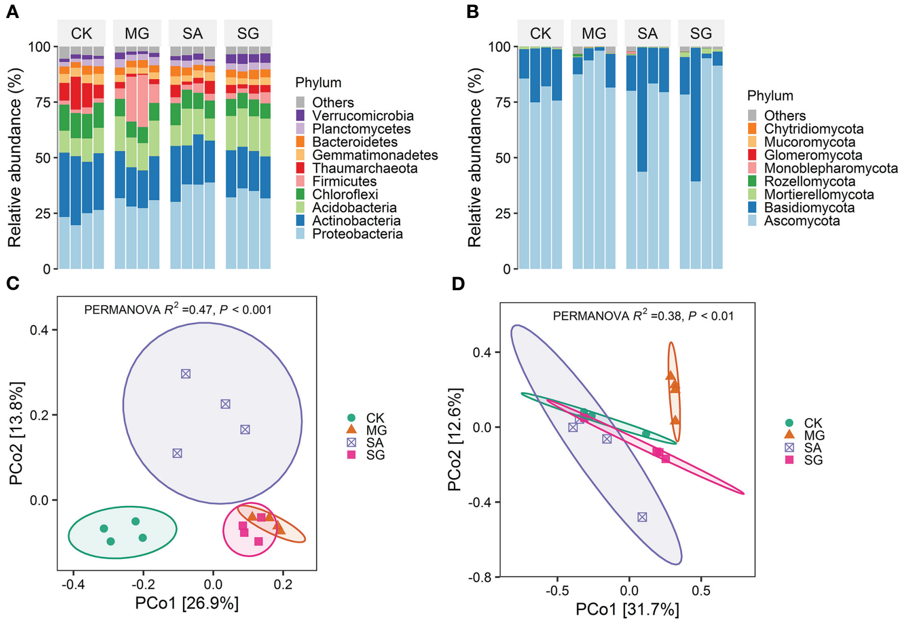

FIGURE 2
Effects of different restoration modes on soil bacterial and fungal communities. **(A)** Distribution of dominant bacterial groups at the phylum level. **(B)** Distribution of dominant fungal groups at the phylum level. **(C)** Principial coordinates analysis (PCoA) of bacterial community composition based on Bray-Curtis distances. **(D)** Principial coordinates analysis (PCoA) of fungal community composition based on Bray-Curtis distances. CK: extremely degraded grassland. MG: planting mixed grasses. SA: planting shrub with *Salix cupularis* alone (SA). SG: planting shrub with *Salix cupularis* plus mixed grasses.

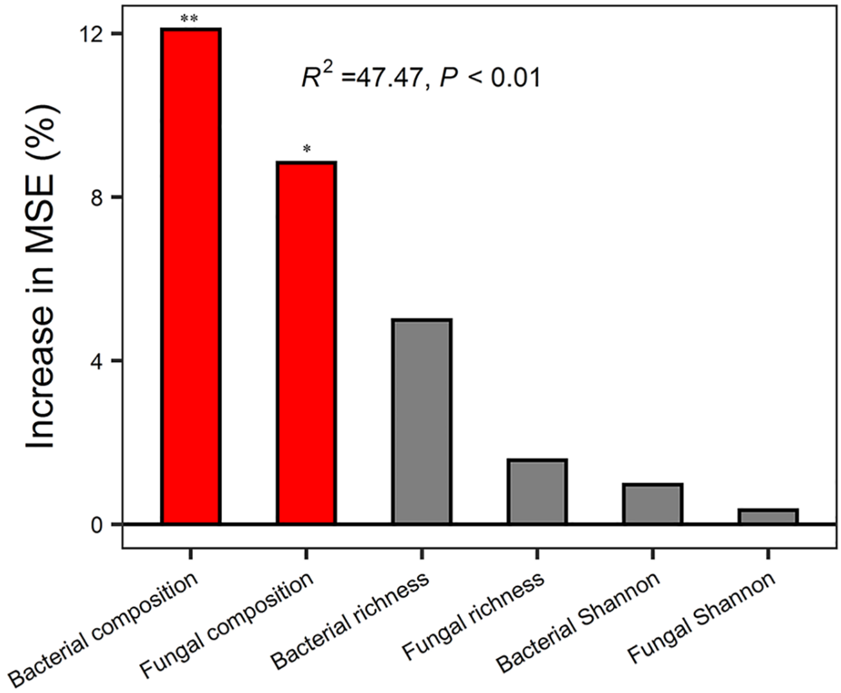

FIGURE 3
Random Forest regression model showing the mean predictor importance (% of increase of MSE) of microbial drivers of ecosystem multifunctionality. MSE, represents the mean square error. * indicates $P < 0.05$ and ** indicates $P< 0.01$ (both meaning that the associated driver had a significant effect on multifunctionality). Bacterial composition and fungal composition were represented by scaling 1, the first component of PCoA analysis. Bacterial richness and fungal richness were represented by Chao1 index.

positively correlated with SOC, TN, AN, DOC and DTN ($P < 0.05$) (Supplementary Figure S3).

4 Discussion

4.1 Responses of ecosystem functions to ecological restoration

In alpine degraded grasslands, the major challenge is to develop the sustainable and effective restoration mode to solve a series of ecosystem degradation problems caused by human disturbances and climate change (Xu Y et al., 2021). Our findings demonstrate that long-term restoration have a positive effect on multifunctionality index and most individual ecosystem functions, including plant biomass, soil fertility, and microbial activities. These results align with previous studies (Xiao et al., 2021; Zhou et al., 2022), which also indicated that different restoration modes exert varying effects on ecosystem multifunctionality.

Specifically, treatments MG and SG exhibited a significantly higher positive effect on the multifunctionality index compared to the CK and SA treatments. This finding supports the argument made by Zhao et al. (2022) that mixed-species restoration is a viable strategy for restoring ecosystem functions and services in degraded ecosystems. Furthermore, in terms of each component of ecosystem multifunctionality, MG and SG treatments were more effective than the SA treatment in restoring AGB, SOM, TN, enzymes activities and MBC. Several factors can account for these differences. Firstly, compared to the SA treatment, the higher vegetation coverage in MG and SG treatments facilitates the accumulation, distribution, and cycling of soil nutrients, consequently promoting plant growth (Zhao et al., 2022). Secondly, the increase vegetation coverage in MG and SG treatments mitigates wind or rainfall erosion, enhancing soil stability and improving soil quality, thereby stimulating the growth of vegetation and microbes (Singh et al., 2018; Dong et al., 2022). Thirdly, the presence of different growth forms and co-dominant species in MG and SG treatments may lead to higher amounts of root exudates, also improving soil properties and microbial activities (Chen et al., 2019; Huang et al., 2022). Additionally, treatments SA and SG exhibited increased litter biomass, as shrubs contribute significantly to the input of fallen leaves and twigs.

4.2 Responses of soil microbial communities to ecological restoration

The alpha diversity of bacteria and fungi in the MG and SG treatments was higher than in the SA and CK treatments. One possible explanation is that the higher soil fertility of MG and SG created a more suitable microenvironment for bacteria and fungi to survive, and consequently enhanced the diversity of soil bacterial and fungal community (Lu et al., 2022). Moreover, mixtures of plant species in the SG and MG treatments likely provided the microbes with greater accessibility to organic materials and a variety of root exudates, which results in more niches to support higher diversity of bacterial and fungal taxa (Zhao et al., 2022).

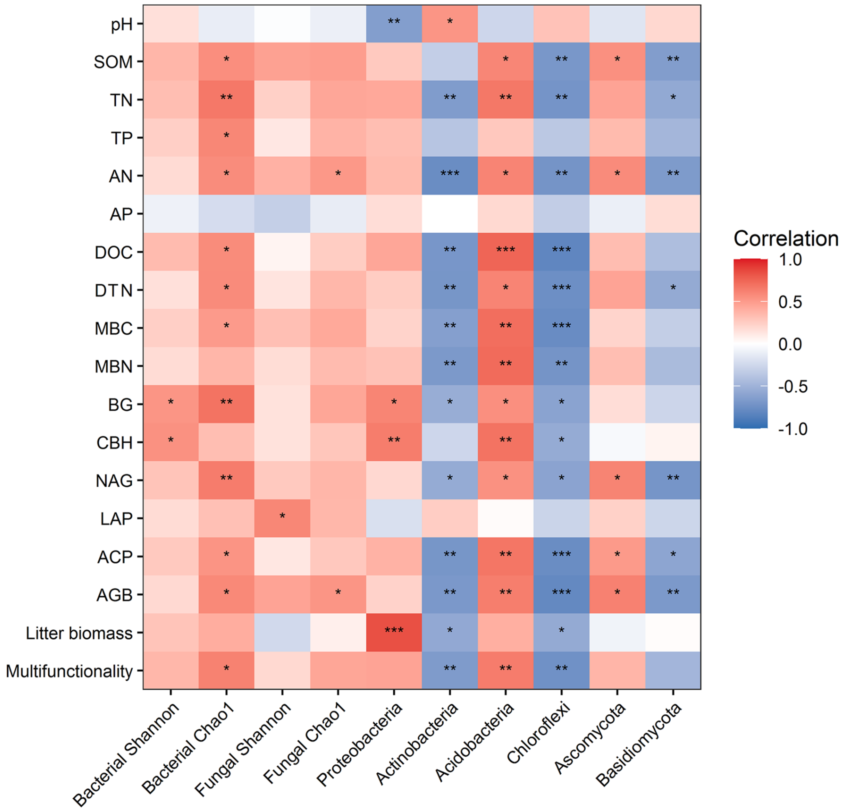

FIGURE 4
Relationships between ecosystem functions and the diversity and dominant phyla of microbial communities. * indicates $P < 0.05$, ** indicates $P < 0.01$, *** indicates $P < 0.001$.

Soil properties are the key factors influencing the structure of soil microbial communities (Bahram et al., 2018). Our results showed that soil pH was an important factor altering soil bacterial communities under varying conditions of ecological restoration, also consistent with studies conducted at either local or larger spatial scales (Bahram et al., 2018; Delgado-Baquerizo et al., 2018; Lu et al., 2022). This presumably due to the relatively narrow optimal pH for bacterial growth (Shu et al., 2022). SOM, TN and DTN were the other major factors influencing the bacterial community structure. SOM was also a key factor influencing the fungal community structure. Our results are in line with those of Lu et al. (2022), who found that soil microbial community structure was closely related to soil nutrients and particularly SOM content.

4.3 Relationships between EMF and the diversity and composition of soil microbial communities

Clarifying how microbial diversity and composition influence ecosystem multifunctionality in ecological restoration is critical for restoring and managing degraded grassland ecosystems. We observed positive relationships between microbial diversity with ecosystem multifunctionality, as well as with most individual functions, which is consistent with previous studies (Chen L et al., 2021; Jing et al., 2015). Higher diversity can promote better performance in ecosystem functions due to the potential high functional redundancy of microbial communities (Le Bagousse-Pinguet et al., 2019). We also found positive relationships between soil microbial diversity and EMF, although not all soil microorganisms played an equally important in regulating EMF. Our findings suggest that the diversity and composition of bacterial communities, rather than fungal communities, drove EMF. Soil bacteria are considered the main component of microbial communities, accounting for 99% of total soil microorganisms in degraded grassland ecosystems (Zhang et al., 2021). Soil bacteria encompass a relatively broad taxonomic grouping with diverse traits and functions; while fungi represent a narrower taxonomic grouping with a more limited range of functions (Jing et al., 2015; Mori et al., 2016). Additionally, we observed a significant positive correlation between plant above-ground biomass and the Chao1 index of bacteria and fungi, confirming that the importance of soil bacterial and fungal richness in biomass production (Yang et al., 2021).

The composition of bacterial and fungal communities emerged asa strong predictor of ecosystem multifunctionality. In this study, the phyla Proteobacteria, Actinobacteria, Acidobacteria, and Chloroflexi were the most abundant bacterial taxa, which is consistent with findings from local and regional studies (Baubin et al., 2019; Feng et al., 2020). The higher relative abundance of Proteobacteria and Acidobacteria may have contributed to the recovery of ecosystem functions. These bacterial groups are

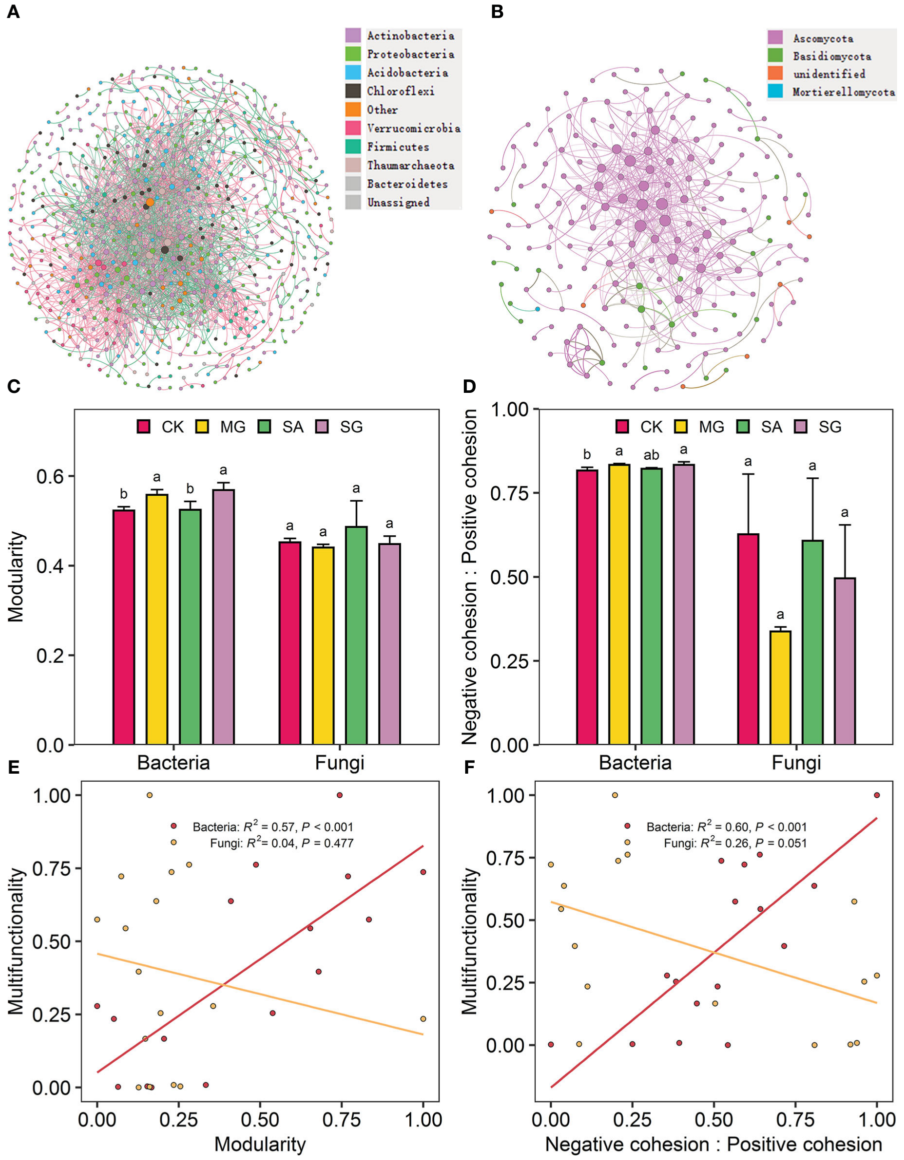

FIGURE 5

Co-occurrence patterns in soil bacterial and fungal communities as affected by restoration and the relationships of ecosystem multifunctionality and the stability of bacterial and fungal communities. Co-occurrence network of soil bacterial communities **(A)** and fungal communities **(B)**. The modularity **(C)** and the ratio of negative cohesion to positive cohesion **(D)** of soil bacteria and fungi co-occurrence patterns from extremely degraded grassland (CK), planting mixed grasses (MG), planting shrub with *Salix cupularis* alone (SA), and planting shrub with *Salix cupularis* plus mixed grasses (SG). The relationships of ecosystem multifunctionality to modularity **(E)** and the ratio of negative cohesion to positive cohesion **(F)** of soil bacteria and fungi co-occurrence patterns.

associated with soil health and quality due to their effects on various biogeochemical processes and strongly influenced by degradation and land use (Crowther et al., 2019). Proteobacteria tend to thrive in nutrient-enriched environments and play a critical role in complex and labile C decomposition (Yao et al., 2017). Acidobacteria is a keystone taxa in soil, involved in soil organic matter decomposition (Costa et al., 2020), nitrogen cycling, and plant growth promotion (Eichorst et al., 2018; Kalam et al., 2020). Actinobacteria and Chloroflexi are defined as oligotrophs, thriving in soils with low nutrients (Chen L.F et al., 2021; Fu et al., 2022). In contrast to degradation, ecological restoration can improve soil organic matter content and nutrient availability, which may explain the decline in the relative abundance of Actinobacteria and Chloroflexi. Furthermore, Ascomycota showed a significant positive correlation with SOM, NAG, ACP and plant above-ground biomass, supporting its critical role in nutrient cycling and supporting plant growth (Challacombe et al., 2019).

Several studies have concluded that temperature, precipitation, inorganic nutrients, and organic matter exhibit marked seasonal differences, which strongly affects ecosystem properties (Singh et al., 2018; Lin et al., 2021; Xu C et al., 2021). Alsterberg et al. (2017) observed that both ecosystem multifunctionality and the structure and diversity of soil bacterial communities are significantly affected by seasonal dynamics. Du et al. (2019) found clear seasonal changes in tthe biomass and necromass of fine roots during vegetation succession. Yang et al. (2022) demonstrated that plant litter inputs, soil carbon availability, microbial functional genes, and the composition and diversity of soil microbial communities exhibit strongly seasonal varations. Moreover, the relationships between soil microbial composition and soil-related functions are dependent on the sampling season. In this study, we focused solely on investigating the effects of different long-term restoration modes on ecosystem functions and microbial communities during the summer season. Due to the lack of observational data, we cannot determine how restoration impacts ecosystem functions and its relationship with the composition and diversity of bacterial and fungal communities in different seasons. Therefore, future studies should consider seasonal variability to provide a more comprehensive evaluation.

4.4 Linkages between EMF and soil microbial network stability under ecological restoration

The study of microbial stability is fundamental but has been largely overlooked in ecological investigations of restored ecosystems. Exploring how long-term ecological restoration may influence microbial co-occurrence networks provides new insights into understanding the stability of microbial communities. Community stability can be characterized by various network topological properties, such as modularity and cohesion (Hernandez et al., 2021). Modularity quantifies how strongly taxa are compartmentalized into groups of interacting/co-occurring taxa. Generally, communities with higher network modularity tend to be more stable as they have more functionally interrelated members (Ye et al., 2021). Meanwhile, the ratio of negative to positive cohesion among microbial taxa is a good indicator of community stability, as stability is often associated with negative interactions. A high proportion of negative correlations within a community is considered to be more stable (Coyte et al., 2015). In this study, we observed that the ratio of negative to positive cohesion of bacterial network increased in MG, SA, and SG, suggesting that negative associations between taxa dominate in these restoration treatments. Additionally, the modularity of bacterial network were significantly higher in the MG and SG treatments compared to the CK and SA treatments, indicating that MG and SG can stabilize bacterial networks. The increase stability of bacterial network in MG and SG treatments may result from enhanced resource availability, which promotes microbial richness and stability (Supplementary Figure S3). This finding is consistent with recent research indicating that microbes in low-stress habitats exhibit high modularity and higher ratios of negative to positive cohesion compared to communities in high-stress habitats (Hernandez et al., 2021). Importantly, we found a significant positive correlation between EMF and the modularity and the ratio of negative cohesion to positive cohesion of bacteria. This suggests that ecological restoration could stabilize bacterial communities and improve their ecosystem functions by promoting the compartmentalization of bacterial associations and fostering bacterial communities dominated by negative associations.

It is crucial to recognize that the effects of ecological restoration on the structure, functions and stability of degraded ecosystems occurs over time, so the evaluation of the influence and effectiveness must consider the necessary time frame (Hastings, 2016). Previous studies indicate that the positive effects of ecological restoration on soil fertility and biodiversity can increase with restoration time. For instance, Guo et al. (2021) found that soil multifunctionality, plant richness, and microbial richness increased concomitantly with restoration time. Our previous research based on a 34-year time series found that soil fertility and plant biomass increased with the increasing plantation period of shrub with *Salix cupularis* alone (Hu et al., 2018). Huang et al. (2019) conducted a meta-analysis and revealed that the biodiversity of the restored state increased by 34%, 51%, and 122% for restoration durations of 0-10, 10-20 and >20 years, respectively, compared to the unrestored (degraded) state. However, evidence suggests that biodiversity does not necessarily increase with restoration time. For instance, van der Heyde et al. (2020) found that both soil bacterial diversity and fungal diversity did not consistently increase with restoration age at different sites. Additionally, a recent global meta-analysis showed that the positive effects of restoration on plant biomass, soil carbon, soil fertility, and SOM decomposition increased with increasing of restoration age, while plant diversity and microbial biodiversity did not (Zhou et al., 2022). The community structure and diversity of soil microorganisms can vary significantly on the scale of days, months, and years, making it difficult to identify a single general trend (Chernov and Zhelezova, 2020). In this study, we observed that MG and SG treatments increased microbial richness, stabilize bacterial network, and promote multiple ecosystem functions after 14-years establishment period. However, it remains unclear whether the positive effect of these modes on microbial richness and network stability will presist across different restoration ages. Considering the significance of microbial community richness and network stability for ecosystem stability (Yang et al., 2018; Yuan et al., 2021), we recommend that future studies investigate the effects of different ecological restoration modes on microbial richness and microbial network stability over a longer time span to gain a more comprehensive understanding.

5 Conclusions

Our study revealed that three restoration modes had a significant positive effect on ecosystem multifunctionality, compared to degraded (unrestored) grassland. We observed that the composition and diversity of bacterial communities played a crucial role in determining ecosystem multifunctionality, while the influence of fungal communities was comparatively less pronounced. Furthermore, our results highlight the strong association between soil bacterial network stability and ecosystem multifunctionality. Notably, the combination of planting shrubs and grasses demonstrated to be an effective restoration mode for enhancing ecosystem multifunctionality, as well as promoting microbial diversity and stability. These findings provide valuable insights into the role of soil microbiota in driving ecosystem multifunctionality within the context of ecological restoration. Moreover, they have significant implications for the implementation of large-scale restoration projects and strategies aimed at enhancing multifunctionality in ecosystems.

Data availability statement

The original contributions presented in the study are publicly available. This data can be found here: https://www.ncbi.nlm.nih.gov/bioproject/PRJNA945234.

Author contributions

XS and WL: Writing - original draft, Funding acquisition, Writing – review &editing, Visualization, Methodology. YH: Funding acquisition, Writing - review & editing. LX, YYZ, KF, YLZ and WZ: Writing - review & editing. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpls.2023.1173962/full#supplementary-material

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Climate, not grazing, influences soil microbial diversity through changes in vegetation and abiotic factors on geographical patterns in the Eurasian steppe

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Livestock grazing has a significant impact on the biodiversity of nature grassland ecosystems, which is mainly regulated by climate factors. Soil microbes are essential components of biogeochemical cycles. However, the coupling effects of grazing with MAT (mean annual temperature) and MAP (mean annual precipitation) on soil microbial communities remain inconsistent. Our study considered the various climates in four grasslands as natural temperature and precipitation gradients combined with grazing intensity (GI). We collected and analyzed vegetation and soil physiochemical properties from four grasslands. Our results showed that climate factors (CF) changed β diversity of soil bacteria and fungi while grazing intensity and their interaction merely affected fungi β diversity. Furthermore, climate factors and grazing intensity impacted changes in vegetation and soil physiochemical properties, with their interaction leading to changes in EC and MBC. Our analysis revealed that climate factors contributed 13.1% to bacteria community variation while grazing intensity contributed 3.01% to fungi community variation. Piecewise SEM analysis demonstrated that MAT and MAP were essential predictors of bacteria β diversity, which was significantly affected by vegetation and soil carbon and nitrogen. At the same time, MAP was an essential factor of fungi β diversity and was mainly affected by soil nitrogen. Our study indicated that bacteria and fungi β diversity was affected by different environmental processes and can adapt to specific grazing intensities over time.

KEYWORDS

climate factors, grazing intensity, soil microbe, vegetation, soil physicochemical properties

1 Introduction

Grasslands are a significant resource that accounts for nearly 40% (59 million km^2) of the global ice-free land area, and have multiple functions in the ecology system and service (Hufkens et al., 2016; Hautier et al., 2018). Different climates are the primary reason for various grasslands, profoundly affecting grassland ecosystems by changing precipitation patterns, increasing temperatures, and regulating the entire ecosystem processes (Berdugo et al., 2020; Hu et al., 2022). Livestock grazing provides essential survival supplements and is vital for herder's livelihood and maintaining multiple ecosystem functions. Anthropogenic disturbances such as grazing and fire, connected with global climate change, may have complex effects on grasslands (Jing et al., 2015). Most of our earth is undergoing climate warming, changing precipitation patterns, and increased extreme climate events (Showstack, 2013; Hoover et al., 2022). These phenomena have significantly impacted terrestrial ecosystems, including altering vegetation productivity. Previous researches have examined the influence of changing temperature and precipitation on grassland ecosystems, while still existed inconclusive results (Nolan et al., 2018; Berdugo et al., 2020). Experiments by Ma et al. (2017) in Tibetan Plateau found that precipitation changes did not affect biomass levels. At the same time, climate warming reduced the temporal stability of biomass, primarily affecting dominant species related to community biomass stability instead of plant species diversity, such as *Stipa aliena* and *Elymusnutans* (Ma et al., 2017). Therefore, it is crucial to consider the context-dependent of climate change or precipitation-altering plant community biomass or biodiversity, which is closely linked with the local environment and their grassland ecosystem types (Gherardi and Sala, 2019; Liu et al., 2021). Additionally, aboveground primary productivity (ANPP) was highly sensitive in arid sites and primarily limited by precipitation in local places. Meanwhile, plant growth is limited by other resources, such as nutrients, light, and temperature. However, a recent global meta-analysis found that the vegetation Shannon index H and species richness was not significantly affected by climate warming, even showing negative relationships under drought, while they were positively related to local MAP (Liu et al., 2021).

Climate change also significantly impacts soil physicochemical properties through vegetation (as intermediation), with plant allocation of carbon to their above- and below-ground organs constituting terrestrial carbon dynamics. The quantity and quality of carbon input are closely associated with plant types, which are primarily limited by climatic conditions and their interactions with soil environments (Henneron et al., 2020; Mekonnen et al., 2021). The climate is considered the dominant factor in controlling soil carbon pool dynamics on global or regional scales, inextricably linked with nutrient cycling and soil microbial communities, which have a significant impact on the biogeochemical cycling of macronutrients, micronutrients and other primary elements essential for the growth of plant and animal (Bardgett and van der Putten, 2014; Schimel, 2016). Recent research has also highlighted how climate changes affected soil microbial communities, with direct effects tracing back as far as 1,000 years ago, with paleoclimate imprinting on contemporary soil bacteria (Fordham et al., 2017; Liu et al., 2023; Luo et al., 2019). Climate change also strongly affects bacterial richness and community through pH, soil properties, and soil organic carbon concentration in forest ecosystems on a global scale (Looby and Treseder, 2018; Zheng et al., 2020). However, the impacts of climate change on soil microbial communities remain understudied in grassland systems.

Grazing is a precious utility pattern for grasslands, providing humanity with economic growth through low investment, high returns, and ecosystem stability (Bai et al., 2004). However, while herbivores can change plant biomass and biodiversity, soil biogeochemistry, and microbial communities through activities such as defoliation, trampling, and returning dung and urine, grazing effects on the soil microbial community still need to be determined to technical and methodological constraints. The advent of high-throughput sequencing and metagenomics is instrumental in demonstrating microbial diversity and composition in various soil ecosystems, providing practical approaches for different ecosystem responses to various climate change scenarios. Over the past 15 years, numerous studies have explored the influence of grazing on grasslands, which was controversial globally. Different grazing intensities can change aboveground plant biomass directly, and moderate grazing can maintain grassland system diversity. The feeding preferences of herbivores alter the dominant vegetation species in grassland communities (Koerner et al., 2018). Grassland biomes store 10%–30% of global soil organic carbon, and grazing and global climate change are essential factors in grassland carbon dynamics and the global carbon process (Follett and Reed, 2010; Zhou et al., 2019). Meta-analyses showed that soil carbon content increased under light grazing in the subsoil layer (>20 cm), while it decreased on the topsoil under moderate and heavy grazing. Grazing also reduced soil carbon and nitrogen pools in grassland ecosystems and decreased soil microbial biomass carbon and nitrogen (21.62% and 24.40%) (Jiang et al., 2020; Zhang et al., 2018). Soil microbial communities play pivotal roles in ecosystem feedback under global climate change, extensively researched in recent decades. However, their interactions with human activities, such as grazing on grassland ecosystems, are poorly understood. Warming increased some proportion of oligotrophic lineages; However, it reduced those of active saprotrophic fungi and arbuscular mycorrhizae, and no interaction between warming change and grazing for soil fungi communities (Che et al., 2019). In Tibetan alpine meadows, microbial functional genes are tremendously altered by the interaction of grazing and warming rather than their individual effects (Jiang et al., 2020). While grazing has asynchronous influences on soil microbial community, increasing top and deep soil bacterial diversity, it does not significantly affect deep soil fungal diversity (Wu et al., 2022).

Understanding and predicting the influences of climate factors and grazing intensity on soil microbial community is a grand challenge in our grassland ecosystems. Our study aimed to answer three critical issues through field experiments in the northwest grasslands of China: firstly, which factors contribute more significantly to the soil microbial community? How does soil microbial diversity respond to climate factors and grazing intensity? Moreover, what is the influence of vegetation and soil physiochemical properties on the soil microbial community? We hypothesized that climate factors influence soil microbial community more than grazing intensity on a large spatial scale. Both climate factors and grazing affect soil microbial biodiversity independently without interaction effects. Climate factors and grazing intensity also changed microbial communities via vegetation and soil physiochemical properties.

2 Materials and methods

2.1 Study sites

We carry out our study in four sites in northern China, from Inner Mongolia to Qinghai-Tibetan Plateau; Meadow steppe (MS, lat. 49°19′ N, long. 119°56′ E, 666-680 m) is located in Hulunbeer, the average annual precipitation is 375 mm and the annual average temperature is -3.5 °C, which is dominated by *Leymus chinensis*, *Stipa baicalensis*, soil type of it is chernozem; Typical steppe (TS, lat. 44°15′ N, long. 116°32′, 1111-1121 m) is located in Xilinhaote, the average annual precipitation is 350 mm and the annual average temperature is -0.1 °C, which is dominated by *L. chinensis*, *S. grandis*, soil type of it is chestnut; Desert steppe (DS, lat. 41° 56′ N, long. 111°09′, 1000-1031 m) is located in Suniteyouqi, the average annual precipitation is 177.2 mm and the annual average temperature is 4.4 °C, which is dominated by *Stipa breviflora* Griseb., *Cleistogenes songorica* (Roshev.), soil type of it is brown carcic soil; Alpine steppe (AS, lat. 36°92′ N, long. 100°93′, 3200) is located in Xihai Town, Qinghai-Tibetan Plateau, the average annual precipitation is 424.82 mm and the annual average temperature is 1.4 °C, which is dominated by *Kobresia humilis, Lemus secalinus*, soil type of it is clay loam. Figure 1 shows the coverage of the four grassland types in the region.

2.2 Experimental design

Study platforms were established and set different grazing intensities in 2008 (MS), 2010 (DS), 2014 (TS), and 2018 (AS) respectively. Grazing intensity was reasonably distributed across four gradients, namely, CK, Light grazing (LG), Moderate grazing

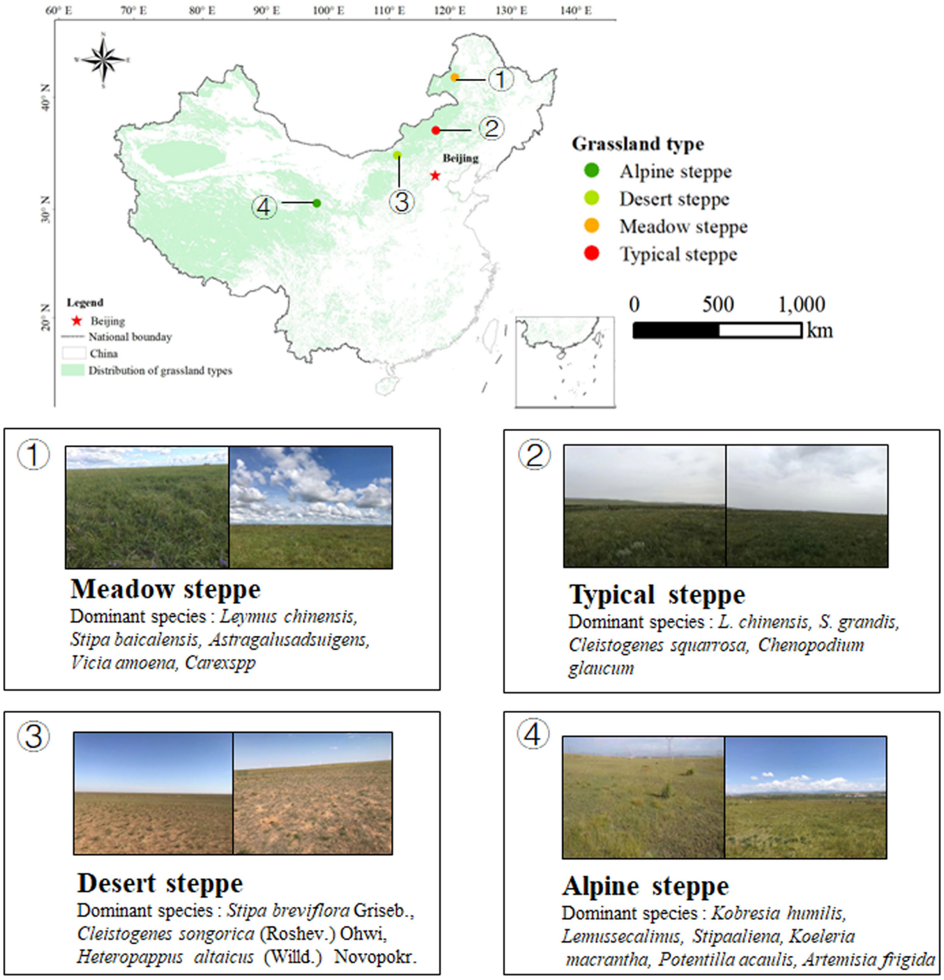

FIGURE 1
The location of the sampling sites.

(MG), and Heavy grazing (HG) in four grassland types, considering grassland productivity, herd types, and areas. Grazing periods were limited to June to October, with no grazing allowed during the rest of the year. The grazing experiments followed a randomized block design. We investigated and collected vegetation and soil samples in these four sites in August 2019.

2.3 Measurement of vegetation and edaphic properties

The plant biodiversity and biomass were assessed by randomly selecting three 0.5m×0.5m quadrats in each plot in four sites. The samples were then classified according to the species composition, and the biomass was recorded before drying them into an oven at 65°C (48 h). The soil properties were determined using three cylindrical soil cores collected from where above-ground biomass had been sampled. Soil samples were homogenized, sieved, and divided into three subsamples, each passing through a 2 mm sieve. The first subsample was under air-dried to measuring the physicochemical properties; The second subsample was reserved at 4°C and immediately analyzed soil ammonium (NH_4^+-N) and nitrate (NO_3^--N) contents, soil microbial biomass carbon C (MBC), and soil microbial biomass carbon N (MBN); The third subsample was stored at -80°C for DNA analysis.

Soil parameters were analyzed as follows: pH of soil was measured using a deionized, and water soil ratio of 2.5:1; Soil water content (SWC) was measured by gravimetric method; Elemental analysis (Elementar Analysensysteme GmbH) measured Soil organic carbon (SOC); Elemental Analyzer (vario MACRO cube, Elementar, Germany) measured total nitrogen (TN); Soil inorganic nitrogen was extracted with a 2M KCl solution used to extract soil ammonium (NH_4^+-N) and nitrate (NO_3^--N), then analyzed with a FIAstar 5000 (FOSS Analytical) (Pang et al., 2020); Olsen method measured available phosphorus (AP) content; Two 10 g fresh soil subsamples were used to measure the MBC and MBN contents using the chloroform fumigation extraction method, one of which was fumigated with chloroform for 24 h, and the other was not fumigated. After finishing fumigation, both soil subsamples were extracted with 25 ml 0.5 M K_2SO_4 on a shaker for 30 min (Vance et al., 1987). The extracts were filtered and then measured by a multi C/N analyzer (Multi N/C3100, Analytik Jena AG, Germany).

2.4 Soil DNA extraction and PCR analyses

To extract whole microbial genome DNA from the soil samples, three replicates of 0.5g of soil were used and processed by the FastDNA SPIN for soil kit (MP Biomedicals, Solon, USA) based on the instructions of manufacturer. 1.0% agarose gel electrophoresis used to quantify DNA and a NanoDrop® ND-2000 spectrophotometer (Thermo Scientific Inc., USA) before being stored at -80°C. The bacterial 16S rRNA (V3-V4) and fungal ITS genes (ITS1F_ITS2R) were amplified by primers pairs 338F (5'-ACTCCTACGGGAGGCAGCAG-3') and 806R (5'-GGACTACHVGGGTWTCTAAT-3') for bacteria and primers pairs (ITS1F: 5'-CTTGGTCATTTAGAGGAAGTAA-3' and ITS2R: 5'-GCTGCGTTCTTCATCG ATGC-3') for fungi (Liu et al., 2016). The PCR reactions included 4 μL 5× Fast Pfu buffer, 2 μL 2.5 mM dNTPs, 0.8 μL of each forward and reverse primers (5 μM), 0.4 μL Fast Pfu polymerase, 10 ng of template DNA, and ddH_2O to a final volume of 20 μL. PCR amplification cycling conditions constituted of initial denaturation at 95 °C for 3 min, and following by 27 cycles of denaturing at 95 °C for 30 s, annealing at 55 °C for 30 s, and extending at 72 °C for 45 s, and a single extension at 72 °C for 10 min, following by a final step at 4 °C. The PCR product was using the AxyPrep DNA Gel Extraction Kit (Axygen Biosciences, Union City, CA, USA) and quantifying by the Quantus^{TM} Fluorometer (Promega, USA). It was then sequenced on the Illumina MiSeq PE300 platform/NovaSeq PE250 platform (Illumina, San Diego, USA) according by Majorbio Bio-Pharm Technology Co. Ltd (Shanghai, China).

2.5 Statistical analyses

Our data were statistical analyses by R 4.2.1 (R Development Core Team, 2022). Two-way ANOVA was performed to analyzing the soil microbes community, soil physicochemical properties, plant communities, and climate factors (MAP and MAT), grazing intensity, and their interactions as fixed factors. The connection between plant, soil properties and soil microbe communities were assessed by redundancy analysis (RDA). The contribution percentage and significance of climate factors, grazing intensity, soil, and vegetation to the soil bacterial and fungal community were calculated by the rdacca.hp package, and visualized by the UpSetVP package to show hierarchical segmentation. The association between soil property (e.g. TN, SOC, NO_3^--N, NH_4^+-N) and bacterial or fungal β diversity was analyzed using PicewiseSEM after accounting for multiple key ecosystem factors such as Microbes (MBC, MBN), plant (richness, Shannon, AGB, BGB) (Lefcheck, 2016). All measured variables were considered in this model and analyzed as composite variables using the "piecewiseSEM" and "lme4" packages (Bates et al., 2014). Fisher's C test confirmed correctness of the results, and the models were modified according to the significance value ($P < 0.05$).

3 Results

3.1 The effect of climate factors and grazing intensity on microbes

Our study examined impacts of climate factors (CF) and grazing intensity (GI) on soil microbe diversity and the interaction between the two. As shown in Figure 2, CF had a significant effect on many measures, including fungi β diversity, fungi Simpson, fungi Shannon, fungi sobs, bacteria β diversity, bacteria sobs ($P < 0.05$), fungi chao, bacteria Shannon ($P < 0.01$), and bacteria chao ($P < 0.001$). However, GI and the interaction between CF and GI did not significantly impact microbe diversity,

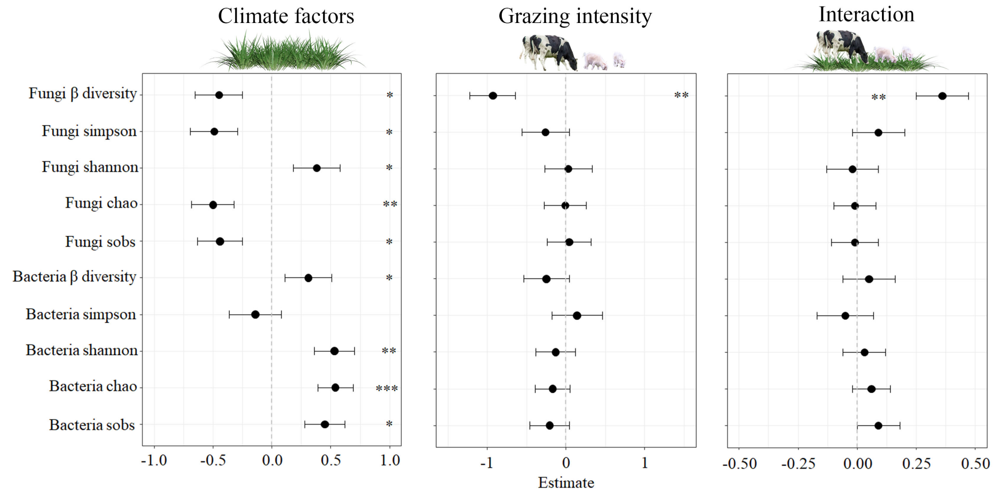

FIGURE 2

Effects of climatic factors, grazing intensity and their interaction on standardised soil microbes for the four study sites. The significant effects (*$0.01 < P < 0.05$; **$0.001 < P < 0.01$; *** $P < 0.001$) are labelled with * Fungi β-diversity, fungi Simpson, fungi Shannon, fungi chao, fungi forbs, bacteria β-diversity, bacteria Simpson, bacteria Shannon, bacteria chao, bacteria sobs.

except for fungi β diversity ($P < 0.01$). Labels in Figure 2 indicate the significant effects observed.

3.2 The interaction of climate factors and grazing intensity for plant and soil property

Our study examined impacts of grazing intensity and climate factors on plant community and soil physicochemical properties, as well as the interaction between the two. As presented in Figure 3, both climate factors and grazing intensity had significant effects on plant Shannon, soil MBN ($P < 0.05$), plant richness ($P < 0.01$), SMC, NO_3^--N, NH_4^+-N, TN, SOC, MBC, plant AGB and plant BGB ($P < 0.001$). However, pH, EC, and plant evenness ($P > 0.05$) were no significant effects. Grazing intensity significantly affected on NH_4^+-N, MBN ($P < 0.05$), MBC ($P < 0.01$), and AGB ($P < 0.001$), while pH, EC, SMC, NO_3^--N, TN, C/N, SOC, AP, BGB, plant richness, plant evenness, and plant shannon index have not significant effects. The only significant responses observed for CF*GI were for EC and MBC. Labels in Figure 3 indicate the significant effects observed.

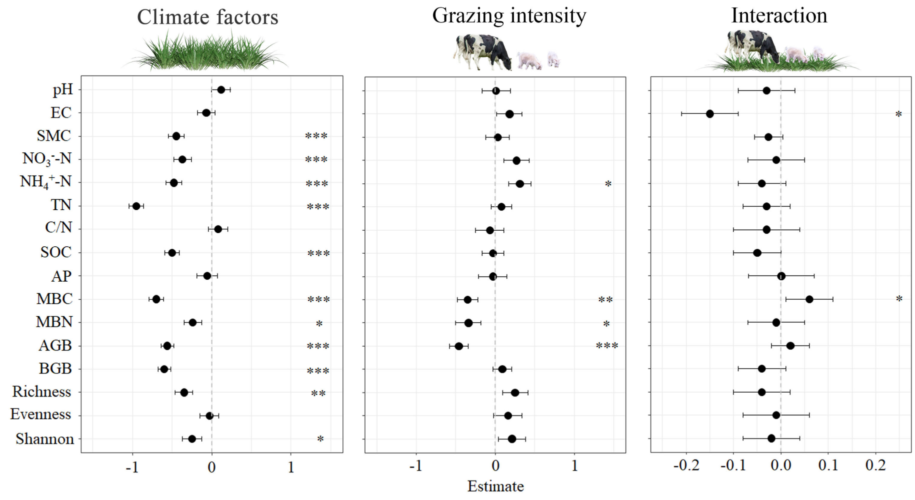

FIGURE 3

Effects of climatic factors, grazing intensity and their interaction on standardisation soil and vegetation parameters for the four studied sites. Significant effects (*$0.01 < P < 0.05$; **$0.001 < P < 0.01$; *** $P < 0.001$) are indicated by * pH, EC, SMC, NO_3^--N, NH_4^+-N, TN, C/N, SOC, AP, MBC, MBN, plant AGB and plant BGB, plant richness, evenness and Shannon.

3.3 Contributions of plant and soil indicators for β diversity of microbes

Our study explored the contributions of biotic (plants and microbial communities) and abiotic factors (soil, CF, GI) to changes in bacteria and fungi β diversity, with varying degrees of influence observed (Figure 4). Of the explanatory factors, the soil had the highest contribution rate (13.76%), with significant contributions, also observed for GF and microbes (P < 0.01). Conversely, the contribution rates of plant and GI for β diversity were relatively low (7.41% and 1.62%, respectively). Some factors were found to commonly explain β diversity, with soil, CF, microbes, and plant accounting for 5.2%, CF and microbes for 5%, and soil and CF for 5.1%. Regarding fungi β diversity, both biotic and abiotic indicators have had significant impacts, with soil having the highest contribution rate (11.32%), followed by CF (8.58%), microbes (5.99%), and plant (4.06%). Grazing intensity significantly affected fungi β diversity, with soil and microbes commonly explaining its variation, along with soil, microbes, and GI.

3.4 The response of microbes β diversity to biotic and abiotic in various grazing types

We utilized PiecewiseSEM to examine the direct and indirect pathways through which regulatory factors impacted climate factors in microbes β diversity (Figure 5). Our results revealed that vegetation characteristics and soil physicochemical properties collectively played a significant role in explaining climate factors in both bacteria and fungi β diversity. Additionally, soil physicochemical properties, including climate factors (MAT,

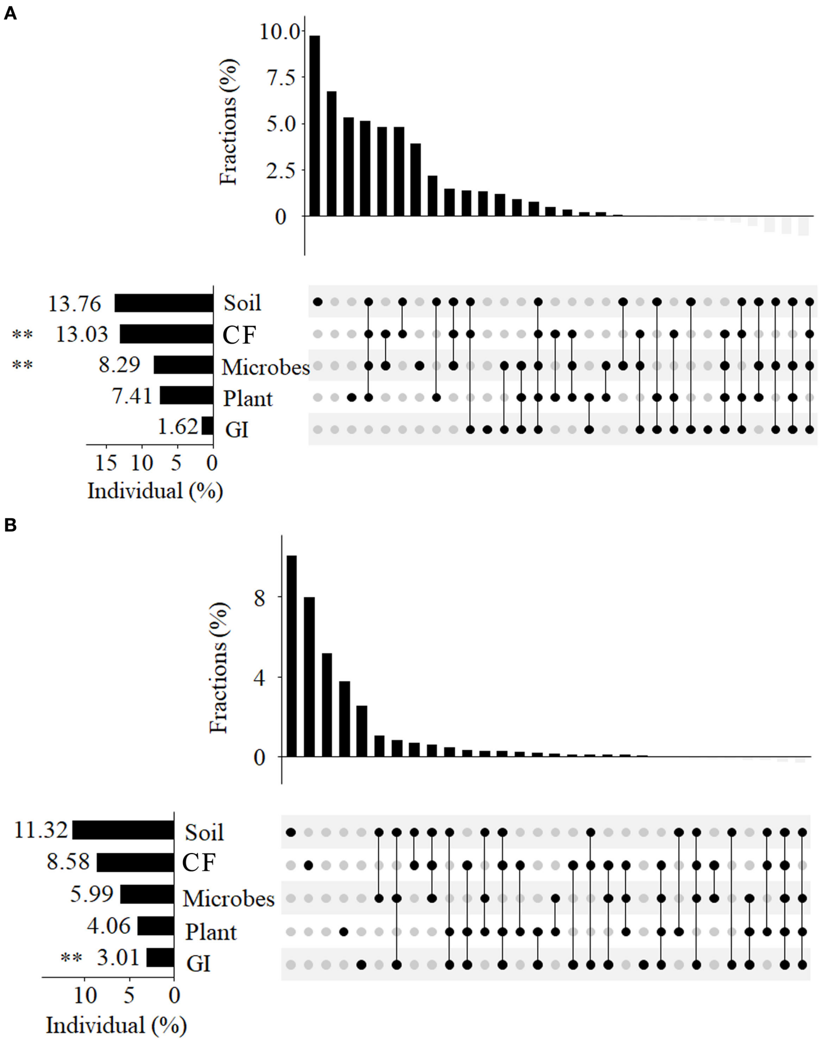

FIGURE 4
We utilized UpSetView variation-partitioning to analyze pure and shared contributions of soil properties, CF, microbes (microbial carbon and nitrogen), plant, and GI to variations in soil bacteria **(A)** and fungal **(B)** communities. The graphs depict the percentage of variance explained by the environmental factors, with dot matrices and associated bars above showing the values of exclusive and shared contributions. Negative values resulting from adjustment of R-squared were not included in the graph, but were incorporated in the total contribution of each variation, as indicated on the edge of the dot matrix. The significant effects *0.01 <P < 0.05; **0.001 < P < 0.01; *** P < 0.001.

MAP), consistently demonstrated significant regulation of microbes β diversity by directly and indirectly altering SOC, NO_3^--N, MBN, BGB, TN, NH_4^+-N, and MBC. MAT and MAP were important predictors of bacteria β diversity among climate factors. In contrast, factors such as soil properties, CF*GI, and CF collectively explained variability in fungi β diversity. CF*GI and MAP were found to impact fungi directly β diversity, with additional indirect effects on microbes that altered soil properties (e.g. NO_3^--N and NH_4^+-N).

4 Discussion

4.1 Interactive effects of climate factors and grazing on soil microbes

Soil microbes play a crucial role in determining fitness and health of grassland and regulating ecological system. Microbial diversity, both alpha diversity which explores the structure or composition of microbial communities in a single habitat or treatment, and beta diversity, which represents the combination of microbial communities with environmental gradients, are commonly used to measure microbial communities (Gülay and Smets, 2015; Luo et al., 2018; Zhang et al., 2016). Our studies found the α diversity and β diversity of soil bacteria and fungi respond significantly to climate factors.

Warming has shown inconsistent effects on soil microbes in many studies. In Tibetan grasslands, warming after six years have significantly altered soil fungal communities. However, three-years of warming did not alter soil fungi communities. Seven years of warming did not significantly affect bacteria diversity, but it changed the fungi and bacteria communities. Therefore, the influence of climate for soil microbes depended on time of warming (Jiang et al., 2021). Similarly, warming changed α diversity of soil bacteria in the first year at temperate steppe of Inner Mongolia. However, there were no significant changes in the next two years. This suggests that the bacterial community is sensitive and adapted to warming, and increased the stability and complexity of the bacterial network structure (Ibarra et al., 2020). In contrast, a meta-analysis on a global scale has shown that warming increases microbial populations but decreases biodiversity (Guo et al., 2019). Besides warming, precipitation is also a significant factor that influences soil microbes. Drought, a probable consequence of grassland ecosystems in the future, has observed noticeable changes in richness, composition, and function of soil bacteria in North America and Australia but lesser changes in fungi (Ochoa-Hueso et al., 2018).

Fungal community changes are directly proportional to the precipitation gradient (Ochoa-Hueso et al., 2018; Wu et al., 2020). In Inner Mongolia, soil bacteria diversity significantly differs by habitat, while fungi taxa are less affected by declining precipitation. This suggests that bacteria are more sensitive than fungi, and the community structure of microbes is context-dependent (Wang et al., 2021).

Additionally, our results indicate that grazing intensity significantly changes fungi β diversity but does not affect the diversity of bacteria, which supports our hypothesis. Surface disturbance has an inconsistent effect on soil microbial community. Soil microbial communities can recover quickly following disturbance treatment events, and their diversity is not highly affected by grazing disturbance treatment due to their resilience (Comer and Perkins, 2021). Overall, our experiments suggest that climate factors significantly impact soil microbes more than grazing intensity, which is consistent with our hypothesis. A probable reason for this is that a relatively long grazing history on four steppes have conferred high ecosystem resilience to different grazing and gradually adapted to different grazing intensities. However, future studies are required to determine the effects of both grazing and climate change on soil microbes. Soil microbial reaction to environmental changes is often subject to temporal lags, given that their biogeochemical responses to various environmental

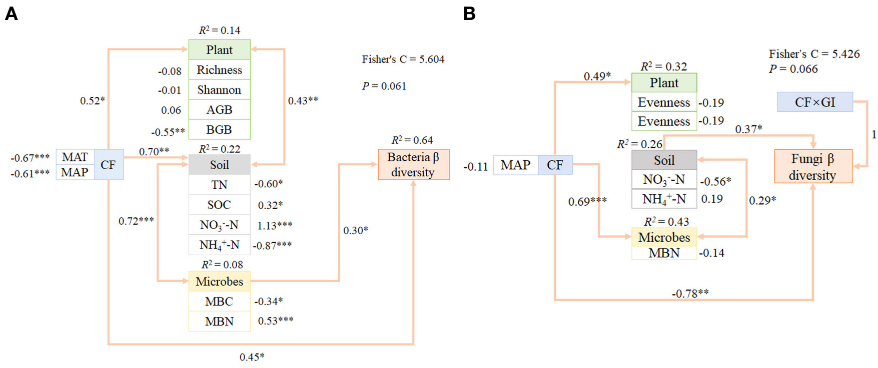

FIGURE 5
We utilized PiecewiseSEM to investigate the pathways through which climate factors and grazing intensity impacted soil bacteria and fungi communities via plant and soil properties at a large spatial scale. Composite variables were created for the soil properties, plant, and microbes. The signed path coefficients shown on the arrows represent the standardized effect size of the relationship, with non-significant relationships among residual variables of measured predictors not included. The significant effects (*0.01 <P < 0.05; **0.001 < P < 0.01; *** P < 0.001). Our results showed that the responses of soil bacteria β diversity **(A)** and fungi β diversity **(B)** were impacted by multiple direct and indirect effects of climate factors, grazing intensity, plant and soil properties. Pathways linking these variables were identified and the strength of their relationships were established, providing insight into the mechanisms that shape microbial community structure in grassland ecosystems.

changes often take time as the soil microorganisms adaption. Nonetheless, soil microorganisms can lead microbial reactions and metabolic interactions in instantaneous microscale conditions.

4.2 Interactive effects between climate factors and grazing for vegetation and soil physicochemical property

Livestock grazing is widely regarded as the most widespread and intensive land use on Earth, especially in northern China, which includes some of the most extensive remaining grasslands on the Eurasian steppe (Kemp et al., 2013). Grazing has multiple effects on soils, including physical disturbance, such as soil compaction, and chemical disturbance, such as nutrient cycling via animal dung, which can alter plant productivity and ecosystem function. Both climate factors and grazing intensity significantly affect plant and soil physicochemical properties, including aboveground biomass (AGB), richness, nitrate- and ammonium-N, soil microbial biomass carbon (MBC), and soil microbial biomass nitrogen (MBN).

A regional-scale study on a global scale has shown that livestock grazing has negative effects on aboveground biomass and belowground biomass (Díaz et al., 2007), similar to our findings under grazing intensity (Supplementary Tables S1, S2). Our study discovered that grazing mainly reduced AGB, possibly due to livestock preference for perennial bunchgrasses and rhizome grass (Semmartin et al., 2010). The grazing optimization hypothesis suggests moderate grazing increases aboveground biomass through compensatory vegetation growth. However, grazing decreased AGB at 10 sites (Li et al., 2020), suggesting that grazing effects on AGB have exceeded compensatory growth (Wang and Wesche, 2016). Global models of biomass for grazing showed that grazing has negative effect on aboveground biomass (decrease 23%) but positive effects on belowground biomass (increase 20%), with the effects compensated for by nearly equivalent (Milchunas and Lauenroth, 1993). However, our regional-scale study showed that grazing reduced AGB and BGB. Grazing affects the biomass of vegetation and biodiversity, while these changes are not synchronous. Our research has shown that grazing intensity significantly changes plant richness, which was determined by vegetation composition, soil environment (context-dependency of the environment), and biodiversity indices such as species richness and vegetation evenness (Melendez Gonzalez et al., 2019). Our results indicated that livestock grazing did not affect plant species' evenness. However, they positively affected richness, resulting in unchanging species diversity (Shannon index). These results contradict previous studies suggesting that grazing increase plant diversity due to light limitation, reducing competition by circumjacent plants (Borer et al., 2014; Guo et al., 2023), as well as influencing soil nutrients or water availability at the same time (Eldridge and Delgado-Baquerizo, 2018). Meta-analysis in large-scale shows that plant richness and aboveground net primary productivity decreased but evenness and belowground net primary productivity increased under livestock grazing. The decrease in plant richness due to grazing may be due to the level of herbivory for diet preference, with selective effects on plant community composition (Wan et al., 2015). The alteration of plant evenness resulting from grazing may attribute to livestock's paramount ingestion for aboveground biomass of constructive species, and providing chance for other plant species to have higher resource accessibility (Wan et al., 2015). Domestic livestock of grazing significantly affected the C and N dynamic circulation in grassland ecosystems (Wu et al., 2014). Global meta-analysis showed that livestock grazing significantly decreased belowground C and N pools in global grassland ecosystems. Light grazing benefits soil C and N sequestration, while other grazing (gradient moderate and heavy grazing) significantly reduced C and N reservoir (Zhou et al., 2017), as in our findings with different climate factors under grazing intensity (Tables S1, S2). Livestock grazing decreased soil C and N pools by planting ingestion, reducing aboveground plant biomass, and decreasing root elongation and biomass, which reduced C allocation to roots (McSherry and Ritchie, 2013). Specifically, above-belowground biomass may increase under light grazing, stimulating more photosynthate entering into belowground roots and fixing C, leading to more root biomass and root exudates. More root exudates can increase C accumulation and enhance soil N inputs (Zhang et al., 2015). However, moderate and heavy grazing sharply decreases soil C and N pools, which is attributed to higher grazing intensity removing more aboveground vegetation at semi-arid and arid ecoregions (Smith et al., 2012). Soil microbial biomass carbon and nitrogen decrease with the same trend as C and N under moderate and heavy grazing.

4.3 Pathway of vegetation and soil physicochemical property for soil microbes

Soil microbes are vital for biogeochemical cycles in the ecosystem. They interact with plants and soil properties, meanwhile can be influenced by climate factors and human activities. Studies showed that difference of diversity of soil microbes depend on soil and vegetation variables (Ma et al., 2021). Grassland ecosystems existed a strong and consistent connection with plant communities and soil microbes at different scales (Bai et al., 2022). Grazing can alter the soil microbes community and diversity by affecting plant growth and soil properties (soil C/N ratio, soil moisture, and so on) (Wang et al., 2022).

Plant diversity is crucial in distribution of soil bacterial communities. Our study showed that bacteria β diversity is indirectly affected by plant belowground biomass, associated with root properties such as root exudate release, root cell death, and litter biomass deposition (Ma et al., 2022). These factors influence the soil organic matter and contribute to soil carbon and nitrogen accumulation. Plant community, including biomass, community composition, and biodiversity, ultimately determines the quantity and quality of soil composition. The variation in plant communities can change microbes' communities, while soil properties play essential roles in this process.

Our research found that soil C and N content were the driving factors for bacteria (such as soil organic carbon, nitrate-nitrogen, and so on). The soil nutrient content was reduced with grazing intensity increased, ultimately regulating the bacteria community. Interestingly, MAP significantly influenced the β diversity of fungi, which was indirectly correlated with soil properties such as nitrate-nitrogen and ammonium-nitrogen. Soil moisture changes are also strongly correlated with the composition of fungi, dominant taxa, and specific groups in our study.

In conclusion, soil microbes are critical engines for biogeochemical cycles and interact with plants and soil properties. Research has shown that diversity of soil microbes altered because of soil and vegetation variables. Plant community and soil properties are essential in regulating the microbial community, which is complex. Future research should focus on understanding how these factors interact and influence each other in ecosystems.

5 Conclusions

Soil microbes are small but essential components of grassland ecosystems. Our study has shown that climate factors, as well as grazing intensity, can affect soil microbes. Different climate factors can influence microbial communities in various ways, as different climate patterns can impact vegetation and soil properties. The pathways through which climate factors and grazing intensity impact soil microbial communities are diverse. Bacteria β diversity is influenced by vegetation and soil carbon and nitrogen, while fungi β diversity is mainly affected by soil nitrogen.

The effect of grazing types on soil microbes is more significant than grazing intensity. Grazing intensity primarily affects vegetation and soil properties rather than soil microbes. This means that the response of soil microbes to grazing intensity can have a time lag and be inconsistent. Our research provides an innovative and comprehensive perspective on how human activity and regional scale can alter soil microbial communities.

In conclusion, soil microbes are crucial components of grassland ecosystems, and our study demonstrates climate factors and grazing intensity can influence these microbial communities. Bacteria and fungi microbes respond differently to these factors, and grazing types can have a more significant effect than grazing intensity. This research provides new insights in human activities and grazing intensity can alter soil microbial communities.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Author contributions

YZ, NL and GY conceived the ideas and designed the study. BQ, BW, YW, ML, and YB collected the data. BQ and BW analyzed the data. BQ wrote and revised the draft. and YZ revised the manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationship that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpls.2023.1238077/full#supplementary-material

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Responses of community traits and soil characteristics of *Achnatherum inebrians*-type degraded grassland to grazing systems in alpine meadows on the Qinghai-Tibet Plateau

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Introduction: Scientific grazing management is of great significance for the ecological health and sustainable use of alpine meadows.

Methods: To explore appropriate management methods of alpine grasslands of the Qinghai-Tibet Plateau degraded by *Achnatherum inebrians* (Hance) Keng ex Tzvele presence, we studied the effects of different grazing systems on the *A. inebrians* population, grassland vegetation community traits, soil characteristics and soil microbial community structure for cold- season grazing plus supplementary feeding pasture (CSF) and four-season open public pasture (FOP) in Tianzhu County, Gansu Province.

Results: Compared with FOP, the CSF site showed significantly inhibited reproduction of *A. inebrians*, especially the crown width, seed yield and number of reproductive branches per plant were as high as 50%, significantly increased the aboveground biomass of edible forage and soil water content by 57% and 43–55%, better soil nutrients, and significantly reduced soil bulk density by 10– 29%. Different grazing systems affected the composition and diversity of soil microbial communities, with a greater effect on fungi than on bacterial flora. The most abundant phyla of bacteria and fungi were Proteobacteria and Ascomycota for CSF (by 30–38% and 24–28%) and for FOP (by 67–70% and 68–73%), and the relative abundance and species of bacterial and fungal genera were greater for CSF than FOP. The α-diversity indexes of fungi were improved, and the β-diversity of fungi was significant difference between CSF and FOP. However, the grazing utilization time was prolonged in FOP, which reduced the diversity and abundance of soil bacteria and increased soil spatial heterogeneity. The use of *A. inebrians*-type degraded grassland in the cold season, and as a winter supplementary feeding and resting ground, could effectively inhibit expansion of *A. inebrians*, promote edible forage growth, enhance grassland productivity and community stability, and improve soil structure.

Discussion: The results guide healthy and sustainable utilization of *A. inebrians*-type degraded grassland in the Qinghai-Tibet Plateau.

KEYWORDS

grazing system, *Achnatherum inebrians*, plant communities, soil microbial communities, alpine meadows

1 Introduction

As a unique geographical unit of the earth, the Qinghai-Tibet Plateau is an important ecological security barrier in northwest China, with a wealth of habitat types and biological species (Fan and Fang, 2022). It has a profound impact on the surrounding area, China and the world. Alpine meadows are the most widely distributed grassland type in the Qinghai-Tibet Plateau (Niu et al., 2019), and play an important role in maintaining the ecosystem balance, including for animal husbandry development, climate regulation and water conservation (Ma et al., 2022). For decades, grazing was the dominant use in alpine meadows of the Qinghai-Tibet Plateau. However, these grasslands have also experienced spread of poisonous weeds following desertification and salinization because of the dual influence of natural and human factors, including climate change and overgrazing (Wei, 2013). This has reduced species diversity and edible forage yield, restricted the development of grassland animal husbandry and seriously threatened the livestock–soil–grassland ecosystem balance and productivity (Guo et al., 2017; Chai et al., 2019). Therefore, it is very important to study the impact of grazing on poisonous weed-type degraded grassland ecosystems in Qinghai-Tibet Plateau alpine meadows.

Achnatherum inebrians (Hance) Keng ex Tzvele is a perennial grass in the family Gramineae that is becoming increasingly widespread in northwest China, including in Gansu, Xinjiang, Qinghai, Tibet and Inner Mongolia (Liu et al., 2021; Liang et al., 2023). Relevant studies showed that the harmful area was 3×10^5 hm^2 in Gansu, accounting for 17.08% of the poisonous weed degraded area in the province (Guo et al., 2017). The distribution area of *A. inebrians* reached 5.3×10^5 hm^2 in Xinjiang's natural grassland, with coverage of up to 85% in some areas (Sun et al., 2014), and its distribution area reached 5.7×10^5 hm^2 in Qinghai. In recent years, the distribution area and coverage of *A. inebrians* tended to expand in different regions, with serious economic losses to animal husbandry and also leading to grassland ecological imbalance. *A. inebrians* is the host and mutualist symbiont of the *Epichloë* endophyte, with a carrier rate of up to 100%. *Epichloë* contains high levels of ergot alkaloids (i.e., ergopeptine and ergovaline), which make it poisonous (Miles et al., 1996), and accidental feeding and starvation of juvenile or foreign livestock have caused serious losses for animal production (Yang et al., 2015). Moreover, the *Epichloë* endophyte can enhance biotic and abiotic resistance (Moon et al., 2007; Zhang et al., 2012). Li et al. (1996) showed that livestock that mistakenly ingest *A. inebrians* can quickly identify and avoid further feeding on it, so that it has a greater advantage in interspecific competition within grassland communities and continues to spread in degraded grassland, causing serious harm.

Current research on *A. inebrians* mainly focuses on control (Jin et al., 2017), characteristics (Li, 2005), seed germination (Chen et al., 2021), toxic ingredients (Liu et al., 2022) and *Epichloë* endophyte resistance (Zhang et al., 2012) in the *A. inebrians* population. Research on prevention and restoration of *A. inebrians*-type degraded grassland focuses on responses of *A. inebrians* population traits, edible forage yield and grassland community diversity to fencing, mowing, manual digging and sowing excellent forage (Li et al., 1996; Mcdaniel and Sterling, 2007; Jing et al., 2014; Yang et al., 2015). However, Sun et al. (2020) showed that long-term fencing provided no ecological and economic benefits; believed that mowing and manual digging were only suitable for *A. inebrians* grasslands with small distribution area and high growth density, and sowing was a seemingly simple but complex improvement measure. Therefore, grazing is the most important and direct utilization and management method affecting grassland biodiversity and ecosystem function, and seasonal grazing is widely used for managing degraded grassland (Zhang et al., 2023). However, there is a lack of research on the response of poisonous weeds of grasslands to grazing systems in the Qinghai-Tibet Plateau (Wei, 2013), and the comprehensive effects of different grazing systems on grassland communities, microorganisms and soil require further study.

In this study, our main objective was to study how vegetation community traits and soil characteristics of *A. inebrians*-type degraded grassland under long-term different grazing systems, explore the relationship between soil microbial community structure, soil and vegetation traits in *A. inebrians*-type grassland, and provide a theoretical basis for the restoration and health of poisonous weed-degraded alpine meadow ecosystems. More specifically we hypothesized that: (i) grassland vegetation community traits with grazing systems vary, (ii) soil physicochemical characteristics and microbial community composition change with grazing systems, (iii) the vegetation–

soil–microbe are interrelated, (iv) cold-season grazing plus supplementary feeding pasture can effectively regulate *A. inebrians*-type degraded grassland.

2 Materials and methods

2.1 Study area and sampling collection

A vegetation community survey and soil sampling for this study were conducted on two separate grasslands, situated in the alpine meadow eastern edge of the Qinghai-Tibet Plateau in the administrative region of Tianzhu County, Gansu Province, China (37°11′N, 102°46′E). According to the guidance of local grassland ecological experts and herders, the *A. inebrians*-type degraded grassland was selected as the research area, which was open public grassland with basically the same vegetation as 35 years ago, with *A. inebrians* as an absolute dominant species. In 1993, it was divided into two areas: (i) one, rested in summer, had always been grazed by Tibetan sheep + yak and as a supplementary feeding site in winter, and had been fenced; and (ii) the other was still used as an open public pasture, with the same livestock grazing all year round. The distance was 20 m between cold-season grazing plus supplementary feeding pasture and four-season open public pasture, so the physical environment was similar (soil substrate and topography were the same). The altitude is 2910 m, annual mean temperature is −0.1°C, with monthly mean temperature ranging from −18.3°C in January to 12.7°C in July, and average annual accumulated temperature of 1380°C. The average annual precipitation is 416 mm, mainly concentrated in July–September and mostly terrain rain. There are only cold and warm seasons in the year, with the cold season in October–May, the warm season in June–September and the plant growth period generally April–September. The two grasslands are termed cold-season grazing plus supplementary feeding pasture (CSF) and four-season open public pasture (FOP).

2.2 Index determination and methods

During 15–18 August 2022, nine quadrats (1 m × 1 m) with representative and uniformly distributed vegetation were selected from each pasture for the vegetation community survey and soil sample collection. On September, 50 A. *inebrians* plants were selected from each pasture to calculate their population characteristics.

Soil samples were collected using a soil drilling core (d = 3.5 cm) divided into 0–10, 10–20 and 20–30 cm, with nine replicates in each quadrat; nine drills from each layer were mixed in bags and taken back to the laboratory. Each sample was divided into two subsamples and allocated to the following measurements: (i) soil nutrients and enzyme activity (air-dried soil) and (ii) soil microbial sequencing, for which 5–8 g of soil was dispensed into sterilized centrifuge tubes, stored on dry ice and brought back to the laboratory and stored at −80°C. Soil bulk density was sampled by a ring knife (100 cm^3 volume) and an aluminum box dried in advance was used to determine soil water content.

2.2.1 Survey of aboveground vegetation

The coverage of each species and the total coverage of the quadrat were measured by the needle-punch method. Ten plants of each species in each quadrat were randomly measured for their natural height. The aboveground biomass of each species was removed by the cutting method in each quadrat, put into an envelope, brought back to the laboratory, dried at 105°C for 30 min, then oven-dried at 65°C to constant weight and weighed. A sampling quadrat was tossed randomly 50 times into the plot and the frequency of each species recorded in each quadrat (Ren, 1998).

2.2.2 Reproductive capacity of *A. inebrians*

The crown size of *A. inebrians* was determined using a steel tape measure, and then a single plant was harvested and dried it at 65°C to constant weight and weighed. Another 30 clusters of *A. inebrians* were randomly selected to count the number of reproductive branches, and the ears were removed, put into an envelope; then their length was measured, they were threshed by hand and the weight of 100 grains was determined by 0.001 g electronic balance. Thirty reproductive branches were randomly selected and their spikelets were counted; 30 spikelets were randomly selected to count the florets and seeds per spikelet.

2.2.3 Soil properties

The soil bulk density, soil water content, total nitrogen, total phosphorus, available nitrogen, available phosphorus and soil organic matter were determined by ring knife method, drying method, Kjeldahl nitrogen method, molybdenum antimony anti-colorimetric method, alkaline diffusion method, $NaHCO_3$ leach-colorimetry method and external heating of $K_2Cr_2O_7$; and total potassium and available potassium were determined using a flame photometer (Model 2655–00, Digital Flame Analyzer, Cole-Parmer Instrument Company, Chicago, IL, USA), respectively (Bao, 2000). The urease, alkaline phosphatase, sucrase and catalase activities in soil were determined using sodium phenolate-sodium hypochlorite colorimetry, benzene disodium phosphate colorimetry, 3,5-dinitrosalicylic acid colorimetry and potassium permanganate titration, respectively (Guan, 1986). Soil pH was measured using a soil pH meter (PB-10, Sartorius, Göttingen, Germany). Soil samples were sent to Weikemeng Technology Co., Ltd. for Illumina MiSeq sequencing.

2.3 Data calculation and analysis

The Richness, Shannon–Wiener, Simpson diversity and Pielou evenness indexes were used to describe the species diversity of L and S, using the following formulas (Ma, 1994).

$$Pi = (C' + H' + B' + F')/4$$

$$D = 1 - \sum_{i=1}^{N} Pi^2$$

$$H = -\sum_{i=1}^{N} Pi ln Pi$$

$$Pi = \frac{H}{lnN}$$

where C' is relative coverage, H' is relative height, F' is relative frequency, B' is relative biomass (Lindsey, 1956), N is the total number of species in a quadrat and Pi is the importance value of species in the quadrat.

The soil microbial community used the Illumina NovaSeq platform for two-ended sequencing. The amplicon sequencing data (16S rRNA and ITS) were quality controlled, denoised and spliced to generate operational taxonomic unit, taxonomic annotation, species screening, basic statistics, significant difference comparison, α-diversity analysis, β-diversity analysis and correlation analysis using the DADA2 plugin in Qiime2 software. The species annotation information was obtained by comparing with the database [16S rRNA default Greengenes Database (version 13_8), ITS default United database (version 8.2)] The Shannon and Simpson indexes were used to assess the species diversity of samples, the Chao1 index was used to reflect species richness, and the Kruskal–Wallis method was used to determine whether there was a significant difference in an α-diversity index between the groups. Principal coordinate analysis of β-diversity was based on the weighted UniFrac distance calculation, and the significance of β-diversity was determined using Permutational multivariate analysis of variance. Besides, the closer the distance between the dots of different colors, the more similar the species composition and structure, and the closer the distance between the dots of the same color, indicating that the samples are better clustered in the group. The correlations between environmental factors and the relative abundance of soil microbiota at the phylum level were analyzed using Redundancy analysis, and the significance of the ranking axis feature values used the Monte Carlo permutation test.

All statistical analyses of vegetation community and soil physicochemical indexes were performed using SPSS software (version 19.0), including Shapiro–Wilk normal distribution assessment and independent sample t-test ($p< 0.05$). The measurement results are expressed as mean ± standard deviation. The data were plotted using Origin 2021.

3 Results

3.1 Characteristics of grassland plant communities in different pastures

3.1.1 Vegetation community characteristics and plant diversity

The aboveground biomass, coverage and height of *A. inebrians* for CSF were 52.73%, 94.32% and 19.00% lower than those of FOP, respectively ($p< 0.05$); the aboveground biomass and height of edible forage in CSF were 56.82% and 123.35% higher than those of FOP, respectively ($p< 0.05$), and there was no significant difference in the sum of the coverage of each edible forage between CSF and FOP ($p > 0.05$).

The vegetation community diversity differed between the two pastures: the Simpson and Pielou indexes for CSF were 12.86% and 26.03% higher than those of FOP, respectively ($p< 0.05$), but there were no significant differences in Richness and Shannon–Wiener indexes between CSF and FOP ($p > 0.05$) (Table 1).

3.1.2 Reproductive ability of *A. inebrians*

The length of the long and minor axes, dry weight and crown width of *A. inebrians* were 36.28%, 35.76%, 36.13% and 59.26% lower for CSF compared to FOP, respectively. The reproduction of *A. inebrians* was significantly lower for CSF than FOP, especially the seed yield and number of reproductive branches per plant were as high as 52% ($p< 0.05$) (Table 2).

TABLE 1 Vegetation community characteristics and plant diversity of different pastures.

Vegetation characteristics	Cold-season grazing plus supplementary feeding pasture	Four-season open public pasture
Aboveground biomass of *A. inebrians* (g)	22.09 ± 5.83b	146.73 ± 16.46a
Aboveground biomass of edible forage (g)	201.25 ± 29.63a	128.33 ± 26.91b
Coverage of *A. inebrians* (%)	3.30 ± 1.53b	58.60 ± 7.09a
Sum of sub-coverage of edible forage (%)	113.00 ± 7.21a	100.60 ± 6.43a
Average height of *A. inebrians* (cm)	53.50 ± 3.50b	66.00 ± 0.96a
Average height of edible forage (cm)	19.61 ± 3.22a	8.78 ± 1.73b
Richness index	7.67 ± 0.58a	9.00 ± 1.00a
Simpson index	0.79 ± 0.04a	0.70 ± 0.02b
Shannon–Wiener index	1.87 ± 0.26a	1.60 ± 0.13a
Pielou index	0.92 ± 0.10a	0.73 ± 0.07b

The data are expressed as mean ± standard deviation, and different lowercase letters after the standard deviation number indicate a significant difference between the two pastures ($p< 0.05$).

TABLE 2 Reproductive ability of *A. inebrians* in different pastures.

Indexes	Cold-season grazing plus supplementary feeding pasture	Four-season open public pasture
Length of the long axes	30.44 ± 1.54b	47.48 ± 0.89a
Length of the minor axes	23.89 ± 0.73b	37.19 ± 0.51a
Dry weight	12.90 ± 1.21b	20.19 ± 3.57a
Crown width	754.67 ± 82.23b	1852.33 ± 36.81a
Ears length (cm)	11.29 ± 0.55b	13.08 ± 0.47a
Seed yield (kg·hm^{-2})	35.27 ± 1.63b	74.11 ± 2.67a
Number of reproductive branches per plant	5.97 ± 0.35b	12.60 ± 0.26a
Spikelets per reproductive branch	32.50 ± 1.15b	38.63 ± 1.47a
Number of florets per spikelet	6.62 ± 0.06b	9.18 ± 0.09a
Number of seeds per spikelet	13.17 ± 0.45b	18.63 ± 0.57a
1000-grain weight (g)	0.98 ± 0.05b	1.13 ± 0.01a

The data are expressed as mean ± standard deviation, and different lowercase letters after the standard deviation number indicate a significant difference between the two pastures ($p < 0.05$).

3.2 Soil properties in different pastures

3.2.1 Soil physicochemical properties

Soil pH and bulk density tended to increase with greater soil depth in both pastures. However, soil water content, nutrients and organic matter tended to decrease (Figures 1, 2). Compared with FOP, CSF had significantly lower bulk density (by 29.46% and 10.53%) and greater soil water content (by 43.54% and 55.10%) for 0–10 and 20–30 cm, respectively ($p < 0.05$). Besides, CSF had significantly greater total nitrogen and total phosphorus in 0–10 cm (by 39.52% and 5.02%, respectively) and in 20–30 cm (by 33.59% and 45.23%), and had significantly greater total phosphorus and total potassium by 11.16% and 2.06% in 10–20 cm, respectively ($p < 0.05$). Compared with FOP, CSF had significantly greater soil organic matter, available nitrogen, available phosphorus and available potassium in 0–10 cm (by 29.67%, 28.45%, 68.42% and 23.77%, respectively) and 10–20 cm (by 10.68%, 11.25%, 93.75% and 31.20%, respectively). There were no significant differences for pH in the three soil layers, for bulk density, soil water content, total nitrogen and total phosphorus in 10–20 cm, for soil organic matter in 20–30 cm ($p > 0.05$).

3.2.2 Soil enzyme activities

The urease and sucrose activities tended to decrease with greater soil depth, which was opposite to the trend of catalase activity; and alkaline phosphatase activity tended to initially increase and then decrease in both pastures (Figure 2). Compared with FOP, CSF had significantly greater urease and sucrose activities by 8.31% and 45.71% only in 0–10 cm, respectively ($p < 0.05$). There were no significant differences in activities of the four enzymes in the other soil layers ($p > 0.05$).

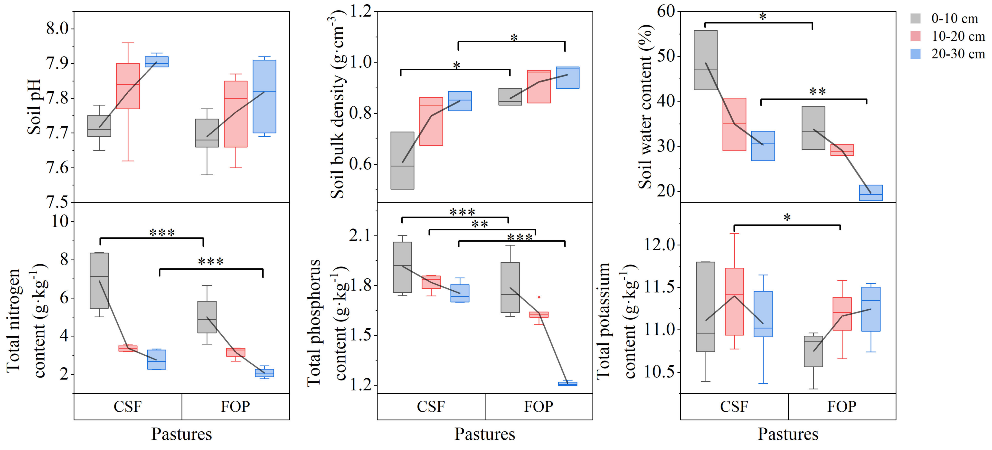

FIGURE 1
Soil physicochemical characteristics and total nutrients of different pastures. CSF and FOP are cold-season grazing plus supplementary feeding pasture and four-season open public pasture, respectively. *, ** and *** Significant at the 0.05, 0.01 and 0.001 probability level.

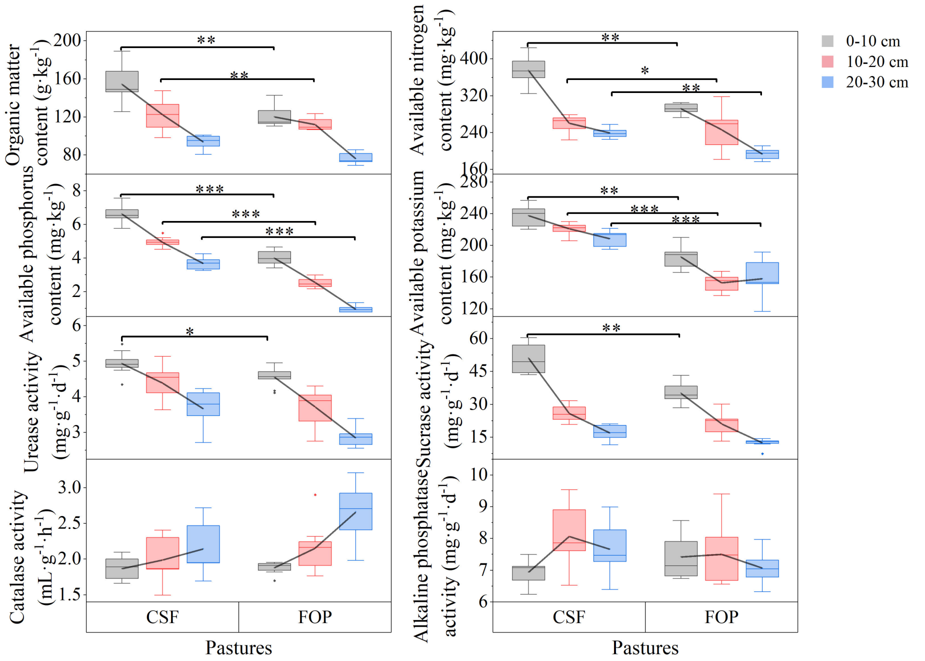

FIGURE 2
Soil available nutrients and enzyme activities of different pastures. CSF and FOP are cold-season grazing plus supplementary feeding pasture and four-season open public pasture, respectively. *, ** and *** Significant at the 0.05, 0.01 and 0.001 probability level.

3.3 Soil microbial community structure in different pastures

3.3.1 Soil microbial community composition

3.3.1.1 Bacterial community

The dominant bacterial phyla were Proteobacteria, Actinobacteriota and Acidobacteriota, but their relative abundances varied. The highest relative abundance was for Proteobacteria in 0–10, 10–20 and 20–30 cm, which was 37.78%, 30.16% and 32.99% in CSF, and 27.67%, 25.20% and 24.00% in FOP, respectively – all were higher for CSF than FOP. This was followed by Actinobacteriotaiota, with relative abundances of 16.87%, 24.33% and 26.91% in 0–10, 10–20 and 20–30 cm for CSF, respectively, and 22.68%, 28.96% and 31.67% for FOP. A total of 25 genera were detected in CSF and FOP, and nearly 30% of the bacterial taxa could not be classified clearly into any genus (i.e., designated unclassified). *Sphingomonas* was the dominant genera in 0–10 cm in CSF and FOP, with relative abundances of 3.91% and 3.94%, respectively, 67_14 and *Ralstonia*, *Pseudomonas* and 67_14 were the dominant genera in 10–20 and 20–30 cm, which was 4.51% and 6.04%, and 6.48% and 4.88%, respectively (Figure 3).

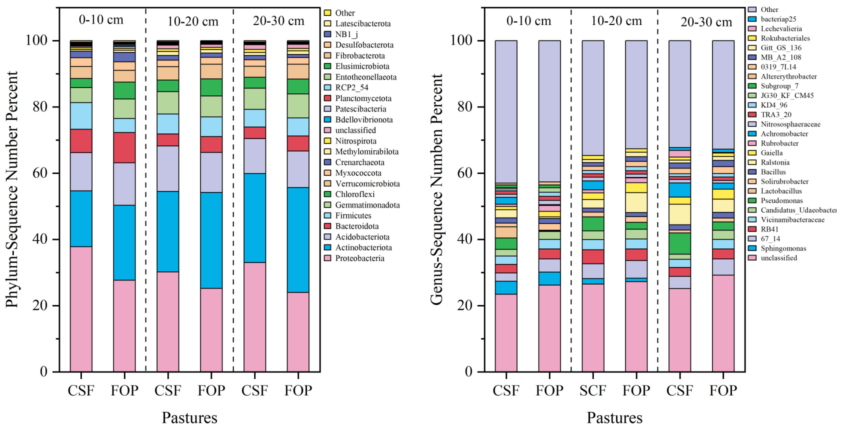

FIGURE 3
Relative species abundance of soil bacteria at phylum and genus levels in different pastures. CSF and FOP are cold-season grazing plus supplementary feeding pasture and four-season open public pasture, respectively.

3.3.1.2 Fungal community

The dominant fungal phyla were Ascomycota, Mortierellomycota and Basidiomycota, and their relative abundances varied. The highest relative abundance was for Ascomycota in 0–10, 10–20 and 20–30 cm, with 70.38%, 66.93% and 68.95% in CSF, respectively, and 73.03%, 68.42% and 70.1% in FOP – all were lower in CSF than FOP. This was followed by Mortierellomycota, with relative abundances of 16.20%, 16.59% and 14.68% for CSF, respectively, and 14.83%, 15.42% and 12.49% for FOP. A total of 32 genera were detected in CSF and FOP, with nearly 35% of the fungal taxa not able to be classified clearly into any genus (i.e., unclassified). *Mortierella* was the dominant genus in 0–10, 10–20 and 20–30 cm for CSF with 15.00%, 11.23% and 13.11%, respectively, and 13.95%, 13.98% and 9.61% for FOP (Figure 4).

3.3.2 Soil microbial community diversity

3.3.2.1 α-diversity

Bacterial α-diversity was overwhelmingly dominant in CSF and FOP, with the Shannon and Chao1 indexes significantly higher than those for fungi ($p< 0.05$). In the bacterial community, the Simpson index for FOP was significantly higher than for CSF in 0–10 cm by 1.41% ($p< 0.05$). In the fungal community, the Shannon, Simpson and Chao1 indexes for CSF were significantly higher than for FOP in 0–10 cm ($p< 0.05$), being 6.13%, 1.5% and 12.85% higher, respectively. There was no significant differences for α-diversity indexes in the other soil layers between CSF and FOP ($p > 0.05$). In addition, the α-diversity indexes were higher for FOP compared to CSF in the three layers of soil for bacteria, and for the Simpson index in 10–20 cm for fungi. The α-diversity indexes were higher for fungi in 0–10 and 20–30 cm of CSF compared to FOP (Figure 5).

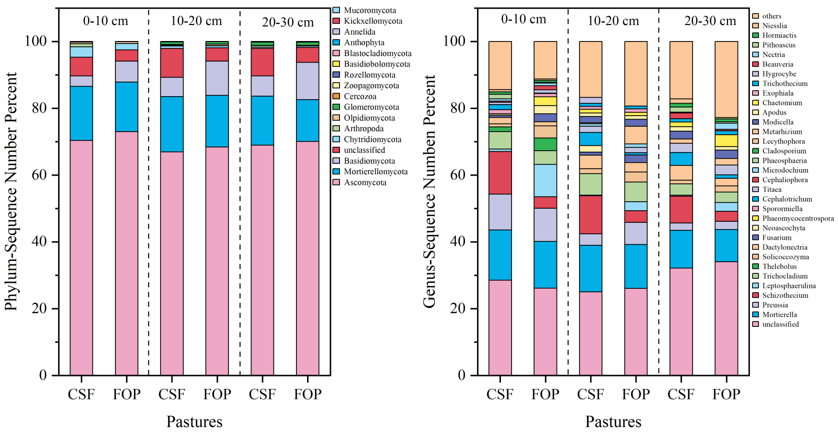

FIGURE 4

Relative species abundance of soil fungi at phylum and genus levels in different pastures. CSF and FOP are cold-season grazing plus supplementary feeding pasture and four-season open public pasture, respectively.

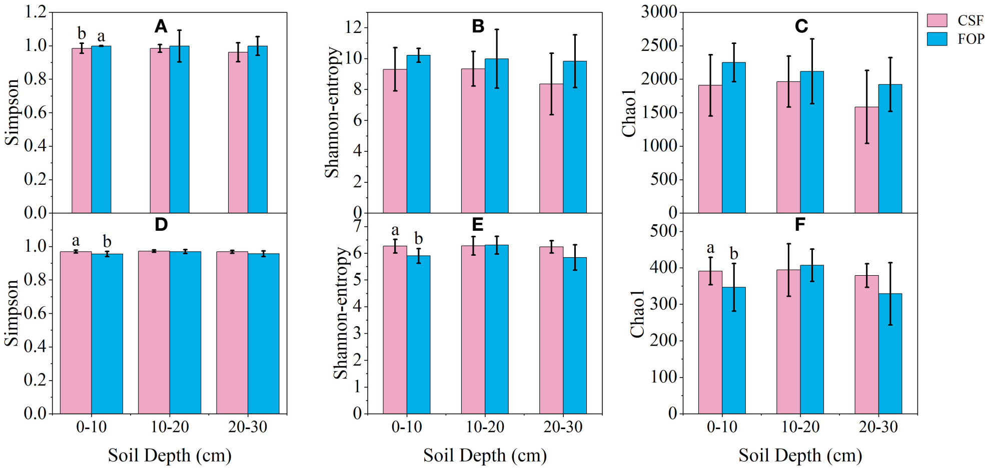

FIGURE 5

The α-diversity indexes of soil bacterial **(A-C)** and fungal **(D-F)** communities in different pastures. CSF and FOP are cold-season grazing plus supplementary feeding pasture and four-season open public pasture, respectively. Different letters indicate significant variation at the level of p=0.05.

3.3.2.2 β-diversity

The Bray–Curtis Permutational multivariate analysis of variance showed a significant difference in 0–10 cm for bacteria ($p< 0.05$), but no significant difference in deeper soil between the two pastures ($p > 0.05$). The fungal communities significantly differed in the three soil layers between CSF and FOP ($p< 0.05$) (Figure 6; Table 3).

3.4 Vegetation–soil–microorganism interrelationships in different pastures

Vegetation communities and soil physicochemical indexes were screened using Principal component analysis (Figure 7). The vegetation and soil factors were screened by PC1 load values greater than 0.28 and 0.30: the important vegetation factors were

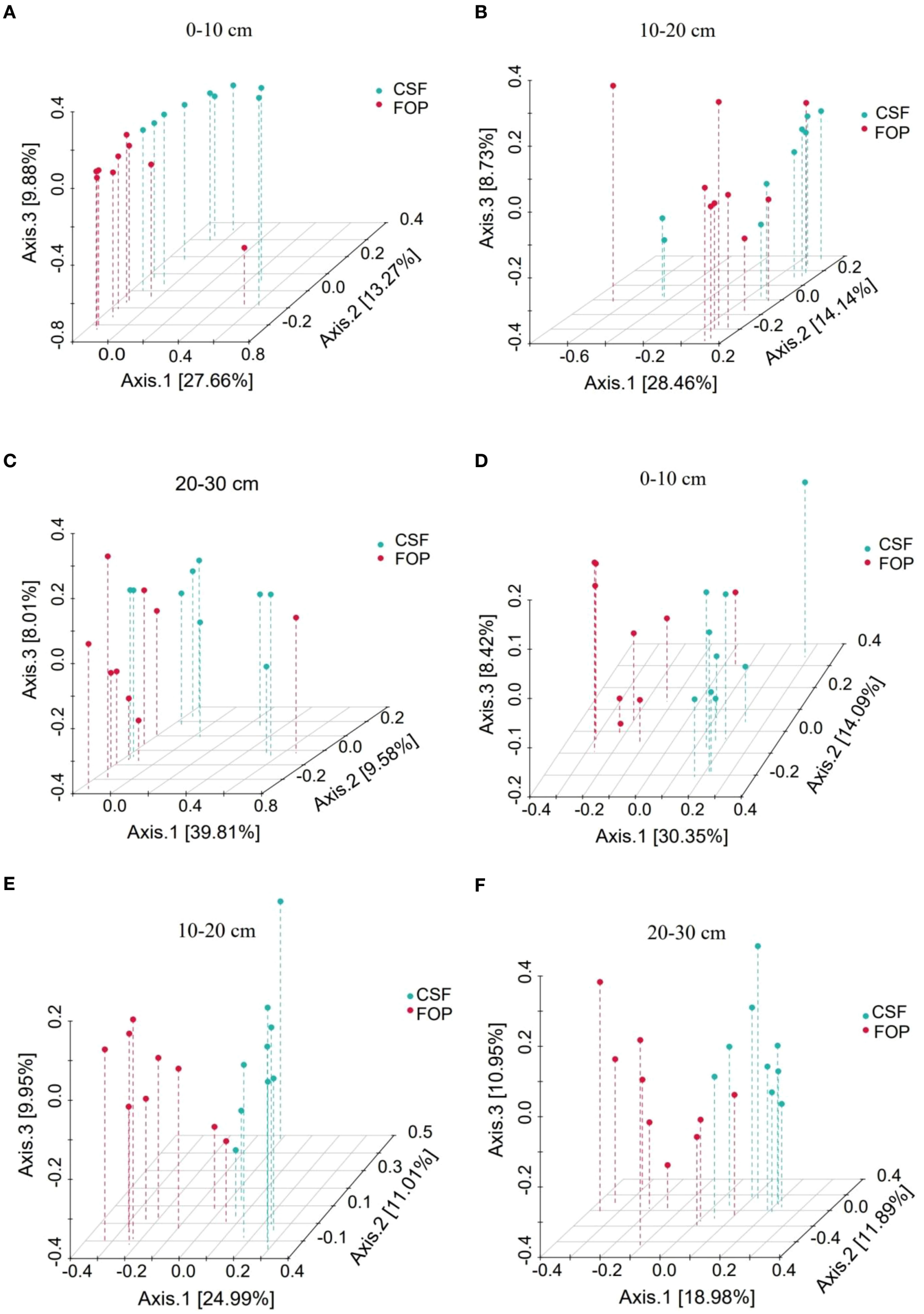

FIGURE 6
PCoA of β-diversity of soil bacterial **(A–C)** and fungal **(D–F)** communities in different pastures. CSF and FOP are cold-season grazing plus supplementary feeding pasture and four-season open public pasture, respectively. – This applies in other tables and figures below.

TABLE 3 Analysis of β-diversity between groups based on Permanova.

	Bacteria			Fungi		
Soil depth (cm)	0-10	10-20	20-30	0-10	10-20	20-30
Group 1	CSF	CSF	CSF	CSF	CSF	CSF
Group 2	FOP	FOP	FOP	FOP	FOP	FOP
Sample number	18	18	18	18	18	18
pseudo-F	2.093	1.6193	1.3813	5.886	3.899	2.771
p	0.005	0.079	0.162	0.001	0.001	0.001

CSF and FOP are cold-season grazing plus supplementary feeding pasture and four-season open public pasture, respectively.

aboveground biomass, coverage crown width, number of reproductive branches and seed yield of *A. inebrians*. The important soil factors were total nitrogen, total phosphorus, soil organic matter, and soil available nutrients in 0–10 cm; soil organic matter, available phosphorus and available potassium in 10–20 cm; and total nitrogen, total phosphorus and soil available nutrients in 20–30 cm.

3.4.1 Correlations among soil bacteria, vegetation and soil physicochemical properties

The cumulative contribution rates of the first and second axes were 45.34%, 45.63% and 46.67% in 0–10, 10–20 and 20–30cm, respectively (Figure 8) . The most abundant phyla were Proteobacteria, Actinobacteriota, Acidobacteriota and Bacteroidota, in 0–10 cm, which had large positive correlations with *A. inebrians* reproductive capacity; and Proteobacteria and Bacteroidota had high positive correlations with soil available nutrients. Proteobacteria, Acidobacteriota and Actinobacteriota were the most abundant phyla in 10–20 cm, which were influenced by available potassium, soil organic matter and crown width of *A. inebrians*, respectively. Proteobacteria and Actinobacteriota were the most abundant in 20–30 cm, with positive correlations with available nitrogen and seed yield of *A. inebrians*. Soil bacteria were most strongly correlated with the *A. inebrians* reproductive capacity and soil organic matter in 0–10 cm of CSF and FOP. In 10–20 cm, soil bacteria were strongly correlated with soil organic matter, available phosphorus and potassium in CSF, and seed yield, number of florets per spikelet, coverage and number of reproductive branches of *A. inebrians* in FOP. Soil bacteria were also highly positively correlated with crown width, number of reproductive branches, number of

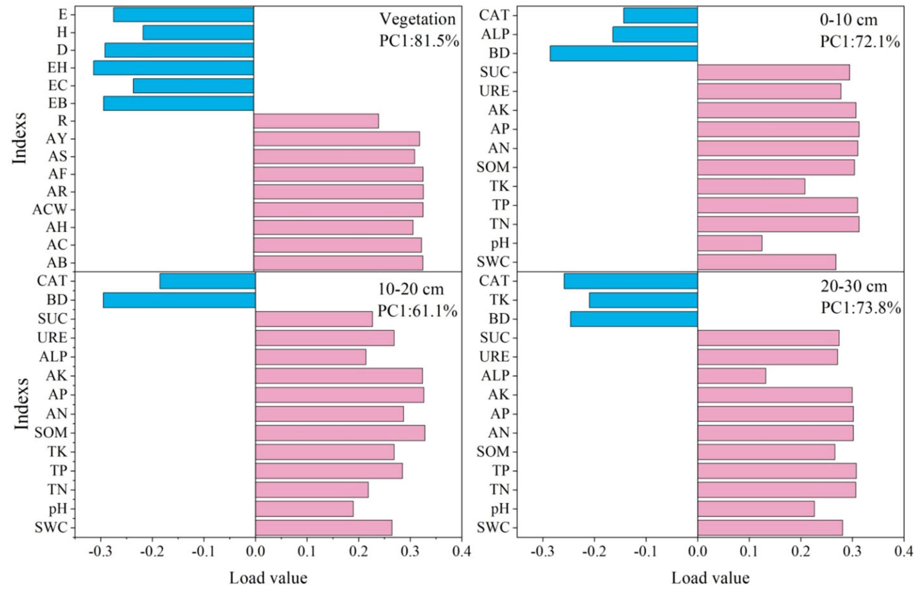

FIGURE 7
Vegetation community traits and soil characteristics of PC1 (Principal component analysis) axis load value. AB, AC, AH, ACW, AF, AR, AS, AY represent aboveground biomass, coverage, height, crown width, number of florets per spikelet, number of reproductive branches, spikelet per reproductive branches, seed yield of *A. inebrians* in turn; EB, EC, EH represent aboveground biomass, coverage and average height of edible forage in turn. E, Pielou evenness; H, Shannon–Wiener; D, Simpson diversity; BD, SWC, TN, TP, TK, SOM, AN, AP, AK, ALP, URE, SUC and CAT represent soil bulk density, water content, total nitrogen, total phosphorus, total potassium, soil organic matter, available nitrogen, available phosphorus, available potassium, alkaline phosphatase activity, urease activity, sucrase activity and catalase activity in turn. – This applies in other tables and figures below.

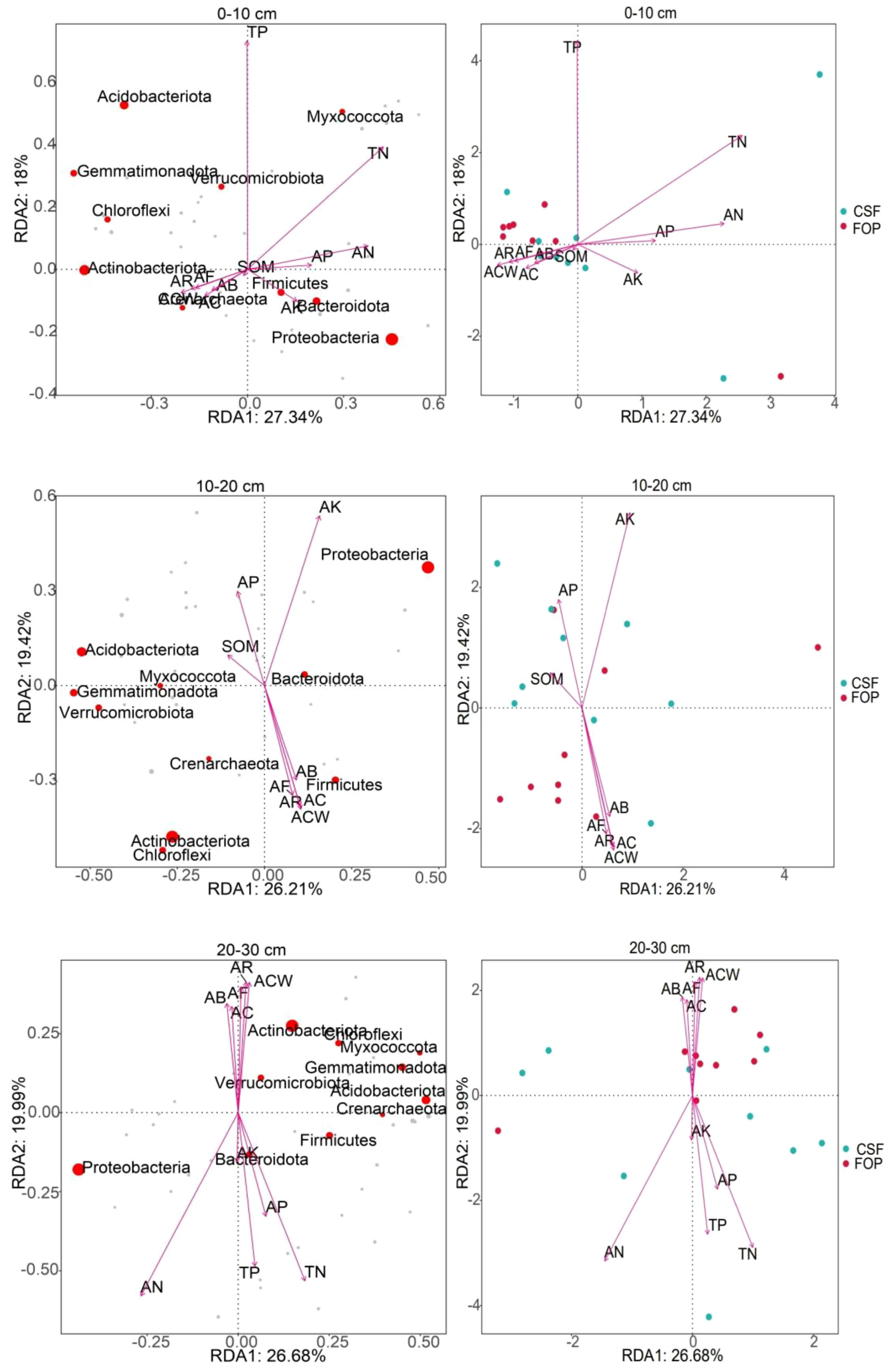

FIGURE 8
RDA of soil bacterial communities at the phylum level and environmental factors in different pastures.

florets per spikelet of *A. inebrians* in 20–30 cm of FOP, but the dispersion of CSF sample points was high. Combined with a Monte Carlo permutation test, soil bacteria were significantly correlated with available nitrogen only in 20–30 cm ($p< 0.05$), and had no significant correlations with each factor in the remaining two layers ($p > 0.05$) (Table 4).

3.4.2 Correlations among soil fungi, vegetation and soil physicochemical properties

The cumulative contribution rates of first and second axes were 51.58%, 54.61% and 48.64% in 0–10, 10–20 and 20–30 cm, respectively (Figure 9). The most abundant phyla were Ascomycota and Mortierellomycota in 0–10 cm, both with high positive

TABLE 4 Monte Carlo permutation test between soil bacteria, vegetation and soil physicochemical properties.

Soil layers	Indexes	RDA1	RDA2	r^2	*p*-value
0–10 cm	AB	−0.8555	−0.5178	0.0508	0.8111
	AC	−0.8414	−0.5404	0.0621	0.7256
	ACW	−0.9406	−0.3395	0.0864	0.5462
	AR	−0.9418	−0.3363	0.0736	0.6352
	AF	−0.9384	−0.3454	0.0679	0.6867
	TN	0.7339	0.6793	0.2267	0.1224
	TP	−0.0021	1.0000	0.2875	0.0600
	SOM	−0.5102	−0.8600	0.0092	0.9500
	AN	0.9808	0.1952	0.1508	0.2854
	AP	0.9977	0.0683	0.0787	0.6087
	AK	0.8332	−0.5530	0.0728	0.6302
10–20 cm	AB	0.2924	−0.9563	0.1670	0.2529
	AC	0.2581	−0.9661	0.2114	0.1699
	ACW	0.2571	−0.9664	0.2165	0.1534
	AR	0.2585	−0.9660	0.2105	0.1629
	AF	0.2261	−0.9741	0.1900	0.1999
	SOM	−0.7362	0.6768	0.0762	0.5557
	AP	−0.2502	0.9682	0.1647	0.2594
	AK	0.2815	0.9596	0.2991	0.0725
20–30 cm	AB	−0.0893	0.9960	0.1891	0.2114
	AC	−0.0518	0.9987	0.1833	0.2259
	ACW	0.0751	0.9972	0.2255	0.1484
	AR	0.0523	0.9986	0.2261	0.1444
	AF	0.0201	0.9998	0.2172	0.1579
	TN	0.3264	−0.9452	0.3070	0.0555
	TP	0.0949	−0.9955	0.2661	0.0905
	AN	−0.4184	−0.9083	0.3481	0.0410
	AP	0.2269	−0.9739	0.1837	0.2209
	AK	−0.0193	−0.9998	0.0853	0.5297

correlations with number of reproductive branches of *A. inebrians* and available potassium. Ascomycota and Mortierellomycota were the most abundant phyla in 10–20 cm, and Ascomycota was positively correlated with the *A. inebrians* population, and Mortierellomycota was strongly positive correlations with soil organic matter, available phosphorus and potassium. The fungal phyla with high abundance in 20–30 cm was consistent with abundances in shallower soil but were not highly correlated with each factor. Soil fungi were strongly correlated with soil chemical properties in CSF, and *A. inebrians* population traits in FOP. Sample point dispersion was high in 20–30 cm of CSF and FOP. Combined with the Monte Carlo permutation test, for 0–10 cm, fungi were significantly correlated with all factors except total phosphorus ($p< 0.05$), and very significantly correlated with aboveground biomass, coverage, crown width, number of reproductive branches and number of florets per spikelet of *A. inebrians*, soil organic matter and available nitrogen ($p< 0.01$); for 10–20 cm there were very significant correlations of fungi with all factors ($p< 0.01$). There were no significant correlations in 20–30 cm ($p > 0.05$) (Table 5).

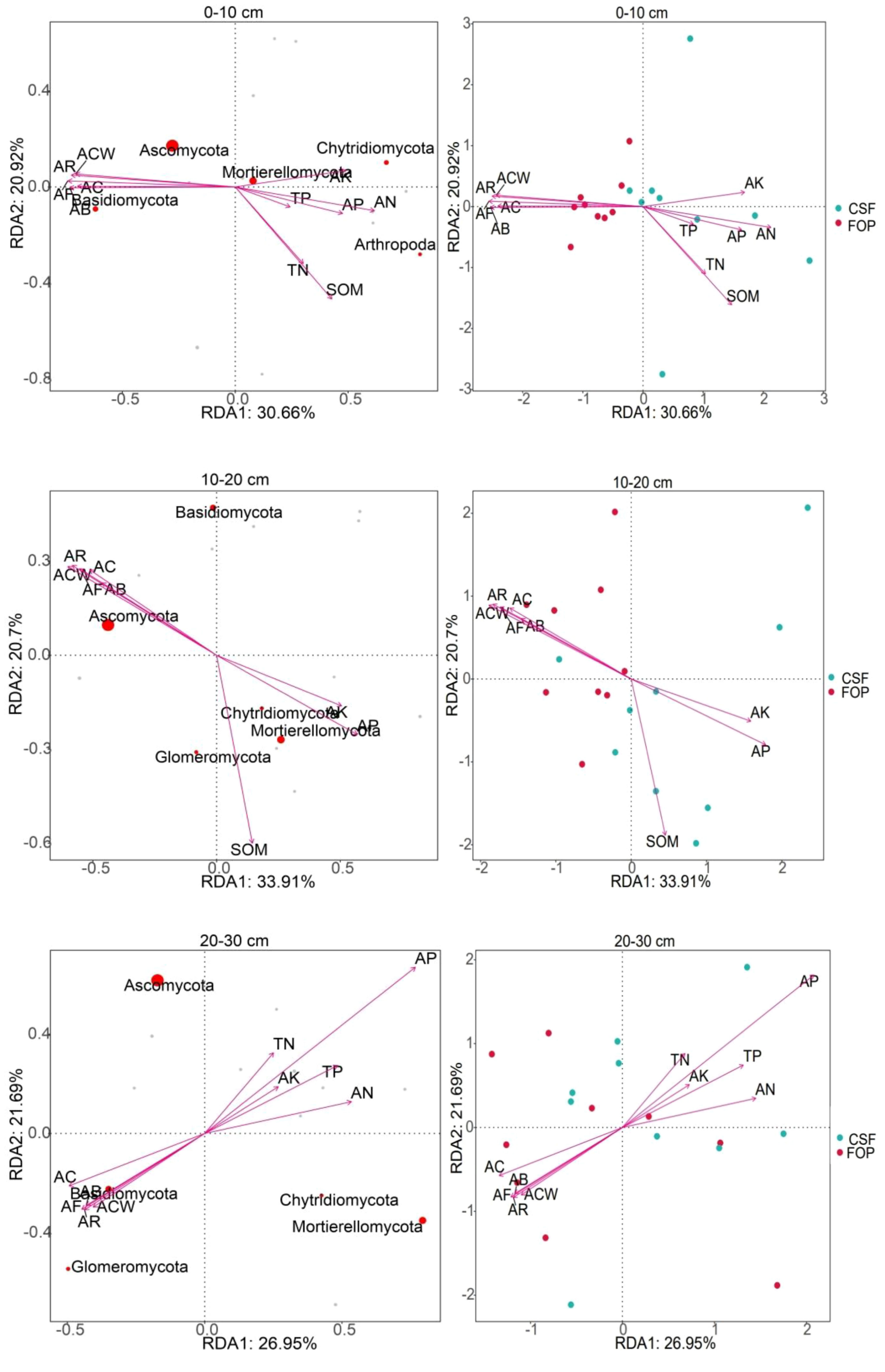

FIGURE 9
RDA of soil fungal communities at the phylum level and environmental factors in different pastures.

4 Discussion

4.1 Effects of grazing system on plant community characteristics

The ecological restoration of poisonous weed-type degraded grasslands is not only reflected in the poisonous weeds themselves but also in other plants and environmental changes in grassland communities. This study focused on *A. inebrians*, edible forage and community diversity, and attempted to study the vegetation community's changes in different pastures from multiple perspectives. The aboveground biomass and height of edible forage in the CSF were significantly better than in the FOP, while *A. inebrians* performed the opposite, and had the strongest inhibition of its coverage. Wang (1962) studied the "camping circle" of sheep in Tianzhu grassland in Gansu Province and found that the grass yield

TABLE 5 Monte Carlo permutation test between soil fungi, vegetation and soil physicochemical properties.

Soil layers	Indexes	RDA1	RDA2	r^2	*p*-value
0–10 cm	AB	-1.0000	–0.0046	0.5408	0.0005
	AC	-1.0000	0.0042	0.5157	0.0005
	ACW	–0.9971	0.0766	0.5230	0.0005
	AR	–0.9977	0.0679	0.5372	0.0005
	AF	–0.9994	0.0341	0.5476	0.0005
	TN	0.6863	–0.7273	0.3236	0.0480
	TP	0.9461	–0.3238	0.1896	0.2144
	SOM	0.6757	–0.7372	0.4670	0.0065
	AN	0.9875	–0.1578	0.4606	0.0065
	AP	0.9741	–0.2261	0.3601	0.0220
	AK	0.9904	0.1385	0.3649	0.0275
10–20 cm	AB	–0.8947	0.4467	0.4449	0.0085
	AC	–0.8830	0.4694	0.4979	0.0040
	ACW	–0.9045	0.4264	0.5708	0.0005
	AR	–0.8973	0.4414	0.5580	0.0010
	AF	–0.8947	0.4467	0.5308	0.0010
	SOM	0.2340	–0.9722	0.5297	0.0055
	AP	0.9136	–0.4066	0.5339	0.0015
	AK	0.9524	–0.3047	0.4553	0.0095
20–30 cm	AB	–0.8296	–0.5584	0.1447	0.3073
	AC	–0.9193	–0.3935	0.1496	0.2914
	ACW	–0.8069	–0.5907	0.1400	0.3238
	AR	–0.8179	–0.5753	0.1488	0.2984
	AF	–0.8258	–0.5639	0.1508	0.2924
	TN	0.6103	0.7922	0.1143	0.4113
	TP	0.8700	0.4931	0.1549	0.2824
	AN	0.9724	0.2333	0.1531	0.2829
	AP	0.7530	0.6580	0.2836	0.0845
	AK	0.8179	0.5754	0.0913	0.4763

and the proportion of Gramineae with excellent quality were increased significantly compared with outside the circle, and poisonous and pest grasses decreased significantly, consistent with our results. The reasons were that resting from grazing during the pasture rejuvenation period protected the plant's underground organs from being trampled by livestock, and resting from grazing during the pasture vigorous growth period prevented livestock feeding on plants with good palatability, and so these plants had stronger community competitiveness than plants with poor palatability (Yao, 2019). Thus, resting from grazing provided more abundant grass resources for grazing in the cold season, and was conducive to the vegetation renewal of plants with bud bank as their vegetative propagation mode of potential population. Zhang et al. (2018) showed that moderate grazing affected community structure and interspecific relationships, and that the competitiveness of general dominant species was inhibited by grazing, and the coexistence of dominant species and grazing-tolerant species improved grassland productivity and stability.

A. inebrians is the dominant grass species in degraded alpine meadows, the study of its response to different grazing systems plays an important role in the sustainable use and conservation of species diversity in *A. inebrians*-type degraded grassland (Zhang L. et al., 2019). Our studies showed that the *A. inebrians* developed adaptive strategies for different grazing systems, and the population characteristics, seed yield and composition factors had significant differences. The selective feeding of livestock can regulate the competition between liking and not liking forage, inhibit the foragehating and enhance the forage-loving, and then affect the community structure and function and grassland health (Hou and Yang, 2006). Continuous grazing throughout the seasons, without giving the grassland a chance to recuperate, and frequent gnawing of livestock reduces the biomass of edible forage, affects its material energy accumulation and so affects its growth, development and reproduction, and this gave *A. inebrians* an advantage in competition with excellent plant species and so its cluster diameter increased, effective photosynthetic area was larger, and more energy accumulated, which could be used for the production of more constituent factors. Studies in the Qinghai-Tibet Plateau also showed that grazing intensity exceeded the threshold, and the adaptability of *A. inebrians* to grazing environment was stronger than that of *Stipa purpurea* (Zhang et al., 2022). However, moderate trampling of livestock can stimulate and enhance the tillering ability of Gramineae in CSF, the density and coverage are bound to increase, and the ecological conditions in the grassland also change, and the growth of *A. inebrians* is inhibited with the weakening of light, and it will even be expelled from the grass for a long time. In addition, there are few studies on field seed yield in *A. inebrians*, so it cannot be compared with other literature.

As an important part of community structure, grassland plant community diversity plays a vital role in maintaining grassland ecosystem stability and productivity (Song et al., 2018). In this study, the Pielou index was higher for CSF and the Simpson index higher for FOP, indicating that the grassland community composition included fewer weeds, excellent forage grew well and was evenly distributed for CSF, while more weeds invaded FOP. This is likely because Gramineae and Leguminosae with good palatability were eaten first in FOP, which provided a better microenvironment and growth opportunities for some small non-dominant plant species, especially weeds. In addition, frequent grazing provided greater opportunities for livestock hair and hooves to carry and transfer external plant propagules (e.g., seeds and reproductive organs). Studies have also shown that continuous grazing leads to soil compactness, nutrient loss, inhibits compensatory growth of edible pasture, increases the proportion of inferior pasture, and decreases the diversity of community species, while reasonable grazing weakens the growth of dominant species in the community, provides survival opportunities for inferior species, increases community diversity, and then increases system productivity, which is not completely consistent with the our results (Zhang et al., 2022). Therefore, ecosystem function is closely linked to its biodiversity, but biodiversity does not necessarily provide the grazing services provided by ecosystems (Msadek, 2021).

4.2 Effects of grazing system on soil physicochemical properties and enzyme activity

Grassland soil is an important basic factor in the grassland ecosystem, and grassland vegetation change is closely related to changes in grassland soil fertility and activity, which affect each other (Merbold et al., 2014). Our study showed that soil pH increased with deeper soil, because plant roots were mostly concentrated in the 0–20 cm soil layer, so microorganisms were enriched in rhizosphere soil, and the respiration of root and rhizosphere microorganisms produces CO_2 that, combined with rhizosphere water, resulted in lower pH in the surface soil. The soil water content was enhanced and soil bulk density was reduced in CSF, because CSF was rested from grazing in the warm season; grass resources were abundant when grazing in October, grassland vegetation coverage was enhanced and livestock feeding time was shortened. When coupled with the low temperature in the cold season, bedding time was prolonged and walking time was shortened, which reduced the damage of livestock hooves to the turf and the soil water dispersion loss (Wang, 2017).

In terms of soil nutrients, we found that the content of soil total and available nutrients was low in FOP, because the amount of livestock gnawing and trampling rose with the increased grazing intensity, which decreases grassland primary productivity, existing stock of grassland plants and litter decomposition, thereby reducing soil nutrient content (Li, 2022). The non-growing season supplementary feeding and bedding scatter manure layer about 2 cm on the surface in CSF, and when the temperature increases in spring and the snow melts, it has favorable conditions, and the manure layer can decompose to produce a large amount of humus, which is conducive to the formation of soil aggregate structure and microbial activity, thereby improving soil physicochemical properties and fertility. As we all know, sheep's urine is rich in nitrogen fertilizer, which creates favorable nutritional conditions for the growth and development of Gramineae with high feed value, this is consistent with the view that grazing livestock trampling, and return of manure and urine had positive effects on soil nutrient improvement (Wang et al., 2008). So the response of soil physicochemical factors to grazing is uncertain. In addition, Sun et al. (2016) found that grassland degradation presented synchronous degradation of aboveground communities and soil, consistent with our conclusions.

Soil enzyme activity is related to microbial metabolic processes and biochemical cycles of nutrients. In this study, the alkaline phosphatase, urease, and sucrase activities were high in CSF, consistent with the results of Qin et al. (2014) showing that increasing grassland degradation in the Qilian Mountains could gradually reduce soil enzyme activities. The reasons are that soil enzymes are mainly derived from soil microorganisms, plant root exudates and animal and plant residues, continuous grazing in four seasons intensifies grassland degradation, affects plant root aggregation and lowers the amount and activity of soil enzymes (Zhang et al., 2015). Especially entering the grass withering period, the bedding time was shortened, the feeding and walking time was prolonged to eat food-loving plants, and there was even damaged or exposured of the hypocotyl or plumule of seedlings in the cold season. However, urease and sucrose activities in CSF were significantly higher than in FOP, because the high aboveground biomass increased the plant roots in the 0–10 cm soil layer, coupled with less soil compaction and good permeability, and so enhanced soil nutrient utilization, microbial activity and reproductive capacity (Poeplau, 2016). The catalase activity is involved in conversion of soil matter and energy, its activity can characterize the strength of soil biological oxidation process and it showed no significant change in CSF and FOP.

4.3 Effects of grazing system on soil microbial community structure

Soil microbes play an important role in grassland ecosystems. Grazing affects changes in the composition of soil microbial communities that may have direct or lasting effects on ecosystems (Jing et al., 2022). The bacteria with the highest relative abundance in CSF and FOP is Proteobacteria at the phyla level, showing CSF higher than FOP. Since Proteobacteria is the most common phylum in the world, and includes important soil bacteria, with its metabolic activity the most important bacterial activity in soil (Iino et al., 2010), which plays an important role in soil improvement, can degrade waste in the soil, not only can increase the soil nitrogen content, but also reflect the soil quality, so CSF treatment can improve the soil quality of of poisonous weed-type degraded grassland (Lin, 2017). The dominant genera in CSF and FOP were Sphingomonas and 67_14 for bacteria, and Mortierella for fungi. However, their relative abundances varied in the different pastures, which was partly consistent with the results from the degraded grasslands of the Qinghai-Tibet Plateau (Wang et al., 2022). This indicated that although the effects of seasonal grazing on soil microbial community composition differed, dominant microbiota were the same. Basidiomycota and Ascomycota predominate in environments with high soil lignin content and are some of the main decomposers of lignified vegetation debris (Araujo et al., 2017), which may be one important reason for Basidiomycota and Ascomycota becoming the dominant fungal phyla. Finally, there were characteristic microorganisms for CSF and FOP, indicating that grazing in different seasons had different effects on soil microbial species.

Soil microbial diversity is a key indicator reflecting the soil's ecological characteristics. We found that the bacterial α-diversity was higher than that of fungi in CSF and FOP, indicating bacterial dominance in the soil, which may be due to the trampling of livestock made the soil more compact, the aeration decreased, the number of gas-repellent bacteria increased slightly, and the bacteria's ability to adapt to poor environments led to the occurrence of this phenomenon (Yin et al., 2020; Wang et al., 2022). The α-diversity of bacteria and fungi differed only in shallow soil, likely due to the gnawing of livestock allocating more assimilated carbon to roots (Hou and Yang, 2006), while plant roots were mostly concentrated in shallow soil, which stimulates growth and activity of rhizosphere heterotrophic microorganisms. Besides, FOP increased grazing disturbance, had a strong spatial heterogeneity in the sample communities, and the sample information was more dispersed, resulting in greater differences in the abundance and diversity of soil microorganisms within the group, while soil samples had lower heterogeneity in CSF. The Principal coordinate analysis of β-diversity showed significant differences in fungal communities between the two pastures, possibly related to plant species composition differences, species composition variation of grassland vegetation may cause changes of litter and root exudate components, and soil fungal community structure is indirectly affected available substrate (Yin et al., 2020). Studies have also shown that differences in plant diversity mainly affect bacterial rather than fungal β-diversity (Prober et al., 2014).

4.4 Relationships among soil microbial community, vegetation traits and soil physicochemical characteristics under different grazing systems

Different grazing management of poisonous weed-type degraded grasslands cause successional changes in grassland vegetation community structure in alpine meadows, which then lead to soil characteristics changes, resulting in changes soil microbial community structure and diversity and finally feeding back to degraded grassland vegetation communities (Li, 2022), making the relationships among them more complex.

In this study, there were significant differences in plant community composition, soil physical properties, nutrients and organic matter. These factors were the main drivers of changes in the diversity and composition of soil bacterial and fungal flora, and there were differences in their correlations. Variations in plant species affect soil microbial communities by altering the number and diversity of soil rhizosphere exudates, the increase of aboveground biomass of grassland vegetation significantly affects the amount of litter input to the soil, increases the nutrient content of the surface soil, and is of great significance to its dynamic change (Zhang C. et al., 2019; Wang et al., 2022). And soil nutrient content can affect the population and distribution of soil microorganisms, soil microbial habitat change is directly related to changes in soil physical properties (Li, 2022). In addition, soil bacteria and soil organic matter had a high correlation, Milchunas and Lauenroth (1993) also found that grazing affects soil microbiota abundance by changing the amount of organic matter returned to soil. Soil fungi had a high positive correlation with the *A. inebrians* population, which may be related to the fact that *A. inebrians* itself is the host and mutualist symbiont of the *Epichloë* endophyte. Therefore, the grazing system plays an important role in changing the vegetation community's composition and soil characteristics, and causing changes in the soil microbial community's structure and composition (Turatsinze et al., 2021).

The effects of environmental factors on soil microorganisms are complex, and these factors also have complex interactions. When these factors are combined with other factors, such as precipitation, temperature and human disturbance, the interactions among them are more variable. From the perspective of vegetation–soil–microorganism interrelationships, the influence of different grazing systems on poisonous weed-type degraded grassland was studied, and appropriate grazing management strategies were proposed, which will be a vital part of future alpine grassland degradation research.

5 Conclusion

In the cold-season grazing plus supplementary feeding pasture, the aboveground biomass, coverage and reproduction of *Achnatherum inebrians* (Hance) Keng ex Tzvele were significantly inhibited, and the coverage and aboveground biomass of edible forage were significantly increased. And long-term utilization plus supplementary feeding in cold season had positive effects on grassland communities Simpson and Pielou indexes, soil water content, total nitrogen, total phosphorus and available nutrients. Moderate grazing in the cold season affected community structure and interspecific relationships, and dominant species were inhibited, providing opportunities for the growth and development of inferior species. The non-growing season supplementary feeding and bedding help soil agglomerate structure formation and microbial activity, improve soil traits, and increase soil fertility. Soil microbial communities were also affected by grazing systems, with a higher abundance of bacterial dominant species but the lower abundance of fungal dominant species in the cold-season plus supplementary feeding pasture. And only soil fungal community diversity differed significantly between the two pastures. Different grazing systems have a greater impact on vegetation and soil characteristics than microorganisms, and the response of soil microorganisms to grazing systems may be time-lagging and inconsistent, and bacterial and fungal communities respond differently. Therefore, grazing and supplementary feeding in the cold season treatment can effectively inhibit the growth of *A. inebrians*, restore edible pasture, and improve soil nutrients, which is particularly important for the *A. inebrians*-type degraded grassland ecosystem.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: BioProject, PRJNA1013135, https://www.ncbi.nlm.nih.gov/bioproject/?term=PRJNA1013135.

Author contributions

YC: investigation, data curation, methodology, writing – original draft, writing – review & editing. CX: investigation. KM: investigation. QH: supervision, writing – review & editing. XY: supervision, funding acquisition, writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher’s note

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Short-term restoration effects of ecological projects detected using the turning point method in the Three River Headwater Region, China

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The Three River Headwater Region (TRHR) is an important river source area providing important ecological functions. Decades ago, climate change and human activities severely degraded the ecosystem in the TRHR. To restore vegetation, a series of ecological projects have been implemented since 1989. Using net primary productivity (NPP) data from 1988 to 2012, a sequential Mann–Kendall trend test (SQ-MK) method was applied to identify the turning point of vegetation NPP. This approach was able to represent the critical response time of the vegetation to important disturbances. A 3-year time window was set after the implementation of one ecological project to detect and analyze its short-term effects. The ecological projects included the Yangtze River Basin Shelterbelt System Construction Project (YRCP), the TRHR Nature Reserve Construction Project (TNR), the Returning Grazing Land to Grassland Project (RGLGP), and the first phase of the Ecological Conservation and Restoration Project of the TRHR (ECRP). Our results showed that the vegetation in the TRHR responded positively to restoration: 89% of pixels showed an increasing trend and 54% of pixels underwent an abrupt change. The accelerated growth type accounted for the highest proportion among all types of detected turning points. In the ECRP's window, the positive turns rose rapidly, from 41% in 2005 to 86% in 2008, and it showed the most balanced restoration effects across grasslands. The alpine meadow and montane meadow restoration was largely influenced by the ECRP and the RGLGP (both >40%). The alpine steppe restoration was mainly attributed to the ECRP (68%). On the county scale, the positive turns in Yushu at the source of the Yangtze River mainly benefited from the RGLGP (56%), while the positive turns in Maduo at the source of the Yellow River benefited from the ECRP (77%). Nangqian, Tanggula and Zaduo County were still in need of intervention for restoration (< 3%). The results of the study can enhance our understanding of the spatio–temporal distribution of the short-term ecological benefits of different ecological projects, thus provide a scientific and timely reference for future planning and adjustment of the conservation and restoration projects.

KEYWORDS

alpine grasslands restoration, ecological conservation and restoration projects, Mann-Kendall test, short-term effect, turning point detection, Three River Headwater Region

1 Introduction

The Three River Headwater Region (TRHR), located in the hinterland of the Qinghai–Tibetan Plateau, is known as the "Water Tower of China" because of its crucial ecological functions and vital role in providing various ecosystem services for the whole country (Cao et al., 2020). Grassland is the dominant ecosystem type in the TRHR, and it is highly susceptible to the impacts of climate change and human disturbance (Liu et al., 2014; Zhai et al., 2020). Since the 1970s, the TRHR has experienced continuous vegetation degradation, resulting in biodiversity loss, soil erosion, wetland decline and other ecological problems(Liu et al., 2008a; Zhang et al., 2012). To protect and restore the fragile ecosystem, the Chinese government has launched a series of ecological projects. These projects aim to restore the degraded ecological environment through measures such as grazing prohibition, ecological migration, soil improvement and conservation. The projects include: the Yangtze River Basin Shelterbelt System Construction Project (YRCP) in 1989, the TRHR Nature Reserve Construction Project (TNR) in 2000, the Returning Grazing Land to Grassland Project (RGLGP) in 2003, and the first phase of the Ecological Conservation and Restoration Project of the TRHR (ECRP) in 2005 (Shi et al., 2011; Shao et al., 2013; Shao et al., 2016b; Shao et al., 2022).

To quantify the ecological benefits of ecological projects, and to understand the process and regional suitability of restoration measures, a large number of assessments and studies have been carried out in China and elsewhere. In 2002, the US Department of Agriculture launched the Conservation Effects Assessment Project, which assessed the impacts of four ecological conservation programs, such as the Wetlands Reserve Program, by comparing the project areas with the adjacent non-project areas, examining the changes before and after the project implementation, and contrasting the situations with and without the project interventions (Duriancik et al., 2008; Euliss et al., 2011). The Center for International Forestry Research used the Before–After–Control–Impact method to compare and assess the implementation effects of forest conservation projects REDD+ in 15 countries, and evaluated the role and contribution of the projects to carbon sequestration (Börner et al., 2016). The European Union implemented the Desertification Mitigation Assessment Project, which used a participatory evaluation to grade the effectiveness of specific measures for sand prevention and control in 12 countries (Rojo et al., 2012). China has carried out comprehensive benefit assessments of major projects such as the Three-North Shelterbelt System and the Grain for Green Project, and issued a series of National Reports on Ecological Benefit Monitoring of the Grain for Green Project (Administration, 2014) as well as evaluating the ecological effectiveness of ecological engineering in the Loess Plateau (Liu et al., 2017). In studies exploring the impacts of ecological engineering, vegetation characteristics (such as the leaf area index (Tong et al., 2018), vegetation productivity (Yang et al., 2014; Niu et al., 2019), vegetation coverage (Cai et al., 2022), and the vegetation index (Shen et al., 2018; Xu et al., 2020; Zhang et al., 2020)) are often used as the core ecological indicators for assessing the benefits of ecological projects. These indicators not only reflect the changes in vegetation, but also related closely to changes in ecosystem composition, structure and function (LaPaix et al., 2009; Terwayet Bayouli et al., 2021), as well as the environmental pressures that are associated with climate, hydrology and human activities (Ge et al., 2021). However, the restoration of vegetation is gradual and slow, thus it is necessary to identify and evaluate the long-term effects of a project by using long-term data.

Relying solely on long-term effect analysis not only leads to delayed evaluation of the outcomes of ecological projects, but also prevents timely and effective comparison and adjustment. At present, there are deficiencies in regional suitability assessment (Peng et al., 2016) and especially in the timely monitoring of measures (Yin et al., 2009; Liu et al., 2015) in ecological project assessment work. The impact and benefit assessment of ecological projects urgently needs more timely assessment methods. Large-scale analyses of remote sensing data that capture the short-term ecological effects of natural or human disturbances can be applied to monitor the changes in ecosystem conditions after sudden events. For example, Guzmán et al. monitored the short-term impact of oil spills on common shallow-water tidal reef coral (Guzmán et al., 1991). Lin et al. monitored and assessed vegetation recovery within two years of earthquake landslides (Lin et al., 2005). Han monitored vegetation dynamics in areas with different fire severity during the year after fire (Han et al., 2021). These studies all focused on detecting and identifying the rapid response of regional flora and fauna communities to habitat changes. In this study, the detected abrupt change of vegetation productivity was used as an indicator to achieve rapid detection of vegetation response after the implementation of ecological projects. The results obtained are the short-term effects of ecological restoration. We used the sequential Mann–Kendall trend test (SQ-MK) to identify significant turning points in NPP data series to examine vegetation fluctuations in a short period of time. The SQ-MK test is used to detect monotonic trends and turning points in time series data (Sneyers, 1991). It has no assumption for data distribution, high computational efficiency, easy implementation and the ability to identify the change of direction (Wei, 2007). Xulu et al. detected vegetation change using the SQ-MK test in South Africa (Xulu et al., 2021). Tong et al. quantified the effectiveness of ecological restoration projects in the karst regions of Southwest China (Tong et al., 2017). This detection method has been proven to rapidly identify the area and response time of vegetation to abrupt climate change or effective ecological projects. However, the applicability of this method to the high-altitude alpine grassland region, where field investigation and monitoring is more difficult, has not been reported yet. Based on Liu et al.'s findings, NPP is more sensitive to grazing intensity than NDVI in the Qinghai-Tibet Plateau (Liu et al., 2021). Therefore, we used NPP as the primary indicator of vegetation, as it represents both the net carbon sequestration by plants and the livestock production that we are interested in.

To assess the effectiveness and efficiency of the TNR, RGLGP and ECRP ecological projects in the TRHR, this study used NPP data from 1988 to 2012. The SQ-MK test and cluster analysis were applied to detect the trend and turning points in NPP to determine their occurrence and nature. The objectives of this study were to 1) analyze the spatial and temporal variability of the short-term effects and the process of different ecological projects; 2) assess the regional short-term effects of ecological projects after implementation; and 3) explore the reasons for the differences in the short-term effects of different ecological projects and the implications for subsequent restoration. The results of the study can provide a reference for assessing the short-term effects of major ecological projects.

2 Materials and methods

2.1 Study sites

The TRHR is found in southern Qinghai Province, China, a mountainous area of 35.66×104 km^2 between 31°39’–36°12’ N and 89°45’–102°23’ E. The average altitude is 4588 m and the climate is cold and dry with strong radiation. The multi-year average temperature is −5.38°C to 4.14°C and the precipitation is 262.2 mm to 772.8 mm (McGregor, 2016). The TRHR is in the source area of the Yangtze river, Yellow river, and Lancang river. It not only the largest nature reserve in China, but also a key area for global ecological functions (Figure 1). There are ten vegetation types distributed in the TRHR and grassland is the main ecosystem component (Department of Animal Husbandry and Veterinary, 1996). Grassland covers 26.27 million ha, accounting for 73.65% of the total area. In this study, the five major grassland types were selected. The area of alpine meadow was the largest, accounting for 74.79%, followed by alpine steppe, montane meadow, temperate steppe, temperate desert–steppe, accounting for 22.44%, 1.66%, 0.88%, and 0.24%, respectively.

2.2 NPP data

In this study, a 1988–2012 1000m resolution raster dataset of net primary productivity of vegetation in the TRHR was used. The data were obtained from the National Platform for Basic Conditions of Science and Technology–National Earth System Science Data Sharing Service Platform (http://www.geodata.cn). The Global Production Efficiency Model (GLO-PEM) (Prince, 1991; Prince and Goward, 1995; Goetz et al., 2000) is a novel model that estimates both net and gross primary production of terrestrial ecosystems at the global scale by using the production efficiency concept. The NPP dataset was calculated using absorbed photosynthetically active radiation (APAR) with the environmental factors that affect the efficiency of APAR conversion in the GLO-PEM model (Pinker et al., 2010; Wang et al., 2017). This data is reliable for ecological geography studies. It reflects the productivity of plant communities and the quality of terrestrial ecosystems (Shao et al., 2016b; Shao et al., 2016c; Shao et al., 2017; Liu et al., 2018).

2.3 SQ-MK test

In this study the SQ-MK test (Sneyers, 1991) was used to detect approximate trend turning points. It is based on the Mann-Kendall test, which is widely used to analyze the monotonic trends in hydrological and climatological data. Furthermore, it can identify the approximate turning points of a trend by applying the Mann-Kendall test to sequential segments of the data. The advantage of the SQ-MK test is that it has no assumption for data distribution, high computational efficiency, easy implementation and the ability to identify the change of direction (Wei, 2007). The formula for the

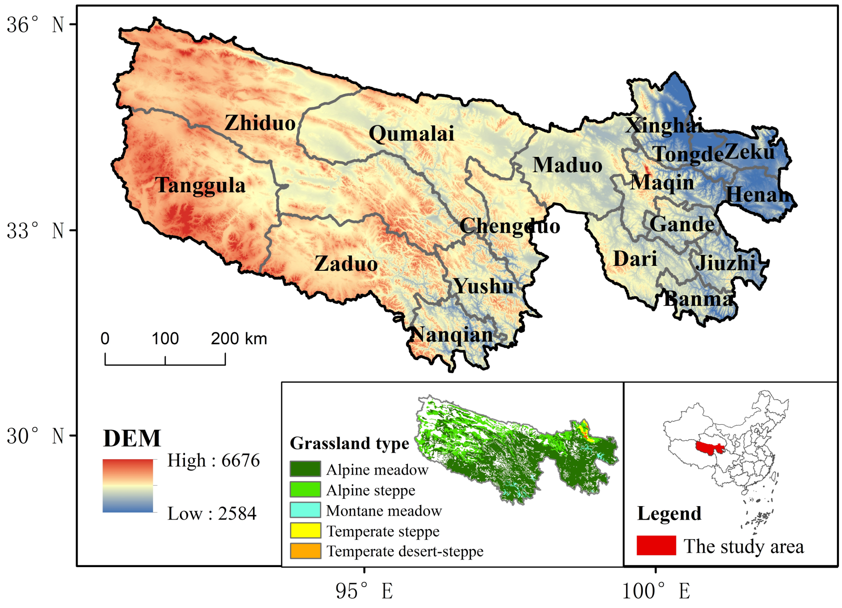

FIGURE 1
Grassland types and location of the Three River Headwater Region.

SQ-MK is as follows:

$$t_i = \sum_{j=1}^{i} n_i \tag{1}$$

$$E(t_i) = \frac{i(i-1)}{4} \tag{2}$$

$$Var(t_i) = \frac{i(i-1)(2i-5)}{72} \tag{3}$$

$$U(t_i) = \frac{t_i - E(t_i)}{\sqrt{Var(t_i)}} \tag{4}$$

The values of y_i, (i = 1, 2, 3,…, n) are compared with y_j, (j = 1, 2, 3,…, j−1), by using the ranked values of y_i from a given time series (x_1, x_2, x_3,…, x_n). In each comparison, the number of cases where $y_i > y_j$ is counted and assigned to n_i. $E(t_i)$ and $Var(t_i)$ is the mean and variance of the statistic t_i respectively. $U(t_i)$ is the standardized values of the statistic. Then, this method produces a forward trend ($UF(t_i)$) and a backward trend ($UB(t_i)$) of the time series calculated at the same time, but the $UB(t_i)$ values are computed by starting from the end of the time series. $UF(t_i)$ is an indicator of a positive NPP trend, while a negative UF indicates a declining NPP trend. The region where the indicators cross and diverge beyond the specified threshold (± 1.96 in this study) is regarded as a statistically significant trend, with the point of intersection indicating the start of a turning point in the trend.

To detect the type of turning point, we employed a segmented linear fitting approach, which involved comparing the linear fitting slopes before and after the turning point for each pixel. Assuming that the slope of the linear fitting before the turning point was a1 and the slope after the inflection point was a2, we defined the following criteria (Figure 2): if a1 > 0 and a2 > 0 and |a1|< |a2|, the type was “accelerated growth”, and if |a1| > |a2|, the type was “decelerated growth”. If a1< 0 and a2 > 0, the type was “positive reversal”. If a1< 0 and a2< 0 and |a1|< |a2|, the type was “accelerated decline”, and if |a1| > |a2|, the type was “decelerated decline”. If a1 > 0 and a2< 0, the type was “negative reversal”. Among the six types, accelerated growth, positive reversal and decelerated decline were defined as a positive turn, and the others were defined as a negative turn.

2.4 Regional short-term effects analysis

Based on positive turn, two indicators were used to compare and analyze the short-term effects of different ecological projects on regions (grassland types/counties). PT_A was the proportion of positive turn pixels to the total number of pixels in a region, reflecting the overall level of grassland restoration in that region. PT_P was the proportion of positive turn pixels from one project’s window (the 3-year time window) to the total positive turn pixels in three ecological projects’ windows (TNR, RGLGP, ECRP), reflecting the relative contribution of a specific project to grassland restoration in that region. The formulas are as follows:

$$PT_A = N_{P(i)}/N_A \tag{5}$$

$$PT_P = N_{P(i)}/\overline{N_P} \tag{6}$$

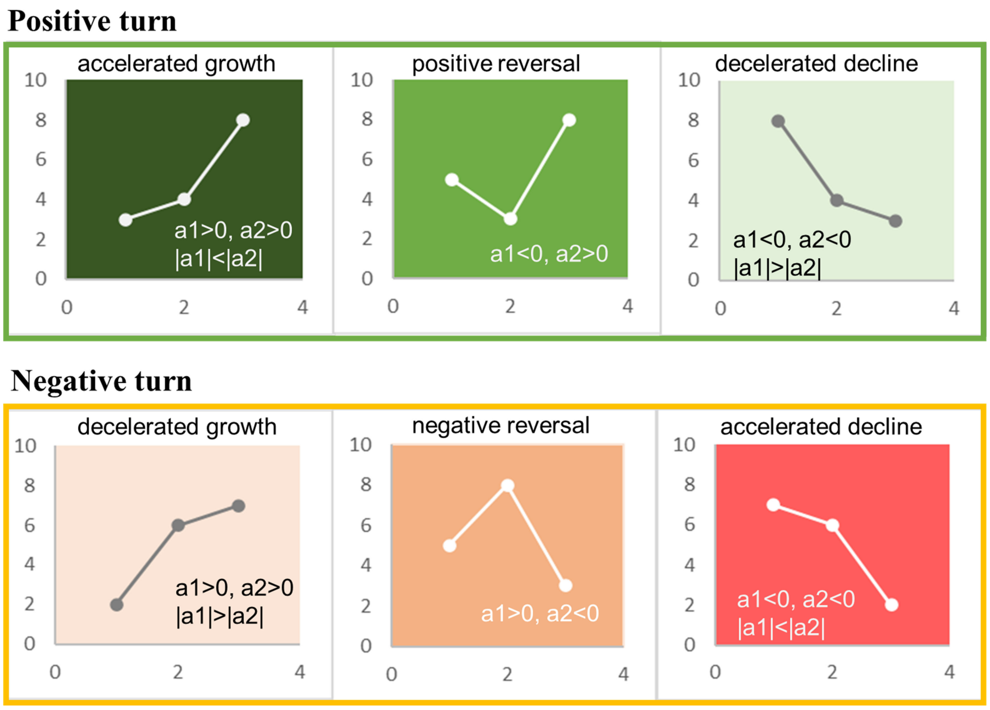

FIGURE 2
Types of turning points.

where $N_{P(i)}$ represents the number of positive turn pixels in the region with a certain project's window. N_A represents the total number of pixels in the region. $\overline{N_P}$ is the sum of positive turn pixels in the region within the three projects' windows.

2.5 Cluster distribution analysis

Spatial autocorrelation on the basis of feature locations and attribute values was measured using the Global Moran's I statistic. If the p-value is very small and the z-score is either very high or very low, then the pattern exhibited is not consistent with the theoretical random pattern represented by the null hypothesis, indicating a tendency toward clustering (Esri, 2021b).

The Optimized Hot Spot Analysis tool can identify statistically significant spatial clusters of high values (hot spots) and low values (cold spots). In this study we applied this method to examine the spatial variation of the timing of the turning points (Esri, 2021a).

3 Results

3.1 Spatial patterns of turning points in the TRHR

The results of the SQ-MK test pixel by pixel are shown in Figure 3A. The vegetation in the TRHR exhibited an increasing trend, with positive trend (UF>0) in 89.07% of the pixels and turning points in 54.47%. In general, 13.96% of the turning points occurred in 1989–1995, which were concentrated in the northern and southern parts of the TRHR. A further 24.95% occurred in 1996–2002, which were more prevalent in the western part; while 34.10% occurred in 2003–2007, which were mainly located in the eastern and central parts. Approximately 27% occurred in 2008–2010, which were situated in the southeast and extended to the central part. It can be observed that the number of turning points increased after 2000. The largest proportion of turning points occurred in 2008, accounting for 17.65% of the total, followed by 2004 with 17.55%.

From the perspective of turning point types (Figure 3B), the most dominant type was accelerated growth (41.06%), which spanned from the east to the west. Negative reversal, accounting for 26.92%, occurred primarily in the southern and northern parts. The other types of turning points were decelerated growth (21.80%), accelerated decline (5.19%), decelerated decline (4.34%) and positive reversal (0.69%).

The results of Global Moran's I (Figure 3C) statistic identified a significant positive spatial autocorrelation pattern with a large z-value and a small p-value, indicating that similar turning values tended to be clustered. According to the results of the Optimized Hot Spot Analysis (Figure 3D), the eastern part was a significant hot spot area and there were local hot spot clusters in the western part. The southwestern part was a significant cold spot area. This implied that the turning point time in the TRHR exhibited a delay from south to north and from west to east.

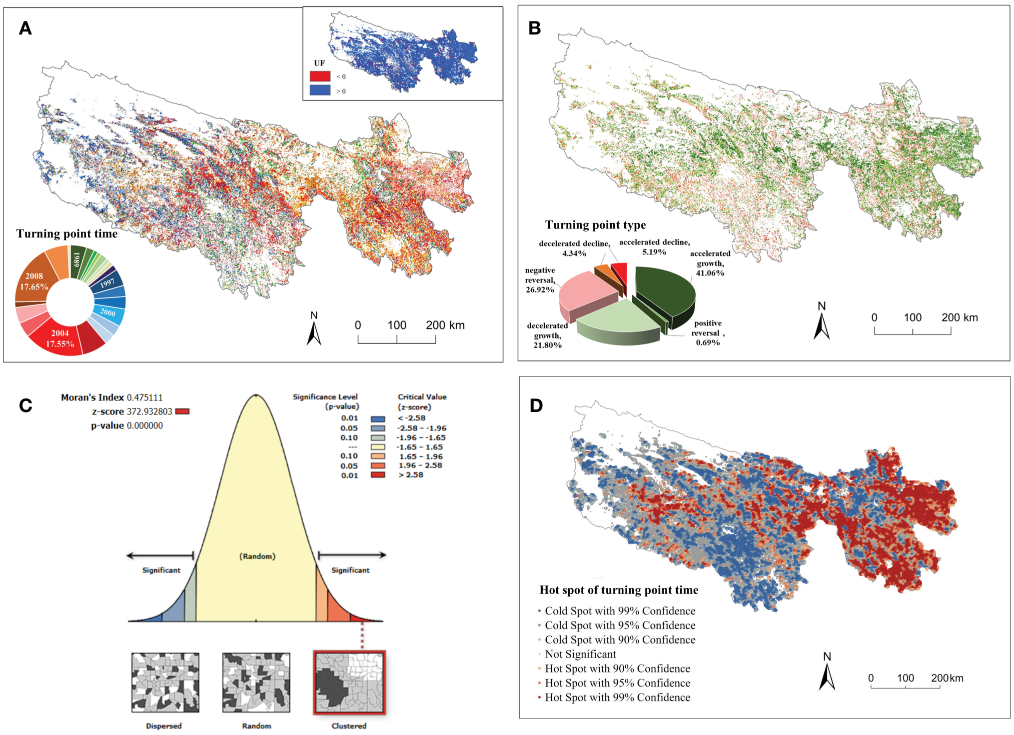

FIGURE 3
The spatial patterns of turning point time **(A)** and turning point types **(B)**; Global Moran's I result **(C)** and the hot spot results **(D)** of turning points in the TRHR.

3.2 Turning points of different grassland types in the TRHR

The turning point time of different grassland types was analyzed (Figure 4A). The most turning points for alpine meadow occurred in 2004 and 2008, accounting for 19.75% and 16.89%, respectively. For alpine steppe, the most turning points occurred in 2008 and 2004, accounting for 28.72% and 12.85%, respectively. For montane meadow, the most turning points were recorded in 2006 and 2004, accounting for 26.70% and 16.73%, respectively, while the turning points in other years were all less than 10%. The most turning points for temperate steppe occurred in 2008, 2010 and 2006, accounting for 38.90%, 15.10% and 14.92%, respectively and those for temperate desert–steppe also occurred in 2008, 2010 and 2006, accounting for 27.97%, 26.27% and 20.34%, respectively. Generally, alpine meadow, montane meadow and alpine steppe had earlier turning point time, while temperate steppe and temperate desert–steppe had later turning point time.

Comparing the turning point types (Figure 4B), it was observed that the majority of pixels in alpine meadow were the decelerated growth type, reaching 35.29%; followed by decelerated decline with 23.36%, positive reversal with 19.15% and accelerated growth type with 17.97%, while the other types were all less than 5%. The majority of pixels in alpine steppe were the accelerated growth type, accounting for 37.76%, while decelerated growth accounted for 27.14%, decelerated decline accounted for 17.59%, positive reversal accounted for 13.71%, and the other types were all less than 5%. The majority of pixels in montane meadow were the decelerated growth type, reaching 38.59%; followed by decelerated decline with 21.14%, accelerated growth type with 19.94% and positive reversal with 15.83%, while the other types were all less than 5%. The temperate steppe also had a majority of pixels of the decelerated growth type, reaching 41.27%; followed by accelerated growth with 32.29% and decelerated decline with 18.70%, while the other types were all less than 5%. The majority of pixels in the temperate desert–steppe was the accelerated growth type, up to 44.56%, while decelerated growth type made up 40.41%, and the other types were all less than 10%.

The proportion of positive turns in different grassland types (Figure 4C) showed that there were obvious peaks in 2004, 2006 and 2008, and that the peak in 2008 was higher than that in 2004 and 2006. The grassland types that had positive turn peaks in 2004 (>10%) were: alpine meadow, alpine steppe and montane meadow. The grassland types that had positive turn peaks in 2006 (>20%) were: montane meadow, temperate desert–steppe and temperate steppe. The grassland types that had positive turn peaks in 2008 (>30%) were: alpine steppe, temperate steppe and alpine meadow. The proportion of negative turns for different grassland types (Figure 4D) showed that there were significant peaks in 1989, 1997, 2004, 2006 and 2008, but the proportions were all less than 25%. In 1989, the negative turns of all grassland types were greater than 10%, and in 1997, the negative turns of alpine steppe and alpine meadow were both greater than 9.00%. In 2004, the grassland types with negative turn peaks (>10%) were: montane meadow and alpine meadow. In 2006, the grassland types with negative turn peaks (>10%) were: montane meadow and temperate desert–steppe. In 2008, the negative turns of temperate steppe and temperate desert–steppe were both greater than 20%.

3.3 Turning points of different counties in the TRHR

From the comparison of the turning points of each county, the years with more than 10% of the turning points were used to show the major turning point times for each county (Figure 5A). The major turning point times for both Zhiduo and Qumalai were in 2004 and 2008; Tanggula was 1998, 2000 and 2008; Xinghai and Maduo were 2004 and 2008; Tongde was 2006 and 2008; Zeku was 2005, 2006 and 2008; Maqin was 2003, 2004, 2006 and 2008, Chengduo was 2004, 2008 and 2009, Henan was 2003, 2004, 2005

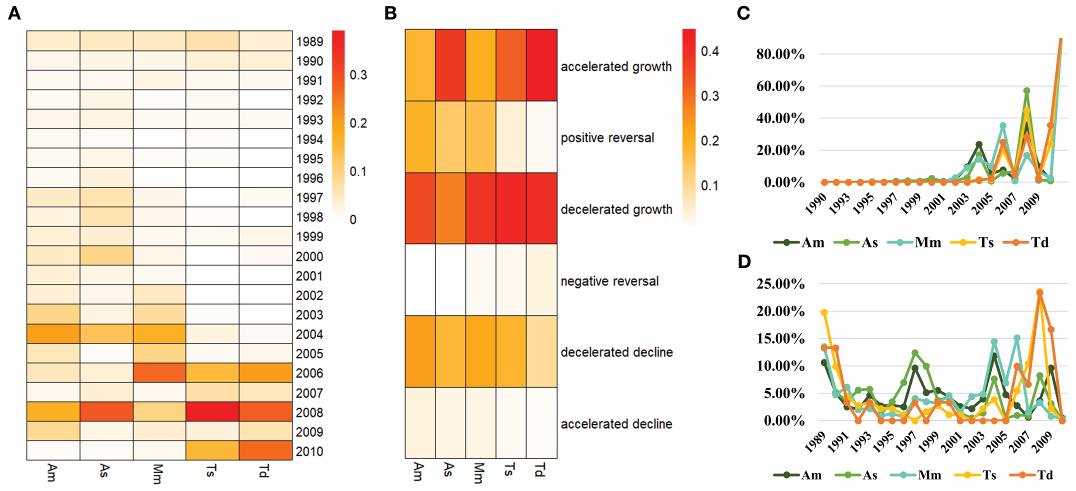

FIGURE 4
Turning point time (A), turning point type (B), the percentage of positive turns (C) and the percentage of negative turns (D) of different grassland types in the TRHR. Am, alpine meadow; As, alpine steppe; Mm, montane meadow; Ts, temperate steppe; Td, temperate desert-steppe.

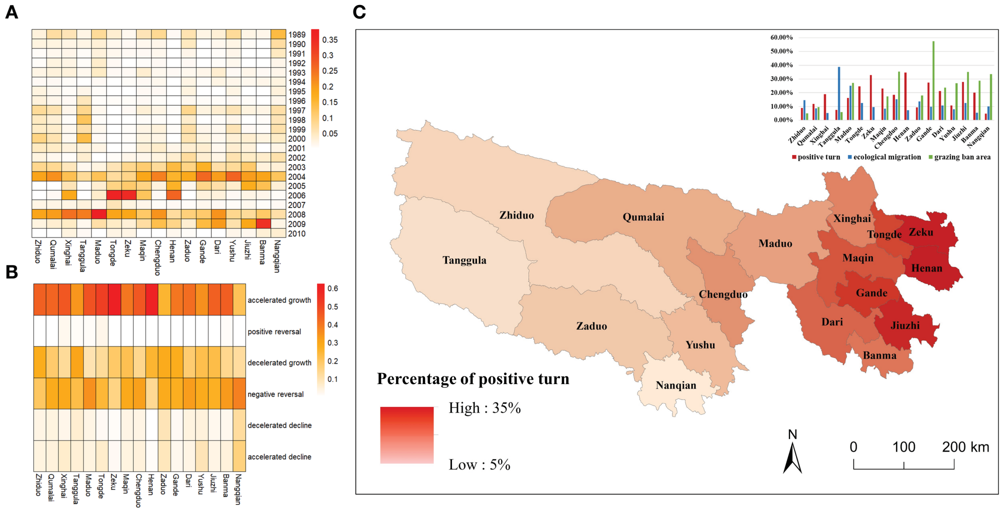

FIGURE 5
Turning point time **(A)** and turning point type **(B)** of different counties; the spatial pattern and percentage of positive turn (accelerated growth and positive reversal), ecological migration and grazing ban area **(C)** of different counties in the TRHR.

and 2006, Zaduo was 2004 only, Gande was 2003, 2004, 2008 and 2009, Dari was 2004, 2008 and 2009, Yushu was 2004, Jiuzhi was 2003, 2004, 2005 and 2009, Banma was 2004, 2005, 2008 and 2009; and Nangqian was 1989 and 2004. In terms of turning point types (Figure 5B), only Zaduo had a majority of pixels with decelerated growth. The other counties all had a majority of pixels with accelerated growth, with the highest proportion in Zeku of 62.21%.

The spatial distribution and the proportion of positive turns in each county was analyzed (Figure 5C). The proportion of positive turns decreased from east to west. Henan County had the highest proportion, accounting for 34.74% of the total area, while Zeku, Jiuzhi and Gande all exceeded 25%. Zaduo, Zhiduo, Tanggula and Nangqian all had proportions less than 10%, among which Nangqian had the lowest proportion, only accounting for 4.71% of the total area. According to the collected data of ecological projects during 2003–2005, Tanggula, Maduo and Chengduo had more than 15% of ecological migration, while Gande, Chengduo and Jiuzhi had more than 35% of the grazing ban area.

3.4 Short-term effects of ecological projects

The turning point types corresponding to each turning point time were analyzed (Figure 6A), and the short-term effect of each major ecological project was identified by applying a 3-year time window. It can be seen that there was no improvement in vegetation in the YRCP’s window for shelterbelts in 1989, because grassland was the dominant vegetation type in the TRHR. Therefore, the following short-term effect analysis only considered the TNR, RGLGP and ECRP.

In the TNR’s window, the proportion of turning points with decelerated growth increased, but so did the accelerated growth, which rose rapidly from 2000 to 2003 and reached 45.39% in 2003. The implementation of the RGLGP in 2003 stabilized the proportion of accelerated growth at approximately 45.00% until 2006. The launch of ECRP in 2005 boosted the proportion of accelerated growth again, from 41.32% in 2005 to 86.22% in 2008. These results indicated a clear trend of rapid vegetation recovery after each project. Spatially, the western part of the region had earlier turning points than the eastern part in the TNR’s window (2000–2003) (Figure 6B) and the RGLGP’s window (2003–2006) (Figure 6C), while the opposite was true in the ECRP’s window (2005–2008) (Figure 6D).

3.5 Regional differences in short-term effects

To compare the short-term responses of different grassland types, we calculated the PT_A for each grassland type in the TNR’s, RGLGP’s and ECRP’s window (Figure 7A). In the TNR’s window, the PT_A of grasslands was not high, with most positive turn in alpine meadow and montane meadow. In the RGLGP’s window, montane meadow had the highest PT_A, reaching 13.33%, followed by alpine meadow, reaching 9.56%. Other grassland types were approximately 3.5%. In the ECRP’s window, the PT_A for different grassland types was similar, with montane meadow still having the highest proportion, reaching 12.32%, followed by temperate steppe (10.88%), alpine meadow (10.50%), alpine steppe (8.23%) and temperate desert–steppe (8.10%). The county-level analysis of the short-term effects revealed that the PT_A varied across different regions in different windows. In the TNR’s window (Figure 7B), Henan (6.58%), Gande (5.15%), and Maqin (3.99%) were the three counties with the highest PT_A. In the RGLGP’s window (Figure 7C), the counties with the highest PT_A were Henan (25.99%), Zeku (21.16%), and Tongde (16.30%), while in the ECRP’s window (Figure 7D), they were Zeku (26.08%), Henan (20.23%), and Tongde (20.20%).

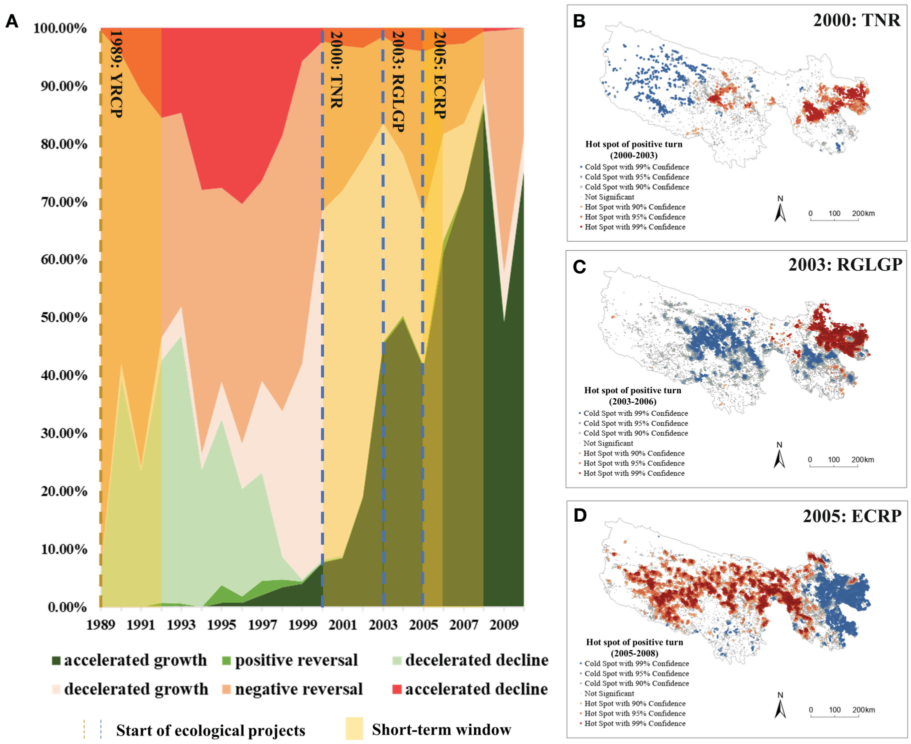

FIGURE 6

The percentage of turning point types in each turning point year **(A)**; hot spot results of positive turns during 2000–2003 (TNR) **(B)**, 2003–2006 (RGLGP) **(C)** and 2005–2008 (ECRP) **(D)** in the TRHR.

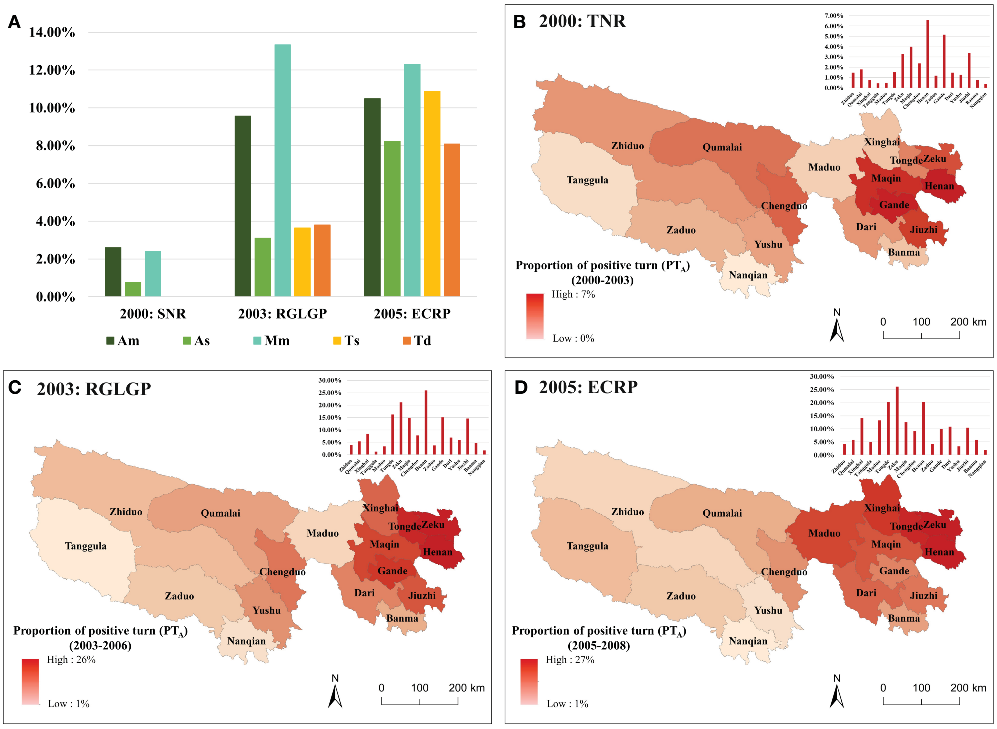

FIGURE 7

The PT$_A$ of different grasslands **(A)**; the spatial pattern of PTA during 2000–2003 (TNR) **(B)**, 2003–2006 (RGLGP) **(C)** and 2005–2008 (ECRP) **(D)** of different counties. Am, alpine meadow; As, alpine steppe; Mm, montane meadow; Ts, temperate steppe; Td, temperate desert–steppe.

An analysis of the source–destination diagrams shows the composition of the positive turns in the 3-year time window of the three projects (Figure 8). In terms of grassland types, the positive turn for montane meadow mainly came from the implementation of the RGLGP and ECRP, and the PT_P was 47.53% and 43.90%, respectively. The same was true for alpine meadow, accounting for 42.32% and 46.32%, respectively. For temperate steppe, temperate desert–steppe and alpine steppe, their positive turns mainly came from the implementation of the ECRP, accounting for 74.92%, 68.00% and 67.94%, respectively. At the county level, Yushu, Jiuzhi, Gande, Henan and Maqin were most affected by the implementation of the RGLGP, with a PT_P higher than 47%. Most other counties were mainly affected by the implementation of the ECRP, with a PT_P higher than 48%.

4 Discussion

4.1 Assessment of the short-term effects of restoration with turning point analysis

Combining the long-term NPP data from 1988 to 2012 and the SQ-MK test to obtain the turning point time and turning point type on a pixel-by-pixel basis, the results showed that the vegetation in the TRHR tended to have a positive response to ecological restoration during the past 25 years. Since 2000, a series of ecological projects for grassland restoration has been carried out in the TRHR. The study found that 72.56% of the pixels had a turning point in the TRHR after 2000 (Figure 3A), 73.55% of which were positive turn (Figure 3B). A study that compared remote sensing images in 2004 and 2012 confirmed that, the overall vegetation in the TRHR was in a stage where the degradation was limited to an initial stage, and some areas showed signs of improvement (Xu et al., 2017). We also found that the negative reversal rate was 26.92%, which means that there was a degradation in some areas. It is consistent with the findings of Shen et al., who compared the vegetation changes inside and outside the TRHR Reserve from 2005 to 2015. They found that the vegetation in some non-protected areas had become severely degraded (Shen et al., 2018).

Vegetation change is driven jointly by human activities and climate change, and the long-term trend in regional vegetation is influenced by the changing climate trend (Ge et al., 2021; Shi et al., 2021). To distinguish and identify the impact of the implementation of ecological projects on vegetation restoration more clearly, the study conducted a short-term analysis (the 3-year time window) of the four ecological projects implemented in the TRHR from 1988 to 2012 (Figure 6A). The study found that the YRCP implemented in 1989 with a long-term forest protection goal was the only project that did not significantly improve the vegetation in short term. This was because it was difficult to afforest the TRHR owing to its high altitude and its poor forestry basis (Zhang and Li, 2001). The TNR in 2000, the RGLGP in 2003 and the ECRP in 2005 did improve vegetation in a short period of time, but there were differences among them. The proportion of positive turns in the TNR's window increased rapidly, from 7.71% in 2000 to 45.39% in 2003. By protecting and rebuilding the balance of the ecological environment, the TNR reversed the rapid decline in biodiversity and curbed the degradation of the ecological environment in the TRHR (Yin et al., 2001). The positive turns in the RGLGP's window showed a slight but fluctuating increase in the short term with a mean rate of 49.41%. One study show that since the RGLGP was implemented in 2003, the grassland coverage in the TRHR increased by 15% to 20% (Wang and Rong, 2012). The proportion of positive turns in the ECRP's window increased significantly, from 41.32% in 2005 to 86.22% in 2008. Relevant

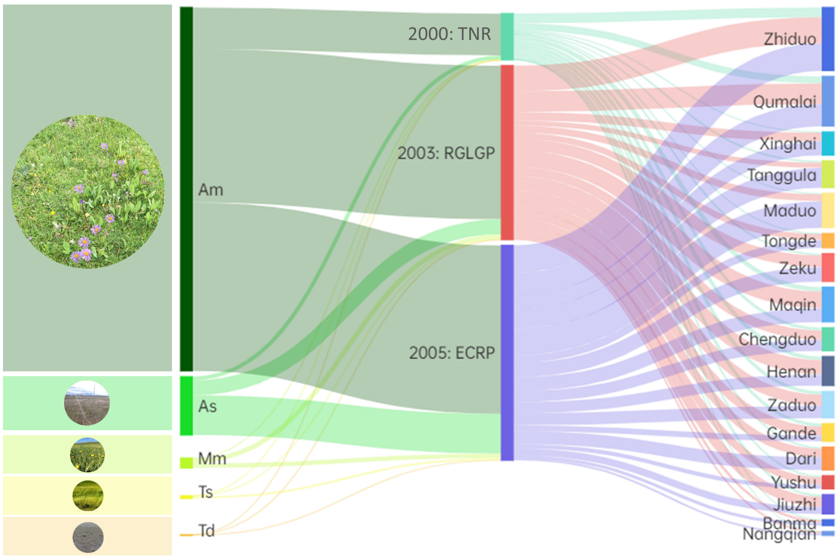

FIGURE 8
The source–destination diagrams of the positive turns from 2000–2003 (TNR), 2003–2006 (RGLGP) and 2005–2008 (ECRP) of different grasslands and different counties. Am, alpine meadow; As, alpine steppe; Mm, montane meadow; Ts, temperate steppe; Td, temperate desert–steppe.

studies found that since the implementation of the ECRP in 2005, the percentage of grasslands with excellent, good, and medium grass conditions had all increased significantly (Wang et al., 2022), which is consistent with the short-term effects observed in this study. From the four cases cited above, it can be inferred that a short-term window is applicable to identify the short-term effects of ecological projects.

Previous studies have used the difference analysis method to compare the short-term effects of ecological projects in the TRHR. The differences in the three-year average NDVI of different projects were used to analyze the vegetation status (Zhai et al., 2020). This method could capture the extent of the vegetation change in a specific period, but it had limited ability to detect and identify the areas with less impact from the projects, because the short-term window resulted in only small changes to the NDVI value of the vegetation. In our study, the turning point detection method was more sensitive and able to effectively capture the short-term spatio–temporal changes from vegetation which was influenced by ecological projects.

4.2 Varied short-term effects of different ecological projects

The ecological projects implemented in the TRHR targeted different grassland types for restoration and improvement, and these grasslands varied significantly among the projects (Figure 7A). The TNR had an impact only on montane meadow, alpine meadow and alpine steppe in the short term (all<3%), possibly because the nature reserve was mainly established in the west of the TRHR to protect the threatened animal and plant resources as well as water resources(He, 2001). Therefore, only the three grasslands mentioned above, located in the core of nature reserve, recovered rapidly in the early stage (Figure 1). The RGLGP significantly recovered montane meadow (13.33%) and alpine meadow (9.56%) in the short term. A previous study indicated that the optimal period of grazing prohibition in alpine meadows should be 5–7 years according to the complexity of plant communities and changes in key species (Zhang et al., 2021). However, in this study, it was found that the NPP of meadow grasslands recovered significantly within 3 years, as detected by the turning point method. The reason could be attributed to the rapid response to composite interventions in the grasslands because the RGLGP incorporated other measures such as over-sowing and fertilization (Shao et al., 2016a). In the short term, the ECRP had obvious recovery effects on all the grassland types and higher proportions of positive turns were witnessed in alpine meadows (12.32%) and temperate steppe (10.88%). The measures implemented by the ECRP, such as ecological migration, ecological compensation, and grazing prohibition and enclosure, were focused on the densely populated areas in the eastern part of the TRHR (Shao et al., 2017; Su et al., 2021). The livestock pressure on grasslands in grazing areas was significantly reduced (Liu et al., 2013; Shao et al., 2017), enabling the high productivity grasslands in the eastern part to show a stronger recovery trend in the short term. In summary, ecological restoration plans should be designed and adjusted based on the specific characteristics and needs of different grassland types and regions, and suitable restoration actions and periods should be selected, to prevent over-interference or omission of certain areas.

The positive effects of vegetation restoration induced by the ecological projects had different temporal and spatial development processes in the TRHR (Figure 5B). After the implementation of the TNR and the RGLGP, the positive turns first occurred in the west (Figures 6B, C), while after the implementation of the ECRP, the positive turns first occurred in the east (Figure 6D). Most long-term studies were able to record vegetation restoration trends and long-term changes in related indicators, but failed to detect the timing and process of restoration effects in short term (Shao et al., 2016b). The detection of short-term effects obtained in this study contributed to an understanding of the implementation and effectiveness process of various ecological projects in this region. The start-up process of the restoration effects might differ owing to the variations in the restoration measures of each project, the distribution of vegetation types in each region, and the composition of dominant species of grassland types. These phenomena indicate that different vegetation types might need different time spans to respond to the restoration measures of the projects. In addition, previous studies indicated that the response times to the restoration measures vary depending on the life history strategies of species that experience environmental disturbance (Albaladejo-Robles et al., 2023): perennial plants tended to respond more slowly than annual and short-lived plants (Yachi and Loreau, 1999; Lan and Zhang, 2008; Ma et al., 2017), and weeds in different plant functional groups tended to respond faster than grasses (Li et al., 2021).

By comparing the effects of different projects, it can be seen that the TNR, which was a protective project, had a lower short-term effect than the RGLGP and ECRP, both restorative projects (Figure 8). Protective ecological projects were more in line with the law of natural succession, but they could not completely prevent the impact of external disturbances and pressures on the ecosystem, nor could they restore the ecological functions and services that had disappeared (Tao et al., 2022). In 2000, the grasslands of the TRHR had formed a degradation pattern(Liu et al., 2008b), and at this time, restorative ecological projects were needed to artificially intervene and rebuild the severely damaged ecosystem (Rohr et al., 2018). Some parts of the TRHR grasslands that had reversed the degradation pattern (Shao et al., 2017) should receive protection-oriented management and utilization in the later stage (Li et al., 2012). When designing and implementing future ecological projects, different evaluation criteria and methods should be applied according to ecological projects of different types, and then integrated with the regional context, to select the most suitable ecological measures.

4.3 Varied regional responses of short-term effects in different ecological projects

Since the implementation of the ecological projects, the proportions of detectable vegetation restoration were different in each county in the TRHR (Figure 7). Evaluating the differences in the generation process and comparing composition of the positive turns in each county (Figure 8) can help to identify effective restoration measures in the region to promote and improve the implementation efficiency of follow-up projects. In the TNR's and RGLGP's window, the short-term effects were more obvious in the eastern counties of the TRHR (Figures 7B, C), which was consistent with the results of long-term observations (Zhai et al., 2020). Further analysis found that the positive turns in eastern counties such as Henan County and Zeku County mostly came from the RGLGP's window (PT_P was greater than 40% in both counties). The RGLGP's restoration measures had outstanding effects in these counties, which has been reported in several case studies of ground-based observations across the project sites (Duojie et al., 2008; Shao et al., 2016a; Xu et al., 2017). However, because the above-mentioned ecological projects only covered a part of the degraded grasslands, the total amount and extent of vegetation restoration in the whole region was relatively limited in analysis using remote sensing (Wang and Rong, 2012). The ECRP, which integrated multiple restoration measures, increased PT_A of 70% (12 out of 17) counties in the short-term window compared with the RGLGP. The uptrend took place mostly in the northeast and central parts (Figure 7D). Maduo County in the headwater area of the Yellow River showed the most obvious increase (of 9.81%), and the ECRP's window contributed to 77.24% of the positive turns. This was consistent with the results of studies on the long-term impact of the ECRP (Liangxia et al., 2014; Shao et al., 2017). The possible reason is that the diversified project measures of the ECRP effectively promoted the restoration of degraded alpine grassland in this area (Wang et al., 2020).

It is noteworthy that although the eastern and central parts of the TRHR recovered significantly, some of the southwest region were still in an ecologically fragile state. The PT_A of Nangqian, Tanggula and Zaduo County in the three projects' windows (TNR, RGLGP and ECRP) was low, with the average PT_A less than 3.50%. Relevant studies found that the vegetation in these three counties declined during 2003–2005 (Zhai et al., 2020). This could possibly be attributed to the fact that the environment of these counties in the southwestern part was relatively fragile and sensitive (Li et al., 2022); persistent ecological degradation, grassland degradation, and desertification were still present in some places (Liu et al., 2013; Cao et al., 2020; Wang et al., 2023); and the intervention restoration measures were insufficient for this special situation (Wang et al., 2021). Although the ECRP had outstanding performance in our analysis, there were still shortcomings with regard to the grazing prohibition and ecological migration of the ECRP (Du, 2012). The measures implemented in some parts with special natural conditions were unsuitable and unsustainable. Overall, the area showed considerable restoration outcomes under human project intervention. However, we suggest that, it is important to strengthen ecological monitoring and assessment of sensitive and vulnerable areas on the Qinghai–Tibet Plateau in the future. And it is necessary to select effective restoration measures through rapid comparison, detection and identification of immediate or short-term effects, and to expand the area covered by these measures (Shao et al., 2016c). Therefore, our study, which used short-term effects to assess the implementation outcomes and the different responses of various vegetation types to ecological projects, will provide a useful reference for restoring the damaged ecosystem on the Qinghai–Tibet Plateau more efficient through regional dynamic adjustment.

5 Conclusions

The study revealed that among the four ecological conservation and restoration projects implemented in the TRHR during 1988–2012, no significant recovery of regional vegetation occurred in a short term following the YRCP. The vegetation gradually recovered from west to east after the implementation of the TNR and the RGLGP. In the ECRP's window, and a significant short-term effect emerged, because the effect of regional vegetation restoration gradually spread from east to west. There were differences in response of different grassland types to the implemented projects. The restoration of alpine meadow and alpine steppe benefitted more from the RGLGP and the ECRP (all>40%); and the restoration of montane meadow benefitted most from the RGLGP, which represented 47.53%. The ECRP was the most effective for restoring different grassland types and the improvement was relatively balanced (all>46%). Approximately 74.92% of the temperate steppe area improved significantly due to the ECRP. For different counties, the TNR and the RGLGP mainly promoted vegetation restoration in the eastern counties, while the ECRP mainly promoted vegetation restoration in the northeast and central counties. The contribution to vegetation restoration in the counties at the source of the Yellow River was mainly came from the implementation of the ECRP, and 77.24% of the positive turns in Maduo County occurred after that. However, the positive turns in Nangqian, Tanggula and Zaduo County remained low (<3%) after each project, and the regional vegetation in these counties was still needed further intervention and restoration. We believe that evaluating ecological projects requires more attention to identifying and evaluating the short-term effects. Compared with long-term project effects evaluated after a long period of implementation, feedback on short-term effects can guide the dynamic adjustment and continuous improvement of ecological projects through timely feedback.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding author.

Author contributions

YL provided the idea for this research and contributed to the analysis design. YZ prepared the primary version of manuscript. YL and YZ collected the data, contributed to the data analysis and figure-making. YL contributed to revision for the manuscript.

Both authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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Changes in bud bank and their correlation with plant community composition in degraded alpine meadows

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Bud banks are considered a crucial factor in regulating the species composition of grassland communities and maintaining the ecological function of alpine grasslands. However, few studies have paid attention to the dynamic changes of bud banks from undisturbed to severely degraded alpine meadows. Therefore, this study examined the correlations between plant diversity and bud bank traits at different stages of alpine meadows degradation. Grass biomasses and plant diversity were found to be highest in moderately degraded meadows, and sedge biomasses were highest in lightly degraded meadows. Lack of disturbance and moderate disturbance by herbivores increased the bud bank density of alpine meadows. Consistent with the changes in bud bank density, bud bank diversity was highest in undisturbed meadows. The structural equation model indicated that the densities of rhizome and the densities and diversities of tiller buds play crucial roles in facilitating the greater diversity of the plant community. Our findings suggest that the diversities and densities of rhizome and tiller buds in the degradation stages are synchronized with changes in plant diversity, and in the regenerative ability of bud banks, which largely determine the outcome of restoration in degraded meadows. These findings could provide a frame of reference for effectively restoring degraded alpine regions by regenerating bud banks. The potential driving force and renewal capacity of bud banks should be taken into account in restoring the Qinghai-Tibet Plateau's degraded meadow.

KEYWORDS

alpine meadow, degraded grassland, bud bank, vegetative reproduction, diversity index

Introduction

Bud banks are defined as collections of buds, such as rhizome, tiller and corm buds, that have the potential to carry out vegetative reproduction (Qian et al., 2014; Liu et al., 2022). Rhizome buds mainly generate from the belowground horizontal rhizomes of dicotyledons and monocotyledons; tiller buds originate from the bases of plant tiller nodes; and corm buds develop from the tips of underground stems (Klimešová and Klimeš, 2007). Previous studies have shown that bud banks play a fundamental role in regulating vegetation communities and plant diversity - especially for plant communities with low seed yields, because seed germination has a negligible contribution to plant regeneration (Clarke et al., 2013; Dong et al., 2015). For example, an alpine meadow with a dense sod layer was dominated by perennial clonal plants. Based on this observation, it can be argued that changes in plant composition, population regeneration, and community dynamics mainly rely on plant bud banks rather than on soil seed banks (Vítová et al., 2017; Wu et al., 2020a).

The reproductive and regenerative capacities of plant bud banks in alpine regions are affected by variable environmental conditions, such as severe drought, fire and disturbances by herbivores (e.g. trampling and feeding) (Enright and Mille, 2007; Klimešová and Klimeš, 2007; Willand et al., 2013; VanderWeide and Hartnett, 2015). Carter et al. (2012) found that drought reduces the density of belowground bud and that the bud densities of grasses and forbs differ in sensitivity to water-deficiency conditions. Bud banks are also reduced in number as mean precipitation decreases (Dalgleish and Hartnett, 2006). Furthermore, fire has positive effects on regulating bud bank density (Benson et al., 2004; Dalgleish and Hartnett, 2009; Russell et al., 2019; Alexandre et al., 2022). For example, Russell et al. (2019) found that grass bud renewal activity is stimulated by burning. Similarly, Alexandre et al. (2022) found that seasonal fires play a vital role in bud bank dynamics in the Brazil's Cerrado savannah and that bud bank densities decrease in the dry season. Some buds can develop into new branches in the rainy season. In tallgrass prairies, the total density of bud banks in burnt grassland is twice that of unburnt grassland (Dalgleish and Hartnett, 2009; Benson et al., 2004). Additionally, herbivores can affect bud banks by removing bud resources or stimulating bud outgrowth (Dalgleish and Hartnett, 2009; Harmony et al., 2009; Ott et al., 2019). For example, Harmony et al. (2009) found that grazing and trampling by herbivores markedly reduces the bud density of heavily grazed tallgrass prairies in North America. Dalgleish and Hartnett (2009) suggested that buds renewal rate increases, but bud density decreases in grazed grassland, compared to un-grazed grassland. Therefore, long-term or intensive grazing by herbivores may result in reducing the reproductive capacities of underground bud banks, which may explain the decrease in or loss of degraded grasslands' self-recovery capacities (Dalgleish and Hartnett, 2009; Ott et al., 2019). Few studies, however, have paid attention to the dynamics of bud density among the different stages of grassland degradation.

Alpine meadows are the most important grassland component of the Qinghai-Tibet Plateau, playing a crucial role in maintaining biodiversity and ecosystem balance, conserving soil and water and regulating global climate change (Yang et al., 2022). However, alpine meadows demonstrate a tendency toward extensive degradation due to the combined effects of climate change, unreasonable anthropogenic disturbances, overgrazing, and rodent burrowing (Min et al., 2011; Fayiah et al., 2020). Previous studies have indicated that bud banks should be regarded as a driving factor of disturbances to plant self-regeneration in perennial grassland ecosystems, and they can be used as effective indicators of the dynamic succession of plant communities (Wang et al., 2008; Rusch et al., 2011; VanderWeide and Hartnett, 2015). Hartnett et al. (2006) attributed 99% of vegetation renewal to the bud banks of perennial caespitose grasses in North American grasslands. Ott and Hartnett (2012) reported that active buds largely determine grasslands' potential renewal, and that bud bank structure and dynamics differ among functional groups, including C3 and C4 species. Interspecific differences in bud bank dynamics also drive the dynamic patterns of aboveground plants. Similarly, Eighty-four percent of the Alps' grasslands are occupied by cloned plants (Wellstein and Kuss, 2011). Furthermore, the density and type of bud banks also demonstrated varied responses to grassland degradation. For instance, total bud banks and the density of rhizome buds correlate positively with total aboveground biomass in lightly degraded (LD) grasslands, while tiller bud density correlates positively with plant diversity in the non-degraded grassland (Yang et al., 2022). However, few studies have clearly elucidated the changes in bud bank type, density and diversity in responding to the structures and functions of grassland communities at different stages of degradation.

The aim of the present study was to examine the dynamic changes in bud bank density and diversity from undistributed meadows to severely degraded (SD) alpine meadows and to clarify the correlation between bud banks and plant diversity at different stages of degradation. Therefore, we conducted a field experiment to investigate the diversity of plant communities and bud banks in degraded alpine meadows. The study addressed the following question: (1) How do plant species diversity and functional group biomass change in differently degraded alpine meadows? (2) How does bud bank density respond to different stages of alpine meadows degradation? (3) Are the effects of alpine meadow degradation on bud bank dynamics consistent with the changes in plant community? The knowledge obtained from this study is helpful in understanding the potential role of bud banks in the restoration of degraded meadows and in predicting the dynamics of plant communities in degraded meadows based on bud banks driving plant regeneration.

Materials and methods

Study site

We conducted this study in Youganning, a town of in the Mongolian Autonomous County of Henan, Qinghai Province, China (34°C44′18"N, 101°C36′31"E, 3523 m), which occupies to the eastern edge of the Qinghai-Tibet Plateau. The experimental site, which has an area of approximately 10 ha, has been a site for the long-term monitoring and annual investigation of grassland communities since 2018. The region has a plateau continental monsoon climate and an average annual temperature of 0.8°C, ranging from -14.6°C in January to 7.9°C in July. Its annual sunlight duration ranges from 2551.8 h to 2577.2 h, and its total amount of daylight radiation ranges from 139.75 kcal to 152.48 kcal. Annual precipitation averages 598 mm, and the plant growth season lasts five months, from May to September (Du, 2015). The vegetation is alpine meadow, which is dominated by clonal, perennial herbaceous plants, including *Kobresia humilis*, *Elymus nutans*, *Festuca ovina*, *Poa pratensis*, *Carex tristachya*, and *Kobresia capillifolia*, and perennial weeds composed of companion species such as *Potentilla anserina*, *Ligularia virgaurea*, *Polygonum viviparum*, *Morina chinensis* and *Elsholtzia densa*. Five plots with an area of 0.5 ha were selected, as follows, in accordance with Li et al. (2016) classification standard for degraded grasslands: undisturbed (ND), lightly (LD), moderately (MD), heavily (HD), and black-soil-type (SD) degraded meadows (Table 1). The distance between plots was at least 5 km (Lin et al., 2016). To ensure the identical grazing intensity of different stages of degradation in designed experimental plots, each plot was enclosed by fence at the beginning of the experiment.

Investigation of plant community traits with alpine meadows of different degrees of degradation

In mid-August 2021, plant community traits were investigated at each plot during the plant growing season. Five replicate subplots with a size of 0.5 × 0.5 m were randomly selected from each plot to measure the height and coverage of each species in the subplot; simultaneously, the stems and leaves of each species were harvested from the surface of the ground (Zhu et al., 2016). The stems and leaves of each species were oven dried to a constant weight at 80°C and then weighed (Ji et al., 2020).

The plant diversities of the degraded alpine meadows were determined by calculating the Margalef index (R_m), the Simpson index (D), the Shannon-Wiener index (H) and the Pielou index (E), using the following formulae (Du et al., 2021):

$$\text{Plant}\quad\text{relative}\quad\text{importance}\quad\text{value}\quad(P_i) = (\text{relative}\quad\text{height} + \text{relative}\quad\text{coverage} + \text{relative}\quad\text{biomass})/3$$

$$\text{Margalef}: R_m = (S - 1)/lnN$$

$$\text{Simpson}: D = 1 - \sum_{i=1}^{S} {P_i}^2$$

$$\text{Shannon} - \text{Wiener}: H = -\sum_{i=1}^{S}(P_i\ ln\ P_i)$$

$$\text{Pielou}: E = -\sum_{i=1}^{S}(P_i\ ln\ P_i)/ln\ S,$$

where P_i is the relative importance value of the i species, N is the total number of species in the plot, and S is the number of species in each subplot.

Examination of bud banks in degraded alpine meadows

To investigate bud bank type and density, three samples (20 cm long × 20 cm wide × 30 cm deep) were randomly selected from the top soil layer and associated vegetation plants and manually excavated with a spade from different degraded grassland sites (Qian et al., 2017). Buds with soil were taken to the laboratory and immersed in a bucket with an inner diameter of 25 cm and a height of 40 cm at room temperature for 24 h. To avoid any damage to the buds, the immersed samples were then gently washed with running water and carefully brushed with a banister brush to clear rhizosphere soil. Plant species were identified and recorded on the basis of their morphological features, either spikelets or inflorescence, and the densities of rhizome, tiller, and

TABLE 1 Detailed information of sampling sites in different degraded alpine meadows.

Number of experimental sites	Degraded degree	Coverage (%)	Proportion of edible forages (%)	Dominating species	Grazing intensity	Duration of grazing
1	Undisturbed meadow (ND)	>85	>80	*Kobresia humilis*, *Kobresia capillifolia*, *Carex tristachya*	0.00 sheep/ha	No grazing
2	Lightly degraded meadow (LD)	70~85	55~80	*Carex tristachya*, *Festuca ovina*, *Elymus nutans*	1.33 sheep/ha	All-year grazing
3	Moderately degraded meadow (MD)	50~70	30~55	*Potentilla anserina*, *Festuca sinensis*, *Carex tristachya*	4.00 sheep/ha	All-year grazing
4	Heavily degraded meadow (HD)	30~50	10~30	*Elymus nutans*, *Poa pratensis*, *Potentilla anserina*, *Ligularia virgaurea*	6.67 sheep/ha	All-year grazing
5	"Black-soil-type" degraded meadow (SD)	<30	<10	*Potentilla anserina*, *Morina chinensis*, *Elsholtzia densa*	11.25 sheep/ha	All-year grazing

corm buds were recorded (Dalgleish and Hartnett, 2009; Kleyer et al., 2008). Furthermore, the degraded alpine meadows' bud diversities were determined by calculating the Margalef, Simpson, Shannon-Wiener, and Pielou indexes using the following formulae (Sun et al., 2020):

$$P_i = n_i/N$$

$$\text{Margalef}: R_m = (S-1)/lnN$$

$$\text{Simpson}: D = 1 - \sum_{i=1}^{S} {P_i}^2$$

$$\text{Shannon}-\text{Wiener}: H = -\sum_{i=1}^{S}(P_i\ ln\ P_i)$$

$$\text{Pielou}: E = -\sum_{i=1}^{S}(P_i\ ln\ P_i)/ln\ S,$$

where P_i is the proportion of individual species i among species, N is the total number of individual species in the sample, and S is the number of species in the sample.

Statistical analysis

One-way analysis of variance (ANOVA) was performed to compare the biomass, plant, and bud diversity indexes among the degraded meadows. The bud number within the area of 0.5 × 0.5 m was transformed into 1 m^2, and one-way ANOVA was used to determine the difference in bud bank density among the degraded alpine meadows. All data are represented as mean ± standard error.

A redundancy analysis (RDA) was performed to analyze the correlation between plant and bud bank diversities (Chandregowda et al., 2018). Furthermore, a structural equation model (SEM) was used to analyze the effects of the density and diversity of bud banks and plant biomass indicators on the diversity levels of plant communities at different levels of degradation. Prior to the SEM analysis, all indicators were screened by correlation analysis, and indicators with high collinearity were deleted. Biomasses of the plant functional groups, bud bank density, and the diversity index were considered as the key factors. Different degradation stages and the plant diversity of alpine meadows were designated as initial and target variables, respectively (Grace et al., 2010). A piecewise SEM module in the R Programming Language was selected to construct piecewise structural equations. All data were analyzed using the IBM Statistical Product and Service Solution (SPSS) software (version 25.0; SPSS China, Shanghai, China), and all figures were produced using SigmaPlot 14.0.

Results

Biomasses and diversity index values of plant communities in the degraded alpine meadows

Significant differences in biomass and diversity index values were found among the degraded alpine meadows (Table 2, Figure 1; $P < 0.05$). The Simpson and Shannon-Wiener index values in the MD were higher than those in the LD, HD, and SD meadows (Table 2; $P < 0.05$) but did not significantly differ from those in the ND meadows (Table 2; $P > 0.05$). Furthermore, the Shannon-Wiener index values in the ND meadows were higher than those in the LD, HD and SD meadows (Table 2; $P < 0.05$) but not significantly different from those in MD meadows (Table 2; $P > 0.05$).

The aboveground biomass of the grasses in the MD meadows was highest (19.96 g/m^2) and significantly higher than that of the grasses in the SD meadows (Figure 1; $P < 0.05$). By contrast, the aboveground biomass of sedges was maximum in the LD meadows (54.75 g/m^2; Figure 1). The biomass of forbs in the black-soil-type of degraded meadow was significantly higher than that of forbs in the degraded meadows (Figure 1; $P < 0.05$).

Density and diversity index values of bud banks in the degraded alpine meadows

The densities of rhizome, tiller, and corm buds differed among the degraded alpine meadows (Figure 2); and the rhizome and tiller bud densities were highest in the MD meadows (average 1216/m^2 and 1750/m^2), whereas the rhizome, tiller, and corm bud densities were lowest in the SD alpine meadows (Figure 2; $P < 0.05$). Furthermore, the rhizome and tiller buds were higher than the corm buds in the ND, LD, MD and HD alpine meadows (Figure 2; $P < 0.05$). The direct examination of bud bank formed plant species in the degraded meadows revealed that 25 species produced buds, 18 and 16 species produced rhizome and tiller buds, respectively, and only 5 species produced corm buds (Supplement Table S1). It was noted that most grasses and sedges simultaneously sprouted rhizome and tiller buds; similarly, some forbs such as *Galium verum* and *Potentilla anserina* produced rhizome and corm buds (Supplemental Table S1).

TABLE 2 Changes of plant diversity index in different degraded alpine meadows.

Number of experimental sites	Degraded degree	Simpson index	Shannon-Wiener index	Pielou index
1	ND	0.88 ± 0.01a	2.65 ± 0.08a	0.84 ± 0.01ab
2	LD	0.76 ± 0.05b	1.81 ± 0.17b	0.79 ± 0.04b
3	MD	0.90 ± 0.01a	2.47 ± 0.09a	0.87 ± 0.01a
4	HD	0.71 ± 0.01b	1.63 ± 0.03b	0.70 ± 0.02c
5	SD	0.68 ± 0.03b	1.56 ± 0.15b	0.77 ± 0.01bc

Different lowercase letters indicate that the plant diversity index of different degradation degrees was significantly differed at 0.05 level.

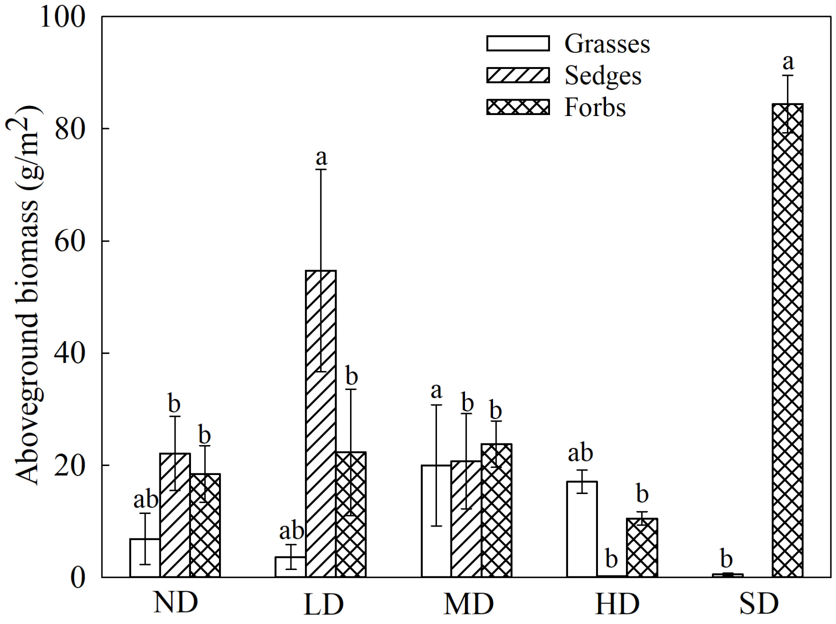

FIGURE 1
Changes in plant aboveground biomass in degraded alpine meadows. The different lowercase letters indicate that the aboveground biomass of the functional groups has a significant difference at the 0.05 level among the different degradation stages.

Significant changes in bud bank diversity were found among the degraded meadows (Table 3; $P< 0.05$). The Margalef and Shannon-Wiener index values of rhizome buds were highest in the ND meadows (1.82 and 1.35, respectively). The Simpson index value of rhizome buds was lowest in the LD meadows (0.13), and the Pielou index value of rhizome buds was highest in the SD meadows (0.91). Similarly, the Margalef, Simpson, Shannon-Wiener, and Pielou index values of tiller buds were highest in the ND meadows (1.49, 0.64, 1.39, and 0.73, respectively). Furthermore, the Margalef, Simpson, Shannon-Wiener, and Pielou index values of corm buds were highest in the ND meadows (0.82, 0.45, 0.73, and 0.8, respectively), while the Shannon-Wiener index value of the corm buds was absent from the HD and SD meadows (Table 3).

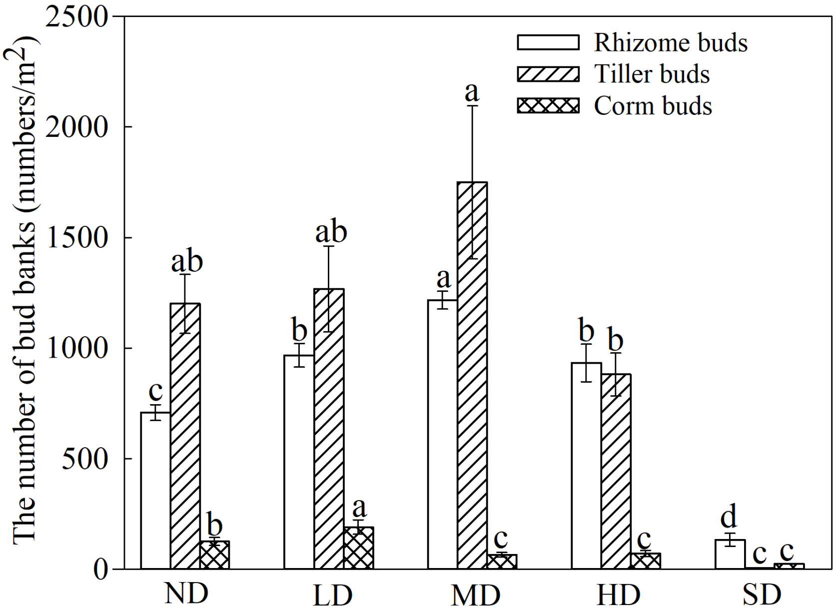

FIGURE 2
Types and densities of bud banks in degraded alpine meadows. The different lowercase letters indicate that the bud bank density of the same type of alpine meadow significantly differed at the 0.05 level between the different degrees of degradation.

TABLE 3 Diversity of bud banks of alpine meadow in different degrees of degradation.

Type of bud bank	Diversity index	ND	LD	MD	HD	SD
Rhizome	Margalef	1.82 ± 0.34a	0.53 ± 0.18c	1.11 ± 0.07ab	1.21 ± 0.11ab	0.77 ± 0.27bc
	Simpson	0.60 ± 0.15a	0.13 ± 0.04b	0.66 ± 0.05a	0.56 ± 0.08a	0.52 ± 0.18ab
	Shannon-Wiener	1.35 ± 0.34a	0.30 ± 0.10c	1.30 ± 0.12a	1.09 ± 0.09ab	0.80 ± 0.28bc
	Pielou	0.68 ± 0.13a	0.27 ± 0.09b	0.78 ± 0.05a	0.66 ± 0.08a	0.91 ± 0.31a
Tiller	Margalef	1.49 ± 0.21a	0.26 ± 0.02c	0.74 ± 0.06b	0.26 ± 0.02c	–
	Simpson	0.64 ± 0.14a	0.29 ± 0.01c	0.56 ± 0.05ab	0.32 ± 0.11bc	–
	Shannon-Wiener	1.39 ± 0.29a	0.46 ± 0.01bc	0.98 ± 0.09a	0.49 ± 0.13b	–
	Pielou	0.73 ± 0.14a	0.66 ± 0.02a	0.71 ± 0.07a	0.70 ± 0.18a	–
Corm	Margalef	0.82 ± 0.30a	0.53 ± 0.23a	0.46 ± 0.15a	–	–
	Simpson	0.45 ± 0.17a	0.39 ± 0.13a	0.20 ± 0.07a	–	–
	Shannon-Wiener	0.73 ± 0.28a	0.64 ± 0.22a	0.35 ± 0.12a	–	–
	Pielou	0.80 ± 0.27a	0.74 ± 0.26a	0.50 ± 0.17a	–	–

Different lowercase letters indicate that the diversity index of the same type bud in different degraded alpine meadows is significantly different at 0.05 level. “-” indicates that the diversity index of bud bank is absent.

Correlations between plant and bud banks among the degraded alpine meadows

The RDA revealed that the Shannon-Wiener, Simpson, and Pielou index values of plants positively correlated with the rhizome, tiller, and corm bud diversities (Figure 3, Supplement Table S2). The Shannon-Wiener index values of plants correlated positively with the diversity of rhizome buds (Figure 3A, Supplement Table S2), and the Simpson index values of plants strongly correlated with the diversities of tiller and corm buds (Figures 3B, C, Supplement Table S2). In addition, the correlation between the diversities of rhizome and tiller buds and the Shannon-Wiener values index of plants were ranked as follows: Margalef > Shannon-Wiener > Simpson > Pielou (Figures 3A, B), whereas the correlations between the diversity of corm buds and the Shannon-Wiener index values of plants ranked as follows: Pielou > Simpson > Shannon-Wiener > Margalef (Figure 3C).

The SEM revealed that the Shannon-Wiener index values of rhizome and corm buds and the density of bud banks decreased as the degradation levels of the meadows intensified (Figure 4, Supplement Table S3). The Shannon-Wiener index of tiller buds and the aboveground biomass of sedges were also significantly reduced (−0.7472 and −0.5813, respectively). By contrast, the aboveground biomass of the forbs increased as the degree of degradation intensified (0.6047). Furthermore, the aboveground biomass of grasses correlated positively with the densities of rhizome and tiller buds (0.5679 and 0.5801, respectively). However, the aboveground biomass of forbs correlated negatively with the densities of rhizome and tiller buds (−0.7179 and −0.4876, respectively). The decreased biomass of the sedges improved the diversities of rhizome and tiller buds, while the decreased biomass of grasses reduced the diversity of rhizome buds. In conclusion, the density and diversity of bud banks and the biomass of sedges were reduced as the degradation of the meadows intensified, while the decreased diversity of tiller buds, the density of rhizome and tiller buds, and the biomasses of grasses and forbs decreased the diversity of the plant community (Figure 4).

Discussion

Bud banks have been considered the dominant driver of plant regeneration and reproduction, and also play crucial roles in regulating plant composition, community succession and ecosystem function stabilization (Hartnett et al., 2006; Pausas et al., 2018; Li et al., 2023). Different types of sexual reproduction mainly through matured seeds, clonal organs, and branches sprouting buds (i.e. mainly through matured seeds, clonal organs and branch-sprouting buds) have the advantage of absorbing nutrients and water from infertile soil, and nutrients stored in buds also facilitate maternal plants' resistance or adaptation to drought, cold, trampling, and other biotic or abiotic stresses (Li et al., 2023). In addition, dormant buds provide substantial ecological benefits in maintaining plant community structure due to their low metabolic consumption and maintenance costs, and plant reproduction through new buds is the most effective and low-cost strategy in responding positively to adverse environmental conditions (Ott et al., 2019). Therefore, the reproduction of new individuals through buds and plant population niches maintained depending on bud banks is an important ecological process for species survival and proliferation in alpine meadows (Dalgleish and Hartnett, 2009; Ott et al., 2019). Furthermore, bud banks are also a key force in the rehabilitation of fragmented vegetation and the regulation of positive vegetation succession in alpine meadows (Fidelis et al., 2014). Our findings indicate that both the higher densities of rhizome and tiller buds and the diversity of tiller buds

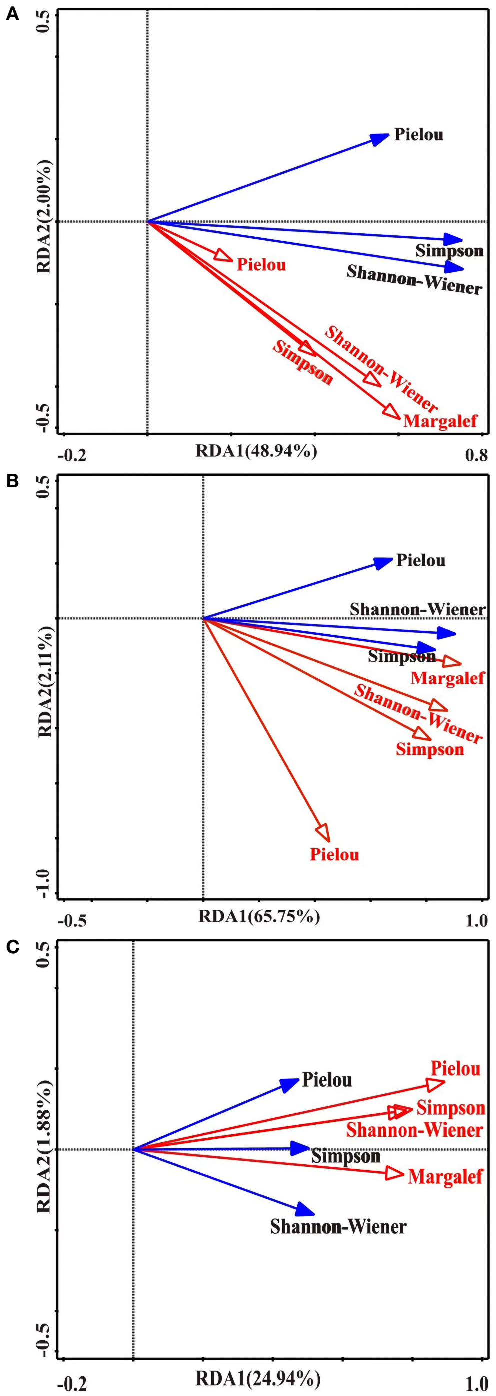

FIGURE 3
Redundancy analysis (RDA) of plant and bud bank diversity. **(A)** RDA between rhizome buds and plant diversity. **(B)** RDA between tiller buds and plant diversity. **(C)** RDA between corm buds and plant diversity. The blue solid line and black letters indicate the Simpson, Shannon-Wiener, and Pielou index values of the plant community, respectively. The red solid line and red letters indicate the Margalef, Simpson, Shannon-Wiener, and Pielou index values of bud banks, respectively.

could facilitate the accumulation of greater biomasses of grasses and forbs. Consequently, in this study, greater community biodiversity was maintained in the degraded alpine meadows. To some extent, the moderate disturbances caused by herbivores through feeding and trampling play positive roles in producing more tillers or rhizomes for grasses and sedges. Thus, in this study, the diversity index values of plant and bud banks were markedly higher in the LD or MD meadows than in the other degraded meadows. Therefore, bud banks should be regarded as the original driving force in renewing plant offspring and maintaining community stability; bud banks with higher diversity may facilitate the rehabilitation of degraded meadows.

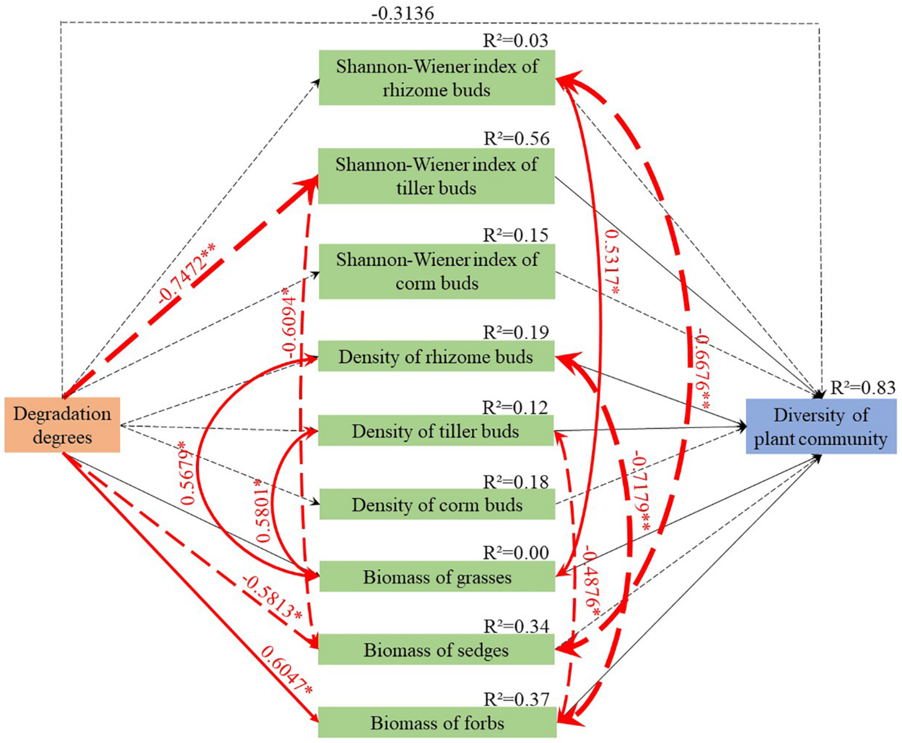

FIGURE 4
Structural equation model for estimating the correlations between functional group biomass, bud bank density, and alpine meadow diversity in degradation stages. The black dotted line indicates the negative correlation between the variables, and the black solid line indicates the positive correlation between the variables. The red dotted line indicates the significant negative correlation between the variables, and the red solid line indicates the significantly positive correlation between the variables. The values above the lines are the normalized path coefficients of the variables, which indicate the strength of the correlationship (*$P < 0.05$, **$P < 0.01$). The width of the line and values above the line are identical to the strength of the correlationship. R^2 indicates the proportion of the interpreted variance. Goodness of fit statistics: AIC = 78.984, BIC = 100.934, Fisher's C = 16.984, and $P = 0.257 > 0.05$.

Differences in functional group biomass and plant diversity in degraded alpine meadows

Our findings indicate that the biomass of functional groups differs largely among degraded alpine meadows and that the grass biomass in MD meadows is significantly higher than that in other degraded meadows. One possible reason for this is that the new rhizome node in sedges and the density of tillers in grasses would be largely increased after undergoing a moderate grazing disturbance (Li et al., 2015). Meanwhile, herbivores' preference for feeding on bunch grasses creates better survival and growth conditions for regenerated buds, with less competitivity (Dalgleish and Hartnett, 2006). In the following spring, the niche widths of grasses and sedges were persistently expanded in the MD meadows, whereas that of forbs was reduced (Jiao et al., 2018). By contrast, the biomass of forbs was significantly higher in the SD alpine meadows than in the other degraded meadows. One possible reason for this may be related to the following: the dominant species of native vegetation, such as grasses and sedges, was replaced by toxic weeds in the SD meadows, and the regenerative capacities of rhizome and tiller buds were completely exhausted because of the combined effects of adverse disturbances such as climate warming, overgrazing, and damage by rodents, which facilitated the seed germination of short-lived weeds from the soil seed bank after rainfall in autumn (Li et al., 2011).

Plant diversity differed largely among the degraded alpine meadows; the Shannon-Wiener index values of the ND and MD alpine meadows were significantly higher than those of the LD, HD and SD meadows, while the Simpson and Pielou index values were highest in the MD alpine meadows. These changes may be attributed to the selective feeding behavior of herbivores, which increased the feeding frequency for palatable grasses such as *Elymus nutans* and *Festuca ovina* in the MD meadows. By contrast, the feeding intensities in forbs and sedges largely decreased, providing better regenerative opportunities for forbs and sedges, especially for some poisonous or unpalatable species (Herben et al., 2018). Thus, the Simpson and Pielou index values were higher in the MD meadows than in the other degraded meadows (Wu et al., 2014). Furthermore, the Shannon-Wiener index value was highest in the ND alpine meadows, which may be related to the markedly lower intensity of disturbances by herbivores in the ND meadows than in the degraded meadows. Eliminating the disturbances caused by herbivores also facilitated plant regeneration and maintained higher plant diversity in the ND meadows. Meanwhile, the absence of disturbances by herbivores provided advantages in accelerating regeneration and improving the diversity of bud banks in the ND meadows, as the high intensity of herbivore feeding strongly suppresses the renewal capacity of bud banks. However, bud regenerative ability can be recovered after the adverse effects of herbivore feeding are removed (Ott et al., 2019). In addition, complicated rhizomes and root nets established through renewal buds can absorb abundant nutrients from soils and transfer them to maternal plants, resulting in latter's growth. The sprouting of new seedlings from buds is thus accelerated, resulting in improving plant diversity (Deng et al., 2014; Herben et al., 2018).

Differences in the composition of bud banks among the degraded alpine meadows

Both bud type and density varied significantly among the degraded alpine meadows. Bud density was highest in the MD meadows. This finding is consistent with the outcome of maintaining higher plant diversity in the MD meadows, as moderate disturbances from herbivore feeding and trampling are conducive to grass's greater production of tillers and rhizomes. The renewal tillers or rhizomes expand their niche widths to facilitate resource utilization and reduce competition with maternal plants for nutrients, water, and other resources (Ding et al., 2019). Therefore, more buds and higher plant diversity emerged simultaneously in the MD meadows (Benson et al., 2004; Ding et al., 2019). In addition, grazing-tolerant and low-input species in the MD meadows have adapted to the negative effects of herbivore grazing and trampling, and their strong root systems facilitated their absorption of more nutrients and water, making grasses and sedges the dominant species in the plant community. Grasses and sedges have the potential to sprout newer buds and branches because the nutrients and water reserved in maternal plants ensure bud regeneration (Zhang D. et al., 2019).

By contrast, bud density was lowest in the black-soil-type degraded meadows, which is attributed mainly to the effects of harsh conditions on plant growth and regeneration (Amine Habib et al., 2014; Zhao et al., 2019). For example, with the combined effects of overgrazing, extreme drought, soil erosion and rodent burrowing, palatable grasses and sedges were completely replaced by poisonous weeds; thus, the renewal capacities of tillers and rhizomes were almost lost (Habib et al., 2014). Furthermore, annual weeds with the traits of fast germination and quick reproduction became dominant species in this habitat; thus, the density of corms sprouting from forbs was outstandingly higher than that of corms sprouting from tiller and rhizome buds (Zhao et al., 2019).

Consistent with the results for bud density, the rhizome, tiller, and corm bud diversities also differed significantly among the degraded meadows, and the diversity index value of rhizomes was lowest in the LD meadows, and the Margalef and Shannon-Wiener index values of rhizome buds in the undistributed meadows were markedly higher than those in the degraded meadows. No significant difference in corm bud diversity was found among the undistributed, LD or MD meadows. A possible reason for this change is that the buffer zone formed by dense litters not only alleviated soil erosion from rainfall but also reduced the evaporation of water from the soil (Sheldrake et al., 2017). This physical safeguard established by litters plays an important role in bud regeneration because water and nutrients are essential factors in the renewal and growth of buds (Guo et al., 2019). Litters also facilitated the colonization of soil microorganisms, as the latter's main source of carbon is decomposed litters (Liu et al., 2021). In return, numerous soil microorganisms also quickly decompose litters into soil organic matter; consequently, soil with higher nutrients has advantages in the renewal and expansion of buds (Zhu et al., 2016). Furthermore, the combined effects of tiller buds that sprout from the bases of grasses and rhizome buds emerging from sedge nodes can enhance the competitiveness of grasses and sedges and facilitate their development into dominant species in undistributed meadows. These findings are partly explained by the fact that the cover and biomass of sedges and grasses were highest in the undisturbed meadows (Liu et al., 2022). Therefore, the coupled effects of the strong competition of maternal plants and the persistent renewing capacity of buds could be regarded as a virtuous cycle in maintaining a higher diversity of buds and dominating species (Li et al., 2022).

The Simpson index was highest in the MD meadows, possibly because the moderate disturbances caused by herbivores had a positive effect on enhancing the proportion of grasses in the alpine meadow community, and because grasses have the capacity to sprout tiller and rhizome buds. Therefore, grasses demonstrated strong interspecific competitiveness for sunlight, water and nutrients, which contributed to their regenerating more tiller or rhizome buds; the Simpson index values of tiller and rhizome buds increased in the MD meadows (Benson and Hartnett, 2006).

Our study confirms that plant diversity is higher in LD meadows than in HD and black-soil-type degraded meadows, but bud bank diversity is lower in the former than in the latter. This may be due to the growth and development of plants not only depending on the bud bank but also on the soil seed bank for sexual reproduction in the LD meadows (Chen et al., 2022). However, it is difficult to develop seeds into plants because of the increased soil bulk density and decreased water and nutrients content due to the feeding and trampling of livestock and human activities in SD meadows (Zhang W. J. et al., 2019). Furthermore, the wide stems and leaves of forbs prevent seed implantation (Klimešová and Klimeš, 2007; Dong et al., 2015). Therefore, bud banks have become the most effective method for population renewal and expansion.

Correlation between plant species and bud banks in degraded alpine meadows

Previous studies have indicated that bud bank diversity plays a crucial role in improving plant diversity and enhancing the stability and function of vegetation communities (Ott et al., 2019; Yang et al., 2022). In our study, the Shannon-Wiener index values of rhizome and tiller buds correlated positively with the plant diversity index, and plant diversity and the diversity index values of rhizome and tiller buds were markedly higher in the MD meadows than in the other degraded meadows. It is interesting that the dynamic change in the density of bud banks preceded the changes in plant and bud bank diversities. The possible reasons for these changes may be summarized as follows: (1) The type and density of bud bank plants largely determined the restoration speed of perennial plants after disturbance by abiotic and biotic stresses such as drought, fire, rodent burrowing, and herbivore foraging (Hämälä et al., 2017). Benson and Hartnett (2006) found that more than 99% of aboveground stems are formed by bud banks in grassland after fire, whereas only 1% of plant regeneration is restored through seed banks. Meanwhile, Zhang et al. (2009) suggested that the propagation and regeneration of plant populations through bud banks demonstrates superiority in growth and adaptivity to adverse survival conditions. Therefore, the succession direction of vegetation was largely regulated by the density and type of bud bank. (2) Perennial sedges and grasses are the dominant species in the alpine meadows' plant community of alpine meadows. Aboveground tissues, including the stems, branches, and leaves of sedges and grasses, withered after their reproduction stage. To ensure the regeneration of tiller or rhizome buds in the next spring, abundant nutrients should be prioritized in the allocation to nutrient storage organs such as roots or buds (Dalgleish and Hartnett, 2009; Carter et al., 2012; Ott and Hartnett, 2014; Zhang D. et al., 2019; Wu et al., 2020b). Dormant buds sprout quickly from the base or rhizome by consuming nutrients stored in buds; consequently, the maternal plant cover increases quickly through the persistent regeneration cycles of tiller and rhizome buds (Wang et al., 2018; Ding et al., 2019). Therefore, bud regeneration was vital to determine vegetation structure and diversity.

Likewise, in our study, the combined effects of greater tiller bud diversity, more rhizome and tiller buds, and higher aboveground biomass of grasses and forbs resulted in higher levels of plant diversity in MD meadows. The probable reasons are as follows: (1) The regeneration rate of the density of tiller buds preceded the changes in bud bank diversity in the degraded alpine meadows, while tiller bud diversity was synchronized with plant diversity. Therefore, the density of tiller buds sprouting from grasses largely determined the diversity of bud banks and grasses in the plant community. It can be concluded that the tiller bud density of grasses could be a predictor of the dynamic change in the plant community diversity (Yu et al., 2020). (2) Grass and sedge coverage in the plant community decreased sharply when grazing intensity exceeded the MD meadows' capacity; by contrast, toxic weeds demonstrated more interspecific competition and became dominant species in the heavily degraded (HD) and SD meadows (Ott and Hartnett, 2012). Although bud bank diversity was relatively high in the HD meadows, bud banks' regenerative capacity was decreased; thus, both the diversity and density of bud banks were sharply reduced in the SD meadows, ultimately leading to the complete loss of the vegetation community's function and regeneration (Ott et al., 2019; Zhao et al., 2019).

Conclusion

The renewal capacity of perennial herbaceous plants was synchronized with the regenerating and expanded abilities of their bud banks, which is a vital survival strategy for species to adapt to the adverse environments of alpine meadows (Ott and Hartnett, 2015). Compared with the function of buds in alpine species, rhizome buds demonstrated stronger spatial expansion underground and better efficiency in absorbing nutrients from the soil, and tiller buds had an advantage in maintaining native populations; whereas corm buds contributed less to plant renewal (Carter et al., 2012). Our study results suggest that the Shannon-Wiener index values of plants and buds were significantly higher in the undistributed and MD alpine meadows than in the LD, HD, and SD alpine meadows. Similarly, the total bud bank density was highest in the moderately disturbed habitats. In addition, the rhizome, tiller, and corm bud diversities correlated positively with plant diversity. As far as we know, previous studies have focused mainly on evaluating the dynamic succession processes of degraded grasslands by monitoring changes in plant composition and evaluating the diversity levels of vegetation communities (Zhu et al., 2016; Wang et al., 2017; Ott et al., 2019; Yang et al., 2022). Our results suggest that bud banks can be considered, in part, the original driving force for vegetation renewal in alpine meadows and that the renewing capacity of bud banks largely determines degraded meadows' restorative efficiency and suppresses their degradation. In addition, our findings also provide convincing theoretical support for the idea that the combined effects of accelerating bud regeneration and reseeding grasses are the most efficient methods for restoring quickly degraded meadows (Ott and Hartnett, 2014). Therefore, the substantial role of bud banks, especially for sedges and grasses, should be considered in the restoration of degraded meadows in alpine areas. Moreover, the results of changes in bud bank type and density caused by herbivore disturbance should be interpreted with caution, because other abiotic factors, such as temperature and precipitation are not to be overlooked in determining the bud banks' traits, and some control experiments regarding the role of other biotic and abiotic factors in regulating bud banks of alpine meadows should be taken into account in future researches.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Author contributions

YL: Writing – original draft. GB: Funding acquisition, Writing – review & editing. PZ: Investigation, Formal Analysis, Writing – review & editing. XF: Data curation, Investigation, Writing – review & editing. JM: Investigation, Methodology, Writing – review & editing. HL: Investigation, Data curation, Writing – review & editing. HS: Methodology, Investigation, Writing – review & editing. XW: Investigation, Methodology, Writing – review & editing. BT: Investigation, Writing – review & editing. KL: Supervision, Writing – review & editing.

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Conflict of interest

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpls.2023.1259340/full#supplementary-material

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Potential short-term effects of earthquake on the plant–soil interface in alpine grassland of the Qinghai–Tibetan Plateau

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Earthquakes are environmental disturbances affecting ecosystem functioning, health, and biodiversity, but their potential impacts on plant–soil interface are still poorly understood. In this study, grassland habitats in areas near and away from the seismo-fault in Madou, a region typical of alpine conditions on the Qinghai–Tibetan Plateau, were randomly selected. The impacts of earthquake on soil properties and plant nutrient content in the short term were emphasized, and their potential relationships with community diversity and productivity were examined. According to the findings of the study, the Maduo earthquake led to a decrease in soil nutrient content in alpine grassland ecosystems, especially soil TC, TN, TP, TCa, AP, AK, NH_4^+-N, and SOC, and inhibited the absorption of N, Ca, and Mg nutrients by plants. In addition, the diversity and productivity of communities were affected by both direct and indirect earthquake pathways. The negative impacts of seismic fracture on soil structure had the most significant direct impact on plant community diversity. Earthquakes also indirectly reduced community productivity by reducing the soil N content and inhibiting the absorption of plant nutrients. Our findings suggested that earthquakes could potentially decrease the stability of the alpine grassland ecosystem on the QTP by affecting nutrient availability at the plant–soil interface.

KEYWORDS

earthquake, alpine grasslands, soil properties, plant nutrient, community diversity, productivity

1 Introduction

Earthquake, a classic disastrous disturbance event, has a significant influence on global biodiversity, causing ecosystem structure and function to degrade and vegetation to be destroyed (Zhang et al., 2011; Cui et al., 2012; Su et al., 2015; Vaux et al., 2022). Disturbances of varying intensities and frequencies not only influence plant diversity and spatial distributions but also affect physiological and ecological processes in plants, and serve as forces of selectivity in their composition (Sousa, 1984; Lindenmayer et al., 2010; Loto and Bravo, 2020). To date, the response mechanism of vegetation after earthquake has remained a topical issue in ecology (Huang et al., 2017; Kang et al., 2021; Kang et al., 2022). Community diversity as well as species richness can be significantly reduced by earthquake, leading to a decline in productivity and serious damage to grassland ecosystems (Mittelbach et al., 2001; Ouyang et al., 2008; Zhang et al., 2011). Eleven years following the Wenchuan earthquake, herbaceous communities still dominated the land recovery, and plant diversity and species evenness were still significantly reduced (Kang et al., 2021). Plant functional traits at the community level that covered multiple organs of grassland plants, including seeds, leaves, stems, and roots, differed markedly compared to plants not affected by the earthquake (Kang et al., 2022). However, we have not gained a clear understanding of what causes the reduction in grassland community diversity and productivity after earthquakes.

Earthquakes may affect community aggregation by completely altering soil structure and nutrient composition, thus affecting community diversity and productivity (Kang et al., 2021). Changes in species diversity can reflect variations in community structure and composition, which are strongly driven by soil factors (Xu et al., 2019). The disturbance of soil structure and nutrients after earthquakes can affect vegetation structure and function, further leading to a reduction in community diversity and loss of vegetation biomass (Zhang et al., 2011; Cheng et al., 2012; Cui et al., 2012). During a major earthquake, original nutrient-rich and well-formed soils are susceptible to disturbance by seismic geological hazards, which can damage the surface soil structure and cause nutrient loss (Lin et al., 2017). In alpine grassland ecosystems, plant productivity is significantly related to soil nutrient status (Xu et al., 2019).

Variations in soil nutrient levels alter the nutrient uptake strategies of plants, while plant nutrient uptake, transport, and utilization control the development and production of plants (Güsewell and Koerselman, 2002; Yan et al., 2019). Despite the fact that plants with high chemical equilibrium can keep nutrient concentrations throughout their tissues largely constant to make adjustments to changes in the environment, reductions in available nutrients can still restrict the development of dominant species and thus impact growth and stabilization of plant communities (Yu et al., 2011; Yu et al., 2015). The plant traits relating to nutrient acquisition and utilization are strongly affected by soil fertility, which results in a close relationship with community diversity and productivity (Zemunik et al., 2015). The change in plant nutrient uptake is one of the mechanisms that explain the connection of biodiversity and primary production (Hooper et al., 2005). At this stage, plant nutrient uptake is being applied to solve ecological issues related to plant development and plant response to soil nutrient variations (Zhang et al., 2019).

The Qinghai–Tibetan Plateau (QTP), located at the boundary between lithospheric plates, is prone to be affected by strong earthquakes (Fattorini et al., 2018; Chen et al., 2021). Alpine grassland is the most important ecosystem to maintain the gene pool of biodiversity of the QTP, and it is usually affected by such disturbance (Dong et al., 2013; Dong et al., 2020). In a previous study, we discovered that the 7.4 Maduo earthquake in May 2021 caused a marked negative effect on alpine grassland plant communities, resulting in diversity loss and productivity decline (Zuo et al., 2022). However, the potential mechanism related to this phenomenon remains unclear. Soil structure and nutrient content will be altered after an earthquake, which will lead to an impact on the plant root system's uptake of soil nutrients (Guo et al., 2013; Lin et al., 2017; Briat et al., 2020). Plant uptake of nutrients is closely linked to the diversity and productivity of the community (Fay et al., 2015; Lü et al., 2019). On this basis, we performed this research to investigate the potential short-term effects of earthquake on the plant–soil interface of alpine grassland with three hypotheses: (1) soil nutrient will be lost due to earthquake disturbance in alpine grassland; (2) the plant nutrient uptake capacity of alpine grassland plants will be limited under the short-term effect of earthquake rupture; and (3) the earthquake inhibits the plant uptake of nutrients by affecting soil nutrients, which is one of the major causes for the reduction in plant diversity and productivity in the long run. Our goal in this study is to inform the recovery and ecological construction of alpine grassland after earthquake and help us understand the adaptive strategies of alpine species responding to the changed environment.

2 Materials and methods

2.1 Field site

The field site of Maduo County of Qinghai Province, China (96° 50′–99°20′ E, 33°50′–35°40′ N), is located in the Yellow River source area in the northeastern part of the QTP. It is an important ecological barrier on the QTP, with an approximate total area of 25,300 km^2 and an altitude mostly between 4,200 and 4,800 m. Maduo County has an alpine grassland climate with an average annual temperature of −4.1°C, a potential annual evaporation of 1,264 mm, and an average annual precipitation of approximately 303.9 mm, 86% of which mainly happens between May and September (Zhang et al., 2010). The vegetation types are mainly grassland, including alpine steppes and alpine meadows, and the kobresia species of the sedge family such as *Kobresia humilis*, *Kobresia tibetica*, and *Kobresia pygmaea* are dominant.

Maduo County is situated within the historically seismically active Bayan Har Block in Qinghai, Province, China, which was struck by an *M*w 7.4 earthquake on 22 May 2021, at a depth of approximately 17 km. The Maduo earthquake was the biggest earthquake on the Chinese mainland following the Wenchuan earthquake in 2008. The earthquake fault spread bilaterally toward both the east and the west, with a rupture length of approximately 170 km and a duration of approximately 38 s, causing the formation of several new seismic fault zones that severely endangered the fragile alpine grassland ecosystem (Feng et al., 2022; Zhang et al., 2022; Zuo et al., 2022).

2.2 Field vegetation and soil sampling

At the beginning of September 2021, eight different seismo-faults were selected randomly as sample points based on the locations of the seismic fracture zones and the principle of consistent site conditions including elevation, slope direction, soil parent material, and human management (Figure 1). At each sampling site, we used an area approximately 3 m near the seismo-fault as the area affected by the seismic fault zone, and an area not affected by the earthquake on the same slope and same aspect approximately 30 m far from the seismo-fault as the control area. The top 10 dominant species of grassland in control and seismo-fault sites were recorded respectively (Supplementary Table 1). In the affected area and control area of each sample site, three areas with a size of 25 cm × 25 cm were randomly selected to collect aboveground plant materials, which were taken back to the laboratory and desiccated at 105°C for 3 h and to a stable weight at 70°C. Then, the dry materials were crushed into fine powder using a vibrating sample mill for subsequent analytical work. Meanwhile, 20-cm-depth soil samples were obtained on the ground at each plant sampling site with soil probes of 3.5 cm diameter. All collected soil samples were then air dried to consistent weight and screened using 0.15-mm sieves.

2.3 Laboratory measurement

The contents of total carbon (TC) and total nitrogen (TN) in plants and soil were determined with an elemental analyzer (EA 3000, Italy). The contents of total phosphorus (P), sulfur (S), potassium (K), calcium (Ca), and magnesium (Mg) in plants and soil, as well as the soil available potassium (AK) and available phosphorus (AP) contents, were determined using inductively coupled plasma spectrometry (ICP) (SPECTRO ARCOS EOP, Germany). Soil nitrate (NO_3^--N) and ammonium nitrogen (NH_4^+-N) contents were taken by a flow injection auto-analyzer (AACE, Germany). The total soil organic carbon (SOC) content was measured with a total organic carbon analyzer (TOC-5000A, Japan). The soil pH in the supernatant was measured with a glass electrode, following 5 g of soil homogeneously mixed with 25 mL of water (Shen et al., 2022b).

2.4 Statistical analysis

All statistical analyses were carried out using SPSS 26.0. A two-tailed *t*-test was applied to the analysis of the influence on soil properties and plant nutrient content of seismo-faults, and a correlation matrix was developed to determine the relation among soil properties and plant nutrient content. GraphPad Prism 9.3 was used to draw the images. In addition, we developed structural equation modeling (SEM) from the AMOSS 26.0 software package to evaluate the causes of the decline in plant diversity and productivity following the earthquake rupture. We examined the most likely path of influence and corrected the original model with calibration factors, resulting in a qualified SEM. Typically, a competent SEM is required to satisfy the following criteria

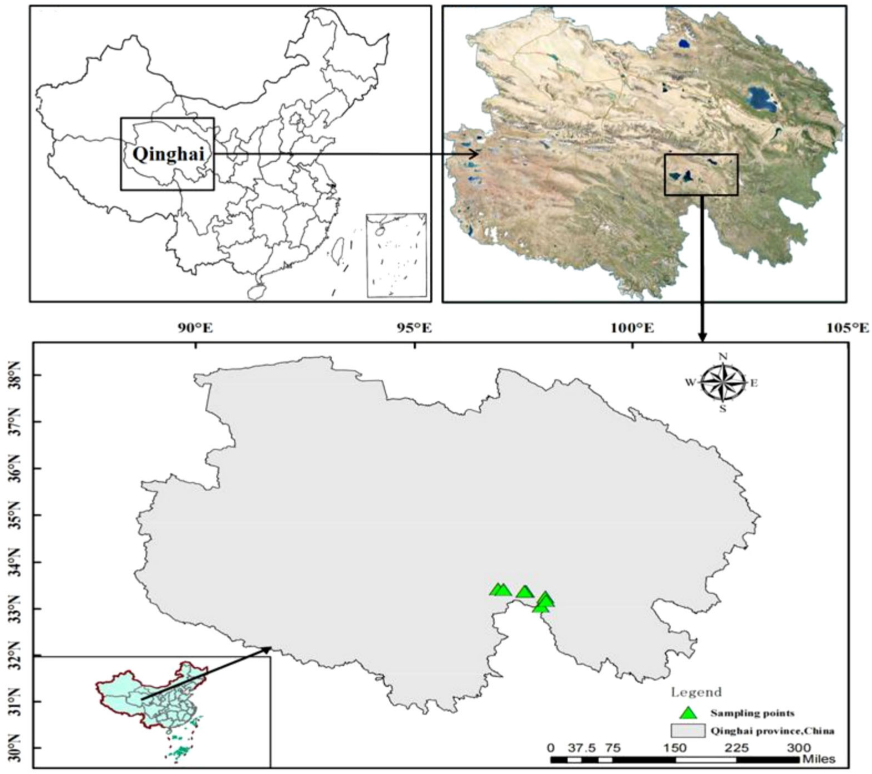

FIGURE 1
Location map of sampling sites.

(Hooper et al., 2007; Jonsson and Wardle, 2010; Wei et al., 2013; Shen et al., 2022a): (1) nonsignificant chi-square test, namely, $p > 0.05$; (2) comparative fit index, CFI > 0.95; and (3) root mean squared error of approximation, RMSEA < 0.05.

3 Results

3.1 Short-term effects of seismic rupture on soil properties

The negative impacts of earthquakes on soil properties were obvious, with soil properties in the seismo-fault sites differing significantly from those in the control area (Figure 2). Seismic rupture caused a significant increase in soil pH ($p < 0.001$) (Figure 2A), resulting in soil salinization intensification. Soil total C, N, P, and Ca contents were all greatly reduced by the earthquake rupture ($p < 0.05$), with decreases of 42.00%, 48.63%, 19.27%, and 29.78%, respectively, compared to the control area (Figure 2C). The contents of soil available nutrients were also strongly affected by seismic fractures (Figure 2D). Soil AP, AK, and NH_4^+-N under the seismo-fault were significantly lower than those in the areas not affected by seismic faults ($p < 0.001$), and the decrease rates were 30.91%, 31.58%, and 43.50%, respectively, while the soil NO_3^--N content was not considerably affected by seismic faults (Figure 2D). In addition, the seismic rupture had an enormous effect on the SOC content ($p < 0.001$), which decreased by 43.88% in comparison to the control (Figure 2B).

3.2 Short-term effects of seismic rupture on plant nutrients

Earthquakes significantly limited plant nutrient uptake. The absorption of N, Ca, and Mg in plants was more sensitive to the short-term effects of the seismic faults. After the earthquake rupture, plant total N, Ca, and Mg contents decreased significantly by 23.97%, 29.73%, and 29.80%, respectively, compared to areas unaffected by the seismo-fault ($p < 0.05$). In contrast, seismic ruptures showed no obvious impact on the total C, P, K, and S contents of plants (Figure 3).

3.3 Relationship between plant nutrients and soil properties

Using data from seismic fault zones and control areas, we evaluated the link between plant nutrient indicators and soil properties using a Pearson correlation matrix (Figure 4). The findings revealed that the plant nutrient contents, which had been significantly altered by the short-term effects of the earthquake rupture, were closely related to the soil nutrient contents (Figure 4). Plant N content was shown to be strongly and positively associated to SOC ($r = 0.40$, $p < 0.01$), soil TC ($r = 0.44$, $p < 0.01$), soil TN ($r = 0.56$, $p < 0.001$), soil TP ($r = 0.48$, $p < 0.001$), soil AP ($r = 0.50$, $p < 0.001$), soil AK ($r = 0.31$, $p < 0.05$), soil NO_3^--N ($r = 0.43$, $p < 0.01$), and NH_4^+-N ($r = 0.34$, $p < 0.05$) contents. Plant Ca content had a great positive connection with SOC ($r = 0.35$, $p < 0.05$), soil TN ($r = 0.36$, $p < 0.05$), soil TK ($r = 0.33$, $p < 0.05$), and soil NH_4^+-N ($r = 0.29$, $p < 0.05$) contents. Plant Mg content demonstrated a significant positive association with regard to SOC ($r = 0.29$, $p < 0.05$), soil TN ($r = 0.46$, $p < 0.001$), soil NO_3^--N ($r = 0.42$, $p < 0.01$), and NH_4^+-N ($r = 0.33$, $p < 0.05$) contents. In addition, the plant Ca and Mg content displayed a strong positive association ($r = 0.69$, $p < 0.001$). Although the pH of soil had no direct correlation with plant nutrient contents, it showed a significant inverse relationship with SOC ($r = -0.35$, $p < 0.05$), soil AK ($r = -0.33$, $p < 0.05$), and soil NH_4^+-N ($r = -0.32$, $p < 0.05$) contents and a significant positive correlation with total soil Mg ($r = 0.51$, $p < 0.001$), thus possibly indirectly influencing plant nutrient contents.

3.4 Direct and indirect drivers associated with earthquake affecting plant productivity and diversity

Earthquakes significantly affected the diversity and productivity of alpine grassland communities. In Supplementary Figure 1, it is evident that seismo-fault obviously reduced the Shannon–Wiener Index and aboveground plant biomass of alpine grassland communities compared to the control area, indicating that the earthquake led to a decline in grassland plant community diversity and a reduction in productivity. Therefore, an SEM was developed to explore the impacts of seismic rupture on plant community

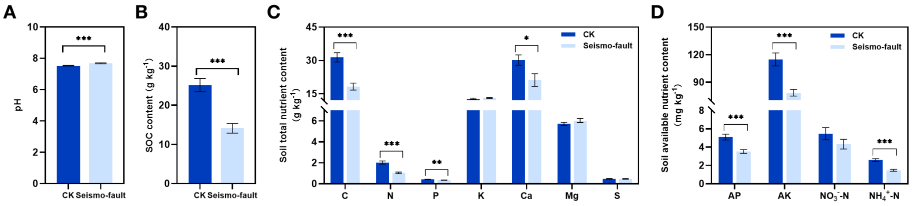

FIGURE 2
Soil properties change under the influence of seismic rupture. **(A)** Soil pH, **(B)** soil organic carbon content, **(C)** soil total nutrient content, and **(D)** soil available nutrient content. The vertical bars reflect the standard error (SE) of the mean. Significant differences between the control and seismo-fault samples are indicated by asterisks on the SE bars (*$p < 0.05$, **$p < 0.01$ and ***$p < 0.001$).

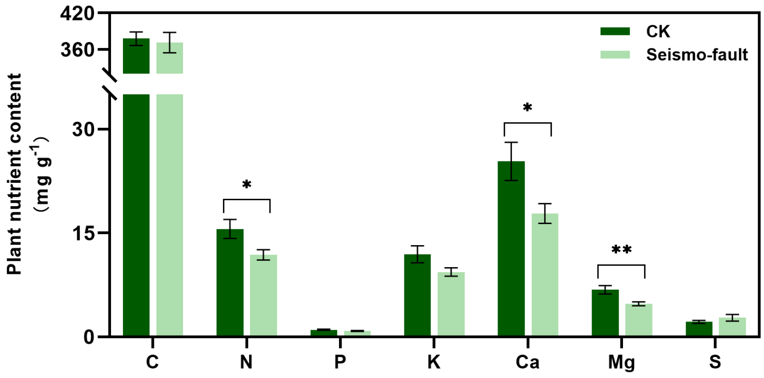

FIGURE 3
Changes in plant nutrient content under the influence of seismic rupture. The vertical bars reflect the standard error (SE) of the mean. Significant differences between the control and seismo-fault samples are indicated by asterisks on the SE bars (*p < 0.05 and **p < 0.01).

diversity and productivity (Figure 5). The results showed that seismic ruptures affected plant community diversity and productivity through different pathways. First, earthquake rupture had a clear direct impact on both the diversity and productivity decline of plants. Although the reduction in soil nutrient content caused by seismo-faults inhibited the absorption of Ca by plants, and the plant Ca content showed a negative relationship with community diversity, the direct effect of seismo-faults was stronger and significantly reduced community diversity. In addition, seismo-faults also affected community productivity through more complex indirect pathways. Seismic fractures inhibited plant uptake of N mainly by affecting the soil N content, thus decreasing the plant N content and reducing aboveground biomass.

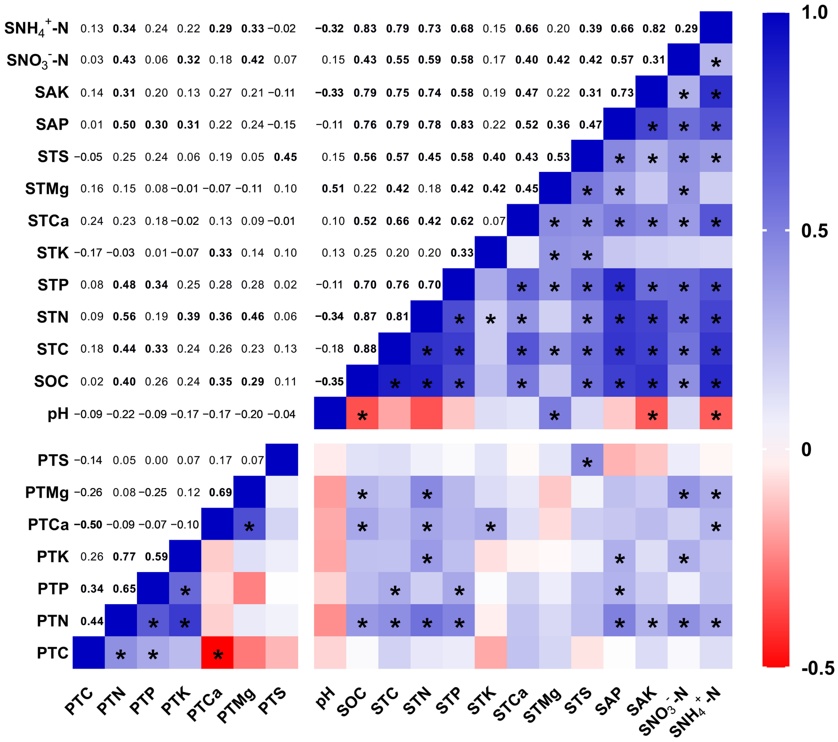

FIGURE 4
Correlation of plant nutrient content with soil properties. PTC: plant total carbon, PTN, plant total nitrogen; PTP, plant total phosphorus; PTK, plant total potassium; PTCa, plant total calcium; PTMg, plant total magnesium; PTS, plant total sulfur; SOC, total soil organic carbon; STC, soil total carbon; STN, soil total nitrogen; STP, soil total phosphorus; STK, soil total potassium; STCa, soil total calcium; STMg, soil total magnesium; STS, soil total sulfur; SAP, soil available phosphorus; SAK, soil available potassium; SNO_3^--N, soil nitrate nitrogen; SNH_4^+-N, soil ammonium nitrogen. * and bolded numbers mean significant differences at the level of p < 0.05.

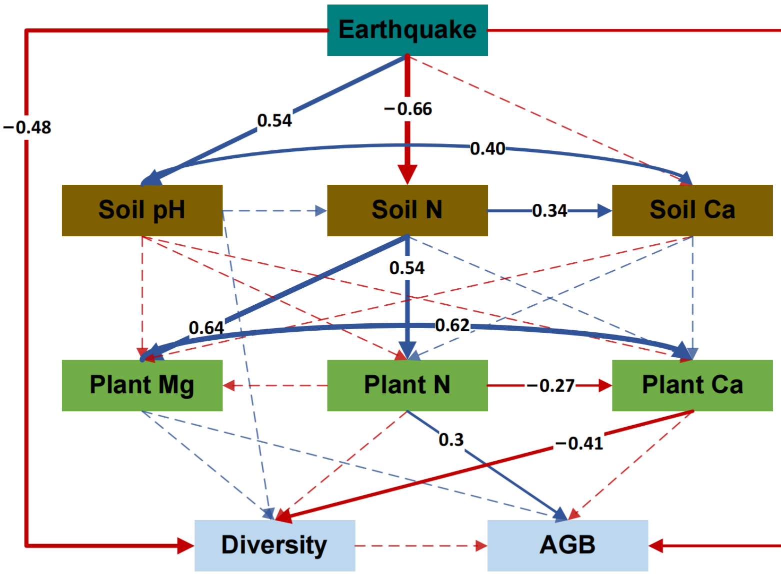

FIGURE 5
Structural equation model (SEM) analysis of the influence path of earthquake on plant community diversity and productivity. Significant positive relationships are denoted by the solid blue lines ($p < 0.05$), while significant negative relationships are indicated by the solid red lines ($p < 0.05$). Weak positive or negative relationships are indicated by dashed blue or red lines, respectively ($p > 0.05$). Arrow width varies directly with the path coefficient's strength. Soil N, soil total nitrogen content; Soil Ca, soil total calcium content; Plant N, plant total nitrogen content; Plant Mg, plant total magnesium content; Plant Ca, plant total calcium content; Diversity, Shannon–Wiener index of the plant community; AGB, aboveground biomass of the plant community. Chi/df = 1.025, $p = 0.414$, GFI = 0.963, CFI = 0.998, RMSEA = 0.023.

4 Discussion

4.1 Earthquake limited plant nutrient uptake by affecting the soil nutrient balance

As a reservoir of nutrients required by plants, soil nutrient changes have an important role to play for plant growth and development (Roca-Pérez et al., 2002; Chaudhary et al., 2008; Friedel and Ardakani, 2020). Undisturbed and well-structured soils, the basic foundation of most of the world's plants, maintain the sustainability, stability, and balance of ecosystems (Rodríguez Rodríguez et al., 2005). Nevertheless, the original nutrient-rich and well-formed soils are susceptible to earthquake disturbance, which destroys the topsoil structure and causes serious soil erosion, further leading to soil nutrient loss (Vittoz et al., 2001; Cui et al., 2012). Our results also suggested that earthquakes greatly contributed to soil nutrients loss, which is in agreement with our first hypothesis. The contents of soil TC, TN, TP, TCa, AP, AK, NH_4^+-N, and SOC were significantly decreased compared with those in areas not affected by the earthquake. This was in keeping with findings by Guo et al. (2013) and Lin et al. (2017) that soil total nutrient content was greatly lost following earthquake, and the contents of SOM (soil organic matter), TN, TP, AHN (alkaline hydrolyzable nitrogen), AP, and AK in the soil were significantly lower in comparison to areas not disturbed by the earthquake. Qiu et al. (2022) also found that soil TC, TP, TN, TS, AP, NO_3^--N, NH_4^+-N, and SOC contents were reduced under alpine wetland environmental conditions after the Maduo earthquake. These nutrient losses may be the result of soil loosening brought on by earthquakes and other secondary geological hazards, which leads to increased aerobic microbial growth and activity, thus speeding up the decomposition of organic matter (Walker and Shiels, 2008; Pupin et al., 2009). Soil pH, an important indicator characterizing soil acidity and alkalinity, strongly influences plant activity (Tsai and Schmidt, 2021). Our findings indicated that earthquakes caused an increase in soil alkalinity and a rise in pH. This phenomenon was also confirmed by the study of Lin et al. (2017). This may be caused by the change in soil profile structure after the earthquake, with deeper layers of carbonate exposed at the surface, leading to an increase in soil pH. An increase in soil pH will raise the negative charge on the surface of plant roots, thus affecting the utilization for nutrients by the plant (Nautiyal et al., 2000; Chaudhary et al., 2008; Barrow and Hartemink, 2023).

Soil nutrients are closely related to plant nutrients. Soil nutrient content is critical to plant growth and is considered a key variable and external factor in plant response (Achat et al., 2018; Briat et al., 2020). The plant root system can take up nutrients from the soil directly, or indirectly from the soil and atmosphere through symbiosis with inter-rooted microorganisms (Patriarca et al., 2002; Katayama et al., 2014). The change in the nutrient content of the soil is the major factor controlling nutrients in plant (Güsewell and Koerselman, 2002; Wang et al., 2018; Zhang et al., 2019). Following earthquake, total and available nutrient contents in the soil were significantly reduced, which led to a decrease in the nutrients available to plants and ultimately led to a loss of nutrient content in the plants. Of these, plants were more sensitive to N, Ca, and Mg uptake, with significant decreases. In arid ecosystems, soil–

vegetation relationships were more associated with Ca, N, and Mg, which confirmed our findings (Pena-Claros et al., 2012). SEM analysis also showed that soil total N played a major role in affecting plant nutrient uptake, which was in agreement with the study of Zhang et al. (2019), where the main factor affecting plant nutrient content was soil total N (Zhang et al., 2019). In short, the earthquake limited the absorption of plant nutrients by affecting soil nutrients, which consequently prevented growth of plants and the development and stability of grassland communities, resulting in profound negative effects on grassland ecosystems. This confirmed our second hypothesis.

4.2 Earthquake directly affected grassland plant diversity

The diversity of plant species is determined by a range of factors at various scales of space (Pena-Claros et al., 2012). Among environmental conditions, soil type and topography have a key part in forming plant diversity, as they both affect the effectiveness of water and nutrients (Potts et al., 2002; Phillips et al., 2003). The structure and diversity of the plant community are influenced by soil nutrients and soil texture in different ways (Pena-Claros et al., 2012). In our research, the decrease in soil nutrients after the earthquake led to a decrease in TN, TCa, and TMg in plants. The nutritional status of plants within a community is closely related to species richness. In some cases, an increase in the nutrient content available to plants will lead to a corresponding decline in species richness. Because of the more limited plant resources, the more niche separation, the greater opportunities for specific trade-offs between different species, the greater the possibility of avoiding competition, and ultimately the coexistence of more plant species (Harpole and Tilman, 2007; Klaus et al., 2013; Borer et al., 2014). Studies have demonstrated that in grassland ecosystems, N and P contents in plant leaves were negatively linked to species richness (Lü et al., 2019) and had a direct impact on plant richness (Harpole and Tilman, 2007). This was similar to our findings, which showed that the N content in plants was negative but not significantly with plant community diversity, while the Ca content was strongly negative with plant community diversity. This may be because plants tend to maintain high community diversity by maintaining low nutrient concentrations in species and improving nutrient utilization efficiency (van Ruijven and Berendse, 2005; Selmants et al., 2014; Lü et al., 2019). However, the low nutrient content of plants in our study did not sustain the increase in diversity, which may be because the decrease in nutrient levels in plants was due to the restriction of lower nutrient content in the soil, rather than the selective absorption strategies of the plants themselves. Grassland community composition is closely related to the concentration of Ca in aboveground biomass, as numerous legumes are accumulators of Ca (Jakobsen, 1993; Bauer et al., 2011). Legumes require higher levels of Ca for the best development (Broadley et al., 2004). This also agrees with our earlier study, i.e., the importance values of legumes decreased significantly after the earthquake rupture (Zuo et al., 2022). Ca levels in plants are highly changeable, but monocots typically have lower Ca concentrations than eudicots, suggesting that low Ca concentrations are more suitable for the growth of monocots like grasses (Broadley et al., 2003). However, the biomass of graminoids was strongly and favorably associated with N content, and the earthquake decreased soil N content, so grassland plant diversity was not enhanced by the decrease in calcium content in plants. Conversely, although a decline in Ca may lead to a reduction in some calciphilous plants and to some extent favor the growth of calciphobe plants, the direct negative short-term effects of earthquakes have a negative impact on all plants and ultimately lead to a decline in diversity. This suggests that the direct effect of the earthquake on decreasing species diversity is significant. Contrary to our third hypothesis, the decrease in plant community diversity from earthquakes may be mainly caused by direct effects such as changes in soil spatial structure.

Several earthquake fault zones were formed directly in the alpine grasslands of the QTP following the M*w* 7.4 Maduo earthquake in 2021. This disruption to the soil structure caused severe soil erosion, leading to an increase in soil permeability and infiltration capacity and a reduction in hydrological regulation, drainage, capacity, and temperature (Vittoz et al., 2001; Cui et al., 2012). In terms of physical properties, the earthquake changed the composition of soil particles, leading to higher sand and clay contents and a decrease in soil moisture content, which replaced previously well-formed soils (Lin et al., 2017), further leading to a decrease in plant community diversity. It has been shown that the Maduo earthquake led to seepage of surface water close to seismic fissures, which caused a reduction in surface water or complete drying, resulting in a reduction in soil moisture, an increase in soil hardness and salinity, and ultimately a loss of vegetation (Qiu et al., 2022).

4.3 Plant nutrient limitation following an earthquake contributed greatly to community productivity reduction

The interaction between plants and soil nutrients shapes plant community structure, which also has a further impact for the productivity of plants (Silva and Batalha, 2008; Wang et al., 2009). Many works have demonstrated that the accessibility of plant nutrients is one of the key elements influencing plant productivity (Elser et al., 2007; Harpole and Tilman, 2007; Fay et al., 2015). Klaus et al. (2013) found that nutrient contents in plants were strongly and positively linked to aboveground biomass and that nutrients were often synergistically co-limited to productivity (Fay et al., 2015). Of these, N is considered a critical determination of aboveground net primary production (ANPP) (Vitousek and Howarth, 1991; LeBauer and Treseder, 2008). This is because N content in plants, an essential nutrient for photosynthetic organ building, is strongly correlated with root tip length or leaf area, while the leaf area index in turn is significantly correlated with total primary productivity (Koller et al., 2015). In agreement with these findings, our study revealed that strong earthquakes caused a decrease in productivity not only through direct effects such as damage to soil structure but also through a decrease in soil N content, limiting plant N uptake and further affecting plant community and productivity. This also confirmed our third hypothesis. Moreover, we can further confirm that N is not only the principal nutrient limiting plant development in grassland ecosystems but also a limiting factor for primary productivity in grassland ecosystems and an essential indicator of grassland productivity (Vitousek et al., 1997; Koller et al., 2015).

5 Conclusion

Our findings showed that the strong earthquake significantly reduced soil quality in the short term, caused soil nutrient loss, and inhibited plant nutrient uptake. The direct negative effect of earthquake was the major cause of the decline in grassland plant diversity in alpine grassland ecosystem on the QTP. Furthermore, in addition to the direct impact pathways of earthquake, earthquake can reduce the productivity of grassland community through the indirect pathway of loss of soil nutrients and inhibition of plant nutrient uptake. The decrease in soil N content after the earthquake significantly inhibited plant nutrient uptake, leading to a significant decrease in plant community productivity. In summary, the earthquake damaged the functional stability of the alpine grassland ecosystem on the QTP. Effective management and restoration methods are desperately required to strengthen the stability and health of grassland ecosystems following strong earthquakes.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

HZ: Formal analysis and Writing—original draft. HShen: Writing—review and editing. SD: Writing—review and editing. SW: Investigation. FH: Investigation. RZ: Investigation. ZW: Investigation. HShi: Investigation. XH: Investigation. YT: Investigation. CM: Investigation. SL: Investigation. YL: Investigation. FZ: Investigation. JX: Investigation. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpls.2023.1240719/full#supplementary-material

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Soil quality and ecological benefits assessment of alpine desertified grassland following different ecological restoration measures

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Introduction: Soil quality plays an irreplaceable role in plant growth for restored grassland. However, few studies investigate the comprehensive effects considering soil and vegetation properties during the restoration of desertified grassland, which restrict the virtuous circle of restored grassland ecosystem.

Methods: By setting three restoration patterns of enclosure plus grass (EG), enclosure intercropping shrub-grass (ESG), and enclosure plus sand-barrier and shrub-grass (ESSG) with three different restoration years (≤5, 7–9, and ≥15 years), we selected 28 physicochemical and microbial indicators, and constructed a minimum data set (MDS) to analyze the influences of restoration measurements on soil quality and ecological benefits in alpine desertified grassland.

Results: The results showed that the MDS comprised seven soil quality indicators: silt, total nitrogen (TN), carbon–nitrogen ratio (C/N), total potassium (TK), microbial biomass carbon (MBC), microbial biomass phosphorus (MBP), and fungi. Soil quality index (SQI) and ecological restoration effect index (EREI) in restored grasslands significantly increased by 144.83–561.24% and 87.21–422.12%, respectively, compared with unrestored grassland, and their positive effects increased with extending restoration years. The increasing effects of SQI and EREI were the highest in ESSG, followed by EG and ESG. The increasing rate of SQI began to decrease after 5 years in EG and ESG, while it decreased after 7–9 years in ESSG, and that of EREI in EG was lower than ESSG in each restoration year. Our work revealed that ESSG was the optimum restoration pattern for desertified grassland, and anthropogenic monitoring and management measurements such as applying organic fertilization and mowing return reasonably should be carried out at the beginning of 5 years in EG and ESG as well as 7 years in ESSG to maintain sustainable ecological benefits.

Discussion: The study highlights that soil quality, including microbial properties, is a key factor to evaluate the restoration effects of desertified grassland.

KEYWORDS

Zoige Plateau, grassland restoration, minimum data set, soil quality index, ecological restoration effect index

Highlights

- Microbial properties had vital contributions to the soil quality of alpine grassland.
- Enclosure and sand barriers plus shrub-grass were superior measurements.
- Management practices need to be applied after 5 years in restored grassland.

1 Introduction

The grassland ecosystem is one of the most widely distributed terrestrial ecosystems in the world (Cai et al., 2020) and plays a key role in regulating climate change by balancing greenhouse gases (Liu et al., 2020). Grasslands also provide the feed demand of ruminants used for meat and milk production (Liu et al., 2023). Nevertheless, alpine grasslands have been threatened by desertification over the past few decades, leading to decline in water retention, species diversity, and grassland productivity (Liu et al., 2019). Therefore, significant efforts have been made to restore desertified grasslands, such as fencing and reseeding. However, after 7 to 8 years of restoration period, some restored grasslands started to deteriorate once more because there are hardly any management practices based on soil dynamic monitoring and quality assessment. (Dong et al., 2014). Consequently, it is essential to monitor and evaluate the soil quality of restored desertified grasslands in order to increase grassland productivity and retain its varied ecological roles.

The core of scientific soil quality assessment predominantly depends on a reasonable evaluation index system that is differentiated in various environmental conditions (e.g., climate and topography) (Zhou et al., 2020; Mamehpour et al., 2021)—for example, bulk density, organic carbon, and carbon–nitrogen ratio can be used to assess the soil quality of grasslands with temperate maritime climate in Ireland (Askari and Holden, 2014). In total, six soil indicators of total nitrogen, available phosphorus, available potassium, organic matter, salinity, and pH were used to assess the soil quality of grasslands with a temperate continental monsoon climate in the Yellow River Delta, China (Wu et al., 2019). Due to the multicollinearity and redundant information among soil properties, how to screen appropriate indicators was extremely vital for soil quality assessment. Fortunately, minimum data set (MDS) as an effective decision-making tool provides a way to address the issue. This is because the MDS can decrease the data dimension and subjective anthropogenic influence, generating the weights of selected indicators at the same time (Wu et al., 2019), which promote the wide application of MDS in the soil quality assessment of grasslands (Yu et al., 2018; Wu et al., 2019; Zhang et al., 2022). However, the assessment indicators of soil quality only included physicochemical properties and ignored sensitive microbial properties in most of previous researches (Askari and Holden, 2014; Wu et al., 2019), which made it hard to comprehensively elucidate the soil quality and its changes in various grasslands. Therefore, soil microbial properties should be considered in soil quality assessment in restored grasslands.

In a restored grassland ecosystem, ecological benefit is an important concern of restoration effect evaluation (Cai et al., 2020). In general, current research mainly focused on the dynamics of vegetation community characteristics to assess ecological benefits during grassland restoration (Scotton, 2019; Liu et al., 2023). Recent studies reported by Liu et al. (2019) and Hu et al. (2022) found that enclosure increased the vegetation coverage, composition, and biomass. In addition, another experiment adopted the patch dispersal index of shrubland to evaluate the ecological benefits (Wu et al., 2022). It is widely known that favorable soil properties are significant in promoting vegetation growth, contributing to positive pairwise feedback between soil and vegetation (Zhang and Zhao, 2015; Raiesi, 2017). Nevertheless, few research considered ecological benefits assessment indexes that were composed of soil and vegetation properties systematically in degraded grasslands (Liu et al., 2017; Wu et al., 2019; Zhou et al., 2020), which lead to inaccurate results of ecological benefits assessment. Furthermore, Li et al. (2023a) pointed out that more attention should be paid to the dynamics of soil quality combined with ecological benefits to maximize the restoration benefits in desertified grasslands. Therefore, assessing soil quality and ecological benefits requires further investigation in restored grasslands.

The Zoige Plateau, located in the northeastern edge of the Qinghai Tibet Plateau, is an important animal husbandry base and a water conservation area, which is dominated by alpine grasslands, accounting for nearly 50% of the entire plateau (Wang et al., 2014; Yang et al., 2021). Nonetheless, the desertification of alpine grasslands has occurred on account of the combined factors of climate warming, pika damages, and grazing. The grassland area has shrunk by more than 30%, which has affected ecosystem functioning in this area (Liu et al., 2020), mainly manifested as the decrease of biodiversity and the destruction of the water storage function of grasslands (Wu et al., 2015). In response to this increasing trend of desertification, a series of restoration measures such as sowing grass, prohibiting grazing, and setting sand barriers (Hu et al., 2016a; Hu et al., 2016b) has been applied to inhibit the tendency of grassland degradation and restore productivity and ecological function, which have achieved beneficial effects successfully (Wang et al., 2012). Some research indicated that vegetation communities and soil quality have effectively improved through the construction of enclosures and the replantation of grass seeds (Hu et al., 2016a; Liu et al., 2019)—for example, Zhang et al. (2022) reported that long-term ecological engineering enclosure improved the soil quality of alpine desertified grasslands. Similarly, Hu et al. (2022) also found that fencing enclosure promoted vegetation growth as well as soil physicochemical and microbiological properties. However, a lot of scholars mainly paid attention to changes of soil and vegetation properties during the restoration of desertified grassland (Liu et al., 2019; Sun et al., 2020; Wu et al., 2023) and ignored the ecological benefits assessment according to soil quality integrated with vegetation parameters in previous research, making it difficult to comprehensively evaluate the ecological benefits of different restoration measurements. Furthermore, few studies about ecological restoration measurements for desertified grassland simultaneously considered restoration patterns and restoration years. It remains unclear whether scientific artificial management measurements based on soil quality and ecological benefits assessment are required in order to avoid grassland degradation again and maintain the stability of restored grassland ecosystems. Based on different restored grasslands, selecting optimal restoration patterns and exploring the restoration year of applying anthropogenic administration need to be further implemented.

To solve the above-mentioned issues, three types of ecological restoration measurements of desertified grassland, including enclosure plus grass pattern (EG), enclosure intercropping shrub-grass pattern (ESG), and enclosure plus sand-barrier and shrub-grass pattern (ESSG) with restoration years for control group (CK), ≤5 years, 7–9 years, and ≥15 years, were performed in Zoige county on Zoige Plateau, where the problems of grassland desertification were particularly severe since 1990s (Hu et al., 2018b). Therefore, it was hypothesized that (1) microbial properties had vital contribution to grassland soil quality, (2) different restoration measurements show various levels of efficiency on the improvement of grassland soil quality and comprehensive ecological benefits, and (3) each restoration pattern is accompanied by an optimal restoration year cooperating with scientific anthropogenic management measures in restored grassland. To address this hypothesis, the objectives of this study were to (1) construct an appropriate evaluation indicator system for soil quality assessment in alpine grasslands, (2) quantitatively assess the effects of different restoration measurements on soil quality and ecological benefits in desertified grasslands, and (3) explore the optimal restoration year requiring management practices in restored grasslands. This research would promote a virtuous cycle of soil nutrients and vegetation growth in desertified grasslands. Moreover, it can also provide a theoretical basis and practical guidance for the scientific restoration and sustainable management of the alpine grassland ecosystem.

2 Materials and methods

2.1 Site description

The research area is located in the central and western part of Zoige County on the northeast edge of the Qinghai-Tibet Plateau (33°43′27″–33°51′43″ N, 102°25′40″–102°33′34″ E), China, which is characterized by arid and semi-arid transitions with a cold alpine climate. Annual precipitation fluctuates between 600 and 750 mm (average 656.8 mm), 90% of which occurs from April to October. The annual mean temperature varies in the range of 0.6°C–1.2°C, with monthly averages of −10.8°C in January and 10.9°C in July. The geological landform is a hilly plateau formed by the intense uplift of the Himalayan tectonic movement and neotectonic movement. The elevation varies from 3,400 to 3,450 m above sea level, and the main water systems are the White River and the Black River (tributaries of the Yellow River). It is interspersed with a subalpine region, river valley plains, and several lake depressions. Subalpine meadows, wet meadows, and marshes dominate the main landscape. The soils in this study area were classified as Cambic Coarsic Leptosols in the World Reference Base for Soil Resources (IUSS Working Group WRB, 2022).

Subalpine meadow grasslands have degraded universally by natural and human factors over 20 years ago. The desertified grasslands were widely distributed in Xiaman Town (33°43′27.3″–33°46′13.6″ N, 102°25′35.3″–102°32′45.1″ E), Maixi Town (33°51′35.9″–33°51′43.8″ N, 102°32′56.7″–102°33′34.7″ E), and Axi Town (33°40′59.7″–33°41′4.6″ N, 102°55′57.8″–102°56′4.2″ E) in Zoige County. The degradation characteristics of grasslands were mainly embodied in decrease of vegetation coverage, biomass, and herbage edibleness. To restore degraded grasslands, a series of restoration measures was carried out by Zoige Forestry and Grassland Administration, China, such as planting *Avena sativa*, *Poa pratensis*, *Elymus nutans*, and *Tamarix ramosissima* artificially. Three primary ecological restoration patterns were carried out in each town respectively, including enclosure plus grass pattern (EG), enclosure intercropping shrub-grass pattern (ESG), and enclosure plus sand-barrier and shrub-grass pattern (ESSG). Each pattern has three restoration periods of ≤5 years, 7–9 years, and ≥15 years. We have not adopted anthropogenic management measurements such as mowing return and applying fertilization during grassland restoration.

2.2 Plot selection and sampling

We set 10 sampling sites, including three restoration patterns with three restoration years, and a control site with unrestored desertified grassland (CK) in each subarea (Figure 1). Then, we selected three sampling quadrats (each 2 m × 2 m) in each sampling site based on the theory of biological replicates. The plant community characteristics (e.g., functional groups, density, and coverage) and biomass were investigated, and we obtained plant samples following the method described in Zhang and Zhao (2015) (Table 1). The soils (0–10, 10–20, and 20–40 cm) were sampled from five random locations at each quadrat, and 90 samples were collected totally. After removing litter and root material, all soil samples from the same plot were mixed and diminished to 800 g approximately. A part of the soil samples was stored in ice bags and reserved at 4°C for measurement of microbial indicators, and the rest of the soil samples were air-dried to determine the physicochemical indicators. Soil bulk density was measured by the cutting ring method simultaneously.

2.3 Soil sample analysis

Soil particle composition was determined by the simple specific gravity method using Stokes' law (Lu, 2000). The total organic carbon (TOC) content was determined by the Walkley–Black potassium dichromate sulfuric acid oxidation procedure (Nelson and Sommers, 1983). The permanganate-oxidizable carbon content was determined following the protocol proposed by Culman et al. (2012). The dissolved organic carbon content was determined by using Vario TOC analyzer (Elementar, Germany) after extracting with deionized water (Chen et al., 2003). The TN content was

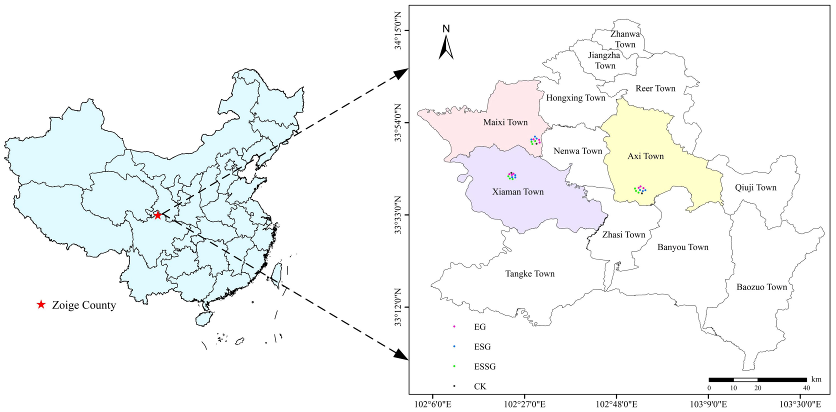

FIGURE 1
Geographical location of the soil sampling sites in Zoige County.

determined by the Kjeldahl method. After 2 mol L^{-1} KCl extraction, ammonium nitrogen (NH_4^+) was determined by indophenol blue colorimetry, and nitrate nitrogen (NO_3^-) was determined by UV spectrophotometry colorimetry (Lu, 2000). The dissolved organic nitrogen (DON) content was calculated as the difference between TN and TIN (the sum of NO_3^-N and NH_4^+–N) (Mariano et al., 2016). The total P and available P contents were measured using the colorimetric molybdenum blue method *via* NaOH fusion and 0.5 mol L^{-1} $NaHCO_3$ (pH = 8.5) extraction, respectively (Lu, 2000). The total potassium (TK) and available potassium (AK) contents were determined using the flame photometer method after digesting in a nickel crucible with NaOH at 750°C and extracted by 1 mol L^{-1} CH_3COONH_4 (pH = 7.0) respectively (Lu, 2000). The number of cultivable bacteria, fungi, and actinomycetes was determined using the dilution plate method (Hou et al., 2014), which were expressed as colony-forming units per gram of soil. The bacteria were incubated in beef protein medium, and the fungi and actinomycetes were cultured in Martin medium and Gauze's synthetic no. 1 medium (Shamiyeh and Johnson, 1973). After soil sampling was performed using the chloroform fumigation–extraction method, Vario TOC cube (Elementar, Germany) analyzer was used to determine the MBC and microbial biomass nitrogen, and MBP was determined by the colorimetric molybdenum blue method (Brookes et al., 1985; Vance et al., 1987). The urease activity was measured by the phenol-sodium hypochlorite method using urea as substrate, which was expressed as milligrams of NH_4^+ per gram of dry soil per hour after incubation at 37°C for 24 h (Samborska et al., 2004). The proteinase activity was determined by the Folin-Ciocalteau reagent and expressed in milligrams of tyrosine per gram of dry soil per hour produced by the incubation of sodium caseinate at 50°C for 2 h (Weber and Tihanyi, 1994). The sucrase activity was measured by the 3,5-dinitrosalicylic

TABLE 1 **Plant community characteristics and biomass in desertified grasslands with different restoration measurements.**

Patterns	Restoration years	Vegetation species	Dominant vegetation	Vegetation coverage (%)	Vegetation density (individual m^{-2})	Grass biomass (g m^{-2})	Shrub biomass (g m^{-2})	Shannon–Wiener index
CK	0	*Rosaceae Goosefoot*	*Potentilla chinensis Agriophyllum squarrosum*	0–13	22	2.20	–	1.44
EG	≤5	*Goosefoot*	*Avena sativa Elymus nutans*	53–63	215	97	–	1.69
	7–9			70–77	481	134	–	1.68
	≥15			88–97	661	156	–	1.65
ESG	≤5	*Tamaricaceae Goosefoot*	*Tamarix ramosissima Avena sativa Elymus nutans Poa pratensis*	57–64	171	90	60	1.55
	7–9			63–69	483	135	270	1.52
	≥15			70–85	673	154	448	1.48
ESSG	≤5	*Tamaricaceae Goosefoot Lamiaceae*	*Tamarix ramosissima Poa pratensis Ajuga lupulina*	37–45	101	78	50	1.74
	7–9			45–59	247	102	980	1.59
	≥15			67–75	565	144	4,770	1.25

EG, enclosure plus grass; ESG, enclosure plus shrub-grass; ESSG, enclosure plus sand-barrier and shrub-grass.

acid colorimetric method, expressed as the amount of glucose released per gram per hour of soil sample in 24 h (Frankeberger and Johanson, 1983). The amylase activity was determined by the dinitrosalicylic acid colorimetric method and expressed as the milligram of maltose in 1 g soil after 24 h (Zhang et al., 2011). Both neutral and alkaline phosphatase activities were determined by the disodium 4-nitrophenylphosphate colorimetric method, which were expressed by the release of 4-nitrophenol per gram of soil samples after incubation at 37°C for 1 h from disodium 4-nitrophenylphosphate (Guan, 1986; Tabatabai, 1994).

2.4 Soil quality assessment

2.4.1 Minimum data set

The MDS approach was used to establish the index system of soil quality (Andrews et al., 2004), aiming to reduce the indicator redundancy (Jahany and Rezapour, 2020). We collected 28 potential soil indicators in the present work, including physicochemical and microbial properties. During this process, principal component analysis (PCA) was used to group the indicators, and only the components with eigenvalues ≥1 were selected. Then, the indicators with loadings ≥0.5 in the same component were classified into one group. If the loading of an indicator in two or more components was >0.5, the indicator was classified into the group where the indicator had the lowest correlations with other indicators. The norm value intended to screen the assessment indicators, representing the comprehensive loading of an indicator in all components. The norm value of each indicator was calculated by using Eq. (1) as follows (Jin et al., 2021):

$$\mathrm{Norm}i = \sqrt{\sum_{i=1}^{k}(uik^2 \times \lambda k)} \tag{1}$$

where Norm_i is the comprehensive loading of indicator i in all components with eigenvalues ≥1, μ_{ik} is the loading of indicator i in component k, and λ_k is the eigenvalue of component k.

The indicator whose norm value was within the 10% range of the maximum value of a group was selected for further correlation analysis (Wu et al., 2019). Subsequently, if the Pearson correlation coefficient of two arbitrary indicators was higher than 0.5, the indicator with a higher norm value was retained in the MDS; otherwise, the indicators were selected.

2.4.2 Soil property scoring

The weight value was calculated by the ratio of norm value for each indicator to the sum of norm values for the selected indicators, as shown in Eq. (2) (Yao et al., 2013). The normalized method is used to convert variables into dimensionless values between 0 and 1 due to the inconsistent units of soil indicators. The relationships among indicators and quality in soils could be divided into three scoring functions: "more is better", "less is better", and "optimum is better" (Santos-Francés et al., 2019). The "more is better" function was applied to the selected indicators because of their positive effects on soil quality in this research. Therefore, the degrees of membership for the selected indicators were calculated using the ascending property function, as shown in Eq. (3) (Biswas et al., 2017). After that, the scores for physicochemical and microbial properties were calculated by combining the degree of membership with the weights of indicators for soil samples as in Eq. (4) (Liu et al., 2017).

$$wi = \frac{\mathrm{Norm}i}{\sum_{i=1}^{n}\mathrm{Norm}} \tag{2}$$

where w_i is the weight of each indicator.

$$S_i = \frac{X_{\max} - Xi}{X_{\max} - X_{\min}} \tag{3}$$

where S_i is the degree of membership of each indicator, X_i is the observed value of each indicator, and $X_{\max}$ and $X_{\min}$ is the maximum and minimum value of each indicator, respectively.

$$F_p = \sum_{i=1}^{n}(wi \times S_i) \tag{4}$$

where F_p is the score of physical, chemical, and microbial properties, and n is the number of soil indicators in the MDS.

2.4.3 Soil quality index

SQI was calculated by the scores of physicochemical and microbial properties in soils and their corresponding weights, reflecting the effects of desertified grassland restoration measurements on soil quality. A larger SQI denotes better soil quality (Liu et al., 2017). The weight values of soil properties were calculated by the commonalities derived from the PCA as shown in Eqs. (5–7) in turn (Mamehpour et al., 2021; Martín-Sanz et al., 2022). SQI was calculated using Eq. (8) (Romaniuk et al., 2011).

$$apj = {}^{fpj}\Big/\sqrt{\lambda j} \tag{5}$$

$$W_{p0} = \sum_{j=1}^{n} a_{pj} \times E_j \tag{6}$$

$$Wp = \frac{W_{p0}}{\sum_{i=1}^{m} W_{p0}} \tag{7}$$

where a_{pj} is the feature vector of property p in component j, f_{pj} is the loading of the property p in component j, λ_j is the eigenvalue of component j, W_{p0} is the weight value of each property, E_j is the explained variance of component j, and W_p is the weight value of property p after normalization.

$$\mathrm{SQI} = \sum_{i=1}^{m}(Wp \times Fp) \tag{8}$$

where SQI is the soil quality index, and m is the number of soil properties.

2.5 Ecological benefits assessment of restoration measurements

PCA was also used to calculate the weight values of indicators, including vegetation coverage, density, and biomass as well as silt, TN, carbon–nitrogen ratio (C/N), TK, MBC, MBP, and fungi in soils. The calculation method of indicator weights was similar to that of soil property weights in soil quality assessment using Eqs. (1) and (2). The degrees of membership of the above-mentioned indicators were calculated using Eq. (3) because these indicators were in accordance with the function of "more is better" (Mamehpour et al., 2021). The ecological restoration effect index (EREI) of restoration measurements was calculated according to Eq. (4).

2.6 Data analysis

The experimental data analyses were performed using SPSS 19.0 (IBM Corp., US) (i.e., maximum, minimum, mean, and standard error). One-way analysis of variance, followed by the Duncan test, was applied to test differences of soil quality indicators among depths, restoration patterns, and years ($p < 0.05$). The correlation coefficients among soil microbial and physicochemical indicators were analyzed *via* Pearson correlation analysis. The figures were drawn by using Origin 2022b (Origin Lab Corp., Northampton, MA, USA).

3 Results

3.1 Soil quality indicators

The soil quality indicators for unrestored grassland (CK) had no significant difference in three subareas ($p > 0.05$) (Supplementary Table S1), and they had no significant differences except bacteria and alkaline phosphatase among depths in the alpine grassland ($p > 0.05$) (Supplementary TableS2). Accordingly, the weighted average of soil quality indicators from different layers was performed for the same quadrat in this research.

As shown in Table 2, the values of soil quality indicators, including physical and chemical properties in restored grasslands, were preferable to those under CK treatment at each restoration year. The soil bulk density and sand content among different ecological restoration patterns were lower than that in unrestored grasslands, and they showed a decreasing trend with increasing restoration years. However, the contents of soil silt, clay, TOC, TN, DON, NH_4^+–N, and NO_3^-N in restored grasslands were significantly higher than those in unrestored grasslands ($p < 0.05$), and they generally significantly increased with increasing restoration years ($p < 0.05$). Moreover, the contents of soil silt and clay in ESSG were significantly higher than in EG and ESG. Meanwhile, our previous results showed that the soil microbial properties, including microbial abundance, microbial biomass, and enzyme activity, in the three patterns of restored grasslands significantly improved ($p < 0.05$) compared with unrestored grasslands (Supplementary Table S4) (Hu et al., 2018a). The improvement effects of the microbial properties enhanced with extended restoration years at each pattern, and those in ESSG were generally better than EG and ESG (Supplementary Table S4) (Hu et al., 2018a).

TABLE 2 Effects of restoration measurements on the soil physicochemical properties.

Indicators	CK	EG			ESG			ESSG		
		≤5 years	7–9 years	≥15 years	≤5 years	7–9 years	≥15 years	≤5 years	7–9 years	≥15 years
BD (g cm^{-3})	1.39a	1.17Bb	1.07Ac	0.94Bd	1.23Ab	1.13Abc	1.05Ac	1.25Ab	0.84Ac	0.97ABc
Sand (%)	96.47a	88.94Cb	89.34Ac	89.37Ac	88.03Bb	88.40Ac	88.4Bd	86.37Ab	86.8Bc	86.63Cd
Silt (%)	1.50 d	6.91Ac	6.83Bb	6.83Ba	8.23Ac	7.37Bb	7.53Aa	7.89Bc	7.23Aa	7.20Bb
Clay (%)	2.03b	4.14Aa	3.83Aa	3.8Ba	3.73 Ba	4.23Aa	4.07Ba	5.74Ca	5.97Aa	6.17Aa
TOC (g kg^{-1})	1.24c	3.24Ab	4.67Ab	9.61Aa	3.22Abc	3.78Ab	7.75Ba	2.98Ac	6.99Ab	9.08ABa
TN (g kg^{-1})	0.05d	0.16Ac	0.26Ab	0.42ABa	0.19Ab	0.21Ab	0.38Ba	0.10Bbc	0.23Ab	0.50Aa
C/N	16.84b	20.15Bab	17.95Ab	23.52Aa	17.32Ba	17.38Aa	20.99Aa	26.19Aa	21.42Ab	18.15Ac
DON (mg kg^{-1})	1.30c	1.58Ac	3.22Ab	4.65Aa	2.13Aa	1.41Ab	1.96Bab	1.65Ab	2.94Ab	5.08Aa
NH_4^+–N (mg kg^{-1})	0.39d	1.37Ac	2.47Ab	3.75Aa	1.68Ab	1.98Aab	2.67Ba	1.85Ab	2.13Ab	3.40Aa
NO_3^-N (mg kg^{-1})	0.46d	1.09Ac	2.11Ab	3.38Aa	1.15Ab	1.55Ab	2.35Aa	1.80Aab	2.38Aab	3.20Aa
TP (g kg^{-1})	0.24d	0.25Bc	0.32Ab	0.35Ca	0.28Bb	0.35Aa	0.39Ba	0.36Ab	0.41Aab	0.50Aa
AP (mg kg^{-1})	1.88c	2.92Ab	2.83Bb	5.00Ba	2.88Abc	4.17ABab	5.47Ba	2.88Ac	4.95Ab	6.57 Aa
TK (mg kg^{-1})	17.96ab	17.76Ab	19.13Aab	19.97Aa	18.44Ab	18.13Bb	17.93Bb	19.30Aa	19.25Aa	18.00Bb
AK (mg kg^{-1})	30.98c	39.20Bab	37.33Bb	48.84Ba	30.26Bb	52.15Aa	50.43Ba	50.13Ab	55.55Ab	68.50Aa

BD, bulk density; TOC, total organic carbon; TN, total nitrogen; C/N, carbon–nitrogen ratio; DON, dissolved organic nitrogen; NH_4^+–N, ammonium nitrogen; NO_3^-N, nitrate nitrogen; TP, total phosphorus; AP, available phosphorus; TK, total potassium; AK, available potassium.

Different capital letters above each bar indicate significant differences among different restoration patterns at $p < 0.05$. Different lowercase letters above each bar indicate significant differences among different restoration years at $p < 0.05$.

3.2 Minimum data set of soil quality

Table 3 indicates that different principal components (PCs) were selected with eigenvalues ≥1 for soil physical, chemical, and microbial properties. PC1 explained 82.39% of the total variance in soil physical properties including four indicators, and soil silt was selected as the appropriate indicator representing physical properties (Table 3). In terms of chemical properties

TABLE 3 Principal component loading matrix and norm values of soil quality indicators.

Soil indicators	Physical properties	Chemical properties			Microbial properties		Group	Norm
	PC1	PC1	PC2	PC3	PC1	PC2		
Silt	-0.986						1-1	1.790
BD	0.921						1-1	1.671
Sand	0.869						1-1	1.577
Clay	-0.849						1-1	1.542
TN		0.929	-0.252	0.099			2-1	2.501
NH_4^+–N		0.904	-0.109	0.192			2-1	2.426
TOC		0.902	0.145	-0.017			2-1	2.416
AP		0.857	-0.033	-0.247			2-1	2.304
TP		0.856	0.113	-0.128			2-1	2.294
NO_3^-N		0.849	-0.085	0.131			2-1	2.275
PXOC		0.813	0.026	-0.061			2-1	2.173
DON		0.769	-0.013	0.308			2-1	2.079
DOC		0.766	0.205	-0.181			2-1	2.069
AK		0.758	0.128	-0.312			2-1	2.054
C/N		-0.156	0.885	-0.345			2-2	1.161
TK		0.129	0.617	0.734			2-3	1.088
MBN					0.948	0.012	3-1	2.768
MBC					0.944	0.039	3-1	2.758
Bacteria					0.932	-0.006	3-1	2.721
Urease					0.926	-0.113	3-1	2.705
Protease					0.912	-0.084	3-1	2.664
Amylase					0.902	-0.097	3-1	2.636
Sucrase					0.881	0.065	3-1	2.574
Neutral phosphatase					0.841	-0.124	3-1	2.459
Alkaline phosphatase					0.822	0.145	3-1	2.403
Actinomyces					0.638	0.383	3-1	1.902
Fungi					0.648	0.533	3-2	1.966
MBP					0.616	-0.707	3-2	1.933
Eigenvalue	3.296	7.137	1.342	1.028	8.527	1.003		
Variance (%)	82.392	59.478	11.183	8.566	71.056	8.360		
Cumulative variance (%)	82.392	59.478	70.661	79.227	71.056	79.416		

PC, principal component; BD, bulk density; TN, total nitrogen; NH_4^+–N, ammonium nitrogen; TOC, total organic carbon; AP, available phosphorus; TP, total phosphorus; NO_3^-N, nitrate nitrogen; PXOC, permanganate oxidized carbon; DON, dissolved organic nitrogen; DOC, dissolved organic carbon; AK, available potassium; C/N, carbon–nitrogen ratio; TK, total potassium; MBN, microbial biomass nitrogen; MBC, microbial biomass carbon; MBP, microbial biomass phosphorus.

encompassing 12 indicators, three PCs explained 79.23% of the total variance, and PC1, PC2, and PC3 explained 59.48%, 11.18%, and 8.57% respectively. Combined with the correlation coefficients of soil chemical indicators, we chose TN, C/N, and TK in the MDS, representing chemical properties on account of their higher loadings and norm values (Table 3; Supplementary Table S3). Concerning microbial properties involving 12 indicators, two PCs explained 79.42% of the total variance, and PC1 and PC2 explained 71.06% and 8.36% of the variation, respectively. MBC, MBP, and fungi were contained in the MDS because of higher loadings and norm values (Table 3; Supplementary Table S4). As a result, sensitive and important indicators comprising soil silt, TN, C/N, TK, MBC, MBP, and fungi were selected to establish the MDS of alpine grassland soil quality.

3.3 Soil quality

As shown in Table 4, the weights of soil physical, chemical, and microbial properties were almost equal. The scores of soil properties increased with increasing restoration years. Figure 2 shows that the value of SQI varied from 0.102 to 0.671. The SQI in ESSG was higher

TABLE 4 Indicator weights and scores of properties in soils.

Properties	Indicators	Years	Scores of properties		
(Weight, w_p)	(Weight, w_i)		EG	ESG	ESSG
Physical properties	Silt (1.00)	0	0.074		
(0.34)		≤5	0.495	0.399	0.197
		7–9	0.662	0.652	0.795
		≥15	0.722	0.909	0.712
Chemical properties	C/N (0.24)	0	0.079		
(0.34)		≤5	0.057	0.047	0.099
		7–9	0.048	0.049	0.151
		≥15	0.072	0.061	0.049
	TN (0.53)	0	0.009		
		≤5	0.117	0.148	0.059
		7–9	0.211	0.167	0.179
		≥15	0.357	0.320	0.435
	TK (0.23)	0	0.045		
		≤5	0.127	0.152	0.183
		7–9	0.177	0.141	0.181
		≥15	0.203	0.134	0.129
Microbial properties	MBC (0.42)	0	0.030		
(0.32)		≤5	0.109	0.136	0.082
		7–9	0.176	0.161	0.166
		≥15	0.268	0.305	0.319
	MBP (0.28)	0	0.024		
		≤5	0.045	0.046	0.101
		7–9	0.068	0.072	0.125
		≥15	0.139	0.113	0.192
	Fungi (0.30)	0	0.046		
		≤5	0.108	0.101	0.057
		7–9	0.144	0.086	0.108
		≥15	0.200	0.167	0.091

C/N, carbon–nitrogen ratio; TN, total nitrogen; TK, total potassium; MBC, microbial biomass carbon; MBP, microbial biomass phosphorus.

than EG and ESG overall (Figure 2). The SQI in each restoration pattern increased significantly with increasing restoration years. The SQI of ≤5 years, 7–9 years, and ≥15 years increased by 144.83–249.14%, 319.63–463.10%, and 506.28–561.24%, respectively, compared with CK ($p < 0.05$) (Figure 2). Moreover, the increasing rate of SQI began to reduce after 5 years in EG and ESG (Figure 2), whereas the increasing rate of SQI between ≤5 years and 7–9 years improved by 120.13% compared with ≤5 years in ESSG, which started to decrease after 7–9 years ($p < 0.05$) (Figure 2).

3.4 Ecological restoration benefits

The value of EREI ranged from 0.104 to 0.547 (Figure 3). There was no significant difference among the three restoration patterns ($p > 0.05$), but EREI in ESSG was generally higher than that in EG and ESG, especially before 7–9 years (Figure 3). EREI increased constantly with increasing restoration years, of which 7–9 years and ≥15 years significantly increased by 6.93%–107.91% and 93.23%–178.89% respectively, compared with 0–5 years ($p < 0.05$) (Figure 3). In addition, the increasing rate of EREI in EG was lower than ESSG. Moreover, the increasing rate of EREI in ESG was lower than ESSG from 5 to 7–9 years, while that in ESG was higher than ESSG after 7–9 years (Figure 3).

4 Discussion

4.1 Evaluation indicator system for soil quality in alpine grasslands

In this research, soil silt, TN, C/N, TK, MBC, and MBP as well as fungi have been selected as soil quality indicators, and they were associated with vegetation growth during grassland restoration. The changes of soil silt content under the application of restoration measurements were the most significant compared with that of sand and clay, similar to the finding of He et al. (2021), which was ascribed to the fact that vegetation restoration could weaken wind erosion, thereby reducing the loss of fine particles (Zhang et al., 2022). The decomposition of plant litterfall increased the soil organic matter under the conditions of planting herbs and/or shrubs plus grazing prohibition in desertified grassland (Yu et al., 2018). Thus, litterfall was enhanced with an increase of aboveground biomass in restored grasslands (Table 1), which induced the changes of C/N and TN contents in soils. The potassium (K) requirement for plant growth greatly increased in the middle and late stage of restoration, which could promote the conversion of soil mineral K to AK *via* the mobilization of organic acids and enzymes from K-solubilizing bacteria, and mineral K was the main form of TK in soils (Zhang et al., 2022). The increase of litter input led to the improvement in soil water storage capacity, which

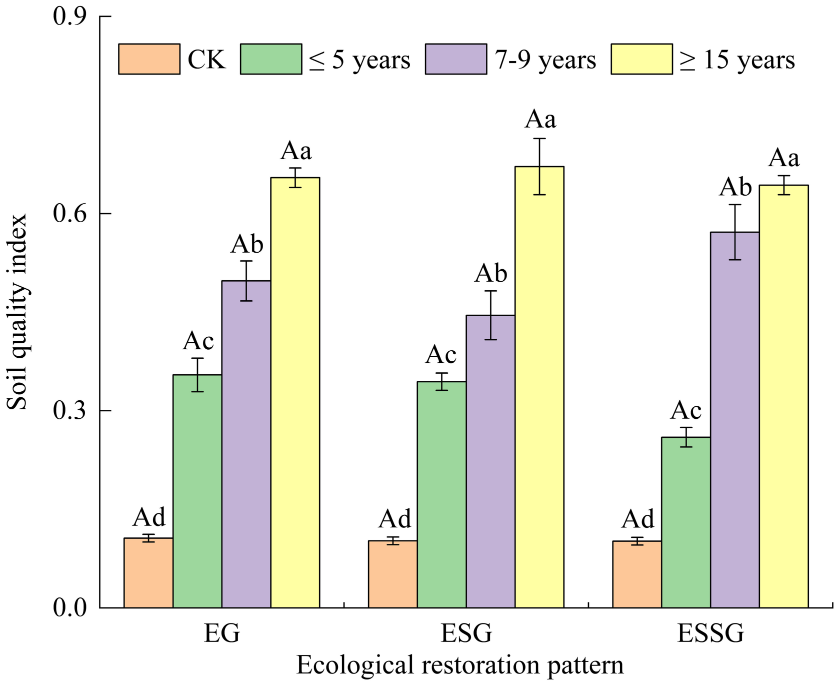

FIGURE 2
Soil quality index of desertified grasslands with different restoration measures. Different capital letters above each bar indicate significant differences among different restoration patterns at $p < 0.05$. Different lowercase letters above each bar indicate significant differences among different restoration years at $p < 0.05$. Vertical bars denote the standard error of the means. EG, enclosure plus grass; ESG, enclosure intercropping shrub-grass; ESSG, enclosure plus sand-barrier and shrub-grass.

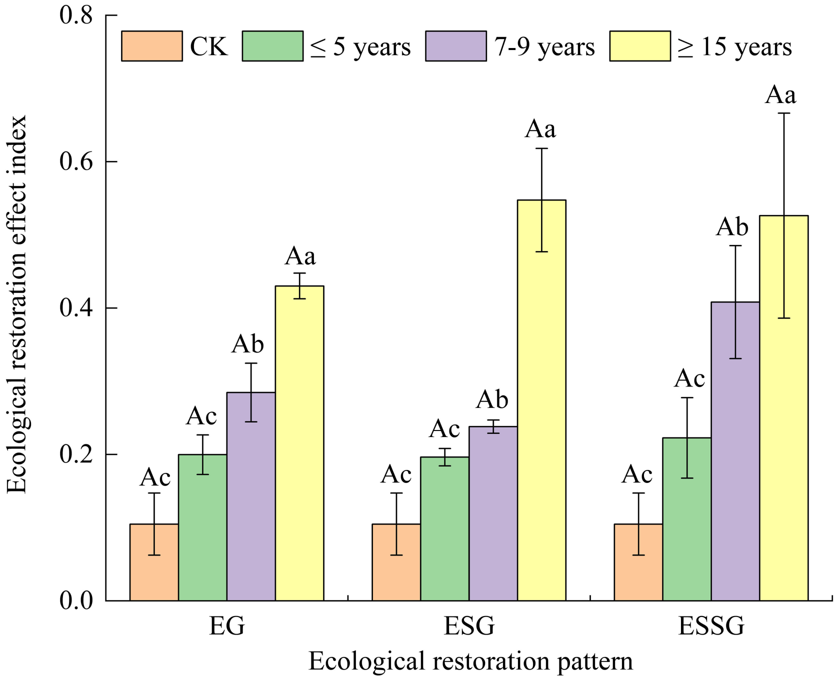

FIGURE 3
Ecological restoration effect index of desertified grasslands with different restoration measures. Different capital letters above each bar indicate significant differences among different restoration patterns at $p < 0.05$. Different lowercase letters above each bar indicate significant differences among different restoration years at $p < 0.05$. Vertical bars denote the standard error of the means. EG, enclosure plus grass; ESG, enclosure intercropping shrub-grass; ESSG, enclosure plus sand-barrier and shrub-grass.

was conducive to the reproduction of microorganisms together and further increased the fungi abundance as well as the contents of MBC and MBP in soils (Liu et al., 2017; Zhang et al., 2021). In recent years, some studies have also established the MDS of soil quality assessment based on physicochemical properties in temperate grassland ecosystems (Wang et al., 2021b; Li et al., 2023b). Nevertheless, our results found that the weights of soil microbial properties were almost equal to the soil physicochemical properties and that the soil microbial properties had positive and significant effects on TN (Supplementary Figure S1), indicating that microbial properties had non-negligible significance to soil quality in this study area. Therefore, microbial properties should be considered to assess the soil quality of alpine grassland under restoration measurements.

4.2 Comparison in the assessment indicators of soil quality among restored desertified grasslands

Different restoration patterns and years had various improvement effects on soil assessment indicators. As far as soil physical properties were concerned, silt content increased, which was similar to the findings of Hu et al. (2022) and can be attributed to the fact that vegetation restoration effectively resisted soil sand outside and promoted the optimization of soil texture (Zhang and Zhao, 2015). Soil structure and texture improved by applying restoration measurements, which may further lead to an increase in soil nutrients (Hu et al., 2022). In this study, the soil nutrient contents of the restored grassland were also significantly higher than those of the unrestored grassland, particularly the significant increase of TN content, similar to the implementation effects of restoration measurements in Shenza County in the Tibetan Plateau as reported by Zhang et al. (2022). This was mainly because the humification of litterfall could directly increase the soil nutrient content, and the improvement of physical properties (e.g., texture, structure, and water retention) might reduce the mineralization of organic matter (Kooch et al., 2022). Previous studies revealed that the vegetation biomass had positive relationships with soil microbial biomass generally (Zhang and Zhao, 2015; Yang et al., 2022). The increase of carbon and nitrogen sources of microorganisms further enhanced the soil microbial biomass (Yu et al., 2018). Therefore, the contents of MBC and MBP as well as the quantity of fungi improved significantly, which was caused by the increase of vegetation biomass together with soil carbon and nitrogen contents in each restoration pattern (Tables 1, 2).

In general, soil quality indicators are gradually optimized due to increased vegetation coverage, density, and biomass (Zhang et al., 2022; Wan et al., 2023). In this research, the vegetation coverage, density, and biomass of restored grassland increased (Table 1), thus inducing soil quality indicators gradually ameliorated with the increasing restoration years, which was similar to the findings of Li et al. (2023c). Furthermore, the contents of slit and MBC in ESSG were significantly higher than EG (Table 2, Supplementary Table S4). These results can be explained by the combined effects of sand barriers and vegetation that were beneficial to sand fixation and water conservation, further effectively improving the soil quality (Wang et al., 2021a; Hu et al., 2022).

4.3 Effects of desertified grassland with different restoration measures on soil quality and ecological benefits

Vegetation biomass had significant positive relationships with SQI and EREI ($R^2 > 0.6$, $p < 0.05$), indicating that soil quality and ecological benefits improved with the increase of biomass in alpine grasslands. We found that the restoration measurements improved the soil quality and ecological benefits of desertified grassland (Figures 2, 3), which was consistent with the findings of positive effects of the fenced enclosure on the soil quality of sandy grassland in the Tibetan Plateau as reported by Zhang and Zhao (2015); Hu et al. (2022), and Zhang et al. (2022). The main reason that was attributed to is that restored vegetation and/or sand barriers could be able to separate the sand sources and resist wind erosion effectively in areas with strong winds (Wan et al., 2023), which was beneficial for soil and water conservation as well as nutrient retention in desertified grassland. Moreover, plants grow preferably based on superior conditions of soil water and nutrients. On the one hand, vigorous plants could retain water and return organic matter *via* litterfall (Yu et al., 2018). On the other hand, the decomposition and humification of dead root and root exudates could promote soil quality (Wu et al., 2023). Therefore, the soil–vegetation system could form positive mutual feedback in restored grassland, further improving soil quality and restoring ecological service functions.

Soil quality and ecological benefits in ESSG were optimal among three restoration patterns because setting sand barriers was of great significance to prevent wind and fix sand as well as reserve moisture in sandy soils (Liu et al., 2019). Particularly, shrubs with deep roots promoted the accumulation of organic matter and nutrients in shallow soils combined with the roles of sand barriers (Kidron and Gutschick, 2013; Wang et al., 2021a), which could strengthen the positive mutual feedback between vegetation and soil. Similarly, Scotton (2019) also reported that combining sand fixation barriers and phytoremediation was a good way to restore the ecology of desertified grasslands.

Vegetation is an important and positive driving force for restoring desertified grasslands, as Wu et al. (2023) have reported. Furthermore, the significant improvement of vegetation (e.g., biomass) with the increase of restoration years was beneficial to restore ecological function directly and indirectly in desertified grasslands (Wang et al., 2023). As the restoration years of degraded grasslands in our study increased, the aboveground and root biomass of vegetation also gradually improved (Table 1). This was conductive to enhance the abilities of retaining water and nutrients and increase litter return and root exudates, which can also further strengthen the positive feedback between soil and vegetation. Thus, soil quality and ecological benefits increased significantly, corresponding to the increasing restoration years in each restoration pattern.

4.4 Optimal restoration year of applying management practices in different restored grasslands

The increasing rate of SQI in EG and ESG as well as EREI in EG began to decrease after 5 years of the application of restoration measurement, indicating that short-term fencing was more beneficial than long-term fencing. A probable explanation for this outcome was that the increasing requirement of plant nutrients slowed down the amount of nutrient accumulation and optimization of microbial characteristics in soils under the circumstances of long-term grazing exclusion (Li et al., 2023c). A similar result has been shown in the study of Sun et al. (2020) and Zhang et al. (2022), respectively, such that longer-term grazing exclusion had a little effect on vegetation growth without the construction of sand prevention belts. Interestingly, the increasing rate of SQI and EREI in ESSG was reduced after 7–9 years. This may be ascribed to the fact that the decay of sand barriers combined with a large amount of requirement of plant nutrients could also slow down the amelioration of soil features after 7–9 years based on the result of Liang et al. (2023). Thus, it was hard to ensure that the soil–vegetation system was constantly a virtuous cycle with the increase of restoration years.

In addition, plant species diversity appeared to decrease along with increased restoration years (Table 1) because the growth of some plants may have been inhibited during grassland restoration (Li et al., 2023c). This would cause a weakening in the stability of ecosystems, according to a research reported by Zhou et al. (2017). As a result, combined with the increasing rate of SQI, EREI, and plant diversity, we suggest that the appropriate time of anthropogenic monitoring and management measurements, such as applying organic fertilizer in soils and mowing return, should be reasonably considered at the beginning of 7 years in ESSG and 5 years in the other two patterns to maintain sustainable ecological benefits.

5 Conclusions

Using the MDS and comprehensive index method, our study assessed the soil quality and ecological benefits in restored grasslands. The MDS of soil quality comprised seven key indicators: silt, TN, C/N, TK, MBC, MBP, and fungi. The increase of vegetation coverage, density, and biomass resulted in such a way that the soil physicochemical and microbial properties as well as the soil quality and ecological benefits were superior in restored grasslands than in unrestored grasslands. Furthermore, the positive effects of soil quality and ecological restoration increased upon extending the restoration years of restored grasslands, and they generally ranked in the order as follows: EG< ESG< ESSG. The increasing rates of SQI decreased after 5 years in EG and ESG and 7 years in ESSG, while that of EREI in EG was lower than ESSG in each restoration year. Therefore, ESSG was the best restoration pattern of desertified grasslands, especially for moving sandy grasslands. Scientific anthropogenic monitoring and management measurements should be carried out at the beginning of 5 years in EG and ESG as well as 7 years in ESSG. We are supposed to pay more attention to the anthropogenic management practices to maintain sustainable ecological restoration effects of desertified grassland in future research—for instance, applying organic fertilizer combined with mowing return might be needed to further form a virtuous cycle of soil–vegetation system.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Author contributions

YiL: Data curation, Writing – original draft, Writing – review & editing. SH: Data curation, Visualization, Writing – review & editing. SL: Data curation, Writing – original draft. YP: Funding acquisition, Writing – review & editing. SZ: Conceptualization, Writing – review & editing. TL: Conceptualization, Data curation, Writing – review & editing. XX: Conceptualization, Validation, Writing – review & editing. YJ: Conceptualization, Visualization, Writing – review & editing. GW: Conceptualization, Writing – review & editing. DY: Funding acquisition, Writing – review & editing. YuL: Visualization, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpls.2023.1283457/full#supplementary-material

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Assessing the win–win situation of forage production and soil organic carbon through a short-term active restoration strategy in alpine grasslands

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Introduction: Grassland degradation has seriously affected the ecological environment and human livelihood. To abate these, implementing effective management strategies to restore and improve the service functions and productivity of degraded grasslands is crucial.

Methods: To evaluate the influences of restoration measures combined with different grazing intensities on short-term (1 year) grassland restoration, the changes in soil physicochemical properties, as well as plant traits under restoration measures of different grazing intensities, reseeding, and fertilization, were analyzed.

Results: Soil organic carbon (SOC) increased to varying degrees, whereas available nutrients decreased under all combined restoration measures. Reseeding, alone and in combination with fertilization, substantially increased SOC, improved grassland vegetation status, and enhanced grassland productivity. The aboveground biomass of Gramineae and the total aboveground biomass increased under the combined restoration measures of transferring livestock out of the pasture 45 days in advance, reseeding, and fertilization (T4). Redundancy analysis revealed a strong correlation between grassland vegetation characteristics, SOC, and available potassium. Considering soil and vegetation factors, the short-term results suggested that the combination measures in T4had the most marked positive impact on grassland restoration.

Discussion: These findings offer valuable theoretical insights for the ecological restoration of degraded grasslands in alpine regions.

KEYWORDS

grassland degradation, ecological restoration, short-term, soil properties, plant

1 Introduction

Grasslands are important components of terrestrial ecosystems that maintain human livelihoods and national ecological security (Gomez-Casanovas et al., 2021). In the last few years, the overuse of grassland resources due to increases in population and animal husbandry and a chronic lack of scientific management of grassland resources has severely deteriorated the ecological environment and productivity of the grassland (Zhang et al., 2019; Bardgett et al., 2021). Previous research claims that nearly 39.06% of grasslands globally have some form of degradation (Liu et al., 2019). Although the overall trend in grassland degradation has been curbed in the last 10 years, grassland degradation in some areas has become more serious, and the productive capacity of some grasslands has been lost completely (Hou et al., 2022). The world's largest alpine grassland ecosystem is found on the Qinghai–Tibet Plateau, which is significant to the development of local animal husbandry, water conservation, and environmental security (Liu et al., 2021). Since the 1970s, the development of animal husbandry on the Qinghai–Tibet Plateau has resulted in overgrazing and a sharp reduction in grassland (Zhao et al., 2022). Natural grassland vegetation coverage and productivity have decreased, inedible forage, poisonous plants, and weeds have increased, and some seriously degraded grasslands have even transformed into "bare lands". This seriously threatens local ecological security and the development of animal husbandry (Shang et al., 2008; Dong, 2023). Therefore, for the sustainable development of the economy, society, and the ecological environment of local pastoral areas, the restoration and management of degraded grasslands have become critical.

Plant–soil interactions determine the stability of grassland formation and development. Two basic characteristics of community stability, species diversity and productivity, are the core indices of the grassland ecosystem (Pennekamp et al., 2018). Species diversity reflects the complex relationship between organisms and their environment as well as the richness of biological resources. The aboveground biomass mirrors the vegetation characteristics and productivity of grasslands and maintains ecosystem diversity (Hector et al., 1999; Dietrich et al., 2023). Grassland degradation contributes to the reverse transformation of the structure and function of grassland ecosystems, simultaneously weakening grassland productivity, which leads to biodiversity loss and community destabilization (Dong et al., 2018; Berdugo et al., 2020). Grassland degradation includes vegetation and soil degradation. Vegetation degradation manifests as decreases in biomass, coverage, the proportion of edible herbage, species diversity, and stability and an increase in poisonous plants and weeds. Soil degradation is manifested in variations in soil physicochemical properties and structure and the deterioration of microbial and enzymatic activities (Xie et al., 2018; Peng et al., 2019; Su et al., 2023). Vegetation degradation is directly caused by soil degradation. Vegetation growth and development are heavily dependent on the supply of soil nutrients. Therefore, vegetation growth is restricted by soil fertility to a certain extent, indicating mutual influence between these factors (Wu et al., 2020; Kooch et al., 2022).

Restoration measures for degraded grasslands mainly include enclosures, restoration of farmland to grassland, turf cutting, no-tillage reseeding, and fertilization. In view of the existing difficulties in the restoration of degraded grasslands in different areas, restoration methods also differ (Gu et al., 2022; Wu et al., 2023) —for example, some researchers have taken measures, such as enclosure, trench excavation, and fish-scale pit construction, to restore degraded grasslands to their typical state in the hill area of the Loess Plateau (Han et al., 2015). Different measures for restoring degraded grasslands have also been studied. In mildly degraded grasslands, fencing, rodent control, and varying grazing intensities and durations have been adopted (Choi, 2007). For moderately degraded grasslands, measures such as reseeding and fertilization have been adopted (Wu et al., 2023). Artificial grassland restoration measures have been adopted in severely and extremely degraded grasslands (Liu et al., 2017; Liu et al., 2022). Several investigations have found that different combinations of measures have different restoration effects on degraded grasslands (Yin et al., 2021; Duan et al., 2022). Compared to single grassland restoration measures, combined measures have a more apparent improvement on degraded grasslands (Wei et al., 2022; Wu et al., 2023).

Previous studies on the restoration of degraded grassland were conducted in grazing-prohibited sites, which focus on the long-term grassland restoration but not on short-term productivity, animal husbandry development, and other livelihood issues (Bai et al., 2020; Dietrich et al., 2023). We used the grassland of Gannan Prefecture to explore the variations in soil properties and vegetation characteristics under different combined restoration measures with different grazing intensities and the relationships between them. The objective was to clarify the short-term effects of different combined measures of restoration on degraded grasslands and determine which restoration measure with regional characteristics is suitable for local traditional production modes. The results of this study may provide new ideas and theoretical references for the future comprehensive solution to production, ecological, and people's livelihood problems.

2 Methods

2.1 Study sites

Our experiment was conducted at Sangke grassland (34°51′N–34°52′N, 102°04′E–102°07′E) in Xiahe County, Gannan Prefecture (Figure 1). The altitude is 3,200–3,500 m, the mean annual air temperature is 2.6°C, and the mean annual precipitation is 500 mm. Rainfall mainly occurs from July to September, when grass growth is strong. The climate is cold and humid, the temperature varies widely from day to night, rain and heat occur during the same season, and the vertical temperature differential is substantial. Absolute non-frost periods are not observed. The vegetation growing season is 120–140 days. The soil type is subalpine meadow soil with alpine and mountain meadow grasslands.

The excellent herbage in grassland vegetation predominantly included *Elymus nutans*, *Carex lanceolata*, *Poa pratensis*, *Lolium*

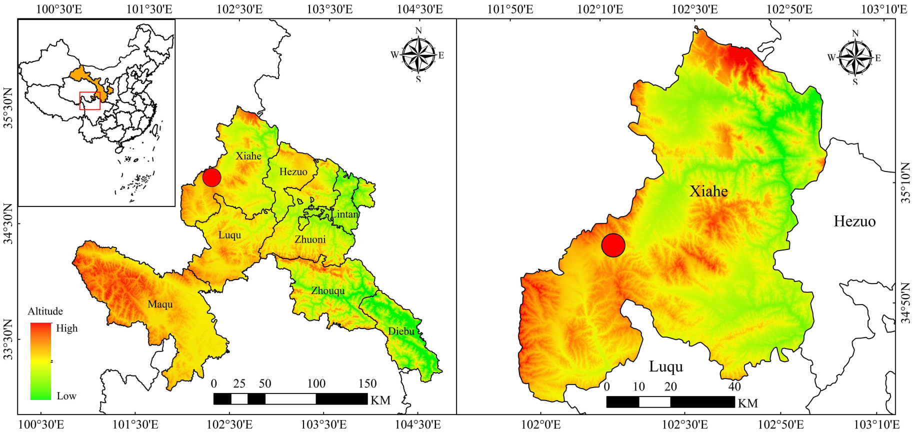

FIGURE 1
Location of the study site in Xiahe County, Gannan Prefecture. The red circle represents the study site.

perenne, *Festuca ovina*, *Polygonum viviparum*, *Kobresia humilis*, and *Trigonella ruthenica*. The poisonous plants and weeds included *Potentilla bifurca*, *Oxytropis kansuensis*, *Leontopodium leontopodioides*, *Gentiana macrophylla*, *Thalictrum aquilegiifolium*, *Achnatherum inebrians*, *Gentiana dahurica*, *Delphinium grandiflorum*, *Ligularia virganrea*, and *Pedicularis kansuensis*.

2.2 Experimental design

Three grazing intensities and four combined restoration measures were used at the study sites (Figure 2). Our study was conducted under the conditions of a certain area of the grassland and the number of livestock (2.5 standard sheep unit/hm^2). The specific times of the three grazing treatments were as follows: CK: normal grazing on May 23, 2020; G1: transfer of livestock out of the pasture 30 days in advance on April 23, 2020; and G2: transfer of livestock out of the pasture 45 days in advance on April 7, 2020. The four restoration measures were as follows: T1: combination of G1 and reseeding; T2: combination of G2 and reseeding; T3: combination of G1, reseeding, and fertilization; and T4: combination of G2, reseeding, and fertilization.

The native grass species used for the mechanical no-tillage reseeding were *E. nutans*, *Poa crymophila*, and *L. perenne*. The seeding rates of the three grasses were 30 kg/hm^2 *E. nutans*, 15 kg/hm^2 *P. crymophila*, and 15 kg/hm^2 *L. perenne*. The three types of grass were mixed during sowing.

An organic–inorganic compound fertilizer was selected. The fertilizer nutrients were as follows: (B + Za + Fe + Mo) 0.1%, (S + Ca + Mg) 3%, (N + P_5O_2 + K_2O) 17%, pH = 6.0–6.5, and organic matter content 30%. The application rate of organic and inorganic compound fertilizers was 1,200 kg/hm^2. Mechanical fertilization, disc harrow cutting, covering of the soil, and other processes were required before sowing to ensure that the fertilizer was fully embedded within the soil.

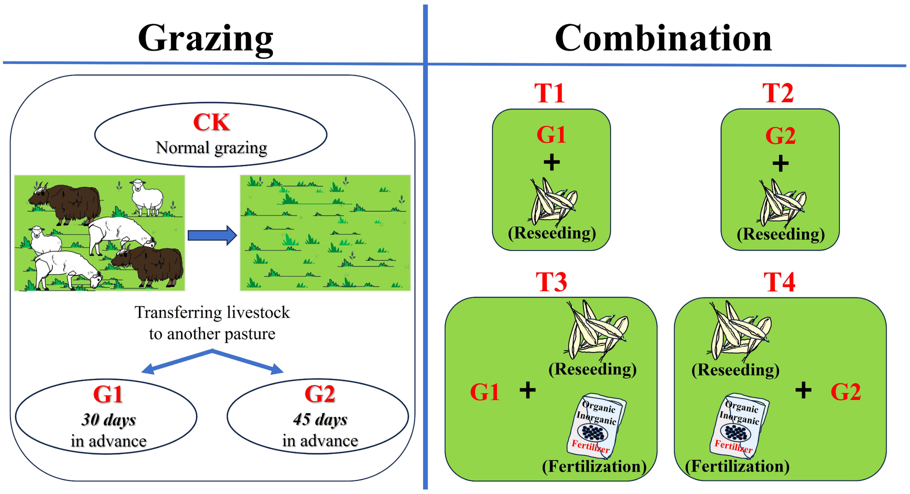

FIGURE 2
Diagram of different restoration measures in degraded alpine grasslands.

2.3 Vegetation and soil sampling

Field survey sampling was conducted in August 2020. The experiment included four sites with different combined restoration measures and three sites with different grazing intensities. Every site was 5 hm^2. We selected three similar plots (0.5 m × 0.5 m) at each site randomly. The coverage and natural height of each species were measured. Within each plot, all plants, including both live and standing dead biomass, were clipped to ground level inside each plot to calculate the total aboveground biomass (AGB). Within each site, soil samples were collected from each of the three replicated plots ($n = 3$) at three different depths (0–10, 10–20, and 20–30 cm), and a total of five soil cores with a diameter of 5 cm were randomly sampled at each depth. We formed a composite sample, which was uniformly mixed using the soil samples from the same depth at each site.

We used the over-drying method to detect the soil water content (SWC) (Thomasson, 1978). The litter, plant roots, and stones in the soil samples were removed manually. Then, the soil samples were air-dried. The soil was ground fully and passed through a sieve with a pore size of 0.25 mm. The soil pH was measured using a pH meter (Sartorlus, Beijing, China). The dichromate oxidation method was used to measure the soil organic carbon (SOC). The soil total phosphorus (TP) was measured using the $HClO_4$–H_2SO_4 method. The Kjeldahl method was used to determine the soil total nitrogen (TN) (Bao, 2000). The available potassium (AK) and total potassium (TK) were detected using a flame photometer after digestion with NaOH and extraction with CH_3COONH_4, respectively (Han et al., 2022). The available soil nitrogen (AN) content was identified using an alkali–hydrolysis reduction diffusion method (Bao, 2000). The ammonium bicarbonate method was used to extract the available soil phosphorus (AP) (Zhang et al., 2018).

2.4 Statistical analyses

The experimental data were processed using SPSS v. 26.0 (IBM SPSS Inc., Chicago, IL, USA), and the mean and standard deviation were used to express the measured outcomes. One-way analysis of variance (ANOVA) was performed to identify the physicochemical properties of the soil as well as the vegetation characteristics (height, coverage, and aboveground biomass of vegetation) under different ecological restoration measures. OriginPro v. 2021 (OriginLab Corporation, Northampton, MA, USA) was used for drawing. The relationship between grassland vegetation characteristics and soil factors was determined using redundancy analysis (RDA) using the “vegan” R package. The Monte Carlo displacement test (999 displacement cycles) was used to explore the significance of soil factors on vegetation change, and the Envfit function (999 displacement cycles) was used to confirm the relationship between various soil factors and vegetation change (Oksanen et al., 2019). Asterisks indicate the significance level between soil factors and plants ($^{**}P < 0.01$).

3 Results

3.1 Effects of soil water content and pH under different restoration measures

The SWC at three soil layer depths under different restoration measures, from highest to lowest, was 0–10 > 10–20 > 20–30 cm. In all three soil layers, the SWC of the T1 site was the highest, whereas that of T3 was the lowest. The SWC showed differences only in the third soil layer, and it was higher in T1 than in the other combination sites ($P < 0.05$) (Figure 3A). A marked discrepancy appeared in soil pH between sites T2 and T4. The soils at all the sites were weakly alkaline (Figure 3B).

3.2 Effects of soil nutrients under different restoration measures

A comparison of the differences in soil nutrients at different sites revealed that the TP, TN, TK, AK, and AP contents in the soil decreased and then increased as grazing intensified. Under different restoration measures, no differences were observed in soil AN in the first soil layer among the different grazing sites ($P > 0.05$), but the soil AN at the T2 and T4 sites was higher than that at the T1 and T3 sites, respectively ($P < 0.05$) (Figure 4A). The soil AP content did not change in the first and third soil layers ($P > 0.05$); however, the soil AP content at the T2 and T4 sites in the second soil layer was higher than that at the T1 and T3 sites, respectively ($P < 0.05$) (Figure 4B). Compared with the T3 site, the soil AK in the first soil layer was higher and the TN in the second soil layer was lower at the T4 site ($P < 0.05$). The AK in the second soil layer and TN in the third soil layer at the CK site were the highest among all three grazing sites ($P < 0.05$) (Figures 4C, D). There was no difference in soil TP in the first and second soil layers ($P > 0.05$), and the TP in the third soil layer at the T2 site was higher than that at the T1 site ($P < 0.05$) (Figure 4E). The soil TK content at the T2 site in the first and third soil layers was higher than that at the T1 site ($P < 0.05$) (Figure 4F). The SOC content at the CK site was the lowest of all three grazing sites (Figure 4G). The soil C:N ratio in the first soil layer was higher at the T1 site than at the CK and G2 sites ($P < 0.05$). In the second soil layer, the soil C:N at the T2 and T4 sites was higher than that at the T1 and T3 sites, respectively ($P < 0.05$). The C:N at the G1 site was higher than that at the CK site in the third soil layer ($P < 0.05$), and that at the CK site was the lowest among all three grazing sites (Figure 4H).

3.3 Effects of aboveground vegetation biomass under different restoration measures

The aboveground vegetation biomass under different restoration measures was compared. No reduction in the G2 site was found compared with the CK site in the aboveground biomass of Gramineae

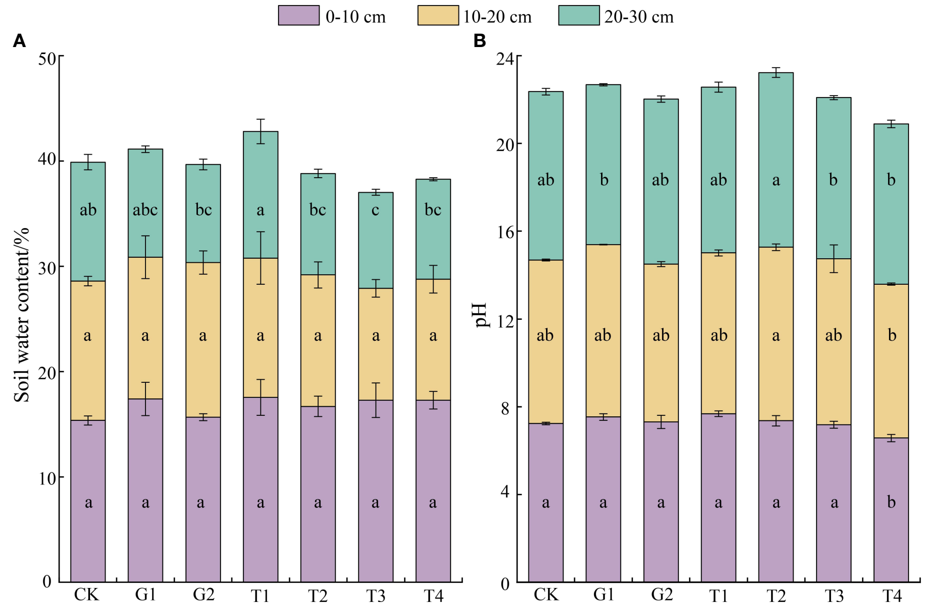

FIGURE 3
Soil water content and pH under different restoration measures (*n* = 3 in each site). **(A)** Soil water content; **(B)** Soil pH. Different lowercase letters in the same color indicate significant differences between treatments at the same soil depth (ANOVA, significance level = 0.05). CK, normal grazing; G1, transfer of livestock out of pasture 30 days in advance; G2, transfer of livestock out of pasture 45 days in advance; T1, combination of G1 and reseeding; T2, combination of G2 and reseeding; T3, combination of G1, reseeding, and fertilization; T4, combination of G2, reseeding, and fertilization.

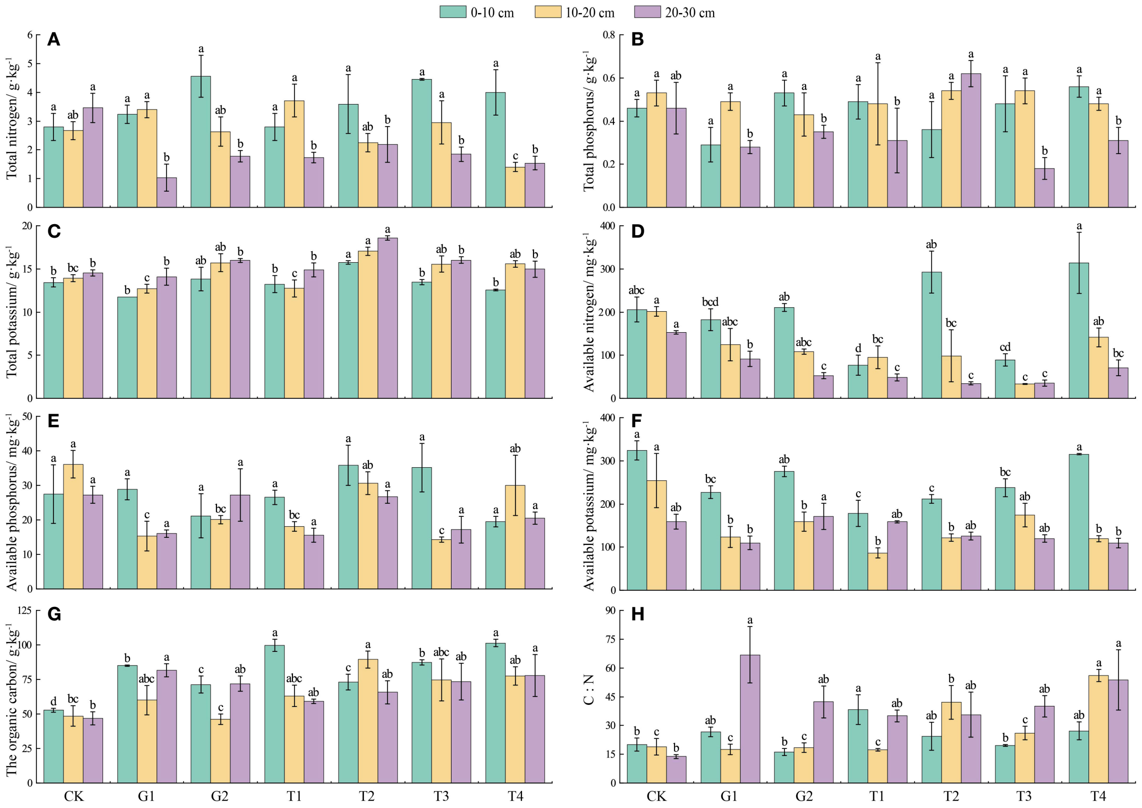

FIGURE 4
Soil nutrients under different restoration measures (*n* = 3 in each site). **(A)** Soil total nitrogen; **(B)** Soil total phosphorus; **(C)** Soil total potassium; **(D)** Soil available nitrogen; **(E)** Soil available phosphorus; **(F)** Soil available potassium; **(G)** Soil organic carbon; **(H)** C:N. Different lowercase letters in the same color indicate significant differences between treatments at the same soil depth (ANOVA, significance level = 0.05). CK, normal grazing; G1, transfer of livestock out of pasture 30 days in advance; G2, transfer of livestock out of pasture 45 days in advance; T1, combination of G1 and reseeding; T2, combination of G2 and reseeding; T3, combination of G1, reseeding, and fertilization; T4, combination of G2, reseeding, and fertilization.

($P > 0.05$), but that at the other sites varied significantly ($P < 0.05$). The aboveground biomass of Gramineae, from highest to lowest, was T4 > T3 > T1 > T2 > G1 > G2 > CK (Figure 5A). There were no Leguminosae at the G1, T3, and T4 sites, and the aboveground biomass of Leguminosae at the T1 site was the highest among the remaining four sites ($P < 0.05$) (Figure 5B). Cyperaceae did not appear at sites T3 or T4. The aboveground biomass of cyperaceous plants at the CK and G2 sites was higher than that at the T1 and T2 sites ($P < 0.05$) in the following order: CK > G2 > G1 > T2 > T1 (Figure 5C). The aboveground biomass of Forbs at the T3 and T4 sites was higher ($P < 0.05$), and that at the G1 site was the highest of all three grazing sites ($P < 0.05$) (Figure 5D). No inedible herbage appeared at the T4 site. The aboveground biomass of inedible herbage was highest at the T2 site ($P < 0.05$), and that at the CK site was the highest ($P < 0.05$) (Figure 5E). The AGB at the T3 and T4 sites was higher than that of the other two combined restoration sites ($P < 0.05$). The AGB was the highest at the G1 site among the three different grazing sites ($P < 0.05$) (Figure 5F).

The vegetation height at the CK site was the lowest, and this increased to varying degrees at the other treatment sites. Compared with all three sites with different grazing intensities, both reseeding and the combination of reseeding and fertilization increased the vegetation height in the degraded grasslands ($P < 0.05$) (Figure 6A). The vegetation coverage at the CK and G2 sites was lower than that at the G1 and four combined restoration sites ($P < 0.05$) (Figure 6B).

3.4 RDA of vegetation characteristics and soil factors

The RDA indicated that the first two ranking axes (RDA1 and RDA2) explained 41.50% and 11.60% of the vegetation characteristic changes, respectively, and soil factors explained 53.10% of the vegetation characteristic changes, indicating that RDA1 and RDA2 explained the correlation between soil factors and vegetation features well. A Monte Carlo permutation test was used to identify the variation in soil factors and vegetation characteristics, and the result was significant ($P < 0.05$) (Figure 7; Table 1).

We used the *envfit* function to explore the relationships between soil properties and changes in vegetation characteristics. In the RDA ranking correlation coefficient, r^2 represents the determining coefficient of the explanatory variable (soil factors) for vegetation characteristics. The correlations between the soil factors and vegetation change were ranked as follows: SOC > AK > SWC > TK > AP > pH > TN > TP > AN. Organic carbon and available

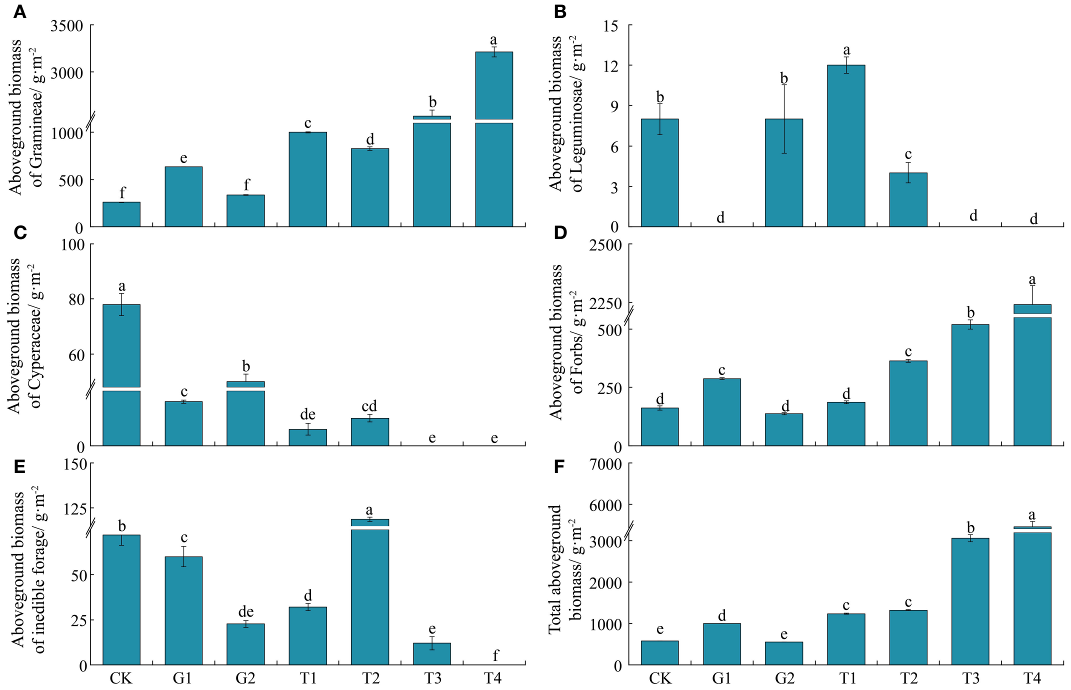

FIGURE 5
Aboveground vegetation biomass under different restoration measures (n = 3 in each site). **(A)** Aboveground biomass of Gramineae; **(B)** Aboveground biomass of Leguminosae; **(C)** Aboveground biomass of Cyperaceae; **(D)** Aboveground biomass of Forbs; **(E)** Aboveground biomass of inedible forage; **(F)** Total aboveground biomass. Different lowercase letters indicate significant differences between treatments (ANOVA, significance level = 0.05). CK, normal grazing; G1, transfer of livestock out of pasture 30 days in advance; G2, transfer of livestock out of pasture 45 days in advance; T1, combination of G1 and reseeding; T2, combination of G2 and reseeding; T3, combination of G1, reseeding, and fertilization; T4, combination of G2, reseeding, and fertilization.

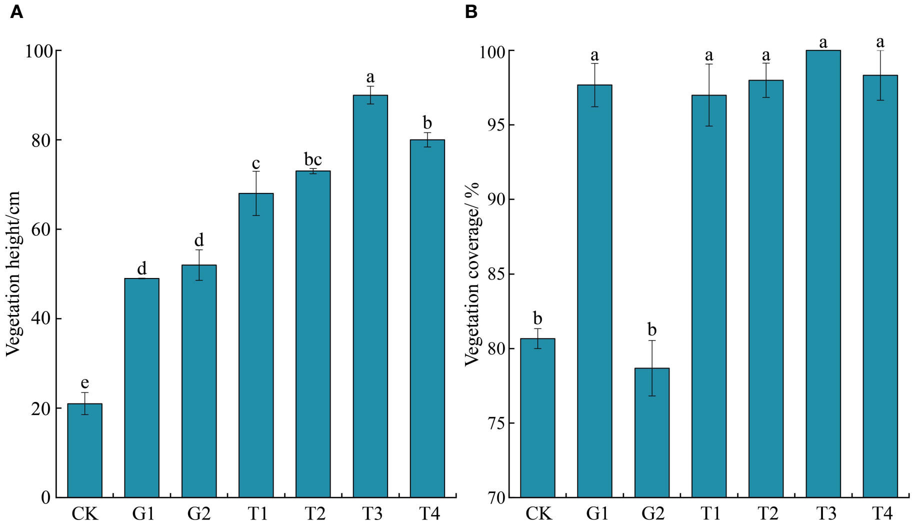

FIGURE 6
Vegetation height and coverage under different restoration measures (*n* = 3 in each site). **(A)** Vegetation height; **(B)** Vegetation coverage. Different lowercase letters indicate significant differences between treatments (ANOVA, significance level = 0.05). CK, normal grazing; G1, transfer of livestock out of pasture 30 days in advance; G2, transfer of livestock out of pasture 45 days in advance; T1, combination of G1 and reseeding; T2, combination of G2 and reseeding; T3, combination of G1, reseeding, and fertilization; T4, combination of G2, reseeding, and fertilization.

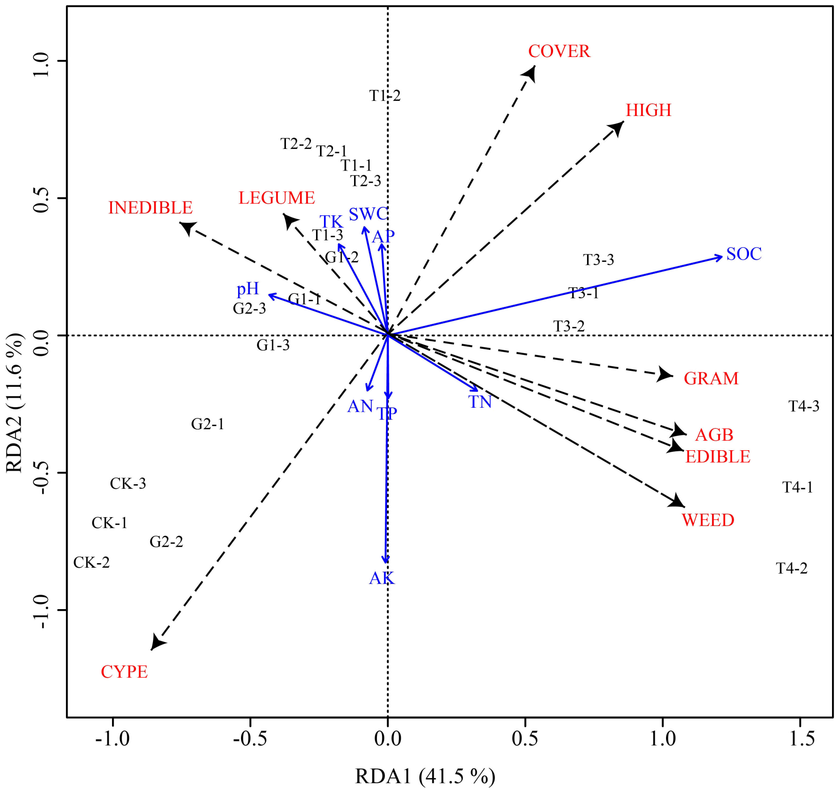

FIGURE 7
Redundancy analysis (RDA) ranking of vegetation characteristics and soil factors. SWC, soil water content; pH, soil pH; SOC, soil organic carbon; TN, total nitrogen; TP, total phosphorus; TK, total potassium; AN, available nitrogen; AP, available phosphorus; AK, available potassium; LEGUME, aboveground biomass of Leguminosae; HIGH, vegetation height; INEDIBLE, aboveground biomass of inedible forage; CYPE, aboveground biomass of Cyperaceae; COVER, vegetation coverage; WEED, aboveground biomass of Forbs; GRAM, aboveground biomass of Gramineae; AGB, total aboveground biomass; EDIBIO, aboveground biomass of edible forage; CK, normal grazing; G1, transfer of livestock out of pasture 30 days in advance; G2, transfer of livestock out of pasture 45 days in advance; T1, combination of G1 and reseeding; T2, combination of G2 and reseeding; T3, combination of G1, reseeding, and fertilization; T4, combination of G2, reseeding, and fertilization.

TABLE 1 Redundancy analysis (RDA) results of vegetation characteristics and soil factors.

Parameter	RDA1	RDA2
Eigenvalues	3.735	1.044
Percentage change in soil factor (%)	41.500	11.600
Cumulative percentage change in soil factor (%)	41.500	53.100
Soil factor–percentage change in vegetation characteristics (%)	66.700	18.650
Soil factor–percentage cumulative change of vegetation characteristics (%)	66.700	85.350
Monte Carlo replacement test	$P = 0.038$	

potassium were strongly correlated with changes in grassland vegetation characteristics ($P < 0.01$) (Table 2).

4 Discussion

4.1 Responses of soil physicochemical properties to different restoration measures

Grassland degradation can directly or indirectly change the soil nutrients and environment of grassland ecosystems, while soil moisture greatly affects grassland productivity (Deng et al., 2016). The first part of this study revealed that SWC was relatively high under moderate grazing conditions (G1) and relatively low under normal grazing conditions (CK), and soil pH did not change substantially among all restoration measures. Overgrazing and grassland degradation can reduce the SWC (Drewry et al., 2008). Trampling by grazing livestock reduces soil porosity; once large pores are lost, water infiltration and SWC decrease (Sanjari et al., 2008). In addition, the decrease in vegetation coverage caused by grassland degradation affects surface evapotranspiration and infiltration, resulting in a decrease in SWC. The relatively high SWC in the 0–20-cm soil layer at all restoration sites was probably due to increased grassland vegetation coverage and decreased surface evaporation caused by moderate grazing and reseeding. The increase in subsurface biomass in the soil would also enhance the water storage capacity of soil (Wang et al., 2023).

pH is an index used to measure soil acidity and alkalinity. A suitable pH is conducive to vegetation growth (Liu et al., 2017). In the current study, restoration measures had a small impact on soil pH in the short term, and soil pH among the different treatments was similar. However, the pH was relatively low in the first soil layer at the T4 site. Fertilization and reseeding reduced the evaporation of soil water, and salt accumulation did not occur in the surface layer, which decreased the pH (Duan et al., 2022). An increase in grazing intensity also leads to an increase in pH (Attard et al., 2008). The T4 site combined light grazing with reseeding and fertilization, which may be a reason for the decrease in soil pH.

Soil nutrients form the basis for plant growth and development. They also play a decisive role in grassland ecosystems (Li et al., 2021). Soil nutrients differed under the different grasslands and restoration measures. With an increase in grazing intensity, the SOC content first increased and then decreased. In contrast, the TN, TP, TK, AP, and AK contents first decreased and then increased. In the case of moderate grazing, the quality of topsoil and litter is improved by the trampling effect of livestock and fecal and urinary regression (Chen et al., 2020). The activities of soil microorganisms and nutrient cycling at the ecological interface between vegetation and soil are further promoted, thereby increasing SOC (Pang et al., 2020). Restoration measures such as grazing, reseeding, and fertilization affect soil microorganisms in the short term, which indirectly affects the decomposition of litter in soil and its corresponding nutrient contents (Bilotta et al., 2007; Drewry et al., 2008; Waring et al., 2022; Su et al., 2023). As a result, soil nutrients at the sites were higher under a relatively heavy grazing intensity. Furthermore, the “compensated growth” of grassland vegetation makes them absorb more nutrients from the soil under grazing conditions. Therefore, some of the soil nutrients are transferred to the ground for vegetation growth (Su et al., 2004; Peng et al., 2023). These results were also reflected in the study by Wang and De (2017), who found that reseeding restoration

TABLE 2 Redundancy analysis (RDA) ranking of correlation coefficients between vegetation characteristics and soil factors.

Soil factor	RDA1	RDA2	r^2	Pr (>r)
SWC	-0.141	0.990	0.115	0.342
pH	-0.879	0.476	0.078	0.499
SOC	0.939	0.344	0.552	0.001**
TN	0.715	-0.699	0.065	0.545
TP	0.009	-0.999	0.038	0.727
TK	-0.327	0.945	0.091	0.444
AN	-0.226	-0.974	0.031	0.759
AP	-0.048	0.998	0.079	0.489
AK	-0.002	-1.000	0.494	0.002**

SWC, soil water content; pH, soil pH; SOC, soil organic carbon; TN, total nitrogen; TP, total phosphorus; TK, total potassium; AN, available nitrogen; AP, available phosphorus; AK, available potassium.
**Significance level, $P < 0.01$.

measures substantially increased the accumulation of TK, AP, and SOC in the soil in their study of the changes in soil nutrients in an alpine meadow under different supplementary sowing years. However, in the current study, the AN and AK contents at the reseeding and fertilizing sites were lower than those at the sites with different grazing intensities. Notably, this decrease might be caused by the increased interaction between the soil and vegetation due to reseeding and fertilization. Fertilization measures increase soil nutrients and promote vegetation growth. Simultaneously, reseeding greatly increased the aboveground vegetation, intensifying the soil nutrient consumption of plants. During the short repair years, the soil nutrients do not fully recover or reach a relatively stable state (Gao et al., 2019; Wang et al., 2023). The SOC content at the normal grazing sites was the lowest and increased to varying degrees at the other sites. This is probably because the decrease in grazing intensity followed by moderate grazing was conducive to soil nutrient accumulation and soil structure restoration in the grassland (Yang et al., 2018; Zhang et al., 2023). This concurs with the results obtained by Zhang et al. (2021) regarding the influences of grazing on soil properties in the eastern margin of the Qilian Mountains. Reseeding can affect the soil aggregate structure and enhance SOC sequestration (Liu et al., 2022). Fertilization can increase the SOC content by increasing the input of soil organic matter (Fang et al., 2012). Therefore, the SOC at the T4 restoration site was higher than that at the three different grazing and reseeding sites. The available nutrients at the T4 restoration site were higher than those at the T3 restoration site, which is in line with that of Hou and Guo (2021), who studied the dynamic response of plant nutrients to grazing intensity. The plant nutrient transfer rate differed under different grazing intensities, which resulted in an increase in available nutrients at the T4 restoration site (Hou and Guo, 2021).

4.2 Relationship between vegetation characteristics and soil factors

Different restoration measures have different effects on the soil properties and vegetation characteristics of grasslands (Keller et al., 2023). In grassland ecosystems, the physicochemical properties of soil are important factors that directly affect grassland vegetation. Therefore, understanding the correlation between soil factors and grassland vegetation characteristics provides a theoretical reference for the restoration of degraded grassland soils. Vegetation degradation is the primary cause of soil degradation and *vice versa* (Wu et al., 2020; Kooch et al., 2022).

Different disturbance conditions have different effects on the species structure, coverage, and biomass of grassland plant communities. Fertilization increases species diversity, enhances community competitiveness, promotes plant growth, and enhances soil nutrients (Zong et al., 2021). Our findings suggest that SOC and AK are two key factors affecting the vegetation characteristics of restored grasslands, and they have significant positive effects on grassland vegetation. SOC content is an important index for evaluating soil fertility. Reseeding measures can substantially promote SOC accumulation, and fertilization can also increase SOC content (Fang et al., 2012; Liu et al., 2022). In particular, the rate of organic carbon mineralization is relatively high within the first few years of fertilization (Lan et al., 2016). Under the comprehensive restoration measures at the T4 site, reseeding and fertilization increased the SOC content, promoted the absorption of nutrients by vegetation, and improved the grassland productivity (Dee et al., 2023). However, in short experimental years, the nitrogen and phosphorus contents in the soil were greatly affected by comprehensive factors, and the influences of fertilization on plant nutrients were greater than those on soil nutrients (Gao et al., 2019; Zong et al., 2021; Keller et al., 2023). At the T4 site, no Leguminosae, Cyperaceae, or inedible forage appeared, and the aboveground biomass of Gramineae, Forbs, edible herbage, and AGB was substantially higher than those under other treatments. An explanation for this result is the increased species richness and nutrient content of grasslands under relatively low grazing intensity, reseeding, and fertilization measures (Li et al., 2018), which promoted nutrient cycling between the vegetation and soil and asymmetric competition between vegetation and accelerated the growth of dominant species in grasslands (Donald, 1958; Hautier et al., 2015).

4.3 Challenges in grassland restoration

Our study investigated the short-term effects of different restoration measures combined with grazing intensity, reseeding, and fertilization on degraded grasslands. Most scholars have focused on the positive effects of artificial restorations (Feng et al., 2010; Wu et al., 2010; Zhang et al., 2020; Gu et al., 2022); however, there are also some negative effects. Improper timing and restoration techniques can also cause severe grassland degradation—for example, fertilization transforms underground plant competition into aboveground light competition (Donald, 1958; Niu et al., 2008), thereby reducing plant diversity (Harpole et al., 2016; Seabloom et al., 2020) and community stability (Song and Yu, 2015). The potential negative impact that fertilization could have on grasslands is dependent on the fertilizer application amount and fertilization time (Chen et al., 2013). Although no-till supplementary seeding causes less damage to grasslands than other supplementary seeding measures, it can be easily excluded by competition from native vegetation when the selection of supplementary pasture species is incorrect. This leads to a low species survival rate in no-till supplementary seeding, high improvement costs of supplementary seeding, poor stability of the grassland community, short service life of supplementary seeding grasslands, and other problems (Zhang et al., 2020). The combination of fertilization and reseeding can enhance grassland productivity and improve grassland conditions in the short term. However, the restoration succession of degraded grasslands is a very long process (Shang et al., 2017). Short-term studies can address productivity and livelihood issues but cannot explain the impact of restoration measures on vegetation diversity. Only long-term research can accurately evaluate the restoration of grasslands, and the corresponding restoration measures and models can be more reliable and convincing.

5 Conclusions

Based on the short-term restoration of degraded grasslands in an alpine meadow, reseeding and a combination of reseeding and fertilization effectively increased the SOC content but caused a decrease in available nutrients. Transferring livestock out of the pasture in advance, reseeding, and fertilization improved the height and coverage of grassland vegetation and markedly increased the grassland productivity. SOC was the main factor positively affecting the growth of grassland vegetation. Further restoration and management of degraded grasslands are needed to consider the sustainable development of grassland ecosystems. A long-term study should be conducted to select appropriate combinations of measures according to the local conditions. This should then be combined with a reasonable grassland management and utilization system to achieve the best restoration effects. The findings of this study may offer valuable theoretical insights for the ecological restoration of degraded grasslands and local development in alpine regions.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

YW: Data curation, Formal Analysis, Investigation, Methodology, Software, Visualization, Writing – original draft, Writing – review & editing. ZW: Data curation, Investigation, Methodology, Software, Visualization, Writing – review & editing. YK: Resources, Software, Visualization, Writing – review & editing. ZZ: Investigation, Resources, Writing – review & editing. DB: Investigation, Resources, Writing – review & editing. XS: Investigation, Resources, Writing – review & editing. JS: Conceptualization, Funding acquisition, Investigation, Project administration, Supervision, Validation, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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Consequences of plateau pika disturbance on plant-soil carbon and nitrogen in alpine meadows

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The presence of burrowing mammals can have extensive effects on plants and soils, creating bare soil patches in alpine meadows and potentially altering plant-soil carbon (C) and nitrogen (N). This study focuses on the plateau pika (*Ochotona curzoniae*) to examine the responses of plant-soil C and N to a small burrowing mammal from quadrat scale to plot scale. The density of active burrow entrances in disturbed plots was used as an indicator of the disturbance intensity of plateau pikas. The study found that the below-ground biomass (BGB) and its C and N, as well as soil C and N concentrations were significantly lower in bare soil areas than in vegetated areas and undisturbed plots. This shows that the quadrat scale limited the estimation of the C and N sequestration potential. Therefore, further research on the plot scale found that the disturbance by plateau pika significantly reduced plant biomass and BGB carbon stock. However, plateau pika did not affect soil C and N stocks or ecosystem C and N stocks. These findings suggest the bare soil patches formed by plateau pika caused plant and soil heterogeneity but had a trade-off effect on plant-soil C and N stocks at the plot scale. Nevertheless, moderate disturbance intensity increased the C and N sequestration potential in grassland ecosystems. These results provide a possible way to estimate how disturbance by small burrowing mammals affects C and N cycling in grassland ecosystems while accurately assessing the effects of small burrowing mammal densities on C and N in grassland ecosystems.

KEYWORDS

grassland ecosystems, bare soil patches, heterogeneity, plant-soil, disturbance intensity

1 Introduction

Grassland covers approximately 40% of the terrestrial area on Earth (Fang et al., 2018; Ge et al., 2022), and as one of the most important vegetation types on Earth (Zhang et al., 2013), grassland ecosystems are important reservoirs of carbon (C) and nitrogen (N) (Gao et al., 2015; Sitters et al., 2020). The maintenance of C is also a key factor in the sustainability of grassland ecosystems (Huang et al., 2022). Nevertheless, grasslands can be modified by multiple biotic and abiotic factors, and their C and N sequestration potential will be severely influenced (Xia et al., 2009; Eekeren et al., 2010).

Among these factors, burrowing mammal is underappreciated but key functional group worldwide (Davidson et al., 2012), and they can profoundly impact C and N in grassland ecosystems by creating plant and soil disturbances. On the one hand, these burrowing mammals usually have distinct effects on plant growth, which directly changes the absorption of atmospheric carbon dioxide (CO_2) by plants and its storage in plant biomass (Yurkewycz et al., 2014; Zhang et al., 2014); on the other hand, burrowing and burying effects on the soils of these burrowing mammals changes the organic matter input and decomposition, thereby inevitably influencing the C sequestration potential in the plant-soil systems (Qin et al., 2023). Generally, the C and N retention in the plant-soil systems is assessed by changes in C and N stocks in plants and soils (Deng et al., 2014), and it is often considered an effective agent for estimating the C and N sequestration potential (Reeder and Schuman, 2002; Evans and Burke, 2013).

The plateau pika (*Ochotona curzoniae*) (hereafter pika), one of the dominant species of burrowing mammals in the Qinghai-Tibetan Plateau, is generally considered to be a pest in China due to its accelerated degradation of alpine grasslands (Zhang et al., 2016; Wei et al., 2023). However, some studies have argued that pika is a keystone species for the alpine grassland ecosystem (Smith and Foggin, 1999; Delibes-Mateos et al., 2011). This is because they can modify biotic and abiotic habitat characteristics. For example, pika can serve as food for many predators, and their burrows serve as breeding habitats for small birds and lizards (Smith and Foggin, 1999). Furthermore, pikas break mattic epipedon on the soil surface layer, reducing runoff and increasing water infiltration (Zhang et al., 2014; Wilson and Smith, 2015). Pikas can also excavate soil from deep layers, and excavated soils capture organic matter on the soil surface. This process increases organic matter input and decomposition, releasing nutrients into the soil (Niu et al., 2019). Although increasing attention has been paid to the role of pika in alpine grassland ecosystems, the influence of pika on vegetation and soil is still controversial. This difference could be due to the sampling methods. In fact, the effects of pika can cause heterogeneous microhabitats by creating bare soil patches interspersed in the vegetated soil matrix (Pang et al., 2021). Typically, many studies have focused on the differences between vegetated and bare soil in the presence of pikas (Yi et al., 2016; Zhang et al., 2016; Zhao et al., 2021). Only a few studies have compared soil C and N in vegetated soil areas with and without pikas (Pang and Guo, 2017). These approaches often led to uncertainty in examining the effects of pikas disturbance on soil C and N of alpine grasslands due to ignoring to select areas without pikas as reference (Davidson et al., 2012; Hagenah and Bennett, 2013; Yu et al., 2017b), or neglecting bare soil patches and great heterogeneity (Pang et al., 2020a). A plot-scale method, simultaneously considering the difference between pika presence and absence and the heterogeneity within the presence of pikas, can be a better way to completely estimate the role of pika. Previous studies have shown plant biomass decreased with increasing disturbance intensity (Qin et al., 2021), but soil nutrients showed a slow upward trend followed by a decrease (Pang et al., 2020a, b). However, plant biomass, soil C, and soil N were studied separately, which limited the estimation of C and N sequestration potential under pika disturbance and different disturbance intensities. The changes in the plant-soil systems can better reflect the effects of pikas on grassland ecosystems and deepen the understanding of the role of pika in the C and N cycle of grassland ecosystems. Therefore, more studies are needed to investigate the effects of pika disturbance and disturbance intensity on C and N retention in plant-soil systems at the plot scale.

The effects of pika disturbance on plant-soil C and N in alpine grasslands are examined across multiple sites to improve our knowledge of accurately evaluating C and N sequestration in burrowing mammals. Based on previous studies, we hypothesize that (1) C and N stored in plants are lower in the presence of pikas because of decreased plant biomass, while C and N stored in the soil will be higher due to the capture of organic matter, resulting in a trade-off in plant-soil C and N; (2) higher pika disturbance intensity will decrease plant-soil C and N because of increased bare patches and reduced organic matter input. The results will help to fully elucidate the effects of pika disturbance and disturbance intensity on C and N cycling in grassland ecosystems.

2 Materials and methods

2.1 Study sites

This study selected four sites on the Tibetan Plateau, located in Gangcha County, Haiyan County, and Qilian County in Qinghai Province and Luqu County in Gansu Province (Figure 1), based on the distribution of pikas in existing studies, combined with cross-environmental gradients. These four investigation sites also include, on a large scale, the effects of pika disturbance on plant-soil C and N under different environments on the Tibetan Plateau. The average elevation of these sites varies from 3,169 to 3,550 m, with average annual precipitation ranging from 444 to 691 mm, and average annual temperature ranging from 0.83 to 3.08°C (Table 1).

Alpine meadows are the main grassland type on the Tibetan Plateau (Ma and Zhang, 2022), and pikas are frequently active in alpine meadows. The dominant plant species at the Luqu study site differed from the other three sites (Table 1). However, the vegetation types were all categorized as alpine meadows, and their soils were alpine meadow soils (Gong et al., 2007). The soil surface is covered by a root mat composed of plant roots, approximately 7-11 cm thick, covering the soil surface and preventing water infiltration (Pang et al., 2020b). In contrast, constructing burrowing systems by pika destroy the root mat and increase soil water infiltration (Wilson and Smith, 2015; Pang et al., 2021).

2.2 Survey design

At each research site, we initially selected 10 disturbed plots affected by pika disturbance, with a distance of 3-5 km between each disturbed plot. Subsequently, we selected adjacent undisturbed plots

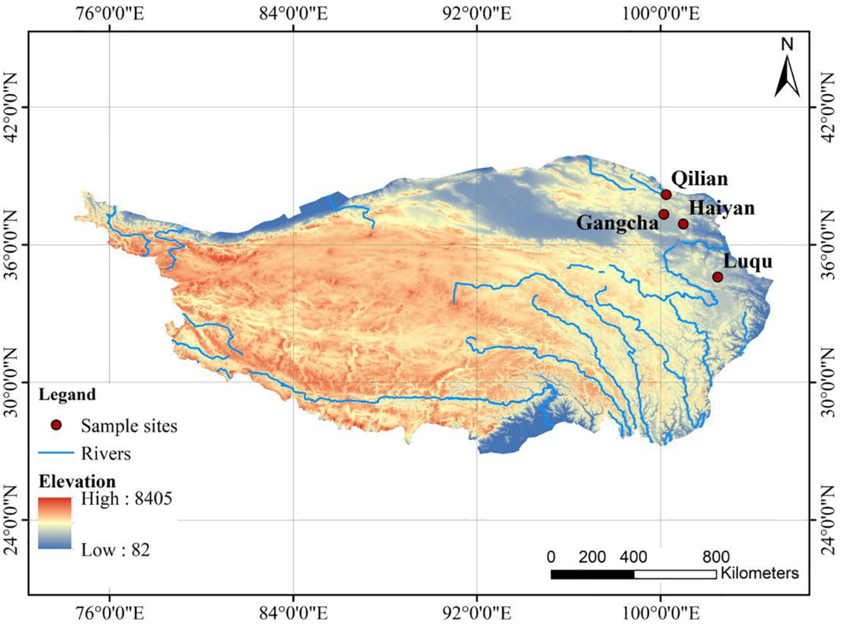

FIGURE 1
Distribution map of the four study sites.

without pika disturbance for each disturbed plot. The distance between the two-paired disturbed and undisturbed plots was approximately 0.5-1 km. There were no significant differences in grassland type, soil type, topography, microclimate, or vegetation composition between the two-paired disturbed and undisturbed plots to ensure the reliability of the results. Undisturbed plots are considered to be potentially suitable areas for pika (Li et al., 2021). Based on the average area of pika's home range (Fan et al., 1999), the area of each plot was set as 35 ×35 m. All plots were situated in cold grasslands, where alpine meadows were fenced from mid-April to October to exclude large herbivores.

2.3 Sampling and analysis

Field surveys and sampling were conducted in early August 2020, when the annual population of pika was the highest (Fan et al., 1999; Qu et al., 2013), accurately reflecting the effects of pika disturbance on the plant-soil C and N. For plots with pikas, the active burrow entrance density (ABED) was used as a proxy for the intensity of the disturbance (Sun et al., 2015). The disturbed plot consisted of vegetated and bare soil surfaces. First, the area of bare soil in disturbed plots was determined by the sum of the areas of bare patches using the split method (Wei and Guo, 2022). Next, five vegetated quadrats (1×1 m) approximately 8 m apart were placed along a W-shape on the vegetated surface of each disturbed plot, and the paired bare soil quadrats were selected for each vegetated quadrat. The distance between each paired vegetated quadrat and bare soil quadrat should not be too far from each other, which was about 1 m. For each undisturbed plot, five vegetated quadrats were placed similarly. Therefore, there are 15 quadrats for each paired undisturbed-disturbed plot, i.e., five vegetated quadrats and five bare soil quadrats within each disturbed plot, and five quadrats within each undisturbed plot.

In this study, all the bare soil patches in the disturbed plots were new bare soil patches with no vegetation cover, so above-ground biomass (AGB) and its C and N at the plot scale, defined as AGB and its C and N measured on the surface of vegetation adjusted for the lack of AGB in bare soil patches, may properly assess the response of AGB and its C and N to the disturbance by small

TABLE 1 Elevation, species richness, dominant species, active burrow entrance density, mean annual temperature, and mean annual precipitation recorded from August 2015 to July 2020.

Site	Elevation (m)	MAT (°C)	MAP (mm)	Dominant species	Species richness	ABED (ha^{-1})
Gangcha	3265	0.83	498	*Kobresia humilis*	23.40 ± 2.23 b	1314.72 ± 67.04 a
Haiyan	3270	1.81	444	*K. humilis*	21.53 ± 0.87 b	1456 ± 123.04 a
Luqu	3550	3.08	691	*Kobresia capillifolia*	30.50 ± 0.80 a	664 ± 82.08 b
Qilian	3169	2.36	476	*K. humilis*	19.00 ± 0.58 b	1368 ± 137.92 a

Different lowercase letters show significant differences among the four sites. Values are means ± SE. MAT, mean annual temperature; MAP, mean annual precipitation; ABED, active burrow entrance density.

burrowing mammal. For each quadrat, all plants were clipped at ground level, and then a root auger (10 cm in diameter) was used to obtain the plant roots at a depth of 20 cm. The clipped plants were oven-dried in the laboratory at 65°C (48 h) and weighed to calculate AGB. Then, the plant roots were carefully washed with water over a 0.5 mm sieve, dried, and weighed to estimate the below-ground biomass (BGB). Total biomass is the sum of AGB and BGB. Five soil cores (3.5 cm in diameter, 0-20 cm depth) were randomly collected from each quadrat after plant samples were collected, mixed, and passed a 2 mm sieve to remove stones and roots. Meanwhile, soil profiles of 20 cm depth were dug using a stainless-steel cutting ring (the volume was 100 cm^3) to collect soil cores to determine soil bulk density. Plant and soil C and N concentrations were analyzed using dry combustion.

2.4 Calculation of plant, soil, and ecosystem C and N stocks

2.4.1 The plant C and N stocks (including AGB and BGB carbon and nitrogen stocks) of disturbed and undisturbed plots were calculated as follows:

$$C/N_{A-stock-dist} = C/N_{stock-VA} \times (1 - BA) \tag{1}$$

where $C/N_{A\text{-stock-dist}}$ is AGB carbon or nitrogen stock of disturbed plots (g m^{-2}); $C/N_{stock\text{-}VA}$ is AGB carbon or nitrogen stock of vegetated areas within disturbed plots (g m^{-2}); BA is the area (%) of bare soil.

$$C/N_{B-stock-dist} = C/N_{stock-BB} \times BA + C/N_{stock-VB} \times VA \tag{2}$$

where $C/N_{B\text{-stock-dist}}$ is BGB carbon or nitrogen stock of disturbed plots (g m^{-2}); $C/N_{stock\text{-}BB}$ is BGB carbon or nitrogen stock of bare soil areas (g m^{-2}); $C/N_{stock\text{-}VB}$ is BGB carbon or nitrogen stock of vegetated areas within disturbed plots (g m^{-2}); BA and VA are area (%) of bare soil and vegetated soil within disturbed plots.

$$C/N_{P-stock-undist} = B_{undist} \times C/N_{UP} \tag{3}$$

where $C/N_{P\text{-stock-undist}}$ is plant C or N stock of undisturbed plots (g m^{-2}); B_{undist} is plant biomass of undisturbed plots (g m^{-2}); C/N_{UP} is plant C or N concentration of undisturbed plots (%).

$$B_{dist} = B_{BP} \times BA \times B_{VP} \times VA \tag{4}$$

where B_{dist} is the plant biomass of disturbed plots (g m-2); B_{BP} is the plant biomass of bare soil areas (g m^{-2}); B_{VP} is the plant biomass of vegetated areas within disturbed plots (g m^{-2}); BA and VA are area (%) of bare soil and vegetated soil within disturbed plots.

2.4.2 The soil C and N stocks of disturbed and undisturbed plots were calculated as follows:

$$C/N_{s-stock-dist} = C/N_{stock-BS} \times BA + C/N_{stock-VS} \times VA \tag{5}$$

where $C/N_{s\text{-stock-dist}}$ is soil C or N stock of disturbed plots (g m^{-2}); $C/N_{stock\text{-}BS}$ is the C or N stock of bare soil (g m^{-2}); $C/N_{stock\text{-}VS}$ is the C or N stock of vegetated soil within disturbed plots (g m^{-2}); BA and VA are area (%) of bare soil and vegetated soil within disturbed plots. The area of bare soil in undisturbed plots was 0, and the area of vegetated soil in undisturbed plots was 100% because only bare soil areas resulting from pika activities were considered in this study.

$$C/N_{s-stock-undist} = [C/N_{US} \times BD_{US} \times T \times (1 - \delta_{US}) \times 0.01] \times 100\,\% \tag{6}$$

where $C/N_{s\text{-stock-undist}}$ is the C or N stock of undisturbed soil (g m^{-2}) and C/N_{US}, BD_{US}, and δ_{US} are soil C or N concentration (%), soil bulk density (g cm^{-3}), and soil fraction of gravel larger than 2 mm of undisturbed soil respectively.

Stocks of C and N in grassland ecosystems were estimated by summing the plant and soil C and N stocks.

2.5 Data analysis

All statistical analyses were performed using R 4.0.3 (R Foundation for Statistical Computing, Vienna, Austria). The effects of pika disturbance on plant biomass, plant C and N concentrations and stocks, and soil C and N concentrations and stocks at four sites were assessed at two scales using a linear mixed model (LMM) with the “lme4” package, where the presence/absence of pikas disturbance and the four sites were fixed factors, and paired designs were random factors. Tukey’s tests were then performed for *post hoc* comparisons using the “emmeans” package. A regression analysis was constructed with ABED as a fixed factor to elucidate the changes in C and N stocks in grassland ecosystems to the disturbance caused by pika. The regression curves of ABED and C and N stocks in grassland ecosystems at the plot scale were obtained using a linear model (LM).

3 Results

3.1 The responses of plant biomass and its C and N to pika disturbance at the quadrat scale

Pika disturbance did not affect AGB or its C and N concentrations at the quadrat scale. BGB was significantly lower in bare soil areas than in vegetated areas and undisturbed plots (Figure 2). Nevertheless, the N concentration of BGB was significantly higher in bare soil areas, and its C concentration was not significantly different between bare soil areas, vegetated areas, and undisturbed plots (Figure 2).

3.2 The responses of soil C and N to pikas disturbance at the quadrat scale

The study found that changes in soil C and soil N concentrations were similar. Specifically, soil C and N concentrations were significantly lower in bare soil areas than in vegetated areas and undisturbed plots (Figure 3).

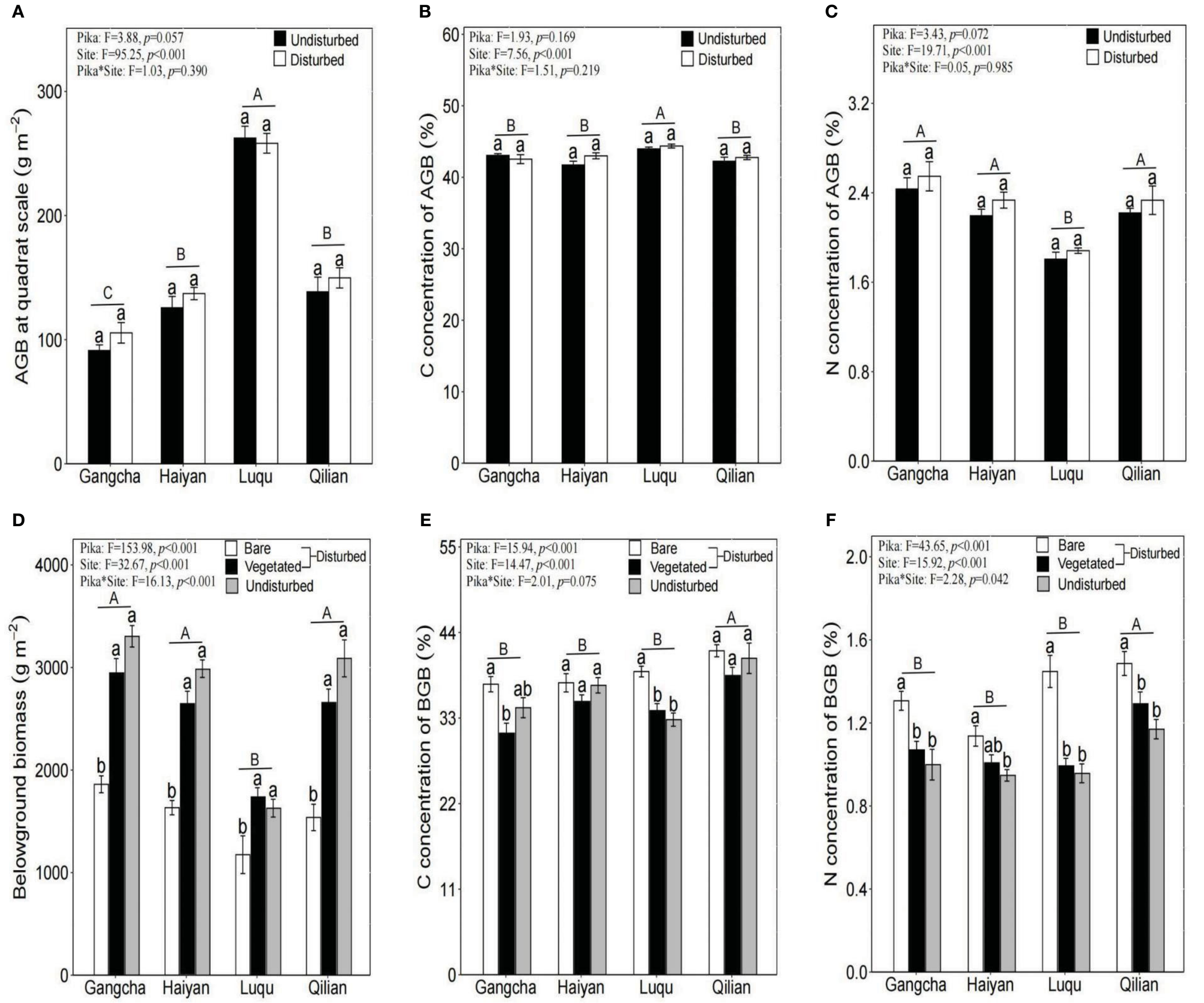

FIGURE 2
Plant biomass (**A:** AGB, **D:** BGB) and its C and N (**B:** C concentration of AGB, **C:** N concentration of AGB, **E:** C concentration of BGB, **F:** N concentration of BGB) at the quadrat scale (mean ± SE). The statistics were obtained from the paired T-test for each site. Different lowercase letters indicate significance between disturbed and undisturbed plots; different uppercase letters indicate significance between sites when the presence and absence of pikas are combined for each site, $P< 0.05$.

3.3 Effects of pika disturbance on plant biomass at the plot scale

According to the study investigations, plant biomass response to disturbance by pikas was similar at all sites except for Luqu. Disturbance by pikas significantly reduced plant biomass (Figure 4). The total biomass in disturbed plots of Gangcha, Haiyan, and Qilian were 18.69%, 18.86%, and 23.52% lower than those in undisturbed plots, respectively. In addition, total biomass was lower at Luqu than at the other three sites (Figure 4). This result is similar to studies at the quadrat scale.

3.4 Response of plant-soil C and N to disturbance by pikas at the plot scale

The disturbance caused by pika reduced AGB carbon and nitrogen stocks and BGB carbon stocks but had no effect on C and N in grassland ecosystems (Figures 5, 6). The studies in Gangcha, Haiyan, and Qilian are consistent with these results. The AGB carbon and AGB nitrogen stocks in disturbed plots of Gangcha, Haiyan, and Qilian were 33.86% and 38.17%, 30.15% and 33.86%, and 25.42% and 32.05% lower than those in undisturbed plots, respectively. The BGB carbon stocks in disturbed plots of Gangcha, Haiyan, and Qilian were 28.91%, 24.33%, and 30.53% lower than those in undisturbed plots, respectively.

However, the effects of disturbance by pikas on C and N stocks were site-specific. Disturbance by pikas had no impact on plant C and N stocks, but significantly increased soil C and N stocks at Luqu (Figures 5, 6). Thus, pika disturbance increased ecosystem C and N stocks at Luqu. The C and N stocks in grassland ecosystems were 33.30% and 37.68% higher in disturbed plots than in undisturbed plots, respectively.

When combining the presence or absence of pikas, Luqu had higher AGB carbon and nitrogen stocks but lower BGB carbon and

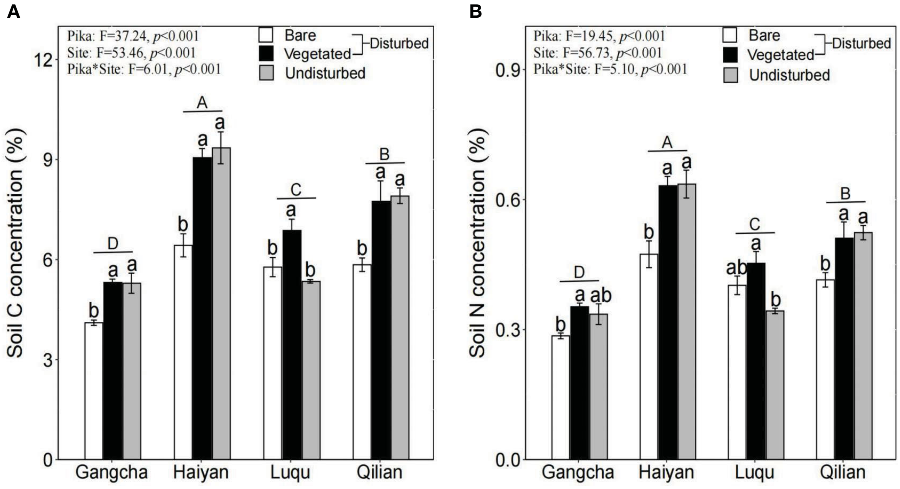

FIGURE 3
Soil C **(A)** and N **(B)** concentrations in bare soil areas, vegetated areas within disturbed plots, and undisturbed plots at each site (mean ± SE). The statistics were obtained from the paired T-test for each site. Different lowercase letters indicate significance between disturbed and undisturbed plots; different uppercase letters indicate significance between sites when the presence and absence of pikas are combined for each site, *P*< 0.05.

nitrogen stocks than Gangcha, Haiyan, and Qilian; and Haiyan had higher ecosystem C and N stocks (Figures 5, 6).

3.5 Effects of pika disturbance intensity on plant-soil C and N in alpine meadow ecosystems

The C and N stocks in grassland ecosystems increased with increased disturbance intensity in Gangcha, Haiyan, Luqu, and Qilian (Figures 7A, B). The ecosystem C and N stocks showed a fast or a slow decreasing trend when the ABED reached a certain value (about 268-489 ha^{-1}).

4 Discussion

Pikas are a key component of alpine meadow ecosystems (Wei et al., 2019). The presence of pikas can cause extensive disturbance to plants and soils, potentially altering plant-soil C and N and affecting C and N cycling in grassland ecosystems (Zhao et al., 2022).

4.1 Effects of plateau pika disturbance on plant-soil C and N at the quadrat scale

This study shows that pika disturbance did not affect AGB and its C and N concentrations (Figure 2). Further research found that

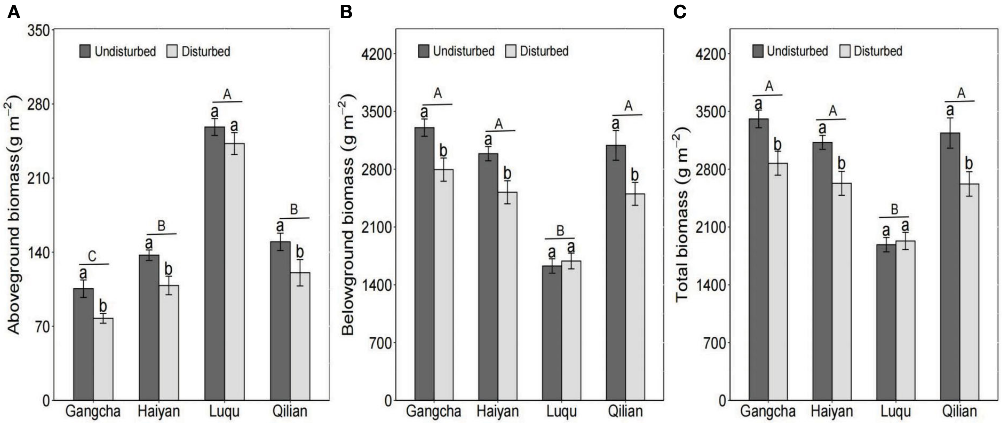

FIGURE 4
Response of above-ground biomass **(A)**, below-ground biomass **(B)**, and total biomass **(C)** to the disturbance by pikas at the plot scale (mean ± SE). The statistics were obtained from the LMMs, using paired plots at each site as random factors. Different lowercase letters indicate significance between disturbed and undisturbed plots; different uppercase letters indicate significance between sites when the presence and absence of pikas are combined for each site, *P*< 0.05.

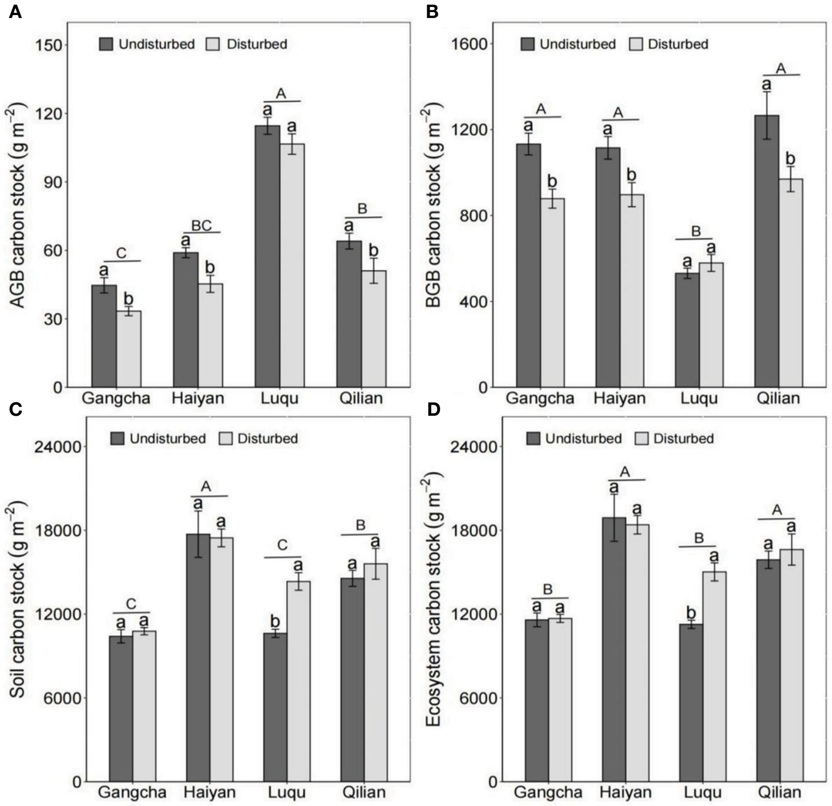

FIGURE 5
AGB carbon stock **(A)**, BGB carbon stock **(B)**, soil carbon stock **(C)**, and ecosystem carbon stock **(D)** in plots disturbed and undisturbed by pikas at each site (mean ± SE). The statistics were obtained from the paired T-test for each site. Different lowercase letters indicate significance between disturbed and undisturbed plots; different uppercase letters indicate significance between sites when the presence and absence of pikas are combined for each site, $P < 0.05$.

BGB, soil C, and soil N concentrations were significantly lower in bare soil areas than in vegetated areas and undisturbed plots (Figures 2, 3). The trend of soil C and N is consistent because N in the soil is mainly bound in the form of organic N compounds (Kelley and Stevenson, 1995). However, the results for soil C and soil N contradicted the first hypothesis. Soil nutrients were also contrary to the study of Yu et al. (2017a), possibly due to inconsistencies in sampling methods. They did not differentiate between bare soil and vegetated areas when collecting soil samples from disturbed areas. The impact of pikas on alpine grassland vegetation and soil is not uniform within the home range of pika families (Wei et al., 2019). Moreover, we studied new bare patches with no vegetation covering the surface of the bare patches. Therefore, there may be three mechanisms for lower soil C and N stocks in bare soil areas: first, reducing vegetation and roots in bare soil areas can decrease the input of soil organic matter (Yu et al., 2017a); second, the digging behavior of pikas moves deep soil with lower organic matter content to the topsoil (Clark et al., 2016); third, the mineralization of soil organic matter in bare soil areas is high (Yu et al., 2017b). However, the N concentration of BGB was significantly higher in bare soil areas (Figure 2). Patterns of C and N nutrient partitioning in above- and below-ground plant organs are among the most important strategies for plant communities to adapt to external changes (Liu et al., 2021). Therefore, the increase in the N concentration of BGB in bare soil areas may be caused by the above-ground vegetation in bare soil areas being heavily foraged and clipped by pikas, resulting in a smaller supply of N to the above-ground vegetation. Plant roots also increased the uptake of N to promote growth. Additionally, effective N increased in bare soil areas (Pang et al., 2020b), and more N became available for uptake and utilization by the roots. These findings suggest that plants and soils in bare soil areas are highly heterogeneous, contributing to the understanding of the role of the pika on C and N cycling in bare patches. Therefore, further research on the relationship between pika disturbance and C and N at the plot scale is required.

4.2 Effects of plateau pika disturbance on plant-soil C and N at the plot scale

At the plot scale, pika disturbance significantly reduced plant biomass, AGB carbon and nitrogen stocks, and BGB carbon stocks (Figures 4–6). The C and N stored in plants decreased as plant biomass decreased. The effects of pikas on plant C and N were consistent with the first hypothesis. However, there were no differences in BGB carbon, soil C, soil N, ecosystem C, and

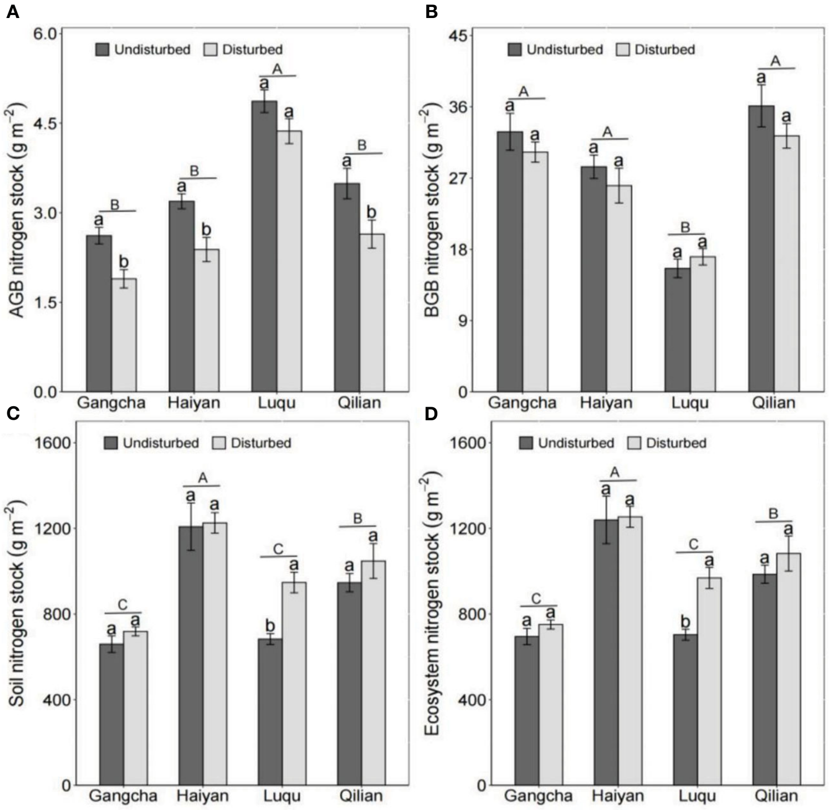

FIGURE 6
AGB nitrogen stock **(A)**, BGB nitrogen stock **(B)**, soil nitrogen stock **(C)**, and ecosystem nitrogen stock **(D)** in plots disturbed and undisturbed by pikas at each site (mean ± SE). The statistics were obtained from the paired T-test for each site. Different lowercase letters indicate significance between disturbed and undisturbed plots; different uppercase letters indicate significance between sites when the presence and absence of pikas are combined for each site, $P< 0.05$.

ecosystem N stocks between disturbed and undisturbed plots (Figures 5, 6). The C and N stored in grassland ecosystems are mainly determined by C and N in grassland soils (Ni, 2002), so pika disturbance maintained the C and N balance of grassland ecosystems. Thus, pika disturbance has a trade-off effect on plant-soil C and N stocks at the plot scale, showing that small mammals interfere differently than large mammals. For example, the trampling of and grazing on grasslands by livestock grazing are

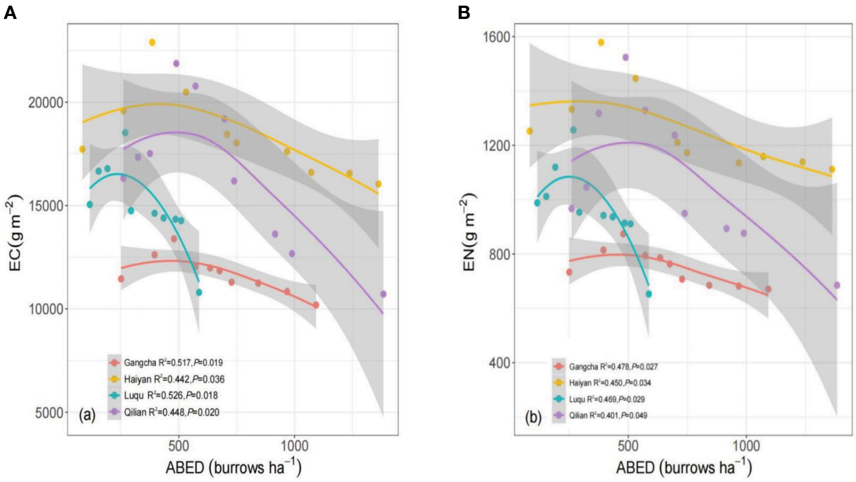

FIGURE 7
Ecosystem carbon **(A)** and nitrogen **(B)** stocks under different pika disturbance intensities based on linear models (lm) for each site. An adjusted local smoothed regression line (color) with its 95% confidence interval (gray) was used to determine the relationship between the disturbance intensity of pikas and the indicators above. EC, ecosystem carbon stocks; EN, ecosystem nitrogen stocks; ABED, active burrow entrance densities.

more severe, resulting in large-scale losses of grassland vegetation and sources of soil C and N (Pringle et al., 2014; Zhou et al., 2017). However, the effects of disturbance by pikas on plant biomass and plant-soil C and N stocks were site specific. In the alpine meadows of Luqu, disturbance by pikas had no impacts on plant biomass and AGB carbon and nitrogen stocks but significantly increased soil C and N stocks (Figures 4–6). Possibly due to higher precipitation and temperature, the dominant plant species at the Luqu study site was *K. capillifolia* with dense above-ground vegetation (Figure 4 and Table 1). Disturbance by pikas can increase the deposition rate of uneaten food and tall plant clippings, thereby increasing the input of organic matter (Liu et al., 2013; Zhang et al., 2016). Moreover, the abundant vegetation was clipped and buried in burrows by pikas, thus storing part of the soil organic matter (Yurkewycz et al., 2014; Clark et al., 2016). Soil C and N are also related to pika density and excretion of feces and urine, contributing to the input of soil organic matter (Yu et al., 2017a). Conversely, higher soil C and N sustain plant growth and development. The survey also found that when combining the presence and absence of pikas, AGB and its C and N stocks were higher but BGB, BGB carbon and nitrogen stocks, and total biomass were lower at Luqu (Figures 4– 6). The average annual precipitation was approximately 691 mm, and the average annual temperature was 3.08°C at Luqu. The relatively high precipitation and temperature favor the growth of above-ground vegetation (Holub, 2002; Ma et al., 2010), but can make the plant roots undeveloped (Ibrahim et al., 1997; Bakker et al., 2006; Qaderi et al., 2010; Xu et al., 2016). The study also found that C and N stored in soil and ecosystem were higher at Haiyan (Figures 5, 6), which could be attributed to the lower temperatures, slowing down the decomposition of soil organic C, thus storing soil organic C.

4.3 Relationship between disturbance intensity and C and N in grassland ecosystems at the plot scale

C and N stocks in grassland ecosystems showed hump-shaped changes with increasing disturbance intensity at all four sites when analyzing the relationship between the disturbance intensity (measured by ABED) and ecosystem C and N stocks. Ecosystem C and N stocks decreased with increasing disturbance intensity when the disturbance intensity exceeded the threshold. This result partially supports the second hypothesis, which may be explained by reducing soil C and N sources at high disturbance intensity (Sun et al., 2015; Pang and Guo, 2017). This result may also be explained by the increase in soil permeability, resulting in the loss of soil C and N (Wilson and Smith, 2015). These findings from the study detail the general pattern of pika disturbance on plant-soil C and N stocks at each site, deepening the understanding of the relationship between small burrowing mammal disturbance and grassland ecosystems on the Tibetan Plateau. Nevertheless, the effects of bare patches of different ages on C and N in grassland ecosystems could not be fully evaluated because the disturbed plots in this study were all new bare patches, and no restored bare patches were considered.

5 Conclusions

This study investigated the relationship between pika disturbance and plant-soil C and N at two scales. The findings suggest that the bare soil patches formed by pikas caused plant and soil heterogeneity but had a trade-off effect on plant-soil C and N stocks at the plot scale. Nevertheless, moderate disturbance intensity increased the C and N sequestration potential in the grassland ecosystems. These findings in this study provide possible ways to estimate how disturbance by small burrowing mammals affects C and N cycling in grassland ecosystems and to accurately assess the effects of small burrowing mammal densities on C and N in grassland ecosystems.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

XX: Data curation, Formal Analysis, Writing – original draft, Writing – review & editing. YW: Data curation, Formal Analysis, Writing – original draft, Writing – review & editing. XW: Data curation, Writing – review & editing. JNL: Data curation, Writing – review & editing. JL: Investigation, Writing – review & editing. DY: Investigation, Writing – review & editing. ZG: Investigation, Writing – review & editing. XP: Data curation, Formal Analysis, Investigation, Writing – review & editing, Funding acquisition.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Response of species dominance and niche of plant community to wetland degradation along alpine lake riparian

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Alpine wetland degradation threatens riparian biodiversity and ecological balance. Our study, conducted in July 2020 along the northern and eastern shores of Qinghai Lake, seeks to unravel the impacts of such degradation on plant species dominance and ecological niches, using advanced network analysis methods to explore the dynamics and survival strategies of plant species. We applied a space-to-time method to delineate three wetland degradation stage: a healthy swamp wetland, a slightly degraded wet meadow, and a degraded dry meadow. Six representative sampling points were chosen. At each point, three sample lines were randomly established, radiating outward from the center of the lake wetland, with each stage of degradation meticulously examined through three replicates to assess the plant communities in terms of species composition, plant height, coverage, and abundance. The results indicated: Species such as *Kobresia tibetica* and *Leymus secalinus* exhibit remarkable abundance across various stages of wetland degradation, indicating a robust tolerance to these conditions. This observation, coupled with the complexity of plant community structures in degrading wetlands, suggests that such intricacy cannot be solely attributed to the dominance of particular species. Instead, it is the result of a diverse array of species adapting to fluctuating water levels, which promotes increased species richness. Despite the prominence of species that exhibit rapid growth and reproduction, the ecological significance of less abundant species in contributing to the community's complexity is also notable. Changes in habitat conditions due to wetland degradation facilitate both competitive and cooperative interactions among species, highlighting the dynamic nature of these ecosystems. Our analysis shows no significant linear relationship between the ecological niche overlap values and niche widths of plant species. However, the strategies employed by dominant species for competition and resource acquisition, as observed in the ecological niche overlap networks, underscore the adaptive capacity of plant communities. These insights underscore the need for tailored restoration strategies to conserve the biodiversity of alpine lake riparian ecosystems. This research not only sheds light on the resilience and adaptability of ecosystems in the Qinghai-Tibetan Plateau but also offers valuable lessons for the conservation of similar habitats worldwide. Our findings underscore the need for tailored restoration strategies to conserve the biodiversity of alpine lake riparian ecosystems. This research not only sheds light on the resilience and adaptability of ecosystems in the Qinghai-Tibetan Plateau but also offers valuable lessons for the conservation of similar habitats worldwide.

KEYWORDS

Qinghai Lake riparian, plant dominance, community structure, niche breadth, niche overlap, network analysis

1 Introduction

Alpine wetlands represent a crucial biome. These ecosystems, irrespective of their size, play a vital role in biodiversity conservation and provide essential habitats for numerous species. As the highest plateau in the world, Qinghai-Tibetan Plateau boasts vast unique alpine wetlands in the size over 1×10^5 km^2, accounting for nearly 30% of the nation's total wetland in China (Li et al., 2016). These wetlands in the forms of lake, river and marsh (Zhao et al., 2015), are primarily distributed in the Three Rivers Source Region, the eastern and southern regions of the Qiangtang Plateau, the Gannan Plateau, and the Zoigê Plateau (Bai et al., 2004). The lake wetland on the Qinghai-Tibetan Plateau is approximately 44,000 km^2 in size, up to 33% of the total wetland area on the Qinghai-Tibetan Plateau (Zhang and Wu, 2014).

These wetlands are distinctive, endowed with irreplaceable ecological, environmental, and societal functions such as water storage, water source replenishment, and climate regulation. They play vital roles in maintaining regional sustainable development, serving as critical areas for biodiversity conservation and reactors and buffers to mitigate global climate change (Liu Z. et al., 2019). Due to its vast area and complex topography, a notable characteristic of the dynamic changes in the high-altitude wetlands of the Qinghai-Tibetan Plateau is pronounced as "east-west" disparity (Li et al., 2011). In recent decades, human activities as the primary driver together with climatic factors as a secondary driver have strongly affected the alpine wetlands on the Qinghai-Tibetan Plateau (Wang, 2007; Hou et al., 2020) resulting in the massive degradation of the alpine wetlands in this region. In the northwestern Qinghai-Tibetan Plateau, warmer and wetter climate has been associated with an overall increase in lake water levels and volume, resulting in enhanced water storage in lake and marsh wetlands (Li and Sheng, 2013). In southern Qinghai-Tibetan Plateau, despite a decreasing trend in precipitation, increased runoff derived from glacier melting has led to an overall increase in water volume, facilitating the natural recovery of many degraded or deteriorating wetlands (Zhang and Wu, 2014; Liu and Liu, 2021). Conversely, in eastern Qinghai-Tibetan Plateau, such as the Zoigê Plateau, the warmer and drier climate in the past three decades have resulted in increased evapotranspiration and declining water levels, leading to a noticeable reduction in water storage in marsh wetlands (Liu Z. et al., 2019; Zhao and Shi, 2020). In the process of wetland degradation, there is a noticeable changes of vegetation composition and structure, exhibiting a succession trend from marsh to wet meadow, to dry meadow, and eventually to desert land (Li et al., 2004).

Qinghai Lake wetland is one of the seven vital wetlands in China and was registered as Wetland of International Importance through the Ramsar Convention in 1992. This wetland is renowned as the "humidifier" of the Qinghai-Tibetan Plateau and serves as a natural bulwark for the maintenance of ecological security with rich biodiversity and the prevention of desertification in the northeastern region of the Qinghai-Tibetan Plateau (Cheng et al., 2013). Since the 1950s, the alteration of land use has exerted significantly negative impacts on the Qinghai Lake's alpine wetland ecosystem, resulting in the decrease in vegetation productivity and shifts of community structure. In recent years, environmental issues in the Qinghai Lake region such as wetland degradation, biodiversity loss, and soil desertification have gradually become more apparent, threatening the sustainability of this precious and unique wetland ecosystem in the world. There are some studies documented the changes of plant diversity and grassland degradation in the Qinghai Lake watershed (Zhu et al., 2006; Song et al., 2011; Cheng et al., 2013). While there has been limited information regarding the changes of vegetation composition and structure with wetland degradation in the Qinghai Lake vicinity. Therefore, there is an urgent need to conduct the studies about the responses of vegetation to the degradation of Qinghai Lake wetland in the dimensions of plant species dominance and niches, the key determining indicators of community composition and structure. The results of such studies could be served as a foundation for the best conservation and restoration practices of alpine wetlands on the Qinghai-Tibetan Plateau and similar regions worldwide.

In the realm of species dominance and niches analysis, numerous studies have been performed in the world to explain the assemble and formation of vegetation in the different biome including wetland since the early stage of the 20th century. These studies have produced the ecological niche theory to explain the inter- and intra-specific relationships for structuring the plant communities. Additionally, the ecological niche theory plays a crucial role in understanding various ecological processes, such as population evolution and community succession (Peterson and Soberón, 2012; Peng and Wang, 2016; Yang et al., 2023). For instance, niche theory can clarify the allocation of resources among species, which reflects the interplay among plant populations and implies the mechanisms shaping the community composition (Nie et al., 2020). In the context of population succession, a species with a broader ecological niche tends to exhibit lower specialization, suggesting a higher degree of competitiveness. Conversely, species with narrower ecological niches display stronger specialization, which can lead to high competitiveness in their specific habitats where they are highly adapted. However, these specialized species may face challenges in resource competition when their habitats undergo significant changes, such as those caused by climate change or environmental degradation (Zhang and Xu, 2013; Wei et al., 2015). Currently, there are two different conclusions on the relationship between width of ecological and the degree of niche overlap, i.e., linear correlation (Li et al., 2014; Wang et al., 2017; Zhao et al., 2023) and non-linear correlation (Miao et al., 2015; Feng et al., 2020). The different outcomes are highly related to environmental conditions and human interventions (Zhang and Xu, 2013). Consequently, definitive outcomes for representative ecosystems in specific regions like Qinghai-Tibetan Plateau's alpine lake wetland require a nuanced, context-specific study. In ecological studies, the concept of a niche plays a pivotal role in understanding species interactions and environmental adaptations. The fundamental niche represents the full range of environmental conditions under which a species can theoretically survive and reproduce, absent of biotic interactions like competition or predation. In contrast, the realized niche is the subset of these conditions under which a species actually exists, considering biotic and abiotic factors in its natural habitat (Hutchinson, 1957; MacArthur, 1958; Chase and Leibold, 2003). This study primarily analyzes the realized niches of species within degraded wetland ecosystems. We emphasize that the observed variations in niche width and overlap among plant species are responses to current environmental conditions rather than alterations in their fundamental niches. Such an approach allows for a nuanced understanding of species' adaptive strategies in the face of changing ecological landscapes.

In addition, most studies on the ecological niche are primarily focused on sole analysis of ecological niche width and niche overlap values. However, very few studies have documented the niche connection and overlap in shaping the community composition and structure. Network analysis methods possess significant potential for exploring interaction, offering a multi-dimensional understanding of relationships, and uncovering potential connections (Deng et al., 2012; Meyer et al., 2020). Hence, identifying the ecological niche width and degree of niche overlap among these populations, and employing network analysis to explore niche overlap network features, enables a deeper understanding of the roles, statuses, and interactions among various species within the plant community during the process of wetland degradation.

Alpine wetlands, vital for biodiversity across sizes, are especially crucial in the Qinghai-Tibetan Plateau's unique environments. This study focuses on the Qinghai Lake riparian area, sets out to test three hypotheses aimed at understanding how wetland degradation affects plant species' ecological niches and community dynamics: 1) Wetland degradation can lead to alterations in the realized niches of plant species by modifying the environmental conditions and competitive dynamics within alpine lake riparian vegetation. These changes can significantly impact the composition of species, as different species adjust their ecological roles and interactions in response to the degraded conditions; 2) Wetland degradation can facilitate species competition through increasing the ecological niche overlap of plant species, leading to a more intricate plant community structure along alpine lake riparian; 3) Increased ecological niche overlap networks with wetland degradation may enhance self-regulatory capacity of plant communities through empowering dominant species' competition for resource acquisition. By focusing on the realized niches, we explore the degradation's impact on species competition and community structure. Our research seeks to illuminate the processes through which degradation reshapes plant communities, with the ultimate aim of guiding restoration and conservation strategies on the Qinghai-Tibetan Plateau and beyond.

2 Materials and methods

2.1 Study area

Qinghai Lake is situated in the northeastern part of the Qinghai-Tibetan Plateau, characterized by a distinct plateau continental climate. Geographically, it spans from approximately 97°53′ to 101°13′ east longitude and 36°28′ to 38°25′ north latitude. The lake's surface lies at an elevation of 3194 meters, with an average depth of 18 meters and a maximum depth of 26.6 meters. Its longest east-west stretch measures around 106 kilometers, while the widest north-south point extends approximately 63 kilometers, giving it a somewhat elliptical shape. The lake's shoreline stretches approximately 360 kilometers (He, 2019). The region encompasses parts of the Haiyan and Gangcha counties in the Haibei Tibetan Autonomous Prefecture, as well as the Gonghe County in the Hainan Tibetan Autonomous Prefecture. Qinghai Lake is recognized as Wetland of International Importance and a key sanctuary for rare bird and fish species, and a natural landscape conservation area on the Qinghai-Tibetan Plateau.

The study area falls within the wetland belt on the northern riparian of Qinghai Lake, part of the Qinghai Lake National Nature Reserve. The region experiences an annual average temperature range of -4.6 to 1°C, a frost-free period lasting 117 to 118 days, an annual sunshine duration of 2800 to 3330 hours, annual evaporation rates ranging from 800 to 2000 mm, and annual precipitation levels between 291 and 575 mm (Wu et al., 2011). The wetland soils predominantly consist of hydromorphic and meadow soils, with marshy and meadow soils being the primary types (Wu et al., 2011).

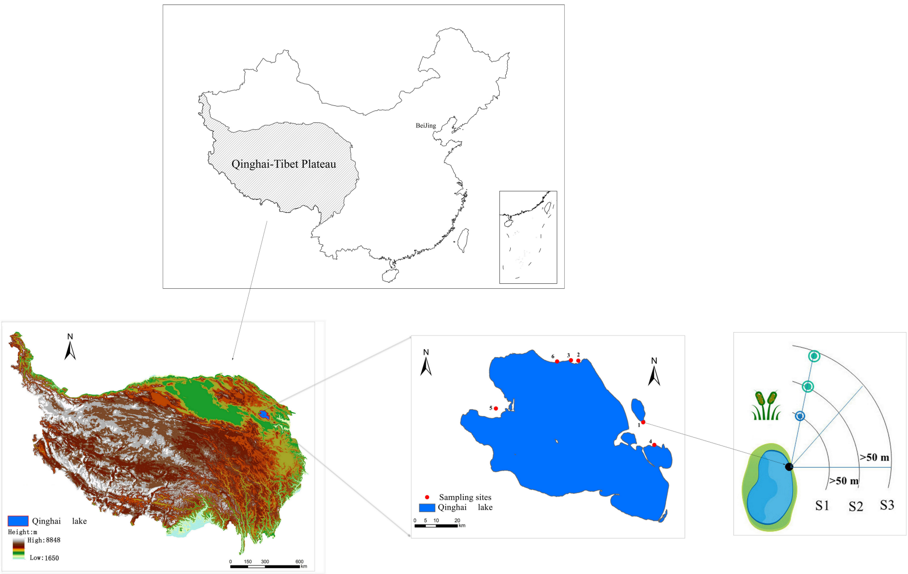

FIGURE 1
Schematic diagram of sampling point distribution and investigation in the study area.

2.2 Experimental design

Six representative sampling sites were selected along the northern and eastern shores of Qinghai Lake. The specific locations (Figure 1) include Gahai, Shaliu River, Shadao Lake, and Xiannü Bay, all of which represent typical wetland areas in the vicinity of Qinghai Lake. The common feature of these areas is that they are typical wetland ecosystems in Qinghai Lake area, which have important ecological value and research significance (Zhang and Yan, 2017). The specific geographical descriptions of the research sites can be found in Table 1.

2.3 Field sampling and measurements

The degradation status of wetland vegetation was investigated following the methodology developed by Ren (Ren, 1998). By using space-to-time method, three stages of wetland degradation along Qinghai Lake riparian were defined along the lake riparian, i.e., typical marsh at the lake riparian represented the healthy wetland (S1, swamp wetland), wet meadow close to riparian represented the slightly degraded wetland (S2, swamp meadow) and dry meadow far from the riparian represented as the degraded wetland (S3, meadow). The categorization of these stages was based primarily on the characteristics of vegetation composition, with each stage typically separated by an approximate distance of 50 meters, reflecting a gradient in vegetation transition and wetland health. The sample line method was applied to sample the vegetation in the wetland riparian at different degradation stage by placing three sample lines randomly for the wetland at each stage of degradation, radiating outward from the center of the lake wetland (at the point where rivers enter the lake). Through data investigation, we have confirmed that all the points on the sampled line were swamp wetlands 40 years ago, which ensures that the spatial sampling can represent vegetation degradation. Three replicated plots of 1 m × 1 m were placed for investigating species composition, height, coverage, and the number of individuals or clumps in the plant community. To minimize potential edge effects, a minimum buffer of 5 meters was maintained between any two survey plots. The elevation and coordinates of each plot were measured using handheld GPS devices. Plant species were further categorized into functional groups of grass, sedge, legume, and forb.

TABLE 1 Geographic locations of sample points for S1stage.

Site	Elevation (m)	Longitude and latitude	
1	3197	E100°35′48.79″	N36°57′24.97″
2	3199	E100°11′48.28″	N37°12′1.82″
3	3198	E100°11′32.60″	N37°12′3.99″
4	3195	E100°39′43.42″	N36°51′53.74″
5	3200	E99°48′5.63″	N36°59′4.59″
6	3199	E100°7′5.11″	N37°11′35.71″

Different diversity indices including Species Richness, and Importance Value (IV) were used to evaluate the structure and composition of plant communities (Agrawal and Gopal, 2012). The Importance Values for species are calculated based on the corresponding heights, cover, and frequency of each species, by averaging these relative metrics to derive the Importance Value for each species. We specifically focused on the Levins' Ecological Niche Width Index (Bi) and Levins' Ecological Niche Overlap Index (Oik) (Levins, 2020), which are instrumental in understanding the actual ecological space occupied by species, influenced by both biotic and abiotic factors. This distinction underscores our analysis of the realized niche, rather than the broader fundamental niche, which theoretically encompasses all environmental conditions under which a species can survive and reproduce. The ecological niche overlap values are categorized into three intervals: <0.3, 0.3-0.8, and >0.8 (Zhao et al., 2023).

2.4 Network analysis

In this study, a network was constructed based on the ecological niche overlap relationship matrix, and modular analysis of the ecological niche overlap network was performed. To analyze network modularity, we used the Modularity index to identify natural divisions within the network. This approach aims to maximize the density of connections within modules while minimizing connections between different modules. Various algorithms can calculate network modularity, and for our study, we identified the division that maximizes this index, thus determining the number of modules. Consistent algorithm and parameter settings were maintained throughout the study to ensure uniformity. In the analysis, nodes in the network represent plant species, with nodes in the same module tending to connect more with other nodes in the module and less with nodes outside the module (Deng et al., 2012). Species with the same color form sub-modules within the ecological niche overlap network, visually differentiated in our representations (Chen et al., 2022). The thickness of edges indicates the magnitude of ecological niche overlap values. In R, we employed the default optimal algorithm to compute the number of modules, which were then visualized in Gephi with distinct colors for each module. This visualization approach allowed us to clearly delineate and present the modular structure within our ecological network. Network modules represent species that tend to coexist in plant communities under similar habitat conditions, possibly through competition or resource sharing strategies.

2.5 Data processing

The calculation of the diversity index, IV, Bi, Oik and network analysis were performed using the “vegan”, “spaa”, “EcolUtils” and “igraph” packages in the program R Studio 1.1.456. The network is visualized by using Gephi 0.10 software.

3 Results

3.1 Impact of wetland degradation on plant community structure

A total of 46 species belonging to 18 families and 33 genera were collected (Table 2). Species with relatively high occurrence frequencies included *Leymus secalinus* and *Poa annua* from Grass functional group, *Kobresia tibetica* from sedge functional group,

TABLE 2 Important value and niche widths of plant species in healthy wetlands (S1), slightly degraded wetlands (S2), and degraded wetlands (S3).

Species No.	Species	Importance value/Niche width (Group ID: a, b, c, d, e)		
		S1	S2	S3
		(Healthy wetland)	(Slightly degraded wetland)	(Degraded wetland)
1	*Kobresia humilis*	—	0.07/1.00 (N/A)	—
2	*Dracocephalum heterophyllum*	0.01/1.00 (b)	0.05/1.23 (b)	0.01/1.80 (b)
3	*Artemisia sacrorum*	0.01/1.80 (N/A)	—	—
4	*Agropyron cristatum*	0.19/2.51 (N/A)	—	0.05/1.00 (N/A)
5	*Descurainia sophia*	—	0.29/1.00 (N/A)	—
6	*Plantago asiatica*	0.01/1.60 (a)	0.15/1.24 (a)	0.04/1.00 (a)
7	*Elymus nutans*	0.09/2.00 (N/A)	0.48/3.09 (N/A)	0.10/5.05 (N/A)
8	*Potentilla conferta*	0.05/3.94 (a)	0.09/1.97 (a)	0.11/3.36 (a)
9	*Astragalus bhotanensis*	0.06/1.00 (b)	0.01/1.47 (b)	0.01/1.00 (b)
10	*Potentilla multifida*	—	0.04/1.00 (N/A)	0.02/1.42 (N/A)
11	*Astragalus polycladus*	—	0.08/1.00 (N/A)	0.05/2.32 (N/A)
12	*Carex kansuensis*	0.4/4.58 (c)	0.24/3.76 (c)	0.21/5.33 (c)
13	*Triglochin maritimum*	—	0.07/1.02 (N/A)	—
14	*Glaux maritima*	0.28/1.18 (N/A)	0.15/3.74 (N/A)	0.05/1.61 (N/A)
15	*Carex atrofusca subsp. minor*	0.35/2.72 (e)	0.24/2.75 (e)	0.03/1.00 (e)

(Continued)

TABLE 2 Continued

Species No.	Species	Importance value/Niche width (Group ID: a, b, c, d, e)		
		S1	S2	S3
		(Healthy wetland)	(Slightly degraded wetland)	(Degraded wetland)
16	*Gentiana pseudoaquatica*	—	0.01/100 (N/A)	—
17	*Potentilla anserina*	0.24/3.90 (a)	0.18/3.50 (a)	0.23/5.57 (a)
18	*Leymus secalinus*	0.4/2.71 (b)	0.45/4.14 (b)	0.71/5.60 (b)
19	*Oxytropis coerulea*	—	—	0.02/1.00 (N/A)
20	*Artemisia frigida*	0.04/2.48 (N/A)	—	0.13/2.27 (N/A)
21	*Oxytropis falcata*	—	0.03/1.72 (N/A)	0.03/1.00 (N/A)
22	*Gentiana squarrosa*	0.04/2.22 (a)	0.09/2.12 (a)	0.05/1.05 (a)
23	*Iris lactea* var. *chinensis*	—	0.08/1.00 (N/A)	0.51/2.95 (N/A)
24	*Silene conoidea*	0.03/1.53 (N/A)	0.03/1.00 (N/A)	—
25	*Ranunculus membranaceus*	0.06/2.90 (a)	0.08/1.95 (a)	0.11/3.12 (a)
26	*Thermopsis lanceolata*	0.26/3.76 (b)	0.37/2.22 (b)	0.13/2.95 (b)
27	*Taraxacum mongolicum*	0.13/2.22 (a)	0.09/3.07 (a)	0.15/2.97 (a)
28	*Koeleria cristata*	—	—	0.05/1.73 (N/A)
29	*Rubia cordifolia*	—	—	0.08/1.47 (N/A)
30	*Lancea tibetica*	—	0.09/1.06 (N/A)	0.01/2.37 (N/A)
31	*Mulgedium tataricum*	—	—	0.01/1.00 (N/A)
32	*Artemisia desertorum*	0.08/2.11 (b)	0.04/1.00 (b)	0.02/1.00 (b)
33	*Saussurea arenaria*	—	—	0.08/1.28 (N/A)
34	*Anemone obtusiloba subsp. ovalifolia*	—	0.03/1.53 (N/A)	—
35	*Triglochin palustre*	0.07/4.92 (d)	0.04/1.00 (d)	0.06/2.92 (d)
36	*Potentilla chinensis*	—	—	0.01/1.00 (N/A)
37	*Polygonum sibiricum*	0.09/2.74 (c)	0.01/1.00 (c)	0.02/1.18 (c)
38	*Kobresia tibetica*	0.68/4.86 (d)	0.64/6.57 (d)	0.67/5.97 (d)
39	*Primula forbesii*	—	0.03/2.51 (N/A)	0.05/1.00 (N/A)
40	*Chenopodium ficifolium*	—	0.03/1.38 (N/A)	—
41	*Kalidium foliatum*	0.03/1.00 (e)	0.03/2.80 (e)	0.01/1.00 (e)
42	*Silene galliea*	0.06/2.39 (a)	0.07/2.21 (a)	0.06/3.40 (a)
43	*Poa annua*	0.31/2.82 (N/A)	0.19/4.64 (N/A)	0.17/3.59 (N/A)
44	*Rumex crispus*	—	0.03/1.80 (N/A)	—
45	*Artemisia scoparia*	0.07/1.35 (b)	0.03/1.00 (b)	0.01/1.00 (b)
46	*Aster tataricus*	0.01/1.00 (N/A)	0.04/1.15 (N/A)	—

The Species No. corresponds to the numerical identifiers used for plant species on the nodes in Figure 2, facilitating cross-referencing between the table and figure. The Group ID indicates the module group to which species are assigned based on Figure 2. Group ID for each stage indicate the module group to which a species belongs during that stage, as identified in the ecological network analysis. "N/A" denotes species that are present at the stage but not assigned to any of the prominent modules with relatively stable module relationships (a, b, c, d, e), and "—" indicates absence from that stage.

Thermopsis lanceolata from Leymus functional group. Species from the Asteraceae and Rosaceae families in the miscellaneous group also appeared frequently. The Importance Value (IV) is a comprehensive indicator of a species' role and status within a community, reflecting its degree of dominance. There were notable differences in the primary plant composition of vegetation communities across different degradation stages (Table 2), indicating species turnover. In the S1 community, the dominant species were *Kobresia tibetica*, co-occurring with *Leymus secalinus*, *Carex kansuensis*, *Carex atrofusca subsp. minor*, and *Poa annua*. In the S2 stage, *Kobresia*

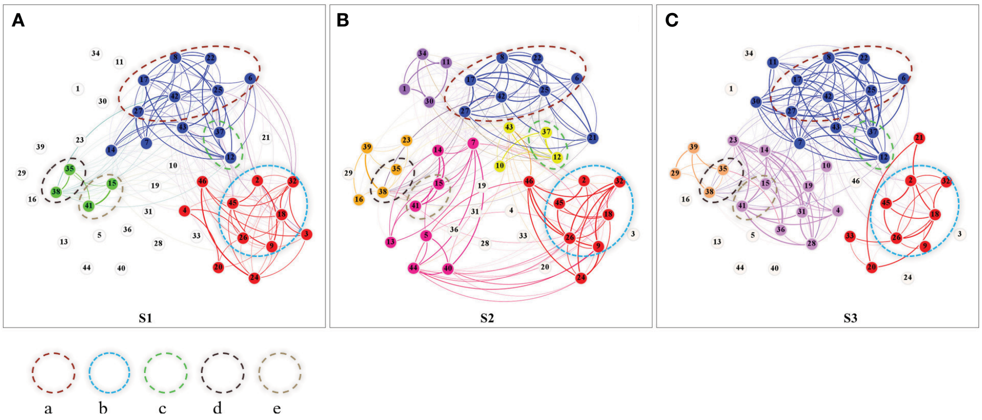

FIGURE 2
Niche overlapping networks and modules at different stages of wetland degradation (**A**: S1, (**B**: S2, **C**: S3). The numbers on the nodes are the species numbers in Table 2, the nodes with the same color belong to the same sub-module, and the thickness of the edge represents the niche overlap value; Dashed circles enclose groups of species with relatively stable module relationships, labeled as a, b, c, d, e based on the number of constituent species. Unconnected nodes (indicated by grey-white circles) represent species not present in the specific stage being analyzed but observed at some point during the overall survey.

tibetica remained the dominant species, accompanied by *Leymus secalinus*, *Elymus nutan*s, and the invasive toxic species *Thermopsis lanceolata* and the miscellaneous *Descurainia sophia*. In the S3 stage, *Leymus secalinus*, *Kobresia tibetica* are co-dominant species. Additionally, the miscellaneous species *Iris lactea* var. *chinensis* and *Potentilla anserina* were observed.

3.2 Impact of wetland degradation on species niche width and overlap

3.2.1 Niche width

According to the niche metrics results, the niche width of dominant species such as Kobresia tibetica and Leymus secalinus was observed to increase in degraded wetland conditions (Table 2). The niche width of the dominant species *Kobresia tibetica* at the S3 stage (5.60) is greater than that at the S1 stage (4.86). The niche width of the dominant species *Leymus secalinus* at the S3 stage (5.60) is higher than that at the S1 stage (2.71). This increase, rather than indicating a shift in ecological strategy, may be more indicative of the species' inherent tolerance to a range of habitat degradation levels. The wider niche width observed in these species at the S3 stage compared to the S1 stage underscores their adaptability to varying environmental conditions.

Some plant species exhibit non-linear relationships between ecological niche width and importance values, implying that species with low importance values may possess broader ecological niches, which could impact the growth of the dominant grasses at the same stage. For example, at the S1 stage, the perennial wetland herb *Triglochin palustre* has an importance value of only 0.07, but it possesses the largest niche width of 4.92. With the progress of wetland degradation, its niche width decreases by 79.66% at the stage S2 and 40.70% at the stage S3. At the stage S3, as one of the salt-tolerant indicators with strong preference for wet conditions, *Potentilla anserina* has an importance value of only 0.23. Nevertheless, its niche width ranks just after *Kobresia tibetica* and *Leymus secalinus*, indicating that this plant competes effectively with other plants despite it has lower importance value than other plant species at the same degradation stage of S3.

Positive correlation between importance values and niche widths of plant species across different degradation stages was observed in regression analysis (Figure 3). With the increase of wetland degradation, the importance values of species become more

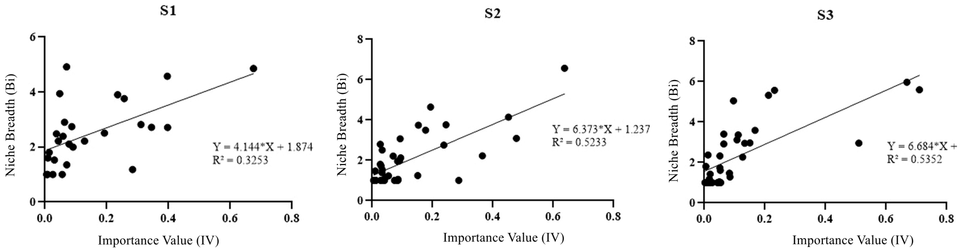

FIGURE 3
Relationship between species weight values and niche breadth species at different degradation stages.

TABLE 3 Intervals of niche overlap values for species in healthy wetlands (S1), slightly degraded wetlands (S2), and degraded wetlands (S3).

	Percentage of each interval (%)			Average niche overlap index
	Niche overlap value <0.3	Niche overlap value0.3-0.8	Niche overlap value>0.8	
S1 (Healthy wetland)	62.94%	28.82%	8.24%	0.27
S2 (Slightly degraded wetland)	61.78%	24.89%	13.33%	0.33
S3 (Degraded wetland)	47.60%	32.69%	19.71%	0.43

significant in determining their resource utilization and environmental adaptation capabilities (Figure 3).

3.2.2 Niche overlap

The overall changes in niche overlap values for the main plant species at different degradation stage are presented in Table 3. In general, species with niche overlap values <0.3 represent the largest proportion with decreasing trend along the wetland degradation gradient, while those with niche overlap values >0.8 represent the smallest proportion with increasing trend along the wetland degradation gradient. The ecological niche overlap index increases with wetland degradation, from 0.27 at the degradation stage of S1 to 0.43 at the degradation stage of S3.

As shown in Figure 4, there are no significant linear relationship between the ecological niche width and niche overlap values of plant species at different degradation stages (with R^2 values of 0.0642, 0.168, and 0.1933), implying that the species with the largest niche width may not necessarily have the highest overlap values with other plant species.

3.2.3 Networks of niche overlap

As shown in Figure 2, the number of network modules increased from 3 at the degradation stage of S1 to 5 at the degradation stage of S3, with the highest number of modules 6 at the degradation stage of S2. There are five groups of species clusters with stable module relationships.

Group "a" consists of *Plantago asiatica* (6), *Potentilla confertam* (8), *Potentilla anserina* (17), *Gentiana squarrosa* (22), *Ranunculus membranaceus* (25), *Taraxacum mongolicum* (27), and *Silene galliea* (42), indicating that these low-growing herbaceous plants form a stable module with shared ecological strategies. Among them, *Potentilla anserina* exhibits more developed creeping stems and higher frequency of occurrence, and a larger ecological niche width, indicating its competitive advantage in this group.

Group "b" is comprised of *Dracocephalum heterophyllum* (2), *Astragalus bhotanensis* (9), *Leymus secalinus* (18), *Thermopsis lanceolata* (26), *Artemisia desertorum* (32), and *Artemisia scoparia* (45). Among them, *Leymus secalinus*, the dominant species in the community, shows the widest ecological niche, followed by *Thermopsis lanceolata*. Other species in this group have importance values less than 0.1 and are relatively short in stature.

Group "c" consists of species *Carex kansuensis* (12) and *Polygonum sibiricum* (37). Group "d" comprises species *Triglochin palustre* (35) and *Kobresia tibetica* (38). Group "e" is composed of species *Carex atrofusca subsp. minor* (15) and *Kalidium foliatum* (41). Groups "c", "d", and "e" are each characterized by a sedge species and a salt-tolerant halophyte. The numbers in the above brackets are network nodes in Figure 2, which correspond to the " Species No." in Table 2.

4 Discussion

4.1 Responses of species dominance to wetland degradation

The changes in plant community succession are reflected in the characteristics of dominant species (Zhang and Sun, 2015). The

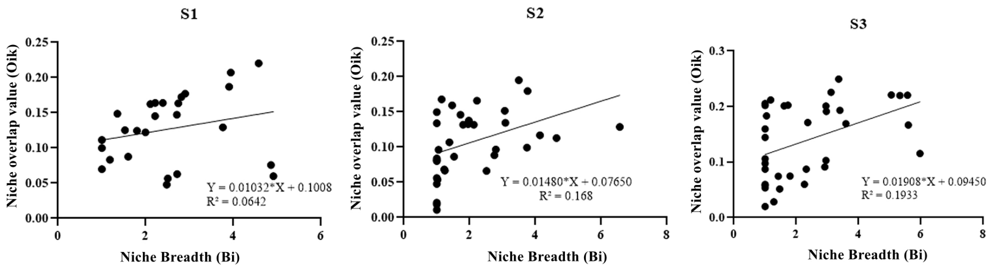

FIGURE 4
Relationship between niche breadth and niche overlap value of species at different degradation stages.

degradation of alpine lake wetlands can result in a more complex vegetation community structure. At the severe degradation stage (S3), the dominant species shifted from sedge species *Kobresia tibetica* to the more drought-tolerant Gramineae species *Leymus secalinus* (Wang et al., 2020). The periodic flooding in moderate degradation stage leads to an increase in soil alkalinity (Liu et al., 2023), which subsequently facilitates the appearance of the salt-tolerant alkaline plant (Wang et al., 2020), i.e., *Cassia lanceolata* in this study at the S2 stage. Moreover, our findings agree with previous study that there is usually an increase in plant community diversity and a higher proportion of dicotyledonous weed species at the degradation stage of S2 (Li et al., 2012). The underlying reason for this phenomenon can likely be attributed to the transitional nature of land cover between wetland and grassland (Zhang and Sun, 2015). At the degradation stage S2, both wetland plants and grassland plants coexist, contributing to an overall increase in diversity and population. Additionally, our on-site observations suggest that the wetland vegetation at the S2 stage have experienced a substantial disturbance from grazing animals of cattle and sheep, which may improve the soil bulk density and nutrient input, promoting the availability of water and nutrients by plants and fostering the compensatory growth of wetland plants (Yang et al., 2021). Therefore, maintaining the ecotone between the marsh and meadow along the alpine lake riparian is vital to preserve biodiversity and supporting sustainable livestock management, although it is a challenge to keep the transitional phase (S2) for the wetland vegetation during their succession.

4.2 Responses of species ecological niche width to wetland degradation

The size of the species' ecological niche width correlates positively with its adaptability to the environment (Chen et al., 2019; Liu X. et al., 2019). Generally, species with broader ecological niches in a community often possess higher environmental resource utilization capabilities, allowing them to more effectively adapt to specific habitat conditions. Species with wider ecological niche width values often become dominant and foundational in a given area (Wang et al., 2014). In this study, we found that an increase in habitat width for *Kobresia tibetica* and *Leymus secalinus* in the process of wetland degradation, meaning these plants are foundational and major dominant species using larger ecological niches to access essential resources.

It is generally believed that the species with larger importance values (alternatively dominance) also exhibit broader ecological niche widths (Chen et al., 2010), especially noted along the wetland degradation gradient, suggests that species with larger importance values may be better positioned to utilize available resources under these changing conditions. This correlation may reflect a response to environmental shifts rather than an inherent adaptive trait, with species importance values becoming more indicative of their current resource utilization strategies in the context of wetland degradation. However, there are some exceptional, e.g., *Osmorhiza aquatica* shows relatively smaller importance values (dominance) at the degradation stage of S1, while it demonstrates larger niche width for higher resource utilization and competitiveness. *Potentilla anserina* is characterized by lower importance values (dominance) at the degradation stage of S3, but it exhibits bigger niche width for higher resource utilization and competitiveness in the community. The presence of these species underscores that dominance is not the sole determinant of ecological niche width (Qi et al., 2011). Likely, these findings may support our first hypothesis that wetland degradation can alter the dominant species and ecological niches of plant species. These changes underscore how degradation modifies environmental conditions and competitive dynamics, significantly altering species composition within the alpine lake riparian vegetation. The adaptation of these species through expanded ecological niches reflects a dynamic response to altered habitat conditions, suggesting a complex interplay between species dominance, ecological niches, and environmental shifts, ultimately reshaping the plant community structure in degraded wetlands.

4.3 Responses of species ecological niche overlap to wetland degradation

Ecological niche overlap reflects the similarity and competitiveness of two or more plant populations in community environments, demonstrating their ability of resources sharing, resource utilization, and inter-species competition. Normally, ecological niche overlap arises when multiple species coexist along a resource gradient and the magnitude of overlap values indicates the similarity in resource utilization strategies among different species (Zhao et al., 2023). In this study, we observed that the average ecological niche overlap indices for all species increased consistently with degradation. These findings imply that the living spaces for meadow plants not marsh plants are improved by reduced inundation, fostering resource proximity among populations and stimulating inter-plant competition, when the alpine lake wetland are degraded. However, an excessive competition was not observed at the stages S1-S3, emphasizing that not all of species ecological niche overlap can result in competition (Feng et al., 2020). These findings support our hypothesis that observed variations in niche width and overlap among plant species are responses to current environmental conditions rather than alterations in their fundamental niches, highlighting the need for conservation efforts focused on habitat preservation and restoration in the context of wetland degradation. Our observations of shifting niche dimensions in response to environmental conditions lend support to Grinnell's niche theory (Grinnell, 1917), while also highlighting the adaptive strategies species employ in degraded habitats.

In contrast to linear relationship between ecological niche width and overlap obtained from the studies in alpine meadow (Wang et al., 2017), semi-arid steppe (Li et al., 2014), and desert steppe

(Zhang and Xu, 2013), our study revealed a non-significant linear relationship between ecological niche width and overlap across all degradation stages. This agrees with the results of studies from artificially enclosed grasslands in semi-arid regions (Liu et al., 2014; Feng et al., 2020). This suggests that in these specific environments, competitive interactions and resource utilization strategies may be more complex, requiring tailored conservation strategies to address these nuanced ecological responses. Essentially, significant ecological niche overlap values do not necessarily manifest between species with large ecological niche widths; instead, it could involve species with comparably smaller niche widths (Zhang and Xu, 2013). This divergence may stem from inherent biological differences among species, resulting in varied environmental requirements (Nie et al., 2021). Additionally, the relationship between species ecological niche width and niche overlap may be influenced by the successional stage (Zhang et al., 2016). In our study, high spatial heterogeneity in environmental resources in marsh, wet meadow and dry meadow at different degradation stage may lead to a disappearance of a pronounced correlation between ecological niche width and overlap (Zhang and Xu, 2013).

4.4 Responses of ecological niche overlap networks to wetland degradation

Our findings indicate a nuanced increase in network module numbers from the initial to the final stages of wetland degradation, with a peak at the S2 stage, suggesting complex species interactions and adaptation strategies. This pattern aligns with the understanding that within-module connectivity reflects shared ecological strategies and resource requirements (Deng et al., 2012; Nie et al., 2020). In present study, we observed the compensatory growth of plants facilitated by the disturbance from the grazing behavior of livestock at the degradation stage of the S2 may increase the demand for resources to intensify competition between species with similar resource utilization strategies (Liu X. et al., 2019), which is reflected in the formation of more small groups with similar resource utilization strategies in this stage. In this study, we further revealed that sedge species, specifically *Kobresia tibetica*, *Carex kansuensis*, and *Carex atrofusca*, tend to form stable subgroups with plants exhibiting distinct halophytic feature. The salt-absorbing and salt-secreting actions of these halophytes contribute to the amelioration of soil conditions (Qi and Chu, 2005), which may suggest an adaptability of the sedge functional group for alpine wetland ecosystems. In our analysis, species not consistently present in each stage or not affiliated with the same-colored module across degradation stages may represent ecological flexibility or niche specificity. Their presence or absence in certain stages or modules could reflect potential adaptation strategies to degradation conditions. However, our study primarily focuses on the dynamics and composition of relatively stable modules and their constitutive species to more clearly represent network structural dynamics. This nuanced understanding of niche dynamics offers fresh insights into species-environment interactions. Additionally, we found from this study that not all of overlap can lead to competition, which agrees with previous researchers that some species can coexist harmoniously when resources are abundant (Wang et al., 2017).

5 Conclusion

In conclusion, our study of Qinghai Lake's wetland riparian degradation revealed several key insights into plant community dynamics and species responses. Firstly, species such as *Kobresia tibetica* and *Leymus secalinus* demonstrated high abundance across varying degrees of wetland degradation, indicating their strong tolerance to these environmental changes. This suggests that certain species maintain their dominance regardless of degradation levels, which is a crucial factor in understanding ecosystem resilience. Secondly, we found that the complexity of plant community structures in degrading wetlands cannot be attributed solely to the dominance of certain species. Instead, this complexity arises from the ability of a diverse range of species to thrive at different water levels, resulting in greater species richness. The presence of both dominant species, characterized by traits favoring rapid growth and reproduction, and less abundant species, each with its unique ecological niche, contributes to the intricate nature of these communities. Contrary to what might be expected, our findings indicated no significant linear relationship between the ecological niche overlap and ecological niche widths of plant species. This highlights the complexity of species interactions and niche dynamics in the context of environmental degradation. Lastly, the observed ecological niche overlap networks during the degradation process shed light on the strategies employed by dominant species for competition and resource acquisition. These strategies are pivotal in enhancing the self-regulatory capacity of plant communities, a vital aspect for ecosystem stability. These findings could be served as the scientific foundations for the best conservation and restoration practices of alpine wetlands on the Qinghai-Tibetan Plateau and similar regions across the world.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding author.

Author contributions

SW: Formal analysis, Visualization, Writing – original draft. SD: Funding acquisition, Project administration, Writing – review & editing. ZW: Investigation, Writing – review & editing. SL: Investigation, Writing – review & editing. CM: Investigation, Writing – review & editing. ZL: Writing – review & editing.

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Conflict of interest

Publisher's note

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Vegetation communities and soil properties along the restoration process of the Jinqianghe mine site in the Qilian Mountains, China

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The study explores the impact of mine grassland restoration on plant communities and soil properties in alpine grasslands, a subject of significant interest due to the observed relationship between grassland changes, plant communities, and soil properties. While prior research has mainly focused on the consequences of grassland degradation on plant diversity and soil characteristics, the specific effects of varying restoration degrees in alpine mining grasslands at the regional scale remain poorly understood. To address this knowledge gap, we established 15 sampling plots (0.5m×0.5m) across five different restoration degrees within alpine mining grasslands in the Qilian Mountains, China. Our objective was to assess the variations in plant diversity and soil properties along these restoration gradients. We conducted comprehensive analyses, encompassing soil properties [soil water content (SWC), available nitrogen (AN), total phosphorus (TP), nitrate nitrogen (NO_3-N), ammonium nitrogen (NH_4-N), total nitrogen (TN), available phosphorus (AP), soil organic carbon (SOC), nitrate nitrogen, soil pH, and electrical conductivity (EC)], plant characteristics (height, density, frequency, coverage, and aboveground biomass), and plant diversity indices (Simpson, Shannon-Wiener, Margalef, Dominance, and Evenness indexes). Our findings included the identification and collection of 18 plant species from 11 families and 16 genera across the five restoration degrees: Very Low Restoration Degree (VLRD), Low Restoration Degree (LRD), Moderate Restoration Degree (MRD), High Restoration Degree (HRD), and Natural Grassland (NGL). Notably, species like *Carex duriuscula*, *Cyperus rotundus*, and *Polygonum viviparum* showed signs of recovery. Principal component analysis and Pearson correlation analysis revealed that soil pH, SWC, SOC, NO_3-N, and AN were the primary environmental factors influencing plant communities. Specifically, soil pH and EC decreased as restoration levels increased, while SWC, AN, TP, NH_4-N, TN, AP, SOC, and NO_3-N exhibited a gradual increase with greater restoration efforts. Furthermore, the HRD plant community demonstrated similarities to the NGL, indicating the most effective natural recovery. In conclusion, our study provides valuable insights into the responses of plant community characteristics, plant diversity, and soil properties across varying restoration degrees to environmental factors. It also elucidates the characteristics of plant communities along recovery gradients in alpine grasslands.

KEYWORDS

alpine mining area grassland, grassland ecosystem, restoration, plant diversity, community, Qilian Mountains

1 Introduction

Alpine grasslands in Northwest China serve as a critical ecological buffer, offering vital ecosystem functions, including livestock grazing, landscape aesthetics, and vegetation production (Wang et al., 2018). However, the alpine grassland ecosystem is notably sensitive to human activities and climate fluctuations, rendering it highly susceptible to issues like grassland degradation, soil contamination, and declining vegetation cover (Lei et al., 2020; Wang and Ali, 2021). Once an ecological imbalance occurs, ecosystem recovery becomes a formidable challenge (Dudley et al., 2020). Northwest China boasts abundant mineral resources, yet imprudent or excessive mining practices can trigger a range of ecological problems, including soil quality deterioration due to human interventions (Wu et al., 2021). Consequently, this contributes to the degradation of mining sites. Achieving equilibrium between the alpine grassland ecosystem and mining grassland ecosystems has emerged as a significant scientific endeavor (Xie et al., 2017).

Plant communities and soil properties share a close relationship, with soil properties serving as a determinant of plant composition (Jochum et al., 2020). Human activities, climate conditions, and soil properties collectively influence the development of alpine grassland ecosystems. Mining, as a significant factor, contributes to grassland degradation and alters plant community composition (Wiegand et al., 2007; Chang et al., 2015). However, it's important to note that variations in soil properties primarily define the plant community in mining grasslands (Zhang et al., 2018; Gao et al., 2021). Although prior research has acknowledged the impact of excessive mining on alpine grassland ecosystems, there remains a gap in understanding the mechanisms behind the changes in grassland restoration levels (Guo et al., 2021; Huang et al., 2021a; Castro et al., 2023). In particular, studying how the plant community evolves can shed light on grassland restoration mechanisms (Kang et al., 2020). Plant community characteristics can provide insights into both plant diversity, encompassing variety and function, and how they respond to different restoration levels (Harrison et al., 2020). Examining the diversity of plant species and their functions across various restoration levels is a compelling avenue of inquiry. While previous studies have predominantly focused on individual plant communities or soil properties at different restoration levels (Feyissa et al., 2021; Stokes et al., 2021), there is a limited body of research on how plant communities and plant diversity change across these levels (Zhou et al., 2019; Schmid et al., 2021). Quantifying plant community and soil properties at different restoration levels can enhance our understanding of how plant communities and plant diversity evolve in alpine grasslands.

The Qilian Mountains National Nature Reserve is a crucial national ecological sanctuary in China, meticulously preserved and protected. It plays an indispensable role in shaping and efforts have been made to enhance the ecological environment in the Western region (Feng et al., 2019). However, mining activities in the Qilian Mountains Reserve have led to ecological damage, resulting in the degradation of the original grassland and soil erosion (Kong et al., 2021). Presently, numerous researchers have been actively involved in managing the ecological environment of mining areas and implementing scientific and rational approaches for the restoration of degraded grassland in these regions. The ecological balance of moderate restoration of its productivity and economic benefits is particularly important (Chen et al., 2020). The mining area in the Qilian Mountains in the Tianzhu region of China has expanded rapidly in recent years, and the largest open mine in the Gansu Province is located in this region. The ecological and environmental damage to the nature reserve has aroused considerable attention. However, there have been few studies on how plant community features and soil properties changes in mining areas have affected the mining grasslands (Chen et al., 2022).

While some studies have explored the restoration of mining areas, there is a notable gap in understanding how restored plant community features vary. Additionally, there has been limited research on plant community features and soil properties across different restoration levels in alpine grasslands (Lorite et al., 2021; Siebert et al., 2021). To address this knowledge gap, our study investigates plant communities and soil properties at various restoration levels within the primary gold mining area of alpine grasslands in the Qilian Mountains, China. We hypothesize that plant communities, plant diversity, and soil properties strongly influence the outcomes at different restoration levels in alpine grasslands. Specifically, our study seeks to achieve the following objectives: (1) Assess the restoration outcomes of alpine mining grassland ecosystems compared to natural grasslands; (2) Investigate how plant communities, plant diversity, functional diversity, and soil properties change at various levels of restoration within the mining area. The findings from this study aim to provide valuable insights into how different restoration levels respond to environmental factors. Additionally, our research intends to establish a scientific foundation for the rational restoration of alpine grassland resources in mining areas.

2 Materials and methods

2.1 Study area description

The Jinqianghe mining area is located in the part of Daiqian village, Zhuaxixiulong Town, Wuwei City, Gansu Province. The geographical coordinates are 37°25'30"-37°25'63"N, 102°51'48"-102°57'82"E (Figures 1A, B), and the altitude is 3267-3323m. This area is located at the junction of Gansu and Qinghai provinces, Zhuanglang River Jinqiang River source of the typical gold mine restoration demonstration area, in Qilian Mountains National Nature Reserve. Soil types in the project area are mainly grassland meadow soils, followed by large black soils and black hemp soils. There is no treatment of the original soil because the sampling places are in the meadow of the Jinqianghe mining area. Jinqianghe upstream alluvial gold mining area is in the headwaters of the Jinqianghe, the source of the Zhuanglang River, the overall topography of the northwest high southeast low, the topography of the undulating changes, elevation generally 3190~4100 m, the relative height difference of the mountains are more than 500 m, the slope of the mountain slope is generally 30~60°, the local section of the slope is greater than 70°. The valley of Jinqianghe is generally 200m~300m wide, and the widest part can reach 1000m, with the first and second terraces developed and third terraces sporadically developed.

The ecological environment was fragile before the mine was restored, the land was barren and the degree of soil erosion was severe, clearly improving the ecological environment after the mine restoration. The region has an alpine semi-arid climate, with seasonal changes of temperature in the region being obvious, with the highest temperature being in July, and the lowest temperature being in January, and a huge diurnal temperature difference. The average annual temperature is 4.8°C. The average annual rainfall and potential evaporation are 650mm and 1400mm, separately, and the rainy season is mainly focused on the June-September. The distinctive feature is clear vertical zoning, low temperatures, high precipitation (more topographic rain) and short frost-free periods. The Northwest winds are prevalent in the area, with the annual average wind speed is 2.1m/s. The main soil type is grassland meadow soil, followed by big black soil, black hemp soil, and other soil types. Before restoration, due to the serious damage to the ecological environment caused by mining activities, a large amount of dumped soil and slag were piled up randomly, the soil was pressed and dug up, and the vegetation cover was extremely low, mainly through the natural restoration method of slag heap leveling, sowing grass seeds and fencing protection. With the expansion of the scale within the area of mining, the waste slag after mining destroyed the vegetation and degraded the vegetation on both sides of the river valley and the ditch, and the vegetation coverage on both sides of the river valley and the ditch before treatment was lower, the mine restoration from 2018 by the same restoration method of natural restoration (Yang et al., 2023a). The primary methods for natural restoration include the leveling of slag heaps, sowing of grass seeds, fence protection, and the facilitation of natural vegetation recovery. Removal of residue piles, backfilling of mining pits, restoration of vegetation in pressure-occupied areas

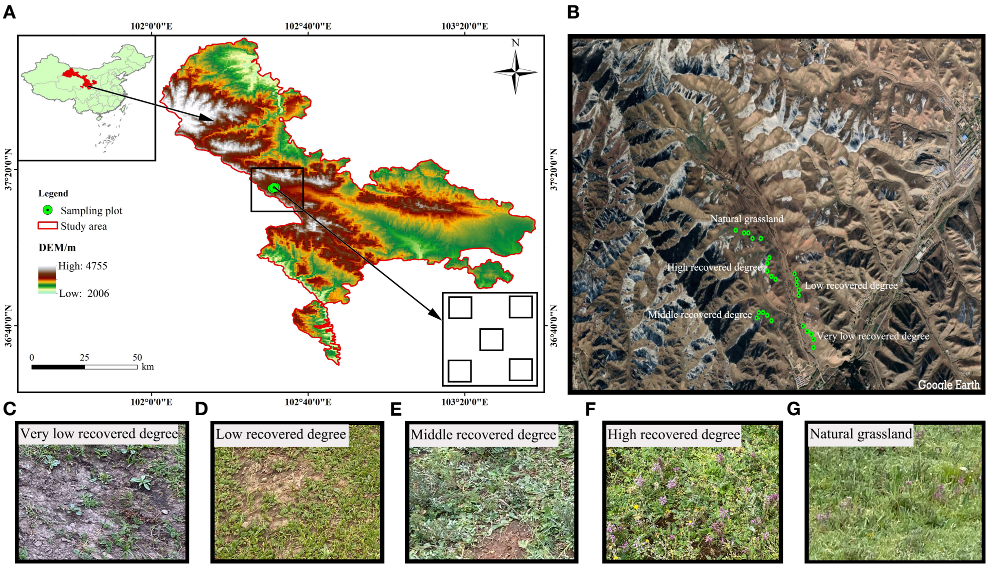

FIGURE 1
Location of the study area on the Chinese Qilian Mountains **(A, B)** and VLRD, very low recovered degree **(C)**, and LRD, low recovered degree **(D)** and MRD, middle recovered degree **(E)** and HRD, high recovered degree **(F)** and NGL, CK natural grassland **(G)**.

and backfilled areas, and restoration of topography and ecological environment to the greatest extent possible. The approach for restoring succession sequences is determined according to the "Soil Erosion Classification and Grading Standard" (SL190-2007) of China. In accordance with the coverage of natural restoration, we used the temporal dynamics of restoration process by replacing the time scale with space, for the investigation, representative grassland restoration in the Qilian Mountains Tianzhu Jinqianghe gold mine was selected. The study encompassed five different levels of grassland recovery based on plant coverage, classified as follows: Very Low Recovered Degree (VLRD), Low Recovered Degree (LRD), Middle Recovered Degree (MRD), High Recovered Degree (HRD), and a reference of Natural Grassland (NGL), with Natural Grassland (NGL) serving as the control (CK), as indicated in Table 1. The vegetation primarily consists of *Cyperus rotundus, Polygonum viviparum, Oxytropis ochrocephala* and *Elymus nutans*, and the animal husbandry industry is the leading industry.

2.2 Sample collection and testing

This study primarily focuses on investigating various soil parameters, including pH, electrical conductivity (EC), soil water content (SWC), soil organic carbon (SOC), total nitrogen (TN), nitrate nitrogen (NO_3-N), ammonium nitrogen (NH_4-N), available nitrogen (AN), total phosphorus (TP), and available phosphorus (AP). The data collection was conducted in August 2022. Three study sites with similar geographic conditions, vegetation composition, and several years of restoration management were selected. To ensure consistency and representativeness in vegetation and soil sampling, we established three large quadrats within each of the five different restoration grassland areas. Within each large quadrat, five small sampling plots (measuring 50×50 cm) were randomly chosen in the mining area for sample collection, with precise GPS coordinates recorded for accurate positioning (Figure 1). Differences in vegetation restoration were observed, particularly in areas closer to the road, due to varying distances from the mine's pollution source. Despite employing the same restoration method, disparities in vegetation recovery persisted. We measured plant circumference, plant height using a steel tape measure, and recorded the plant altitude, longitude, and latitude for each location using GPS devices. Plant community characteristics, including plant frequency, plant density, plant coverage, and plant composition, were documented (Gao et al., 2021). For each sampling plot, we collected soil samples (at depths of 0-20 cm and 20-40 cm) from five points, which were subsequently mixed thoroughly to create a composite sample. These soil samples were transported to the laboratory, where they were naturally air-dried, and any rocks, plant roots, or debris were removed. Afterward, the samples were ground, passed through a 120-mesh sieve, properly labeled, and prepared for testing.

The SWC was measured by the drying method. The soil pH, EC, SOC, TN, NO_3-N, NH_4-N, AN, TP and AP were determined by the electrode potential (Pansu and Gautheyrou, 2006), conductivity meter, dichromate oxidation, element analyzer, Interval-flow analysis, Flow-Injection, alkaline solution-diffusion, Sommers-Nelson, and molybdenum antimony anti-colorimetric methods (Pei et al., 2021), respectively.

2.3 Data processing methods

The indexes of species diversity and functional diversity within the plant characteristics were examined to explore the changing of plant diversity across restoration gradients. Community Importance Value (IV) serves as a crucial criterion for distinguishing various communities and efficiently determining the major components of each community. The calculation method for the Importance Value (IV) is as follows:

IV = (Relative Height + Relative Cover + Relative Density)/3 (Zhang, 2004).

Species diversity is evaluated through factors like species richness, diversity indices, and evenness. This is expressed using measures such as degree and dominance degree (Ma, 1994). The calculation is as follows:

$$H = -\sum P_i \ln P_i \tag{1}$$

$$Ma = (S - 1)/\ln N \tag{2}$$

$$D = 1 - \sum P_i^2 \tag{3}$$

TABLE 1 Sample plots settings.

	VLRD	LRD	MRD	HRD	NGL
Geography coordinate	N37°25’30” E102°51’48”	N37°25’67” E102°52’24”	N37°25’51” E102°52’78”	N37°25’61” E102°52’82”	N37°25’62” E102°52’18”
Altitude/m	3320	3294	3286	3292	3295
Plant coverage	<10%	20%-40%	40%-60%	>85%	>85%
Percentage of bare land	>50%	25%-40%	10%-25%	<5%	<5%
Soil characteristics	Comparatively low level	Low level	Middle level	High level	Nature level
Distance from mine development site	Nearest	Near	Middle	Far	Far

VLRD, very low recovered degree; LRD, low recovered degree; MRD, middle recovered degree; HRD, high recovered degree; NGL, CK natural grassland.

$$\mathrm{Eve} = \mathrm{D}/(1 - 1/\mathrm{S}) \tag{4}$$

$$D_o = \sum \mathrm{P}_\mathrm{i}^2 \tag{5}$$

$$\mathrm{P}_\mathrm{i} = \mathrm{N}_\mathrm{i}/\mathrm{N} \tag{6}$$

In the preceding formula, the symbols are defined as follows: H denotes the Shannon-Wiener species diversity index (1), Ma represents the Margalef richness index (2), D stands for the Simpson diversity index (3), Eve corresponds to the Evenness index (4), Do signifies the Dominance index (5), Pi denotes the species "i" important value ratio (6), N is the sum of the important values of plants in the transect, Ni represents the important value of plant "i" in the plot, and S is the total number of species in the plot.

2.4 Statistical analysis

Soil physical and chemical properties for data analysis were obtained from average measurements at depths of 0-20 cm and 20-40 cm per sample. Plant biomass values were determined for the underlying biomass. To assess differences among restored grassland communities, one-way analysis of variance (ANOVA) was applied. Two-tailed relationships between plant community and soil properties were analyzed using Spearman correlation coefficients in SPSS version 25.0 (IBM, Chicago, USA). Principal Component Analysis (PCA) in CANOCO 5.0 (ter Braak and Smilauer, 2012) was employed to explore diversity variations along recovery degrees for enhanced plant distribution pattern assessment. Important value and diversity index for each herb layer plant were computed using Microsoft Excel 2010. Correlation analysis and graph plotting were performed in Origin 9.0 (Origin Lab Corporation, Northampton, MA, USA), while bar charts and additional data analysis were carried out in Sigmaplot 10.0 (Sigmaplot Lab Corporation, Northampton, MA, USA).

3 Results

3.1 Characteristics of plants at various restoration degrees

The plant characteristics of alpine mining grassland communities exhibited significant variations across different levels of restoration (Figure 2). Vegetation features displayed notable distinctions ($P<0.05$) among the various restoration levels, with the ranking being NGL > HRD > MRD > LRD > VLRD. The height of HRD was 1.66, 2.52, and 4.58 times that of MRD, LRD, and VLRD, respectively (Figure 2A). Additionally, its density exceeded that of MRD, LRD, and VLRD by 1.06, 4.54, and 9.42 times, as shown in Figure 2B. The frequency of HRD surpassed that of MRD, LRD, and VLRD by 1.17, 2.18, and 3.07 times (Figure 2C), while its coverage was 1.48, 3.08, and 4.81 times greater than MRD, LRD, and VLRD (Figure 2D), respectively. Moreover, the aboveground biomass of HRD was 1.64, 2.76, and 3.79 times that of MRD, LRD, and VLRD (Figure 2E). Notably, natural restoration methods did not achieve the level of NGL (CK).

3.2 The composition of plant families, genera, and species varies across different restoration degrees

Table 2 presents the taxonomic structure of alpine mining grassland at various stages of restoration. It is evident that the order of species composition varies with different restoration degrees, with HRD > MRD > LRD > VLRD. The total number of individual genera in the various community types aligns with the species composition pattern. According to the statistical data from our sample survey, the study plot contained 18 herbaceous plant species, which were distributed across 11 families and 16 genera. Among these, Asteraceae had the highest species diversity with 6 genera and 6 species. This was followed by Leguminosae and Cyperaceae, each with 2 genera and 2 species, while Rosaceae, Graminaceae, Ranunculus, Polygonum, Chenopodium, Plantago, Apiaceae, and Geraniaceae each had 1 genus and 1 species. This demonstrates the simplicity of the plant genus and species structure, with a relatively dispersed distribution of plant families. Across all samples, three species—*Carex duriuscula*, *Cyperus rotundus*, and *Polygonum viviparum*—were consistently present. Plant species from five different recovery degrees belonged to the Leguminosae, Asteraceae, Compositae, Rosaceae, and Cyperaceae families, and these families exhibited a high degree of representation. Among them, these five major plant families constituted 67% of the total plant species in the HRD community, 55% in the MRD, 86% in the LRD, and 50% in the VLRD. This pattern is largely attributed to the adaptability of Leguminosae and Graminaceae to the challenging environmental conditions characterized by low temperatures and drought in alpine grassland mining areas. Notably, the plant composition in the NGL (CK Natural Grassland) demonstrated the highest degree of diversity in alpine mining grassland areas.

3.3 Life-form structure characteristics of plant communities

The life-form structure characteristics of plant communities at various restoration levels in alpine mining grassland are shown in Table 3. The life-form classification follows the Whitaker growth type system, which is based on the degree of stem lignification in the community, as described by Yang et al. (2023a). This study categorizes the herbaceous plant community into two groups: perennial plants and annual herbaceous plants. Among the life-form structure characteristics, perennial herbaceous species predominate, with 12 species distributed across 9 families and 12 genera, while annual herbaceous species are less dominant, consisting of 4 species from 3 families and 4 genera. Perennial herbaceous species account for 75% of the total species, while annual herbaceous species make up the remaining 25% (Table 3). There is a significant disparity in the abundance of perennial and annual herbaceous species among various restoration levels in alpine mining grassland, with perennial herbaceous species being abundant and annual herbaceous species relatively scarce. Particularly in the NGL, perennial herbaceous species dominate at 97%, and they also constitute a significant portion in HRD, MRD,

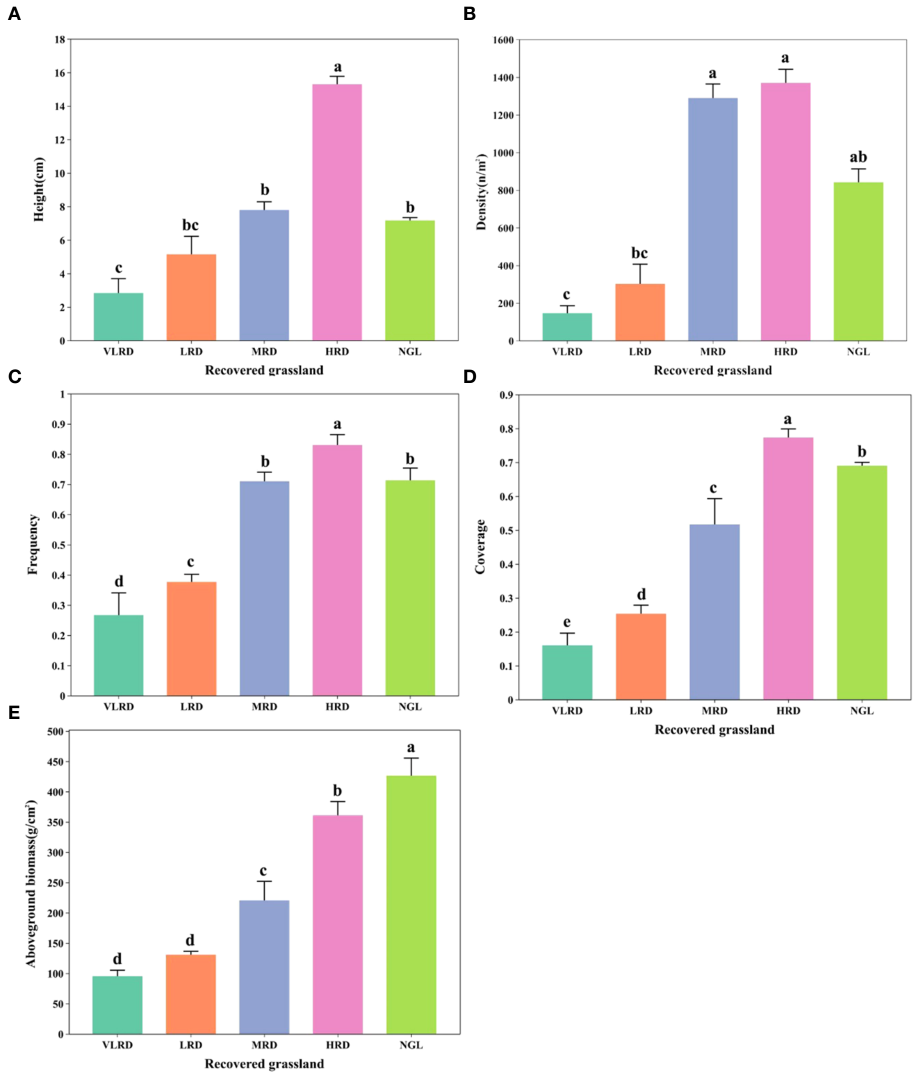

FIGURE 2
Illustrates the vegetation characteristics of alpine grassland at various stages of restoration, with five key attributes: **(A)** Height, **(B)** Density, **(C)** Frequency, **(D)** Coverage, and **(E)** Aboveground biomass. The different restoration levels are represented by the following abbreviations: VLRD (Very Low Recovery Degree), LRD (Low Recovery Degree), MRD (Middle Recovery Degree), HRD (High Recovery Degree), and NGL (CK Natural Grassland). Significant differences at the 0.05 level are denoted by different letters above error bars between the treatments.

TABLE 2 **Composition of dominant plant families, genera, and species at various levels of recovery.**

Recovered degree	Total families	Total genera	Total species	The species distribution of common families						
				Leguminosae	Compositae	Compositae	Rosaceae	Cyperaceae	Total	Rate in total%
VLRD	3	4	4	0	0	0	0	2	2	50%
LRD	6	7	7	1	1	1	1	2	6	86%
MRD	10	11	11	1	1	1	1	2	6	55%
HRD	9	12	12	1	3	1	1	2	8	67%
NGL	11	13	13	1	2	1	1	2	7	54%

VLRD, very low recovered degree; LRD, low recovered degree; MRD, middle recovered degree; HRD, high recovered degree; NGL, CK natural grassland.

TABLE 3 Composition and quantitative traits of communities at different recovery stages.

Life type	Species	Species number in different recovered degrees of alpine grassland				
		VLRD	LRD	MRD	HRD	NGL
Perennial herb	*Cyperus rotundus*	5	22	74	103	71
	Carex duriuscula	9	22	47	71	12
	Taraxacum mongolicum	—	—	6	3	7
	Polygonum viviparum	5	13	10	73	45
	Oxytropis ochrocephala	—	3	48	52	54
	Elymus nutans	—	2	—	10	12
	Potentilla chinensis	—	—	10	—	14
	Plantago Asiatica	—	—	5	15	35
	Daucus carota	21	16	13	6	21
	Cirsium arvense	—	—	—	—	11
	Anaphalis lactea Maxim	—	—	3	2	—
	Geranium pratense	—	—	—	—	5
	subtotal	40	78	216	335	287
	subtotal%	100%	96%	77%	89%	97%
Annual herb	*Chenopodium glaucum*	—	—	64	43	5
	Sonchus oleraceus	—	—	—	1	—
	Heteropappus hispidus	—	3	—	—	—
	Ipomoea nil	—	—	—	—	3
	subtotal	0	3	64	44	8
	subtotal%	0%	4%	23%	12%	3%
	Total	40	81	280	378	295
	Total%	100%	100%	100%	100%	100%

VLRD, very low recovered degree; LRD, low recovered degree; MRD, middle recovered degree; HRD, high recovered degree; NGL, CK natural grassland.

LRD, and VLRD, with proportions of 88%, 77%, 96%, and 100%, respectively. Conversely, MRD has the largest proportion of annual herbaceous species, amounting to 23%. It's worth mentioning that the presence of perennial herbaceous species significantly influences the structure, system function, and stability of the grassland community. Although the species structure of NGL grassland is slightly higher than that of HRD, HRD exhibits the most stable species community structure, followed by MRD, LRD, and VLRD grasslands.

3.4 Plant community value of different restoration degrees

Perennial herbaceous plants occupy a dominant position within various communities, playing a crucial role in shaping community structure, ecosystem function, and overall stability. The importance of plant communities at different restoration levels in alpine grassland is detailed in Table 4. In HRD, LRD, and VLRD, *Carex duriuscula* stands out as the dominant species with importance values of 18.53, 27.33, and 39.22, respectively. The sub-dominant species in these communities are *Cyperus rotundus* and *Polygonum viviparum*. Notably, the importance values for HRD are 16.70 and 15.64 for Cyperus rotundus and Polygonum viviparum, respectively. In MRD, the dominant species is *Carex duriuscula* with an importance value of 21.40, while the sub-dominant species is represented by *Cyperus rotundus* and *Polygonum viviparum* with respective importance values of 4.53. In HRD, the primary companion species include *Chenopodium glaucum* and *Sonchus oleraceus*, boasting importance values of 7.71 and 1.11, respectively. For VLRD, *Carex duriuscula* and *Daucus carota* are the dominant species with importance values of 39.22 and 27.11. The importance values of other companion species are relatively similar and remain below 10. When we compare alpine grassland herbaceous

TABLE 4 Important value of dominant and sub-dominant species under different recovered stages.

Recovered stage	VLRD	Important value	LRD	Important value	MRD	Important value	HRD	Important value	NGL	Important value
Dominant species	*Carex duriuscula*	39.22	*Carex duriuscula*	27.33	Cyperus rotundus	21.40	*Carex duriuscula*	18.53	*Oxytropis ochrocephala*	18.95
	Daucus carota	27.11	*Potentilla chinensis*	26.00	*Carex duriuscula*	18.90	Cyperus rotundus	16.70	Cyperus rotundus	16.92
Sub-dominant	Cyperus rotundus	23.69	Cyperus rotundus	24.13	*Chenopodium glaucum*	15.48	Polygonum viviparum	15.64	*Plantago asiatica*	11.62
			Oxytropis ochrocephala	8.03	*Oxytropis ochrocephala*	14.81	*Oxytropis ochrocephala*	14.43	*Carex duriuscula*	10.79
Main Companion specie	Polygonum viviparum	9.98	Polygonum viviparum	7.61	Polygonum viviparum	8.10	*Chenopodium glaucum*	7.71	*Daucus carota*	9.94
			Elymus nutans	4.27	*Daucus carota*	5.82	*Potentilla chinensis*	6.96	*Elymus nutans*	6.74
			Heteropappus hispidus	2.62	*Taraxacum mongolicum*	5.49	*Plantago asiatica*	6.02	*Taraxacum mongolicum*	6.18
					Potentilla chinensis	4.53	*Daucus carota*	4.28	Polygonum viviparum	6.10
					Plantago asiatica	3.63	*Taraxacum mongolicum*	3.75	*Potentilla chinensis*	3.68
					Ipomoea nil	0.97	*Elymus nutans*	2.67	*Chenopodium glaucum*	3.28
					Elymus nutans	0.88	*Anaphalis lactea Maxim*	1.34	*Geranium pratense*	2.75
							Sonchus oleraceus	1.11	*Ipomoea nil*	2.20

VLRD, very low recovered degree; LRD, low recovered degree; MRD, middle recovered degree; HRD, high recovered degree; NGL, CK natural grassland.

communities across four restoration-degree mining areas, it becomes evident that the importance values of perennial herbs in these communities consistently exceed 10. This underscores the significant role played by perennial herbs in the recovery of alpine grassland mining areas, with HRD approaching the level of NGL, suggesting that HRD has a highly favorable recovery status.

3.5 Variations in community life structure characteristics across different restoration levels

In terms of community life structure, the characteristics of different restoration degrees in alpine mining grassland exhibited a consistent trend between the two life forms—perennial herbaceous plants were significantly dominant, collectively representing more than 83.56% of the total importance values, while annual herbaceous plants had a smaller share (Table 5). Across the various restoration levels, perennial herbaceous plants consistently held higher importance values than annual herbaceous plants. Notably, alpine grasslands with NGL, HRD, and LRD had relatively high importance values for perennial herbaceous plants. In addition, alpine grasslands with HRD and MRD displayed relatively high importance values for annual herbaceous plants. Perennial herbaceous species in these communities primarily belonged to the Graminaceae, Asteraceae, Leguminosae, Rosaceae, and Cyperaceae families. On the other hand, annual herbs were primarily represented by the following four species: *Sonchus oleraceus*, *Chenopodium glaucum*, *Heteropappus hispidus*, and *Ipomoea nil*. When examining alpine grasslands with different restoration levels, HRD featured the highest number of plant species, mainly composed of perennial herbaceous plants, while VLRD lacked annual herbaceous species. Within these restoration grassland communities, perennial herbaceous plants were predominantly *Carex duriuscula*, *Cyperus rotundus*, *Oxytropis ochrocephala*, *Potentilla chinensis*, and *Polygonum viviparum*. Annual herbaceous plants primarily included *Chenopodium glaucum*, *Sonchus oleraceus*, *Heteropappus hispidus*, and *Ipomoea nil*.

TABLE 5 Relative importance of life forms in grassland communities at various recovery degrees (%).

Recovered degree	Important value	
	Perennial herbaceous plant	Annual herbaceous plant
VLRD	100.00	0.00
LRD	97.38	2.62
MRD	83.56	16.44
HRD	90.31	9.69
NGL	94.51	5.49
Total	465.76	34.24

VLRD, very low recovered degree; LRD, low recovered degree; MRD, middle recovered degree; HRD, high recovered degree; NGL, CK natural grassland.

3.6 Variations in plant diversity across restoration levels

The variations in plant diversity across different restoration levels in alpine grassland is displayed in Figure 3. The Simpson index indicates that HRD and MRD have higher diversity indices compared to VLRD, with no statistically significant differences between HRD and MRD, and VLRD (P>0.05). Their respective values are 0.87, 0.86, and 0.71. Likewise, the Shannon-Wiener index is higher in HRD and MRD compared to VLRD, with no significant differences between HRD and MRD, and LRD (P>0.05). The values are 2.20, 2.09, and 1.69. The Margalef species richness index in HRD is significantly greater than in LRD and VLRD (P<0.05). HRD boasts the highest species richness with 12 species, followed by MRD with 11 species, LRD with 7 species, and a minimum of 4 species in VLRD. HRD's composition closely resembles that of NGL. The Dominance index does not exhibit significant differences among different restoration levels in alpine grassland (P>0.05). However, the Dominance index in VLRD is higher than in other restoration levels, with a value of 0.29. Regarding the Evenness index, HRD and MRD surpass LRD, but no significant differences exist between HRD and MRD, and LRD (P>0.05), the values were 0.88, 0.87, and 0.86, respectively.

3.7 Statistical overview of soil properties

Soil properties exhibited significant variations across different recovered grasslands (Figure 4). Specifically, soil pH, electrical conductivity (EC), and soil water content (SWC) at the 20-40 cm soil depth were significantly higher than those at the 0-20 cm depth (P< 0.05). Moreover, soil pH and EC showed a gradual decrease with increasing restoration levels, while soil SWC increased with higher restoration levels. When comparing different restoration levels, the soil pH in VLRD and LRD grasslands at the 0-20 cm soil depth was 44.84% and 33.93% higher, respectively, than that in the NGL. At the 20-40 cm soil depth, the soil pH in VLRD, LRD, MRD, and HRD grasslands was 36.20%, 28.43%, 14.38%, and 7.77% higher, respectively, than in the NGL. Similar trends were observed for soil EC and SWC. Additionally, the HRD exhibited recovery effects that were similar to those of the NGL, indicating the most successful natural recovery. Soil properties, including soil organic carbon (SOC), total nitrogen (TN), nitrate nitrogen (NO_3-N), ammonium nitrogen (NH_4-N), available nitrogen (AN), total phosphorus (TP), and available phosphorus (AP), were significantly higher at the 0-20 cm soil depth compared to the 20-40 cm depth (P< 0.05). In HRD grassland, SOC, TN, NO_3-N, NH_4-N, AN, TP, and AP were significantly higher than in VLRD grassland (P< 0.05). These trends gradually increased with higher restoration levels at 10-20 cm and 20-40 cm soil depths. Once again, the HRD demonstrated recovery effects similar to the NGL, signifying the most successful natural recovery.

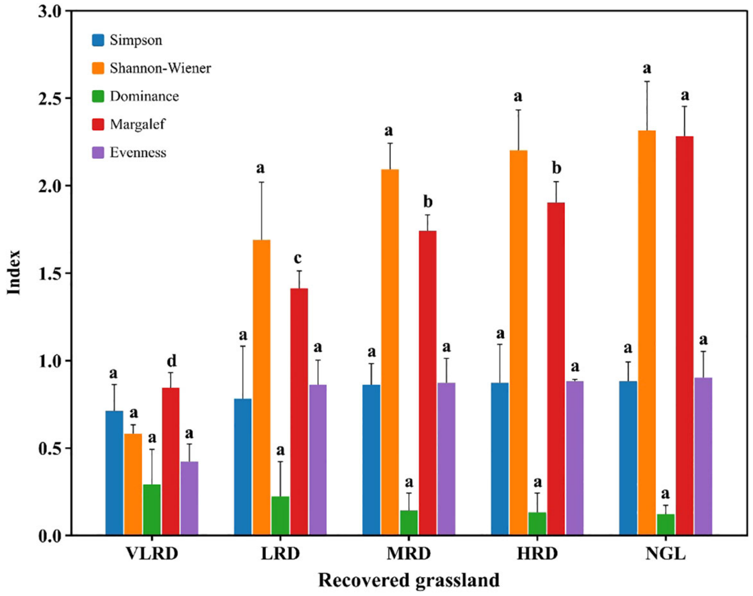

FIGURE 3
Variation in plant diversity in alpine meadows under different restoration degrees. Different colors represents Simpson and Shannon-Wiener Indices, Dominance, Margalef, and Evenness Indexes. VLRD stands for Very Low Recovered Degree, LRD for Low Recovered Degree, MRD for Middle Recovered Degree, HRD for High Recovered Degree, and NGL for CK Natural Grassland. Different letters above error bars between treatments indicate statistically significant differences at the 0.05 level.

3.8 The connection between plant community diversity and soil properties

Pearson correlation analysis was employed to investigate the relationships between plant community diversity and soil properties (Figure 5). The results show that, at the 0-20 cm soil depths, soil properties including soil water content (SWC), available nitrogen (AN), total phosphorus (TP), ammonium nitrogen (NH_4-N), total nitrogen (TN), available phosphorus (AP), soil organic carbon (SOC), nitrate nitrogen (NO_3-N), pH, and electrical conductivity (EC) exhibited a significant and positive correlation with plant frequency, coverage, and biomass ($P< 0.01$). However, these soil properties were significantly and negatively correlated with plant community diversity indices (Simpson, Shannon, Evenness, and Margalef indices) ($P > 0.05$). Furthermore, soil SOC exhibited a significant positive correlation with plant height ($R = 0.65$, $P< 0.01$) (Figure 5A). At the 20-40 cm soil depths, SWC, AN, TP, NH_4-N, TN, AP, SOC, NO_3-N, pH, and EC showed significant and positive correlations with plant frequency, coverage, and biomass ($P< 0.01$). However, these soil properties at 20-40 cm depths were significantly and negatively correlated with plant community diversity indices ($P > 0.05$). Additionally, soil AP demonstrated a significant positive correlation with plant height ($R = 0.66$, $P< 0.01$) (Figure 5B).

Principal component analysis (PCA) was employed to investigate the associations between soil physicochemical properties and the level of soil recovery. The analysis of soil property factors at a depth of 0-20 cm in the recovered grassland at the Jinqianghe gold mine indicated that the first axis accounted for 93.22% of the variance, while the second axis explained 2.32%, resulting in a cumulative explanation of 95.55% (Figure 6A).At 0-20 cm soil depths, soil properties between HRD and NGL displayed positive correlations with soil water content (SWC), electrical conductivity (EC), available nitrogen (AN), total phosphorus (TP), ammonium nitrogen (NH_4-N), total nitrogen (TN), available phosphorus (AP), soil organic carbon (SOC), and nitrate nitrogen (NO_3-N). However, HRD exhibited a negative correlation with soil pH at these depths. At 20-40 cm soil depths, the first axis explained 92.05%, with the corresponding second axis explaining 2.94%, resulting in a cumulative explanation of 94.98% (Figure 6B). Soil properties at these depths between HRD and NGL exhibited positive correlations with SWC, AN, TP, NH_4-N, TN, AP, SOC, and NO_3-N. Conversely, HRD displayed negative correlations with soil pH and EC at these depths.

4 Discussion

4.1 Changes in plant community characteristics

To safeguard the vital aspects of plant diversity, nurture plant growth, and effectively monitor restored grasslands, it is imperative to understand the characteristics of plant communities (Catorci and Gratti, 2010; Tang et al., 2016). Many mining areas have undergone restoration using both artificial and natural methods. However, the outcomes have exhibited significant variability, and it has been challenging to distinguish the effects of different mining areas on grassland environments (Huang et al., 2019; Wei et al., 2019). Consequently, field studies are essential to assess and enhance the restoration levels in alpine grasslands. The species composition within plant communities can serve as a reflection of the external appearance

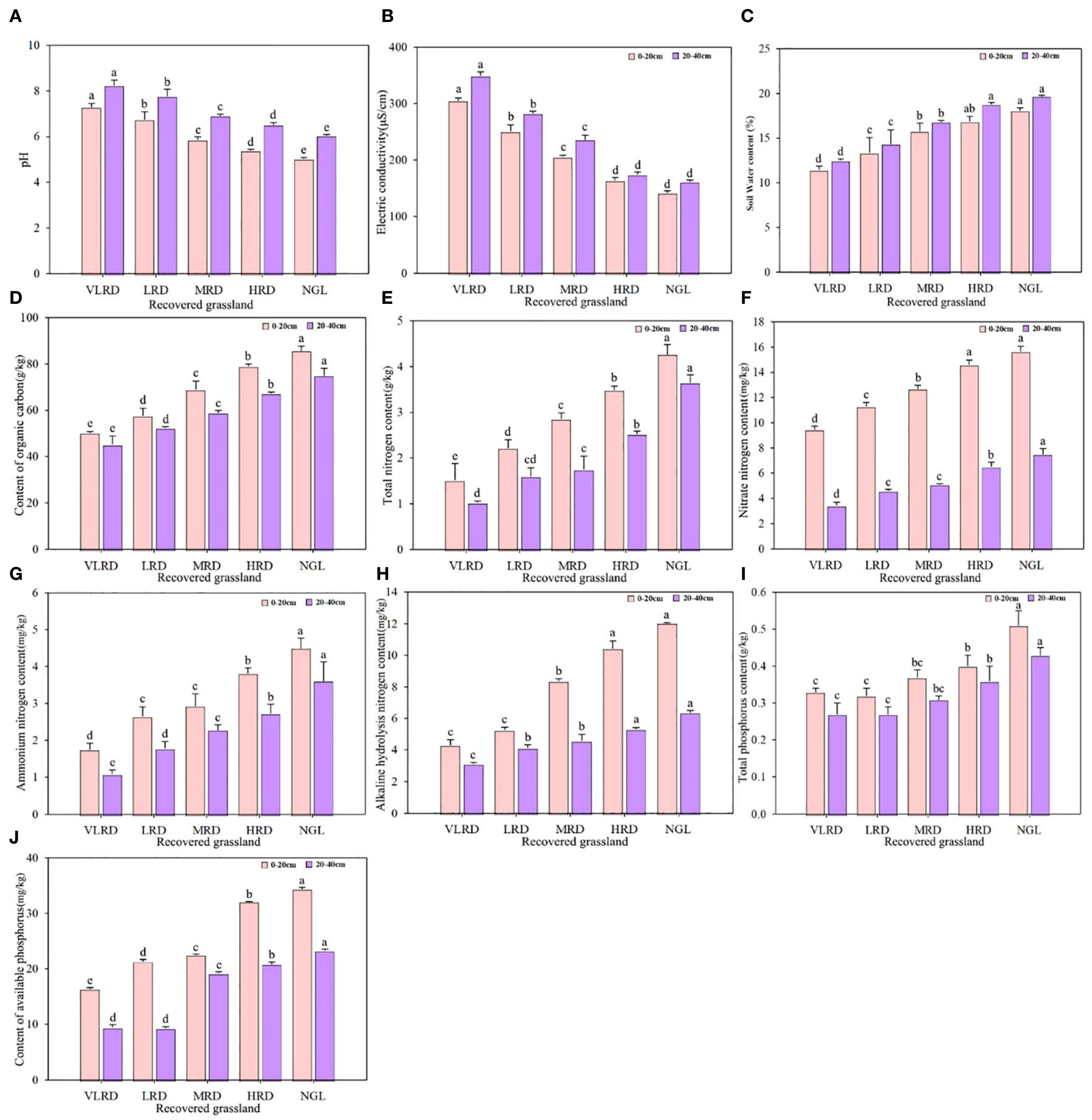

FIGURE 4
Soil properties of alpine meadows, including pH **(A)**, EC **(B)**, SWC **(C)**, SOC **(D)**, TN **(E)**, NO_3-N **(F)**, NH_4-N **(G)**, AN **(H)**, TP **(I)**, and AP **(J)**, Under Different Restoration Degrees. VLRD, very low recovered degree; LRD, low recovered degree; MRD, middle recovered degree; HRD, high recovered degree; NGL, CK natural grassland. Different letters above error bars between treatments indicate significant differences at the 0.05 level.

of the community, which, in turn, represents the comprehensive influence of environmental factors (Deng et al., 2020). In our study, the vegetation types of restored grassland (VLRD, LRD, MRD, HRD, and NGL) in the mine area were *Carex duriuscula* + *Daucus carota*, *Carex duriuscula* + *Potentilla chinensis*, *Cyperus rotundus* + *Carex duriuscula*, *Carex duriuscula* + *Cyperus rotundus* (Table 4). With the degree of restored grassland, the vegetation characteristics showed an increasing trend, the aboveground biomass and coverage increased significantly, and productivity increased (Figure 2). Perennial herbaceous plants played the most important role in different restoration degrees of alpine grassland, while annual herbaceous plants were a few plant components (Table 3). The plant species dominated by Leguminosae, Asteraceae, Graminaceae, Rosaceae, and Cyperaceae usually grow in low-temperature, high-altitude and alpine grassland (Table 2). This is consistent with previous studies that show that these environmental factors preferentially support dominant species' existence and have poor competition among plant species, and the plant community preserves ecological structure with human intervention (Islam et al., 2022).

The impact of major factors influencing plant value perception remains inconclusive due to variations in study subjects across mine restoration research (Li et al., 2019). The relationships between restoration levels and environmental factors are complex, resulting in diverse plant diversity at different restoration stages (Zhao et al., 2019). Plant diversity serves both as a measure of structural characteristics and an indicator of environmental conditions (Bennett et al., 2020). Prior studies have consistently reported that the importance of plants can directly affect plant diversity

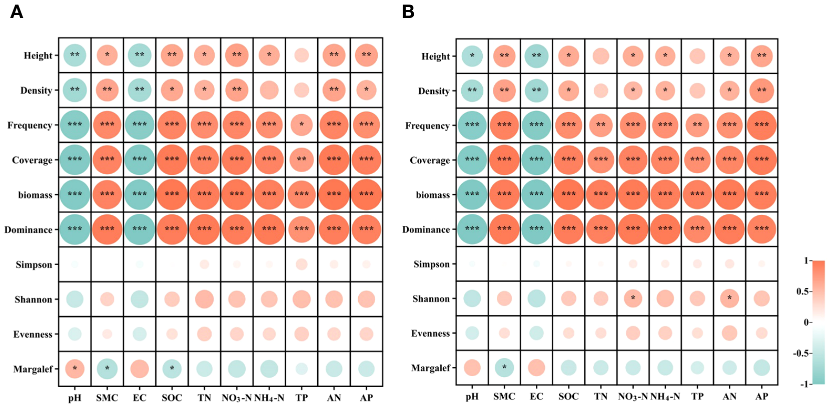

FIGURE 5
Correlations between plant community diversity and soil physiochemical properties in recovered alpine grassland at soil depths of 0-20 cm **(A)** and 20-40 cm **(B)**. pH, soil pH; SWC, soil water content; EC, soil electric conductivity; SOC, soil organic carbon; AP, soil available phosphorus; TP, soil total phosphorus; TN, soil total nitrogen; NO3-N, soil nitrate nitrogen; NH_4-N, soil ammonium nitrogen; AN, soil alkaline nitrogen. * indicates significant correlation ($p < 0.05$), ** indicates extremely significant correlation ($p < 0.01$), *** indicates extremely significant correlation ($p < 0.001$).

(Guo et al., 2020; Hailu et al., 2021). In our findings, the highest number of species was observed in HRD and NGL, whereas VLRD, LRD, and HRD grasslands had *Carex duriuscula* as the dominant species, with corresponding values of 39.22, 27.33, and 18.53, respectively (Table 4). The Shannon-Wiener, Simpson, Margalef, and Evenness indexes displayed an upward trend, while the Dominance index exhibited the opposite trend. The HRD Evenness index surpassed that of other restoration levels, possibly influenced by the number of community species and the uniform distribution of individual plants among species. Appropriate replanting and fencing could reduce the likelihood of invasion and enhance other species within the community, consequently promoting community-level plant diversity (Figure 3). Previous research has indicated that climate, degree of recovery, precipitation, and human activities like grazing and mining can impact the phenological periods and diversity of vegetation (Bao et al., 2014). Our results affirm that HRD grasslands exhibit richness in species, stable communities, and high uniformity. These findings suggest that HRD can serve as the primary management model for local restoration-level grasslands, providing a critical theoretical foundation for ecological restoration efforts in mining area grasslands. In the case of VLRD, vegetation cover was limited, mainly concentrated on both sides of roads and susceptible to trampling by cattle and sheep. Although fences were initially erected to enclose the restoration area, the large size of the area led to fence destruction by livestock. This necessitates enhanced management measures, including the installation of taller fences, in the later stages of restoration, especially in key secondary restoration areas.

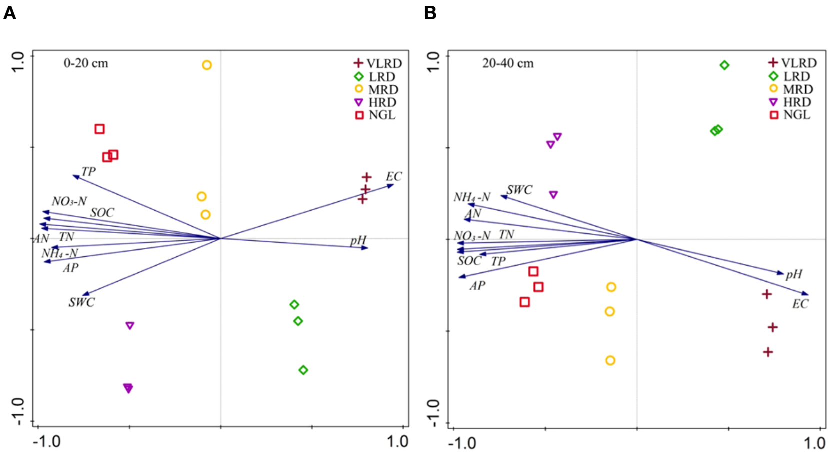

FIGURE 6
The principal component analysis (PCA) of soil physiochemical properties in alpine recovered grassland at soil depths of 0-20 cm **(A)** and 20-40 cm **(B)** was depicted. In the PCA plot, arrows indicate the direction and strength of the associated soil physiochemical indices, with the length of the arrows reflecting the degree of correlation with the variables. Each graph represents the recovered grassland for each sample (three replicates per sample, 1–3). The data are derived from three replicates (1–3) per sample. pH, soil pH; SWC, soil moisture content; EC, soil electric conductivity; SOC, soil organic carbon; AP, soil available phosphorus; TP, soil total phosphorus; TN, soil total nitrogen; NO_3-N, soil nitrate nitrogen; NH_4-N, soil ammonium nitrogen; AN, soil alkaline nitrogen.

4.2 Changes in soil characteristics in different soil layers

Differences in soil fertility as well as geographic location determine differences in vegetation, which in turn absorbs nutrients for plant growth from the soil through nutrients absorbed by the roots into the soil, and to a certain extent plant growth promotes soil nutrients, soil properties play a key role in promoting plant growth, and plant growth can also have an impact on the nutrient properties of the soil (An and Xu, 2013). Among the primary environmental factors affecting plant communities, soil stands out (Yang et al., 2023b). The physical and chemical attributes of soil significantly shape the growth and development of vegetation. In mining grasslands, both soil properties and vegetation growth transform as restoration levels change. Relationships of considerable significance exist among soil characteristics, restoration levels, plant community structure, and plant diversity (Zhang et al., 2020; Huang et al., 2021b). Several studies have shown that restored grasslands could reduce soil pH and EC (Dai et al., 2014, 2017). A similar result was also found in this study, where soil pH and EC were lower from HRD to VLRD due to vegetation growth and sufficient soil nutrients. However, soil SWC, SOC, TN, NO_3-N, NH_4-N, AN, TP, and AP were higher from HRD to VLRD (Figure 4). Soil pH, EC, and SWC were significantly higher from 20-40 cm soil depths to 0–20 cm soil depths, while soil SOC, TN, NO_3-N, NH_4-N, AN, TP, and AP were significantly lower from 20-40 cm soil depths to 0–20 cm soil depths (Figure 4). Low-quality soil is apt to cause vegetation degradation (Li et al., 2020), the varying degrees of vegetation coverage could play a crucial role, as vegetation affects soil chemical properties through leaf litter, root exudation, and associations with microorganisms, while an increase in grassland diversity and aboveground biomass leads to further soil restoration (Han et al., 2020). Our results indicate that restored plant communities (VLRD and LRD) had lower plant diversity and aboveground biomass, which might not recover well. Therefore, it is essential to explore plant composition characteristics and soil properties variation in different restoration degrees and take timely policy measures to protect restoration grassland vegetation.

4.3 Changes in the correlation between vegetation and soil characteristics

The connection between plant communities and soil properties can vary based on the restoration level, geographic location, and study area (Springate and Kover, 2014; Qin et al., 2019). The results of PCA analysis showed that the composition of the HRD plant community significantly differed from that under VLRD and LRD restoration degrees. The dominant controls for the HRD community composition were soil SWC, EC, AN, TP, NH_4-N, TN, AP, SOC, and NO_3-N at soil depths of 0-20 cm and 20-40 cm, respectively. The main reason for this was that the HRD was located at the foot of the mountain, away from the roadside, have sufficient rainfall and was free from human and livestock interference (Figure 5). In other studies, soil nutrients have been proven to be the main factor impacting plant growth, distribution and function (Xu et al., 2016, 2019). Soil nutrients exhibited a strong connection with plant communities in both soil depths (Yang et al., 2023b). In the soil properties at 0-20 cm depth, a positive correlation was observed between HRD and NGL with SWC, EC, AN, TP, NH_4-N, TN, AP, SOC, and NO_3-N, while HRD exhibited a negative correlation with pH at 0-20 cm soil depths. Similarly, at 20-40 cm depth, the soil properties between HRD and NGL displayed positive correlations with SWC, AN, TP, NH_4-N, TN, AP, SOC, and NO_3-N, while HRD showed negative correlations with pH and EC at 20-40 cm soil depths (Figure 6). Furthermore, our results confirmed that the HRD restoration degree was similar to NGL, which could enhance the number of vegetation and soil nutrients, leading to long-term mine grasslands restoration. Knowledge on the impact of mining grassland restoration on plant communities and soil properties can provide a scientific basis for the restoration and sustainable utilization of alpine grasslands.

For future restoration of mining areas, an integrated restoration approach should be applied, based on the findings of this study. Specifically, areas with low vegetation cover, classified as VLRD and LRD, should undergo secondary seeding as part of the restoration efforts. Additionally, fencing should be established to prohibit grazing and trampling, taking into account an integrated evaluation of ecological and socio-economic factors. The use of a diverse mixture of native species is recommended to enhance the resilience and stability of the ecosystem. Soil improvement practices, such as the application of organic materials, should be implemented to enhance soil health and fertility, thereby facilitating quicker vegetation establishment and growth. Monitoring and adaptive management practices should involve the implementation of long-term monitoring plans to track restoration progress, with management strategies adjusted as necessary to ensure the effectiveness of the mining area's restoration efforts.

5 Conclusions

This study investigates how environmental factors influence plant community characteristics, plant diversity, and soil properties at various restoration levels. It also aims to identify plant community characteristics along the recovery gradient in the Qilian Mountains study sites. In these sites, we observed 18 species belonging to 11 families and 16 genera across five restoration levels. Notably, *Carex duriuscula*, *Cyperus rotundus*, and *Polygonum viviparum* dominated the areas showing significant recovery, as indicated by their high importance values and species count. Our findings revealed that the Shannon and Simpson indexes in HRD were notably higher compared to VLRD, LRD, and MRD. Moreover, the recovery effect in HRD was similar to that of NGL, demonstrating the most effective natural recovery. Among the environmental factors, soil pH, SWC, SOC, NO_3-N, and AN played a significant role in regulating the plant community. As restoration levels increased, soil pH and EC gradually decreased, while soil SWC, AN, TP, NH_4-N, TN, AP, SOC, and NO_3-N progressively increased. The results suggest that the improvement in grassland restoration is closely linked to soil restoration, particularly the increase in soil SOC and AN content. Furthermore, the enhancement of grassland community characteristics and diversity contributes to further soil restoration. This study establishes a theoretical basis for the restoration and preservation of mining grasslands by revealing the connection between plant community attributes and soil properties in alpine grasslands.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

XY: Conceptualization, Data curation, Software, Writing – original draft, Writing – review & editing. QF: Funding acquisition, Project administration, Writing – review & editing. MZ: Data curation, Methodology, Software, Writing – original draft. JZ: Investigation, Supervision, Writing – review & editing. LY: Formal analysis, Methodology, Writing – review & editing. CZ: Conceptualization, Validation, Writing – review & editing. ZW: Supervision, Validation, Writing – review & editing. YF: Supervision, Writing – review & editing.

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Conflict of interest

Publisher's note

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The impact of the Qinghai-Tibet highway on plant community and diversity

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Roads are an increasingly prevalent form of human activity that drives the decrease in plant community functions and threatens global biodiversity. However, few studies have focused on the changes in the function and diversity of alpine meadows caused by road infrastructure in the Tibetan Plateau. In this study, the changes in species diversity, functional diversity, and community stability were examined at different distances from the Qinghai-Tibet highway. The results showed that the road intensified the degradation of vegetation, which significantly altered species diversity and community structure. This effect gradually decreased from near to far from the highway. Plant community cover and species diversity were highest at intermediate distances (50–100 m) from the roadway; species diversity and stability were lowest in the grassland most disturbed by the road (0 m), and species diversity and functional diversity tended to stabilize farther away from the road (250 m). Our findings indicate that changes in species diversity are synchronized with changes in functional diversity, which largely determines the outcome of degraded grassland community diversity and stability. Our results provide a reference point for restoring degraded alpine areas and mitigating the ecological impacts of roads.

KEYWORDS

Qinghai-Tibet Plateau, road distance, species diversity, plant functional diversity, road ecology

1 Introduction

Road networks are a ubiquitous phenomenon that creates a driving force from outside the ecosystem causing mortality or serious damage to organisms and changing the availability of resources (Mackey and Currie, 2000). Roads are the basic infrastructure that promotes social and economic progress, and the growth of road transportation is closely related to economic expansion (Meijer et al., 2018). Transportation infrastructure, such as roads, have become a common feature of the contemporary landscape (Skorobogatova and Kuzmina-Merlino, 2017), seemingly covering a small proportion of the land surface but impacting the ecological environment in various ways. Roads have huge ecological impacts, including modifying habitat, disrupting and eroding ecological flows, and increasing pollution (Asher et al., 2020). For example, the 6.3 million kilometers of roads in the United States only cover about 1% of the land, but they impact approximately 20% of the landscape (Forman and Deblinger, 2000). The Netherlands is also affected by the same percentage of roads (Reijnen and Foppen, 2006). Many other developed countries (e.g., the United Kingdom, Germany, and Japan) have road densities that are 2.5 to 4 times higher than those in the United States (Jaeger et al., 2007), with even worse environmental impacts. At least 25 million kilometers of new roads will be built worldwide by 2050; the total length of roads will increase by 60% compared to 2010, and transportation infrastructure will play an important role in shaping the environment (Meijer et al., 2018). The construction of roads represents a pervasive form of natural landscape transformation (Patarasuk and Binford, 2011). Economic development will require the construction of many new roads in the coming decades (Xie et al., 2021), which will extend into once inaccessible mountainous areas; consequently, these areas will face a balance between conservation of biodiversity and economic growth (Miller et al., 2021). Studies of various terrestrial and aquatic ecosystems have shown that many of the most prevalent threats to biodiversity (e.g., habitat destruction, fragmentation, edge effects, invasive alien species, pollution, overhunting, and genetics) are directly or indirectly related to roads (Lapaix et al., 2012), and attention has been paid to study the ecological characteristics of edges associated with roads (Jackson and Fahrig, 2011).

As typically linear corridors, roads serve as conduits to facilitate the movement of species between detached patches of remnant habitat, thereby promoting gene flow and increasing species richness (Lugo and Gucinski, 2000). Roads drive change in the composition and structure of mountain communities through habitat loss, fragmentation, and pollution from vehicles burning fossil fuels (Kitagawa et al., 2018). These changes affect biodiversity and influence ecosystem structure and function (De Pauw et al., 2021). Roads can change vegetation, including the loss of height or biomass, reduced cover, and changes in species composition (Pickering and Hill, 2007). Constructing and maintaining roads removes vegetation, changes land use (Saunders et al., 2002), alters soil structure and leads to an increase in soil compactness (Neher et al., 2013), indirectly affecting soil conditions. This, in turn, affects plant growth and species diversity, and promotes the establishment of invasive plants (Johnston and Johnston, 2004), resulting in the conversion of natural habitats to highly invasive roadside environments (Gelbard and Belnap, 2003). Formerly remote areas are becoming more accessible due to new roads, which not only cause a direct disturbance but also act as corridors for the movement of plant species (Rew et al., 2018). The role of roads as dispersal corridors is often amplified by vehicle traffic (Müllerová et al., 2011). The distance from the road and operating hours may also affect the abundance and distribution of native species. Roadside habitats provide ideal growing spaces for non-native plants, which often benefit from the more favorable microclimatic, the hydrological conditions, and the moderate disturbance (Averett et al., 2016). The success of native plant species fixation may be limited by the road and environmental conditions. For example, vegetation cover is minimal at roadsides but more abundant in interior areas (Cameron and Bayne, 2009).

The Tibetan Plateau is the world's "third pole," and has the largest area of perennial permafrost in the world (Pan et al., 2012). It is a natural barrier to the Asian water cycle and ecological security, and the alpine permafrost grasslands are experiencing climate change and anthropogenic disturbances (Lu et al., 2017). Climate extremes have made alpine grassland ecosystems more sensitive and fragile and particularly vulnerable to human activities (Hua and He, 2011), making restoration of grassland vegetation more challenging (Roy-Léveillée et al., 2014). Large-scale road development and excavation have artificially exacerbated erosion in recent years, leading to the degradation of perennial permafrost, to the detriment of the ecological security in the area. The Tibetan Highway crosses the Tibetan Plateau, a unique and fragile ecosystem. The Qinghai-Tibet Highway is an ideal place to study the effects of road construction and maintenance on species diversity (Zhao et al., 2006). Vegetation, which is the basis of this ecosystem, grows very slowly under localized environmental conditions. In addition, the interaction between anthropogenic disturbances and climate change makes it difficult to restore work in this region (Klein et al., 2004).

Roads are a major cause of the loss of biodiversity in mountainous areas worldwide (Li et al., 2022). Research into the effects of roads on species diversity in mountainous regions has gained momentum during the past two decades. A standardized protocol for monitoring changes in the altitudinal distribution, abundance, and composition of plant biodiversity in mountainous regions due to the interaction between the climate and human pressures has been proposed by previous authors. The protocol was developed by the Mountain Invasions Research Network (MIREN, www.mountaininvasions.org) (Rashid et al., 2021). Studies on the ecological effects of the Qinghai-Tibet Highway have focused on the observation that highway-related activities have exacerbated the degradation of vegetation along the route and have significantly changed the soil physicochemical properties (Liu et al., 2021). Changes in functional diversity and stability of the community structure have not yet been explored. However, the effects of changes in species composition and functional diversity in communities on ecosystem functioning may be equal to or stronger than the effects of changes in species richness (Shi et al., 2016). Plant functional trait diversity is sensitive to perturbations and environmental stress and is decisive for changes in ecosystem functioning. Therefore, assessing road-driven changes in species abundance and changes in functional diversity is critical to understanding the mechanism by which these compositional changes affect community and ecosystem functioning in response to road construction (Li et al., 2022). In addition, analyzing the response of β-diversity at different distances from the road and different elevations and describing the relationship between different diversities is important for understanding the mechanisms of community species coexistence on a landscape scale and conserving species, habitats, and natural ecological processes. Thus, we hypothesized that 1) plant communities at different distances from the road would be differently affected by the road, with plant richness being lower at the road edge, varying across the altitudinal gradient and influenced by climatic factors at the survey site; 2) lower plant functional richness would be detected at the edge of the road compared to different distances from the road; 3) plant community composition will differ by distance from the road, which may affect the plant community network structure. Our study will provide theoretical support for solutions to mitigate road-impacted grassland restoration on the Tibetan Plateau and to achieve mutual conservation benefits for humans and animals.

2 Materials and methods

2.1 Study sites

The effect of the road on plant community diversity at the perennial permafrost zone side of State Route 109 on the Tibetan Plateau was investigated. After crossing the Tanggula Mountain area in the hinterland of the Tibetan Plateau on the 109 National Highway, the terrain is high in the west and low in the north, tilting from west to east (35°18′-36°23′E, 91°47′-94°55′N, Figure 1). The elevation ranges from 4,300 m to 5,135 m, with an average elevation of 4,500 m and many high mountainous peaks (Zhang et al., 2002). To explore the mechanism by which roads affect diversity across altitudinal segments, we categorized the elevations at our sampling sites into high, medium, and low groups for every 600 m. The typical vegetation of the region is highland subtropical semi-arid climate, and the vegetation is mainly alpine grassland dominated by *Stipa purpurea* and the alpine meadow is dominated by *Kobresia* spp. and *Carex* spp. The grassland communities on the side of the Qinghai-Tibet Highway were affected to varying degrees, with the slopes most affected by the highway and differing markedly from the vegetation composition of the interior grassland. Daytime traffic on the Qinghai-Tibet Highway is around 50 vehicles (Yin et al., 2006).

2.2 Field sampling design and survey

Field sampling was conducted during peak biomass and flowering in July–August 2022 to minimize the risk of missing species with early or late phenology. Typical sample strips were systematically set up in grassland communities on one side of the permafrost section of the Qinghai-Tibet Highway. The selected road began at the bottom of the mountainous area through which National Highway 109 passes and reached the highest elevation of the permafrost section of the Tibetan Plateau, with sample lines spaced at 50-km intervals, and the direction of the sample strips was perpendicular to the direction of the highway. Before entering the site to identify the samples, a global positioning system was used to locate the samples as accurately as possible, collect some basic environmental variables (e.g., soil characteristics, and topographic variables), and take photographs of each sample line. Highway mileage ranged from K2886 to K3537, with a total length of 650 km and sample line intervals of 50 km, with 14 sample lines in total.

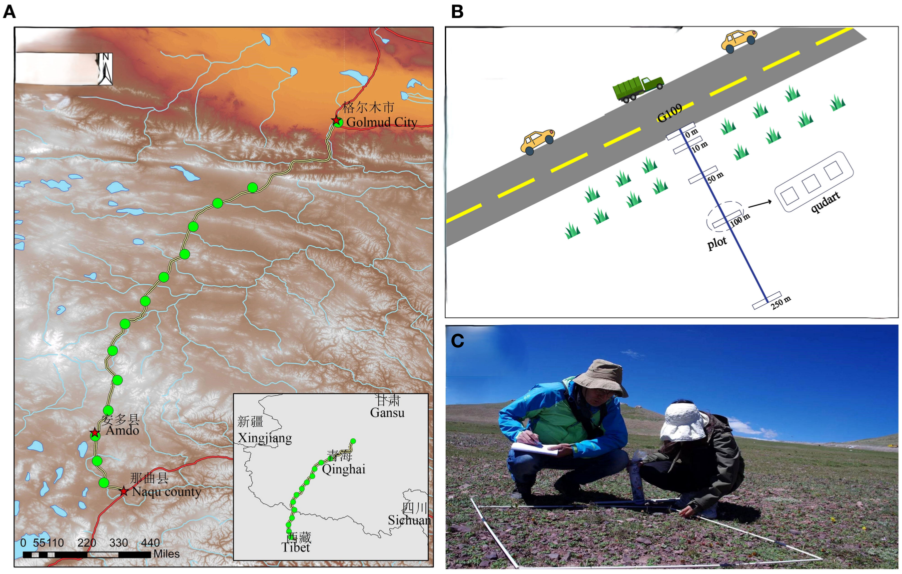

FIGURE 1
Schematic diagram of the distribution and survey of the 14 sample lines on National Highway 109. **(A)** Equal kilometer distribution of 14 sample sites along the road; **(B)** each sample site consists of five 2 m × 50 m plots parallel to the roadside. Plot 1- parallel to the roadside (starting at the first occurrence of roadside vegetation). Plots 2 – 5 represent varying distances from the road; **(C)** exemplary photograph of monitoring a mountain roadside on Qinghai Tibet highway, depicting a survey of plot 1.

Five 2 m × 50 m sampling plots were set up parallel to the road on the sample line at different distances from the highway: 0 m from the highway (slopes), 10, 50, 100, and 250 m (the furthest distance that could be extended). Three 1 m × 1 m sample squares were laid out at each site (Figure 1). In each of the three sample quadrats at all sites, we investigated the abundance, coverage, and height of all native and non-native plants. Plant coverage was represented by the ratio of the shaded area of a species to the total area of the quadrat. Functional plant traits were recorded, including leaf shape, leaf texture, seed dispersal mode, life history, light habit, and growth environment. Unrecognized plants were identified to the species level using the most up-to-date local flora.

2.3 Data analysis

2.3.1 Biodiversity measures

α-Diversity and β-diversity were selected to characterize the spatial dynamics of biodiversity in the highway roadside habitats.

Plant relative importance (*Pi*) size value was calculated for each species and *Pi* was calculated using the following formula: *Pi* = (relative cover + relative height + relative abundance)/3. The richness index, the Chao 1 richness index, the Shannon-Wiener diversity index, and the Simpson diversity index were selected to assess species diversity. The total number of species occurring within the sample was used as a measure of species richness (Wei et al., 2022).

$$Margalef: R_m = (s-1)/\ln N$$

$$Chao1 = S_{obs} + \frac{n_1(n_1-1)}{2(n_2+1)}$$

$$Simpson: D = 1 - \sum_{i=1}^{s} P_I^2$$

$$Shannon-Wiener: H = -\sum_{I=1}^{S}(P_i \ln P_i)$$

Partial least squares discriminant analysis was performed based on the species importance values using the mixOmics package, and the results of the analysis were visualized with the ggplot2 package.

Nineteen bio30s meteorological data were extracted in ArcMap using the latitude and longitude of the sampling points (Supplementary Table S1). Pearson's correlation analysis was used to explore the correlations between plant abundance and meteorological factors at different elevation gradients.

2.3.2 Plant functional trait data collection and the functional diversity calculation

The functional traits of the plants were categorized into growth type, height, physiological characteristics, pollination, and dispersal mode. Ten plant functional trait indicators were used (Table 1), most of which were obtained from field measurements and surveys, and some of which were obtained in a literature review.

Plant functional diversity was measured by three dimensions, including functional richness, functional discretization, and functional homogeneity. After assigning values to the data for each functional trait of the plant, the functional diversity indices were calculated using the FD software package, including the functional richness index (*FRic*), the two-dimensional functional discretization indices (*FDiv* and *FDis*), and the functional homogeneity index (*Feve*).

TABLE 1 Types and ways of obtaining plant functional traits.

Functional characteristic	Functional Characteristics Type	Acquisition method
Seed dispersal mode	1. Gravity propagation; 2. Wind propagation; 3. Automatic propagation; 4. Animal propagation.	FO
Pollination	1. Wind-borne; 2. Insect-borne.	FO
Light Habit	1. Negative; 2. Semi-negative; 3. Positive.	FO
Life history	1. Annual; 2. Biennial; 3. Perennial.	FO
Bloom period	Month of flowering	AI, FO
Florescence	Length of flowering period	AI, FO
Leaf shape	1. Round; 2. Oblong; 3. Lanceolate; 4. Elongate	FO
Leaf quality	1. Herbaceous; 2. Fleshy; 3. Leathery	FO
Average height	Standardization of measured data	FO
Total cover	Standardization of measured data	FO

FO, field observation; AI, access to information from references.

2.3.3 Vegetation community network structure

All species occurring in each treatment were included to construct the nodes of the network graph under that treatment. Spearman's correlation analysis was calculated between two species with the species importance value and was used to construct the edges of the network graph for that treatment (Deng et al., 2012). Edges with a significance level greater than 0.05 and an absolute value of the correlation coefficient of less than 0.5 were excluded to clarify the constructed network graph, while the edges were constructed in the psych package. Based on the nodes and edges, the undirected randomized network graphs for each treatment were plotted using Gephi (v. 0.10.1). In the random network, the size of the average degree of connectivity was used to measure the strength of the species interactions in the community, and the higher the average degree of connectivity, the higher the complexity and stability of the vegetation community (Watts and Strogatz, 1998). Average clustering coefficient size was used to measure the level of community organization, and the larger the average clustering coefficient, the higher the level of community organization (Latapy, 2008).

2.3.4 The relative contribution of elevation and distance to species diversity

As the plots were nested for each site and the sites were nested for the road, we used a linear mixed-effects model (LMM) to analyze the changes in the relative importance of the effects of elevation and proximity on the species α-diversity index, and the

TABLE 2 Results from LMM analyses with elevation and distance as fixed effects, and sites as the random effect.

Variables	Fixed effects	Sum Sq	DenDF	F value	*P* value	Deviation explained(%)
Richness	elevation	35.15	12.20	6.30	0.027	22.33
	distance	264.79	184.20	47.46	< 0.001	36.32
	elevation × distance	43.65	185.96	7.82	0.006	41.35
Shannon	elevation	1.51	12.16	8.49	0.013	45.67
	distance	3.99	184.52	22.41	< 0.001	25.67
	elevation × distance	0.23	186.53	1.31	0.254	28.66
Simpson	elevation	0.19	12.35	5.98	0.030	74.78
	distance	0.11	184.71	3.24	0.074	12.03
	elevation × distance	0.00	186.73	0.04	0.835	13.19
Chao 1	elevation	618.54	12.45	10.76	0.006	29.59
	distance	1624.66	185.30	28.26	< 0.001	32.67
	elevation × distance	619.77	187.66	10.78	0.001	37.74
cover	elevation	265.20	12.13	0.58	0.462	14.56
	distance	8712.90	183.88	18.99	< 0.001	41.41
	elevation × distance	1257.50	185.42	2.74	0.099	44.03
height	elevation	7.32	11.77	4.07	0.067	75.92
	distance	9.99	183.01	5.54	0.020	12.51
	elevation × distance	0.47	184.14	0.26	0.609	11.57

The last column reports the marginal R^2 with 95% credible intervals of the model (row: effects) as well as the variance explained by elevation and distance.

proportions of elevation, proximity, and their interactions were explained, where the fixed effects were elevation, distance, and site as a random effect. We used the R package lem4 (Bruelheide et al., 2021) to fit the LMM (Table 2). A hierarchical split was used for the proportion of explanations in each section (Lai et al., 2022). All analyses were conducted in R (v. 4.3.2; The R Foundation for Statistical Computing, Vienna, Austria).

3 Results

3.1 Effects of the road on grassland community diversity

Meadows at five different distances from the road exhibited different plant community characteristics. The elevation, distance, and interaction between the two grasslands significantly affected plant community height and cover ($P_A = 0.462$, $P_D < 0.001$, $P_{A \times D} = 0.099$). At different distances from the road, vegetation cover was significantly lower at the slope (0 m) than at other distances ($P < 0.05$). The plant community cover of the three altitudinal gradients was unimodal with a significant increase followed by a significant decrease with increasing distance from the road (Figure 2A). Inconsistent trends were observed in plant community height at different elevations and distances ($P_A = 0.067$, $P_D = 0.020$). Plant community height decreased from 0 to 10 m and increased from 50 m to 100 m. The plant community heights at 50, 100, and 250 m were higher at high elevations than at the middle and low elevations (Figure 2B).

Road distance and the altitudinal gradient had highly significant effects on the plant community richness index and the diversity index ($P_A = 0.027$, $P_D < 0.001$, $P_{A \times D} = 0.006$). The plant community richness index, the Chao 1 index, and the Shannon index were significantly ($P < 0.05$) higher at high elevations than at medium or low elevations. However, the difference in the species diversity indices between the mid- and low elevations was not significant ($P > 0.05$). The richness index, the Chao 1 index, and Shannon's diversity index increased and then decreased with the increase of distance from the road ($P < 0.05$), being highest at a distance of 100 m. Simpson's index had the opposite trend to Shannon's index, being lowest at 50 m (Figure 3).

The results of community Bray–Curtis heterogeneity analyses revealed significant differences in plant community composition across altitudinal gradients and at different distances from the highway. The 0-m distance had the highest Bray–Curtis heterogeneity at the high, medium, and low elevations. The difference in heterogeneity between 0 and 50 m was significant ($P < 0.05$) at high-elevations. The difference in heterogeneity at 0 and 10 m was significant ($P < 0.05$) at mid-elevation. The differences in heterogeneity were significant at 0, 10, and 250 m ($P < 0.05$, Figure 4) at low elevations.

Among the meteorological factors extracted in this study, plant community composition across the altitudinal gradient was

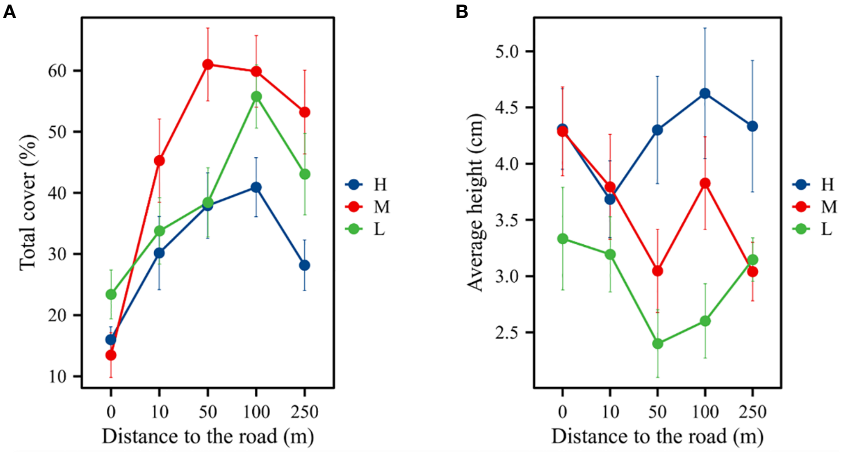

FIGURE 2
Changes in plant community height and cover along the distance gradient.

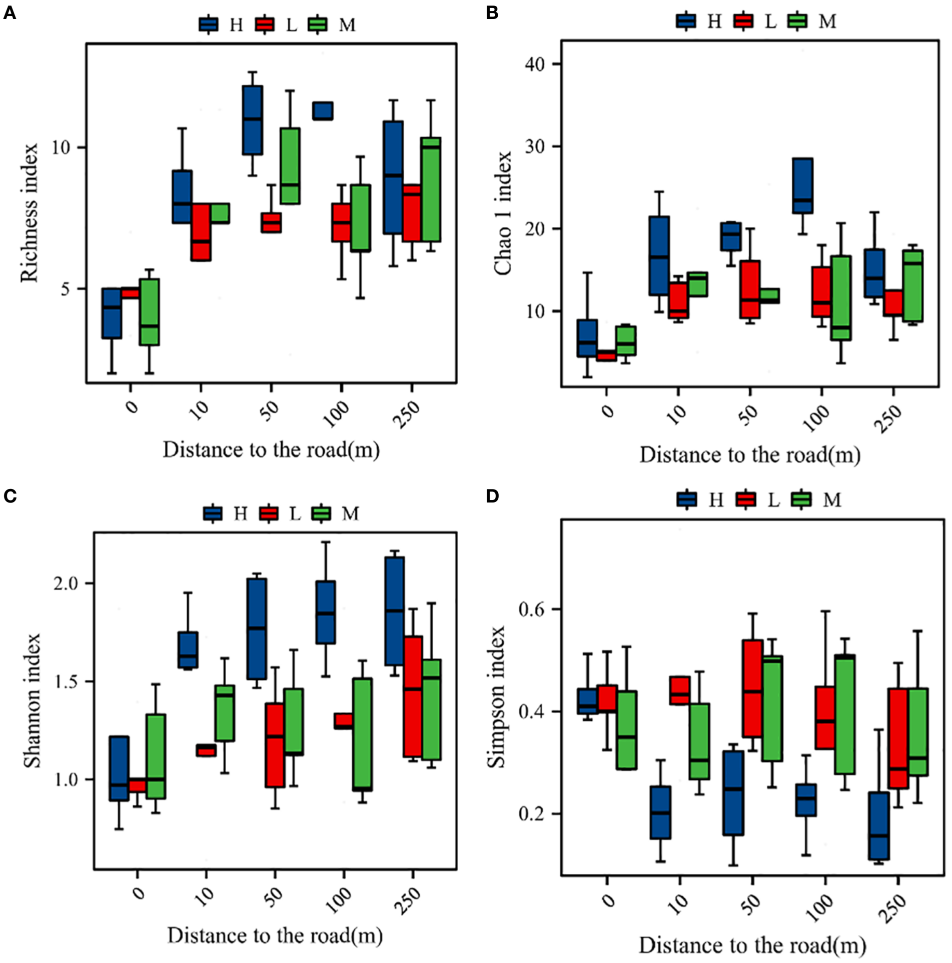

FIGURE 3
Species diversity indices of the plant communities. **(A)** Variation in the richness index with distance at different altitudinal gradients; **(B)** variation in the Chao 1 index with distance at different altitudinal gradients; **(C)** variation in Shannon diversity with distance at different altitudinal gradients; **(D)** variation in Simpson's diversity with distance at different altitudinal gradients; H, M, and L represent high, middle, and low elevations, respectively.

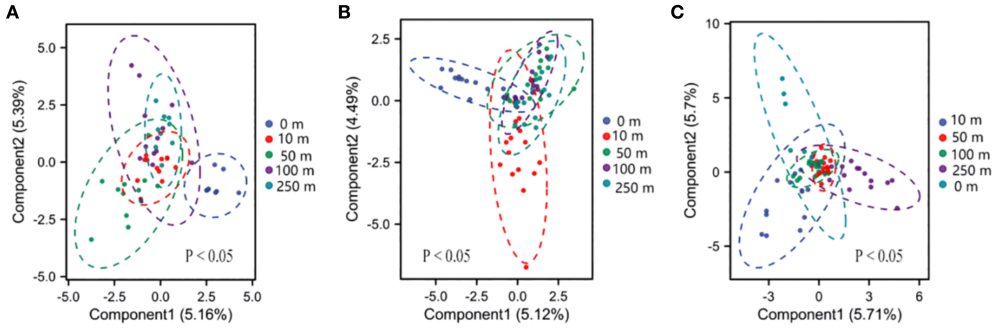

FIGURE 4
Beta diversity of the plant communities. **(A)** High-elevation gradient-biased least squares discriminant analysis (PLS-DA); **(B)** middle-elevation gradient-biased PLS-DA; **(C)** low-elevation gradient-biased PLS-DA.

significantly and positively correlated ($P< 0.01$) with most of the temperature factors (BIO_1–BIO_{11}) and significantly and negatively correlated ($P< 0.01$) with the precipitation factors (BIO_{12}–BIO_{19}). In addition, the effects of different altitudinal gradients on climatic factors were consistent, with mean annual temperature and annual precipitation as the most important factors (Figure 5).

3.2 Effects of the road on plant functional diversity

Road distance had a highly significant effect on the plant community functional diversity indices ($P< 0.01$). However, the effect of the altitudinal gradient was not significant ($P > 0.05$), and the trends in the four functional diversity indices were consistent across the altitudinal gradient. Functional diversity richness (*FRic*) increased significantly ($P< 0.05$) with the increase of distance from the road at 10 m and then decreased slowly, which was consistent with the trend in the species richness indices. Functional diversity dispersion (*FDis* and *FDiv*) showed a single-peak trend of increasing and then decreasing, with lower levels at 0 and 250 m. None of the road distances had a significant effect on the evenness of functional diversity (*FEve*). However, the plant community functional evenness index was significantly ($P< 0.05$) higher at 0 m in the high-elevation zone than at other distances ($P > 0.05$). The degree of uniformity of the plant distribution was essentially the same at different distances (Figure 6).

3.3 Effects of the road on plant community network complexity

A co-occurrence network of the plant communities was constructed by comparing the mechanisms by which different

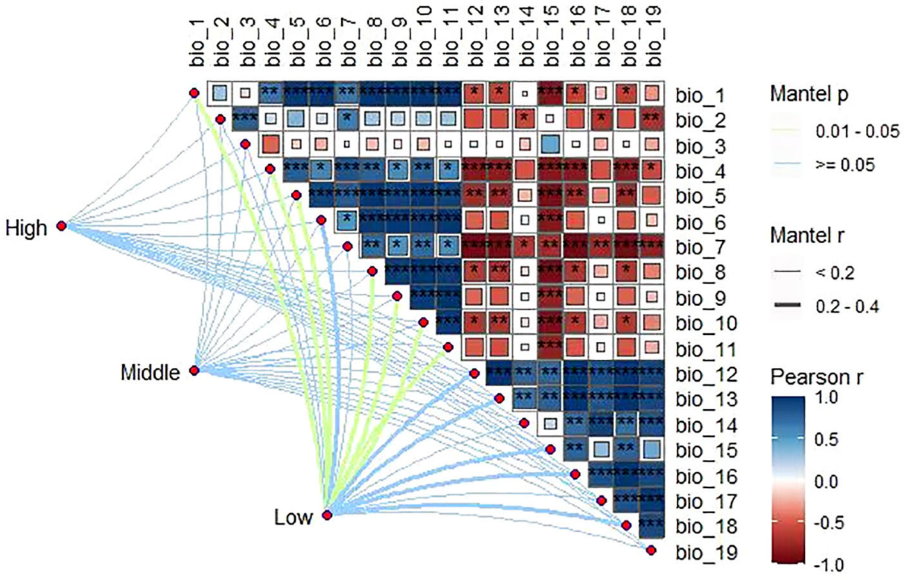

FIGURE 5
Correlation between species diversity and climatic factors at different altitudinal gradients (*, **, and *** indicate p ≤ 0.05, ≤0.01, and ≤0.001, respectively).

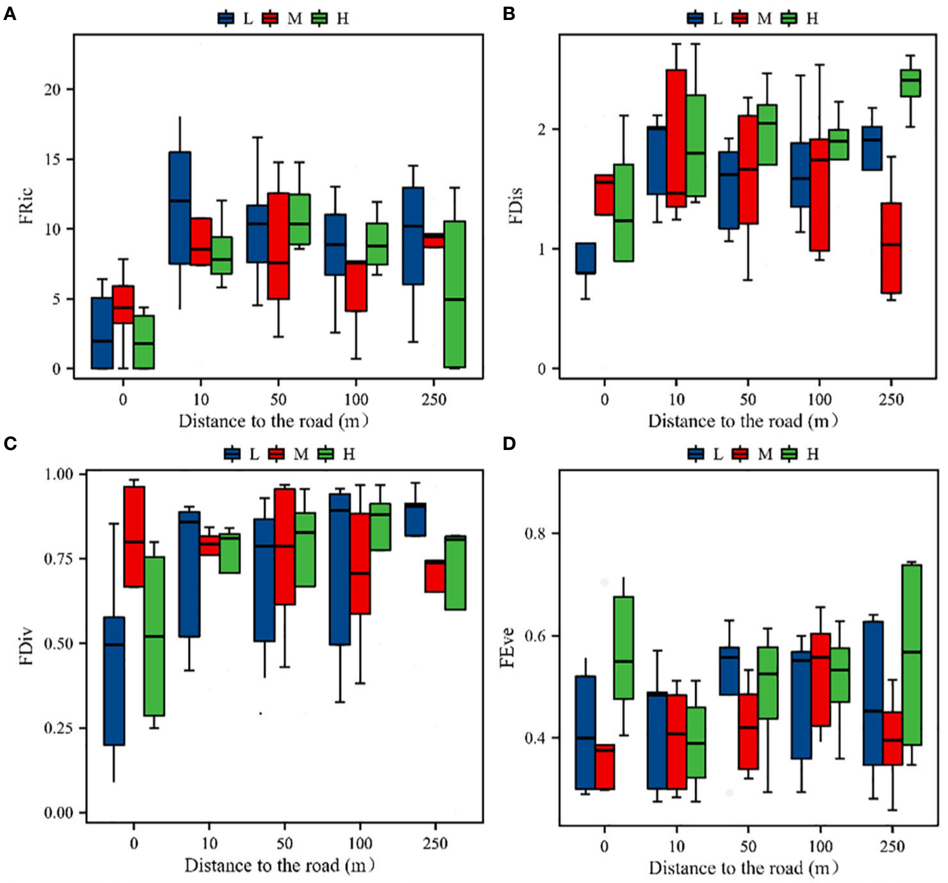

FIGURE 6
Species functional diversity indices of the plant communities. **(A)** Variation in the FRic index with distance at different altitudinal gradients; **(B)** variation in the *FDis* index with distance at different altitudinal gradients; **(C)** variation in the *FDiv* index with distance at different altitudinal gradients; **(D)** variation in the *FEve* index with distance at different altitudinal gradients; H, M, and L stand for high, middle, and low elevations, respectively.

distance gradients from the road affect the complexity of the co-occurrence network of the plant communities. This was accomplished following the importance values of the species at each distance, and various network topology parameters on distance were regressed (Figure 7). The total number of nodes ($R = 0.975$, $P = 0.005$), the total number of connections ($R = 0.975$, $P = 0.005$), and RM ($R = 0.700$, $P = 0.005$) were significantly higher as the distance from the road increased. The mean degree ($R = 0.900$, $P = 0.083$), mean clustering coefficient ($R = 0.700$, $P = 0.233$), and RM ($R = 0.700$, $P = 0.233$) all tended to increase (Figure 8).

4 Discussion

The importance of roads in promoting mountain biodiversity has been documented in a global database of research surveys showing the impact of mountain biodiversity on roads, which has been increasing since 2007 (Haider et al., 2022). However, grasslands at different distances from the road are affected differently. We considered the effects of roads on species richness and abundance, as well as the effects of roads on species functionality and stability. The grasslands at the side slopes were the most affected, reaching the farthest limit of impact at 100 m, while it was virtually unaffected at 250 m, and remained in its original grassland condition, with some sensitive species adapted to this growing condition with relatively low community stability.

4.1 Effects of the road on species diversity

During the construction and operation of a motorway, there will be varying degrees of impact on the soil environment and vegetation of the grasslands along the highway. As we predicted, grassland vegetation in areas close to the motorway was degraded to varying degrees. This result indicates that the closer the motorway is to a site, the lower the cover and diversity of the grassland vegetation, which is consistent with the results of many studies (Dörfer et al., 2013). This damage includes direct cutting and rolling of grass vegetation by construction and access vehicles (Wang et al., 2017). It may also be caused by soil erosion, which would change the topography on both sides of the motorway (Buckeridge and Jefferies, 2007). The impact of roads on roadside vegetation tends to be more severe due to the harsh environmental conditions in mountainous areas (Barni et al., 2007). The 0–10 m area of the road edge is highly affected by vehicles and road management, and the frequency of road construction and rehabilitation may compact

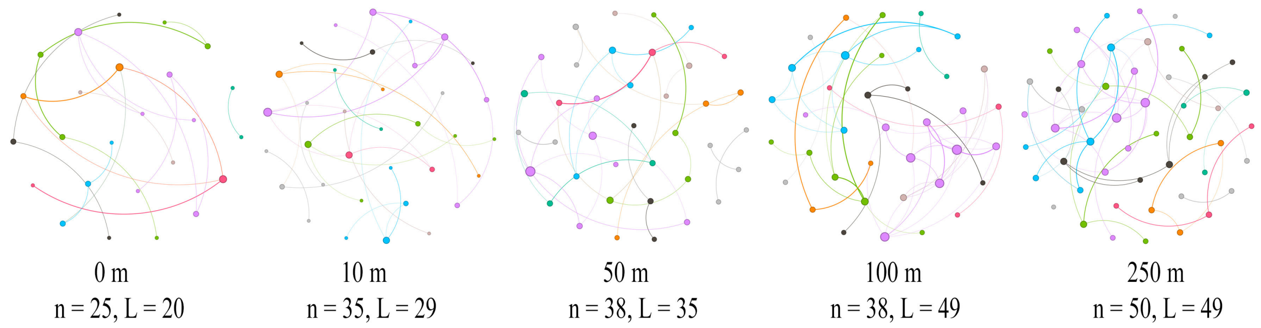

FIGURE 7
Plant community networks at different distances along the highway. Visualization of the constructed network at five different distances, with different modules shown in different colors.

the soil and result in water loss, which may affect plant growth and distribution and hence species richness and cover (Nepal and Way, 2007). These effects have resulted in the decline and disappearance of several sensitive species and have reduced biodiversity. Thus, species richness was lowest in the 0–10 m range, and the increase in species diversity at 10 m may have been due to the dust and water runoff particles from road management that extended into the soil and vegetation of many neighboring habitats, creating favorable conditions for plant growth (Müllerová et al., 2011).

Species richness was greatest at 50 m, and only slight variations in the number of species were observed at 50–100 m, until the threshold at 100 m, beyond which the number of species decreased. One possible explanation is that the 50 m distance represented the transition zone between the grassland edge and the core area, which is subject to road-induced disturbances and a core area relatively distant from the road. The increase in the diversity of the microenvironments for plant growth could increase plant species richness. Core communities, which are represented at distances of 100–200 m, were characterized by a sharp decline in the number of species probably because the new environments in these areas were suitable for a few specific species, and therefore there was lower species diversity.

Several global studies have shown that the richness of native species in the interior and roadside, as well as the assemblage of all species, forms a single-peak pattern with a maximum at lower mid-elevations (Haider et al., 2022). In contrast, our study showed that plant community diversity was significantly higher at high elevations than at low and middle elevations, and there was no significant difference in the diversity changes at low and middle elevations. However, this pattern changes along roads and for non-native species (Liu et al., 2021). Biodiversity patterns are largely shaped by natural factors, such as climatic gradients, and there is growing evidence that mountain biodiversity is affected by climate change (Lenoir and Svenning, 2024). Argentina (interior) and Australia (roadside) have negative correlations between elevation and native species richness (Rahbek, 2005). In contrast, Norwegian native species richness increases with elevation, possibly as a result of reduced shrub competition at higher elevations (Lembrechts et al., 2014). In this study, the difference in the elevation gradient was primarily due to the significant climatic differences along the Qinghai-Tibet Highway, with high temperatures in the south and low temperatures in the north based on latitude. It is windy along the Tibetan Plateau near latitude 32°N, with high winds throughout the year and decreased precipitation from southeast to northwest (Valdés et al., 2015). This climatic factor causes the plant communities along the Qinghai-Tibet Highway to become more diverse as the terrain rises.

4.2 Effects of the road on plant functional diversity and community stability

Many studies have shown that species diversity has a positive effect on community stability (Isbell et al., 2009). As communities become

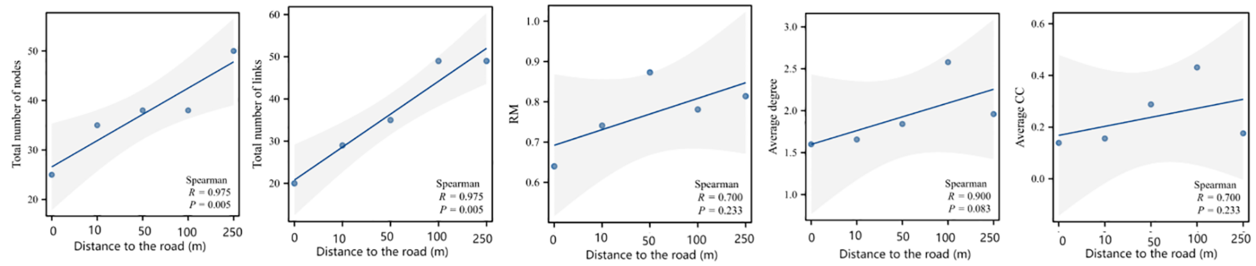

FIGURE 8
Changes in network topology with increasing distance, including the number of nodes, the number of connections, relative modularity, average degree, and the average clustering coefficient.

richer in species and more complex in structure, their stability increases (Campbell et al., 2011). Plant functional traits help to identify adaptive responses and resource allocation strategies in plants (Tilman, 1999). Exploring functional characteristics and functional diversity helps shed light on system stability, community structural mechanisms, and community productivity (Guittar et al., 2016). The results of this study indicate that plant functional diversity richness was significantly higher at 0 m than at the long-range, showing the same trend as species diversity, reaching a maximum at 100 m and decreasing at 250 m.

Analysis of the plant community network structure also showed that the grassland community was most unstable at 0 m. Road development projects require establishing surface processes at the project site, including logging, felling, and embankment construction (Rentch et al., 2005). Such processes disturb the topsoil and remove existing plant communities, turning the site into a barren ecosystem, and leading to long-term soil disturbance with consequences for community stability (Lamsal et al., 2018). As the distance from the road increases, the higher the network topology parameter value, the more stable the grassland community becomes, reaching a maximum at 100 m and then decreasing at 250 m. However, the grassland community was always more stable than the side slopes (0 m). Community stability increases with species diversity with road disturbance of a plant community, and plant community stability is maintained by plant functional diversity. The 100 m distance is critical in disturbed grassland communities, as this is the stage where habitats are most complex, species diversity is highest, and functional diversity reaches a saturation point. The road disturbance is virtually non-existent beyond 100 m; grassland habitats become native habitats, and community stability decreases. This study found that areas close to roads were likely to be colonized by exogenous species (Willard et al., 2007). In addition, plants on road edges change the community by changing basic drivers, such as temperature, moisture, light availability, and wind speed (Zurita et al., 2012). Consequently, the structure of the plant communities in the 0–10 m range is more prone to change, and community stability, distribution, species richness, and cover decrease.

4.3 Patterns of response of different species to road impacts

Heliophilous spp. and open habitat species likely colonize roads and side slopes (Ziegler et al., 2000), as the results of this study show that *Neotorularia torulosa* and *Plantago depressa* are endemic plants that grow on side slopes (0 m). *N. torulosa* prefers to grow in disturbed land, wasteland, sandy land, foothills, or stony clay slopes. *P. depressa Willd* is hardy, drought-tolerant, and adaptable, and has low soil requirements. Areas at the edge of roads are usually characterized by high levels of disturbance, the accumulation of gravel as vehicles pass, poor soil conditions and nutrients, low moisture conditions, and high light. Shade plants and scrub prefer the interior of a meadow. They are less tolerant of light and disturbances and are likely to grow inside undisturbed meadows. Sensitive and slow-growing species are vulnerable to roads, and they can be crowded out by more competitive species, retreating further away because of road and traffic construction. In this study, the endemic species at 250 m, such as *Lysimachia maritima*, grew in the lowlands of the plains, around reservoirs and lakeshores, as well as in the moist areas of mountain valleys (Liu et al., 2023). *Stellaria media* prefers a mild and humid environment (Oladeji and Oyebamiji, 2020). The greater the distance from the road, the less disturbed the grassland community will be, and the more these sensitive species, which require strict growing conditions, will survive (Supplementary Figure S1).

4.4 Potential factors affecting the road

Road distances that shape plant community diversity are strong potential drivers of climate (mean annual temperature, mean annual rainfall, and solar radiation). The destruction of vegetation also harms the road itself. Melting of permafrost under and near the road leads to subsidence of the road base. In addition, desertification of exposed soil occurs rapidly under the influence of strong winds and frequent freezing/thawing cycles. Therefore, the best way to protect vegetation is to apply mitigation measures at the planning and construction stages to keep initial damage to a minimum. Based on our results, we recommend that impacts on biodiversity be minimized by avoiding heavy vehicles that require larger roads or, when new roads are necessary, by methods that require specific planning in conjunction with long-term ecological monitoring and a proper impact modeling phase. Indeed, the geographic literature suggests that mitigation through appropriate road placement is critical to restoring and protecting alpine meadow core habitats, which, in turn, restores all ecosystem services needed for the human economy (Tattoni et al., 2011). Biodiversity can be further improved by the following steps: (1) accurate consideration of the road type and characteristics (Pereira et al., 2002) and historical dynamics may play a key role in detecting changes in biodiversity; (2) indicator taxa, such as animals, typical plants, insects, or birds, can also be used (Lawton et al., 1998). The importance of preserving core remnants of plant communities in the Tibetan Plateau landscapes requires a qualitative and quantitative understanding of the impact of human activities on the entire spectrum of species diversity. Future research on the effects of roads should focus on revealing the relative contributions of the different mechanisms that mediate the effects of roads, including fragmentation, vehicle-induced pollution, and changes in sedimentation rates (Petrin et al., 2023).

5 Conclusions

The impact of roads on species diversity is multifaceted. Increasing habitat diversity and species richness as well as the potential introduction of exotic species can affect plant functional traits, which, in turn, can negatively impact native species. This study investigated the effects of a road on roadside grassland plants at different distances. The results indicated that a road can severely degrade roadside grassland plant communities with reduced species diversity and functional diversity, resulting in low community stability and vulnerability to colonization by invasive alien species. These results will guide the restoration of grassland ecosystems along highways and the selection of road construction options in the Tibetan Plateau region.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding authors.

Ethics statement

Written informed consent was obtained from the individual(s) for the publication of any identifiable images or data included in this article.

Author contributions

ZT: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation. XC: Writing – review & editing, Data curation, Visualization, Investigation, Funding acquisition. YW: Writing – review & editing, Investigation, Data curation, Funding acquisition. SW: Writing – review & editing, Formal analysis, Data curation. RW: Writing – review & editing, Formal analysis, Data curation. BY: Writing – review & editing, Formal analysis, Data curation. YY: Writing – review & editing, Formal analysis, Data curation. YK: Writing – review & editing, Funding acquisition, Formal analysis, Data curation. JQ: Writing – review & editing, Visualization, Software, Resources, Methodology, Funding acquisition, Formal analysis, Data curation.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpls.2024.1392924/full#supplementary-material

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An advanced TSMK-FVC approach combined with Landsat 5/8 imagery for assessing the long-term effects of terrain and climate on vegetation growth

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Introduction: As an exceptional geographical entity, the vegetation of the Qinghai-Tibetan Plateau (QTP) exhibits high sensitivity to climate change. The Baima Snow Mountain National Nature Reserve (BNNR) is located in the south-eastern sector of the QTP, serving as a transition area from sub-tropical evergreen broadleaf forest to high-mountain vegetation. However, there has been limited exploration into predicting the temporal and spatial variability of vegetation cover using anti-interference methods to address outliers in long-term historical data. Additionally, the correlation between these variables and environmental factors in natural forests with complex terrain has rarely been analyzed.

Methods: This study has developed an advanced approach based on TS (Theil-Sen slope estimator) MK (Mann-Kendall test)-FVC (fractional vegetation cover) to accurately evaluate and predict the time and spatial shifts in FVC within the BNNR, utilizing the GEE (Google Earth Engine). The satellite data utilized in this paper consisted of Landsat images spanning from 1986 to2020. By integrating TS and MK methodologies to monitor and assess the FVC trend, the Hurst index was employed to forecast FVC. Furthermore, the association between FVC and topographic factors was evaluated, the partial correlation between FVC and climatic influences was analyzed at the pixel level (30×30m).

Results and discussion: Here are the results of this research: (1) Overall, the FVC of the BNNR exhibits a growth trend, with the mean FVC value increasing from 59.40% in 1986 to 68.67% in 2020. (2) The results based on the TS-MK algorithm showed that the percentage of the area of the study area with an increasing and decreasing trend was 59.03% (significant increase of 28.04%) and 22.13% (significant decrease of 6.42%), respectively. The coupling of the Hurst exponent with the Theil-Sen slope estimator suggests that the majority of regions within the BNNR are projected to sustain an upward trend in FVC in the future. (3) Overlaying the outcomes of TS-MK with the terrain factors revealed that the FVC changes were notably influenced by elevation. The partial correlation analysis between climate factors and vegetation changes indicated that temperature exerts a significant influence on vegetation cover, demonstrating a high spatial correlation.

KEYWORDS

Landsat time series, fractional vegetation cover, spatio-temporal change of vegetation, topographic factors, climatic factors

1 Introduction

Vegetation is an indispensable portion of land ecosystems. It has a critical function in carbon cycling, climate regulation and the maintenance of ecosystem sustainability at both regional and global scales (Duo et al., 2016; Fu et al., 2022b; Li et al., 2023). Nevertheless, there are distinct regional variations in the vegetation response to climate change, influenced by factors such as topography and geomorphology (Palombo et al., 2014; Guo et al., 2016). In environmentally sensitive regions, the impacts of climate change on vegetation phenology are likely to be amplified, especially in mountainous regions situated in geographic transition zones and at high altitudes (Nemani et al., 2003; Hua et al., 2017). National nature reserves are typically situated in mountainous regions characterized by abundant vegetation cover, serving as natural buffer zones that mitigate the impacts of climate variability and natural disasters (Xu et al., 2022). Therefore, amidst global climate change, it is imperative to effectively monitor vegetation within natural reserve areas in order to study how plant phenology responds to fluctuations in climate (Roberts et al., 2020; Zhang et al., 2021).

Earlier studies have utilized NDVI to track the vegetation cover (Zhang et al., 2018). However, NDVI itself has the limitation that it is easy to saturate in high-vegetation cover regions and is difficult to identify the tree canopies in low vegetation cover regions. Nevertheless, these issues can be addressed by calculating the fractional vegetation cover (FVC) (Ma et al., 2021). FVC represents the proportion of the vertically projected surfaces of plant stems, leaves, etc., to the total area within a given region. It can be utilized to track the development of vegetation cover (Marsett et al., 2006; Lehnert et al., 2015). Therefore, FVC can serve as an effective indicator of the vegetation assessment, reflecting the dynamic changes of vegetation affected by various elements such as climate shift, land cover variation, and environmental projects (Geng et al., 2022; Han et al., 2023). On the other hand, long time series-based FVC allows for the analysis of vegetation cover changes in the study area and require the integration of multiple change monitoring methods (Zhu et al., 2021; Fu et al., 2023). Currently, several change detection algorithms have been applied to vegetation monitoring, such as LandTrendr algorithm (Kennedy et al., 2010), continuous change detection and classification (CCDC) algorithm (Zhu and Woodcock, 2014) and BFAST algorithm (Verbesselt et al., 2010). However, commonly used methods of FVC trend analysis include regression analysis and TS (Theil-Sen slope estimator)-MK (Mann-Kendall analysis) analysis (Liu et al., 2022; Fu et al., 2022b). The advantage of TS-MK is that the data do not need to obey a certain distribution law, the data error has a strong resistance to the data, for the significance level test has a more reliable statistical theory basis, so that the results of the operation are more scientific and credible (Zhang et al., 2022b). In addition, Hurst index is widely used in studies of the future sustainability of vegetation cover (Zhang and Jin, 2021; Zhu et al., 2021). Coupling the Hurst exponent with the Theil-Sen slope estimator allows for a more accurate representation of future trends in vegetation. Therefore, this paper integrates the Mann-Kendall, Theil-Sen slope and Hurst index methods to analyze the trend, significance, and future projection of vegetation changes.

Field measurements and remote sensing techniques are available for monitoring the spatial and temporal dynamics of vegetation. However, field measurements encounter limitations such as the inability to gather continuous observation data over extended periods, high monitoring costs and difficulties in realizing large-area monitoring (Han et al., 2023). Remote sensing technology has emerged as a promising approach for monitoring vegetation growth, owing to its ability to provide continuous spatial coverage and long-term data series (Chu et al., 2019; Li and Yang, 2023). Normally, long time-series remote sensing imagery and its derived products can be used to estimate FVC that is beneficial for monitoring the vegetation changes in large river basins, urban agglomerations, and grasslands (Xiao et al., 2017; Geng et al., 2022). Traditional remote sensing analysis methodologies require downloading and pre-processing a large number of images. Google Earth Engine (GEE) has already carried out atmospheric correction, geometric registration, radiometric calibration and other pre-processing of commonly used images. It enables swift realization of image acquisition, batch processing, calculation and analysis by means of on-line programming, which can greatly improve the operational efficiency (Hansen et al., 2013; Gorelick et al., 2017). With the GEE cloud platform, the FVC of the study area can be uniformly and quickly estimated, and the long time series dynamic monitoring of vegetation can be realized (Fu et al., 2022b).

Geographic conditions at high altitudes are relatively complex, with strong spatial heterogeneity in vegetation cover and climate. Therefore, the influence of topographic and climatic factors on highland vegetation has received widespread attention (Wei et al., 2022; Han et al., 2023; Xu and Wu, 2023). At the same time, compared with low-altitude areas, high-altitude areas are often different from each other and cannot be generalized. Even within the same geographic unit, there are differences in the response of vegetation to climatic factors such as temperature and precipitation (Deng et al., 2022b). However, current vegetation monitoring at high altitudes tends to focus on the entire plateau area, using coarse resolution (>500m) AVHRR or MODIS remote sensing imagery to analyze spatial and temporal changes in vegetation (Zhang and Jin, 2021; Han et al., 2023; Huang et al., 2023). It was shown that the spatial resolution of remote sensing images may affect the accuracy of FVC estimation, and suitable remote sensing images need to be selected according to the study area (Zhang et al., 2014; Wang et al., 2022). Landsat imagery has not only higher spatial resolution but also longer time series, which is more suitable for monitoring vegetation at high altitudes at medium regional scales (Wang et al., 2022). Few studies have focused on the investigation of coverage changes of vegetation in mountainous areas. Moreover, the reactions of vegetation to climate variation and topography in complex terrain regions were seldom analyzed. The Baima Snow Mountain National Nature Reserve (BNNR) is located in the transition zone between the Tibetan Plateau and the Yunnan-Guizhou Plateau. The terrain is complex and diverse, with large elevation differences (>3500 m) and a rich variety of vegetation types (Ning et al., 2012). This geomorphological feature makes the vegetation in the BNNR more sensitive to topographic and climatic factors. Therefore, the BNNR is an ideal site for studying the effects of climate change on vegetation growth. By conducting research in the area, it is possible to better understand how topographic and climatic factors interact, providing valuable references and recommendations for ecological conservation. Therefore, in order to realize the monitoring variability of vegetative cover in nature reserves and find relationships of the variations to terrain and climate shifts, the purposes of this research involve: (1) to quantitatively estimate of long time series FVC (1986-2020) in the whole study area with complex terrain, and analyze the spatial and temporal change of vegetative cover; (2) to develop a TS (Theil-Sen slope estimator) MK (Mann-Kendall test) - FVC based approach for accurately evaluating and predicting of the spatio-temporal changes of vegetative coverage, and investigate the reaction of vegetative cover to topography and climate in the BNNR.

2 Materials

2.1 Study area

The Baima Snow Mountain National Nature Reserve is situated in Diqing Tibetan Autonomous Prefecture, Yunnan Province. Its northern portion belongs to Deqin County, while its southern part lies within Weixi County. The geographical coordinates of the BNNR are between 98°57′-99°25′E and 27°24′-28°36′N. Within the core of the Hengduan Mountains is where the BNNR is situated, between the Jinsha River and the Lancang River, the famous Three Parallel Rivers Region. The main river flowing through the reserve is the Zhubaluo River, which originates from the Baima Snow Mountain, with a drainage area of 1835km^2. The BNNR has a prominent monsoon climate characterized by distinct wet and dry seasons, and rainfall is mainly centered in July and August. Furthermore, the BNNR's precipitation distribution is spatially inhomogeneous. Due to topographic and climatic factors, precipitation is much higher in the valley of the Zhubaluo River and the south than in other areas. The BNNR is rich in biodiversity and is an important habitat for the worldwide precious and threatened species and national-level protected animal, the Yunnan snub-nosed monkey. The perpendicular arrangement of vegetation in the region is obvious. Perpendicular distribution of vegetation can be separated into river valley shrubs and tussock, broadleaf forest, coniferous forest, and meadow according to the altitude from 2500m to 5000m (Sun et al., 2017; Su et al., 2022). Examining the features of the vegetation's temporal and spatial distribution as well as the impacts of topography and climate on plants is crucial given the unique topographic and climatic circumstances of the BNNR (see Figure 1).

2.2 Remote sensing data

Satellite images utilized in this study include Landsat 5 (1986-2012) and Landsat 8 (2013-2020). The images were acquired from the USGS. Landsat Surface Reflectance (SR) data for the years 1986–2020 were obtained using the Google Earth Engine (GEE) platform (https://code.earthengine.google.com/). The spatial resolution of the data is 30m, and it has been pre-processed including atmospheric correction and geometric correction. Since most areas of the BNNR were covered by clouds all year round, the remote sensing images need to be de-clouded. The QA quality band of SR remote sensing images was operated bit by bit to realize the filtering of pixel values. Masking of clouds, cloud shadows and snow pixels of remote sensing images to finally remove clouds and snow (Zhu and Woodcock, 2012).

By processing SRTM DEM data, derived data products including altitude, slope, and aspect are generated. The spatial resolution of the DEM data is 30 m. Based on the local conditions of the BNNR and related literature (Wang et al., 2021b; Deng et al., 2022a), the topographic data were reclassified (Figure 2). In order to examine the influence of terrain on vegetative cover, FVC computations will be spatially overlaid with altitude, slope, and aspect data in subsequent analyses.

Meteorological data can be downloaded from the National Earth System Science Data Center website (http://www.geodata.cn/). The dataset includes the 1 km resolution monthly precipitation and average temperature dataset between 1986 and 2020. This data was cropped, resampled and algebraically manipulated to finally obtain the temperature and precipitation data of BNNR (Peng et al., 2019).

Data on vegetative cover categories were downloaded from Data Center for Environmental and Resources Sciences (https://www.resdc.cn/). The dataset comprises 11 vegetation categories, of which 7 are distributed within BNNR.

3 Methods

3.1 The long time series FVC calculation based dimidiate pixel model

NDVI is normally seen as an effective index reflecting large-scale vegetation coverage and growth status, and is among the most

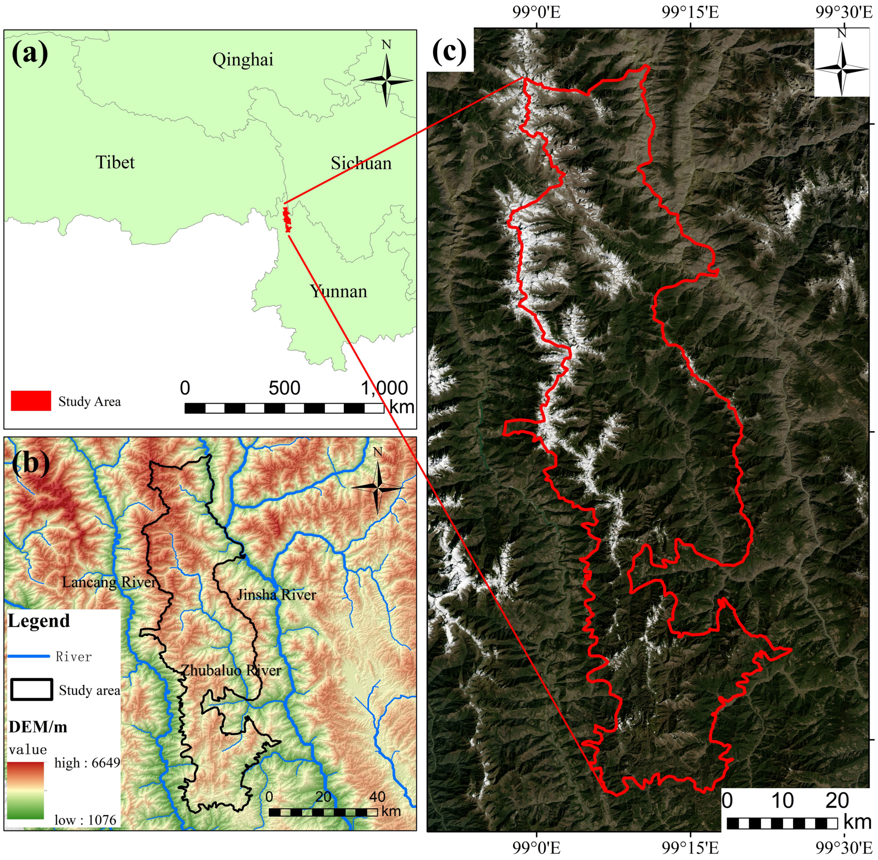

FIGURE 1
Overview of Baima Snow Mountain National Nature Reserve (BNNR); **(A)** location of the BNNR; **(B)** topography; **(C)** Landsat image (2020).

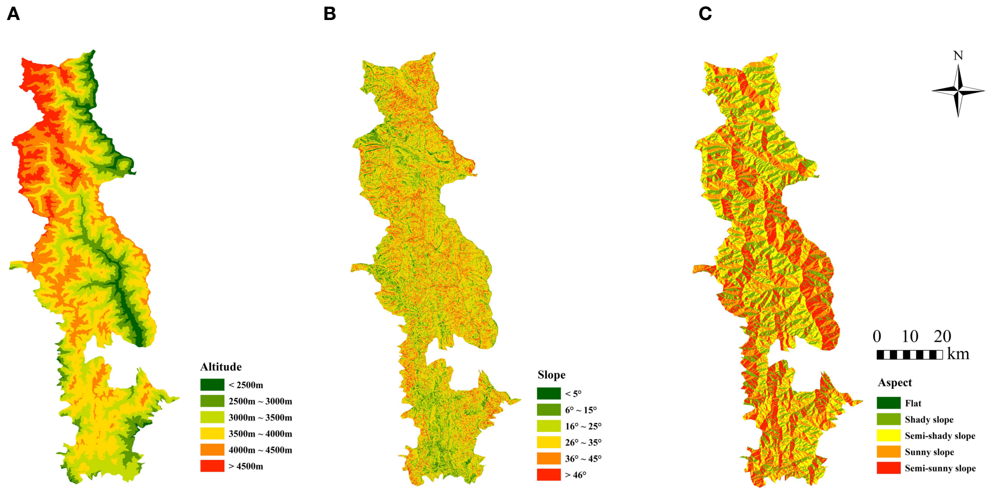

FIGURE 2
Spatial distribution of terrain factor classification results in BNNR; **(A)** altitude was divided into 6 categories; **(B)** slope was categorized into 6 categories; **(C)** aspect is categorized into 5 categories.

extensively applied vegetation indices (Schultz et al., 2016; Lu et al., 2019; Vulova et al., 2023). In this research, Surface Reflectance (SR) images of Landsat were used to calculate NDVI in accordance with GEE cloud platform, and Maximum Value Composites (MVC) were applied to composite the NDVI data spanning from 1985 and 2020 (Lanorte et al., 2014; Liu et al., 2022). Owing to the effects of satellite sensor performance, cloud cover and atmospheric conditions, NDVI time series dataset has serious noise (Goward

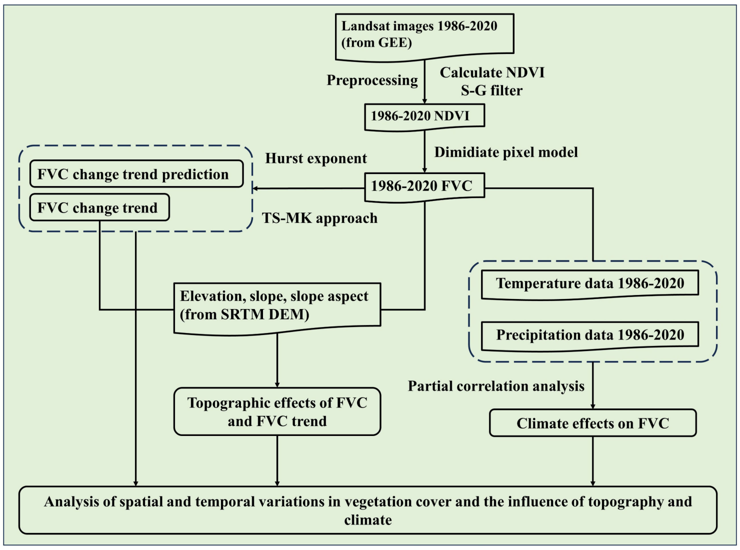

FIGURE 3
Flow chart of assessing and predicting the spatio-temporal variability of vegetation cover based on an advanced TSMK-FVC approach using Google Earth Engine in BNNR.

et al., 1991). Therefore, it was imperative to correctly and effectively remove noise and reconstruct NDVI time series dataset before application. Previous research has demonstrated that S-G filtering can effectively improve the data quality of vegetation index products (Chen et al., 2004; Shao et al., 2016). In this paper, S-G filtering method was for application in rebuild time series of NDVI data to remove noise (see Figure 3) (Zhao and Zhang, 2018; Han et al., 2020).

Further calculation of FVC based on NDVI can help alleviate the issue of NDVI saturation in monitoring areas with high vegetation cover and difficulty in identification in areas with low vegetation cover. In many studies, there were three typical methods to estimate vegetation cover using remote sensing data, such as the Empirical method, the Spectral Mixture Analysis method and the DPM (Jiapaer et al., 2011). The DPM is a fast and effective method for calculating FVC because it is easy to operate and has performed well (Shi et al., 2021b; Hill and Guerschman, 2022). The principle of the DPM involves assuming that the reflectance *(R)* of a pixel consists of two components: the part with vegetation cover (R_V) and the part without vegetation cover (R_S). Subsequently, the spectral information observed through the sensor is synthesized by the linear weighting of these two components.

$$\boldsymbol{R} = \boldsymbol{R}_V + \boldsymbol{R}_s \tag{1}$$

The proportion of the area of a pixel that has vegetation cover is FVC, which is the vegetation cover percentage of the pixel. Consequently, the proportion of the area that is not covered by vegetation is *(1-FVC)*. The reflectance of a pixel is R_{veg} if the pixel is completely covered by vegetation and R_{soil} if it is completely covered by soil. The information contributed by the vegetated portion of the hybrid pixel can be expressed as the product of the purely vegetated reflectance, R_{veg}, and the area covered by vegetation in the image element, *FVC*. And the information contributed by the non-vegetated component can be expressed as the product of R_{soil} and *(1-FVC)*.

$$\boldsymbol{R}_V = \boldsymbol{R}_{veg} \times \boldsymbol{FVC} \tag{2}$$

$$\boldsymbol{R}_s = \boldsymbol{R}_{soil} \times (\boldsymbol{1} - \boldsymbol{FVC}) \tag{3}$$

By solving Equations 1–3, the FVC can be calculated as Equation 4:

$$\boldsymbol{FVC} = \frac{\boldsymbol{R} - \boldsymbol{R}_{soil}}{\boldsymbol{R}_{veg} + \boldsymbol{R}_{soil}} \tag{4}$$

In the inversion of FVC using NDVI, NDVI can be used instead of *R*. This results in the formula for calculating FVC based on NDVI (see Equation 5):

$$\boldsymbol{FVC} = \frac{\boldsymbol{NDVI} - \boldsymbol{NDVI}_{soil}}{\boldsymbol{NDVI}_{veg} + \boldsymbol{NDVI}_{soil}} \tag{5}$$

Since the theoretical values of bare ground $NDVI_{soil}$ and pure vegetation cover $NDVI_{veg}$ should be close to 0 and 1, respectively. The FVC was calculated by intercepting the upper and lower NDVI thresholds with 5% confidence, and averaging the 5% areas with the smallest and the largest NDVI values, respectively, to obtain the $NDVI_{soil}$ and $NDVI_{veg}$.

3.2 FVC dynamic analysis method

3.2.1 Trend in FVC

With the objective of investigating the spatial distribution and temporal variations of vegetative cover in the BNNR from 1986 to 2020. Tendency and stability characteristics of vegetation cover have been investigated utilizing the Mann-Kendall test (MK) and the Theil-Sen slope estimator (TS).

TS is considered suitable for investigating the slope tendency in time series data (Sun et al., 2021). This method has advantages including insensitivity to measurement error and group data as well as high computational efficiency (Peng et al., 2015). MK is one of the commonly used tools for nonparametric trend testing, which is not necessary that the data samples follow a specific pattern, as well as can be used to test the trend of data changes under long time series (Yue et al., 2002; Luo et al., 2020). Combining TS and MK will provide a strong anti-interference ability for data noise, and the specific distribution of analysis data is not a prerequisite (Zhang et al., 2022b). Thus, TS-MK was applied to investigate the trend of the dynamic shifts in FVC of the BNNR. The formula of TS equation is as follows (see Equation 6):

$$S_{FVC} = median\frac{FVC_b - FVC_a}{b-a} \tag{6}$$

Where 1< a< b< n, a and b represent the amounts of years in the time series. FVC_b and FVC_a are the FVC values of time series a and b, respectively. When the slope S_{FVC} is greater than 0, it indicates a growth tendency; when it is less than 0, it indicates a downward tendency.

The calculation formula of Manna-Kendall test is shown in Equations 7–10:

$$S = \sum_{j}^{n-1}\sum_{i=j+1}^{n} sgn(FVC_j - FVC_i) \tag{7}$$

$$sgn(FVC_j - FVC_i) = \begin{cases} 1 & FVC_j - FVC_i > 0 \\ 0 & FVC_j - FVC_i = 0 \\ -1 & FVC_j - FVC_i < 0 \end{cases} \tag{8}$$

$$Z = \begin{cases} \frac{S-1}{\sqrt{Var(S)}} & (S > 0) \\ 0 & (S = 0) \\ \frac{S+1}{\sqrt{Var(S)}} & (S < 0) \end{cases} \tag{9}$$

$$Var(S) = \frac{n(n-1)(2n+5)}{18} \tag{10}$$

Where S is the correlation coefficient of the Mann-Kendall test; Z is the significance index, and its value range is (-∞, +∞), which follows the standard normal distribution. Z-value greater than 0 represents a significant increasing tendency, while a Z-value less than 0 represents a significant decreasing trend.

3.2.2 FVC trend prediction

The Hurst exponent was employed in this research to forecast the FVC trend in the BNNR going forward. Hurst originally introduced the Hurst exponent, which is a way to determine if continuous time series data exhibit long-term correlation (Bashir et al., 2020). This exponent was established using R/S analysis on the basis of long-term hydrological observations (Zhang and Jin, 2021). The Hurst index is generally in the range from 0 to 1. When 0< H< 0.5, the future tendency of FVC will be reversed; when H=0.5, the development trend of FVC is unpredictable; when H is greater than 0.5 and less than 1, the future time series of FVC remains in agreement with what has happened previously (Tong et al., 2018; Liu et al., 2022). The selection of the time window for the Hurst exponent requires consideration of the study object and the cloudiness of the study area (Zhu et al., 2021; Fu et al., 2022b). Since the dominant tree species in the study area are all evergreen and have high cloudiness in the growing season. Therefore, to achieve year-by-year time series FVC estimation in the study area, FVC with a time window of the non-growing season was used for Hurst exponent calculation. The Hurst exponent is calculated as shown in Equations 11–15.

Define the FVC time series as $FVC(\tau)$, The mean of this time series is:

$$\overline{FVC_{(\tau)}} = \frac{1}{\tau}\sum_{t=1}^{\tau} FVC_{(t)}, \tau = 1, 2, 3\cdots, n \tag{11}$$

The cumulative deviation is:

$$U(t,\tau) = \sum_{t=1}^{\tau}\left(FVC_{(t)} - \overline{FVC_{(\tau)}}\right), 1 \le t \le \tau \tag{12}$$

The range $R(\tau)$ is:

$$R_{(\tau)} = maxU_{(t,\tau)} - minU_{(t,\tau)} \tag{13}$$

The standard deviation sequence is:

$$S_{(\tau)} = \sqrt{\frac{1}{\tau}\sum_{\tau=1}^{\tau}\left(FVC_{(t)} - \overline{FVC_{(\tau)}}\right)^2} \tag{14}$$

Calculate the Hurst exponent:

$$R_{(\tau)}/S_{(\tau)} = (\alpha\tau)^H \tag{15}$$

where H represents the Hurst exponent in the range greater than 0 and less than 1.

Afterwards, the Hurst exponent and TS results were overlaid to get coupled data on the changes' tendency and consistency, and the results were classified as: (1) decrease to increase; (2) consistent decrease; (3) increase to decrease; (4) consistent increase (see Table 1).

TABLE 1 Future trend categories of FVC combining Hurst exponent and TS.

Continuation/ FVC trends	FVC decrease trend	FVC increase trend
Consistent trends (0.5< H< 1)	Consistent decrease	Consistent increase
Inconsistent trends (0< H< 0.5)	Decrease to increase	Increase to decrease

3.3 Relevance analysis of FVC with climatic elements

Pixel-by-pixel calculation of the relevance among FVC data and climatic elements for the BNNR from 1986 to 2020. The correlation coefficients were calculated using the Equation 16:

$$R_{ab} = \frac{\sum_{i=1}^{n}(x_i - \bar{x})(y_i - \bar{y})}{\sqrt{\sum_{i=1}^{n}(x_i - \bar{x})^2}\sqrt{\sum_{i=1}^{n}(y_i - \bar{y})^2}} \quad (16)$$

where R_{xy} is the correlation coefficient of factor x and factor y.

When multiple factors are correlated with FVC simultaneously, the use of partial correlation analysis allows individual variables to be analyzed separately for their degree of correlation with FVC (Yuan et al., 2019). The equation of partial correlation analysis is shown below (see Equation 17):

$$R_{xy,z} = \frac{R_{xy} - R_{xz}R_{yz}}{\sqrt{(1 - R_{xz}^2)(1 - R_{yz}^2)}} \quad (17)$$

Where $R_{xy,z}$ denotes the partial correlation coefficient of the x and y variables fixed factor z after. R_{xy}, R_{xz}, and R_{yz} are the correlation coefficients of their variables, respectively. Where the values of the coefficients range from -1 to 1.

4 Results

4.1 Temporal and spatial properties of FVC

4.1.1 Characterization of spatial distribution of FVC

According to the FVC classification standards and pertinent studies (Liu et al., 2022; He et al., 2023), FVC values were categorized into five classes and corresponded to different landscapes (see Table 2). Figure 4A illustrates the spatial distribution of FVC in the BNNR between 1986 and 2020. Areas of higher FVC are situated primarily at the BNNR's eastern and southern regions. The northern and west-central snow-covered areas of the study area have lower FVC. Compared to 1986, the Class V FVC coverage area in 2000 and 2020 showed significant growth, primarily located in the BNNR's central and southern regions.

4.1.2 Characterization of FVC variation over time

The mean FVC value in the research region has exhibited a tendency to increase in a wavering manner over these thirty-five years (see Figure 5A). The average FVC increases from 59.40% in 1986 to 68.67% in 2020, an increase of 0.26% per decade. Throughout this 35-year period, the average annual FVC experienced two significant declines, with the turnaround occurring in 1994 and 2001. The decline in FVC may be attributed to climate-related disasters, and the implementation of ecological policies, such as the return of grazing land to forests, has to some extent contributed to the recovery of vegetation. The highest mean FVC of 72.53% occurred in 2018. The lowest mean FVC was 59.41% in 1986.

TABLE 2 FVC is categorized into five categories and landscapes.

Vegetation coverage value	Categories	Landscape
FVC< 30%	class I	Bare land, snow-covered land, etc.
30% ≤ FVC< 45%	class II	Valley scrub, grassland, etc.
45% ≤ FVC< 60%	class III	Grassland, cropland, etc.
60% ≤ FVC< 75%	class IV	Shrubland, etc.
75%< FVC	class V	Woodland, etc.

Further statistics were made on the changing trend of FVC of different classes in BNNR between 1986 and 2020. Among these classes, FVC for class I, II, III, and IV tended to decline, decreasing by 6.19%, 3.64%, 3.93%, and 5.00%, respectively. The corresponding class V showed an obvious upward trend, rising from 39.28% in 1986 to 58.03% (see Figures 4B, 5B). The improving trend in fast FVC in the BNNR is dominated by the continued growth of high-class FVC.

A total of seven vegetation types (alpine vegetation, coniferous forest, broadleaf forest, meadow, shrub, tussock, and cultivated vegetation) were distributed in the BNNR. The more widely distributed vegetation types are coniferous forest and shrub, accounting for 32.51% and 31.79% of the BNNR, respectively. The FVC of all vegetation types exhibited an upward trend to varying degrees during these 35 years, with the more significant increases mainly in tussock (15.86% increase), cultivated vegetation (14.97% increase), shrub (11.32% increase), and coniferous forest (10.94% increase) (see Figure 5C).

4.2 FVC change trend and prediction

4.2.1 FVC change trend

The results of TS analysis can be classified into three categories based on the slope of FVC changes: S_{FVC}< -0.0005, -0.0005< S_{FVC}< 0.0005, and S_{FVC} > 0.0005, indicating decreasing, no change, and increasing trends in FVC, respectively (see Table 3). As illustrated in Figure 6A, the area of the BNNR with an upward trend is 1651.57km^2 and the area with a downward trend is 619.13km^2, which account for 59.03% and 22.13% of the area, individually.

Among the area proportion of each trend, 61.48km^2 and 118.23km^2 of FVC were significantly reduced and very

TABLE 3 TS (S_{FVC}) and MK (Z-value) were combined to investigate the tendency of FVC and the findings were classified into five groups.

S_{FVC}	Z-value	category	area/km^2
S_{FVC}< -0.0005	2.58< |Z|	Extremely significant decrease	109.38
	1.96< |Z| ≤ 2.58	Significant decrease	63.01
-0.0005< S_{FVC}<0.0005	|Z|< 1.96	No significant change	1901.94
S_{FVC} > 0.0005	1.96< |Z| ≤ 2.58	Significantly increase	284.53
	2.58< |Z|	Extremely significant increase	439.16

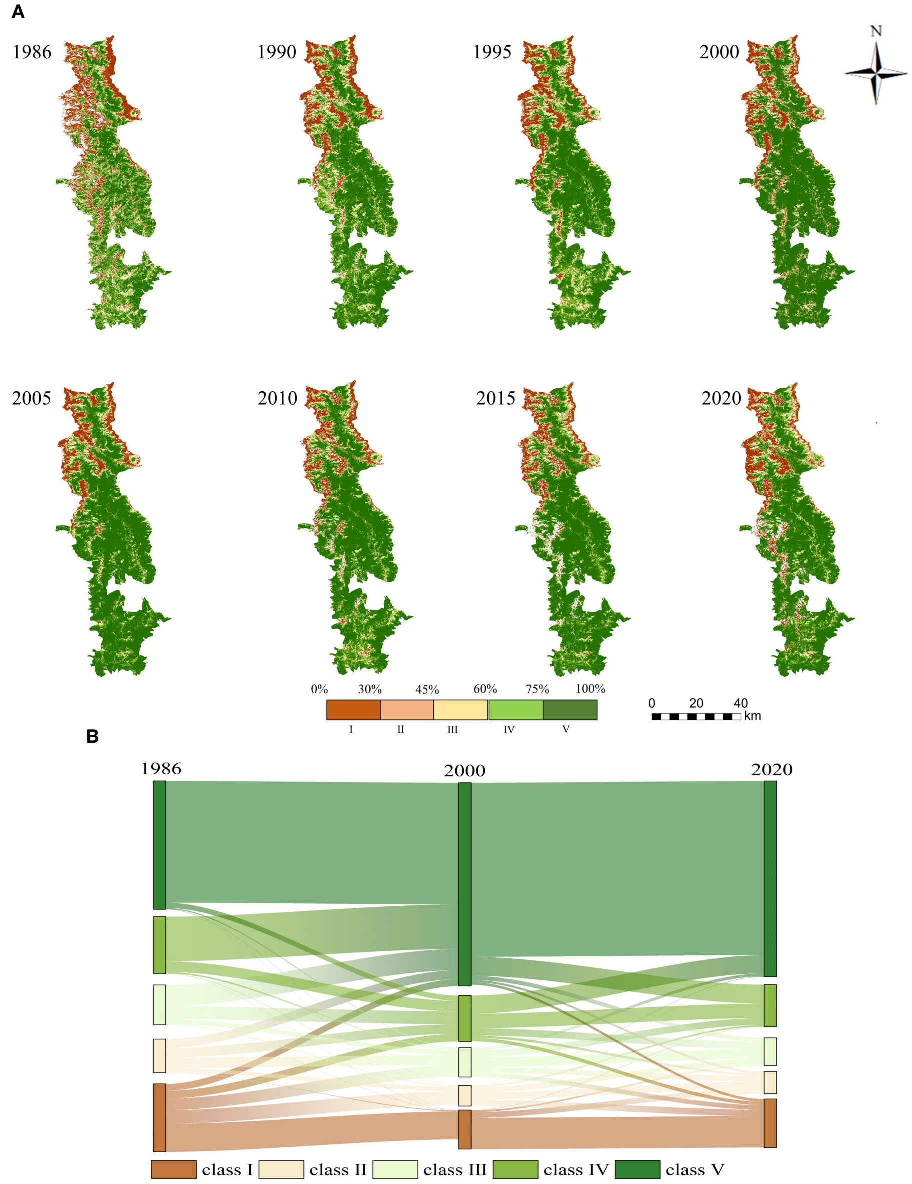

FIGURE 4
Modifications in the space distribution of FVC throughout the BNNR; **(A)** space distribution of FVC by class in the research region from 1986 to 2020; **(B)** sankey diagram of FVC proportion shift of different classes in the research region from 1986 to 2020.

significantly decreased, accounting for 2.20% and 4.23% of the BNNR (see Figure 6B). The area where the decrease of FVC occurred is mainly on both sides of the Zhubaluo River and in the southeastern part near the boundary of the reserve. All of these regions have relatively high levels of human activity. However, there are more areas showing significant vegetation recovery than significant vegetation decline. The areas of significant and extremely significant increase of FVC were 286.24km^2 and 498.44km^2, accounting for 10.23% and 17.81% of the BNNR (see Figure 6B). The regions of vegetation restoration are predominantly situated around the snowy mountains in the north and in the southwestern part of the research region. In addition, in the eastern part of the BNNR, regions of vegetation recovery and deterioration are patchy.

4.2.2 FVC change trend prediction

The overall trend of vegetation change in the BNNR appears to be persistent, as indicated by the Hurst index research. Specifically, the area with a Hurst index greater than 0.5 accounted for 76.7% of the total area of the study area, while the percentage of the area less than 0.5 was 4.0% (see Figure 7A). The results of the TS analysis were integrated with the Hurst index to investigate the degree of sustainability of the FVC. The results of the research are depicted in Figure 7B), where the area transitioning from FVC reduction to growth and sustained growth are 24.17km^2 and 1551.06km^2, respectively. Conversely, the area transitioning from FVC improvement to degradation and sustained degradation are 82.71km^2 and 487.13km^2, respectively. Since the vegetation in most areas will continue the past trend, the distribution of FVC

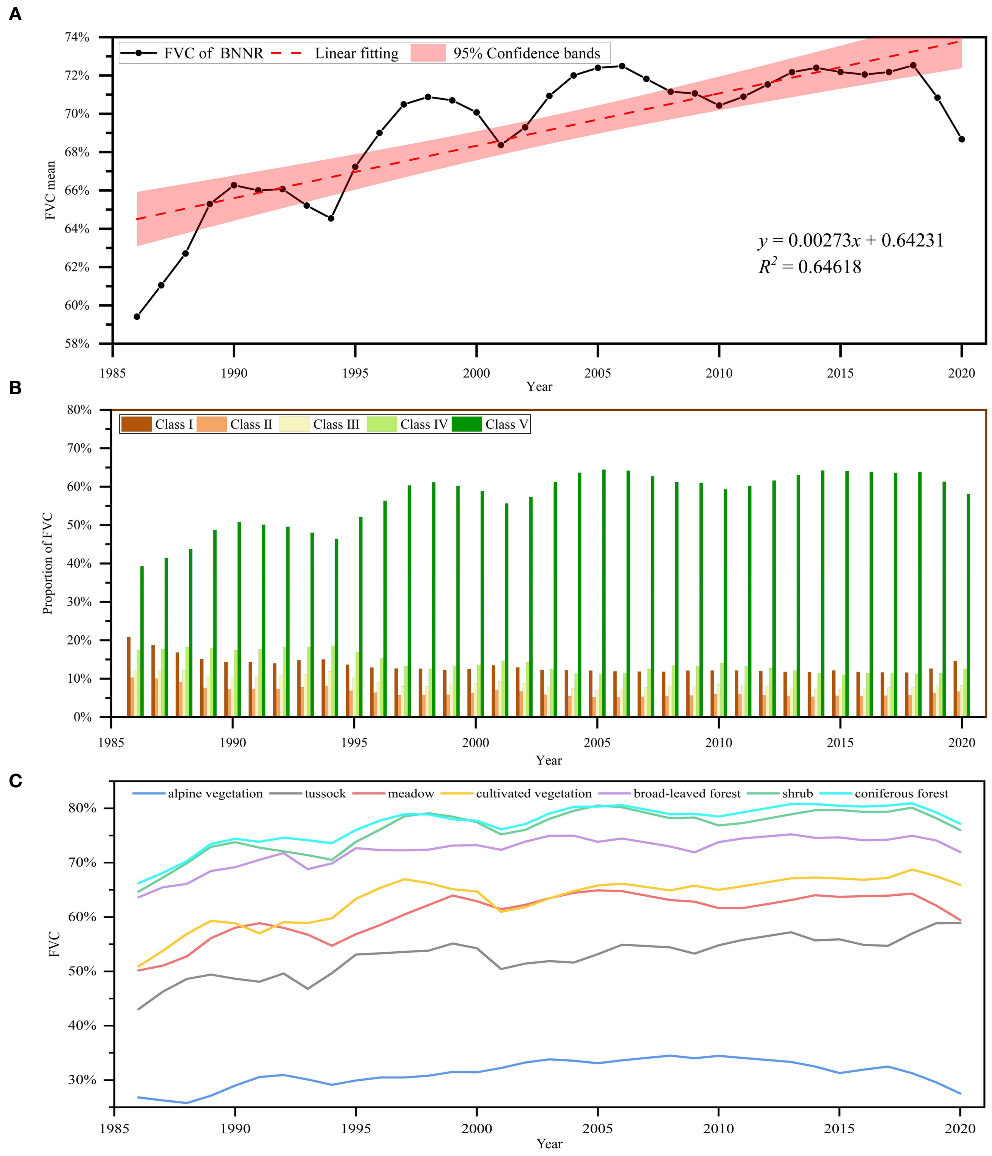

FIGURE 5
Temporal variation in FVC in the BNNR; **(A)** Interannual change in the mean FVC from 1986 to 2020; **(B)** changes in FVC by class in the BNNR from 1986 to 2020; **(C)** variations in mean FVC for various vegetation categories from 1986 to 2020.

growth and decline in the future BNNR will basically coincide with the past trend.

4.3 FVC influence factor analysis

4.3.1 Terrain effects of FVC

Based on the actual situation of the BNNR and related literature, its altitude, slope, and aspect were reclassified to explore the influence of topographic effect on FVC. The area proportion of FVC classes varies significantly with the elevation (see Figure 8A). The proportion of class I fluctuated greatly at different elevations. In the elevation range from 2500m to 3500m, the proportion of class V increases with the elevation, while the proportion of class I and class II decreases in this elevation range. However, in the area with elevation greater than 3500 m, the proportion of class I area increases with the elevation, especially in the area above 4500m, reaching up to 82%. But the proportion of class IV and class V in this area is even less than 1%. The variation trend of FVC also has an obvious terrain response at different elevations (see Figure 8D). Both vegetation deterioration ($P< 0.05$) and recovery ($P< 0.05$) are primarily located at altitudes intervals below 4500 m, and reach the maximum value between 2500 m and 3000 m. The proportion of regions with vegetation deterioration ($P< 0.05$) and recovery ($P< 0.05$) in FVC was 13% and 39%, respectively, at altitudes from 2500m to 3000m. It can be seen that the elevation zones with higher vegetation cover are also the places with the most drastic changes in vegetation cover. In addition, at elevations greater than 3000 m, the percentage of area with significant changes in vegetation decreases with elevation.

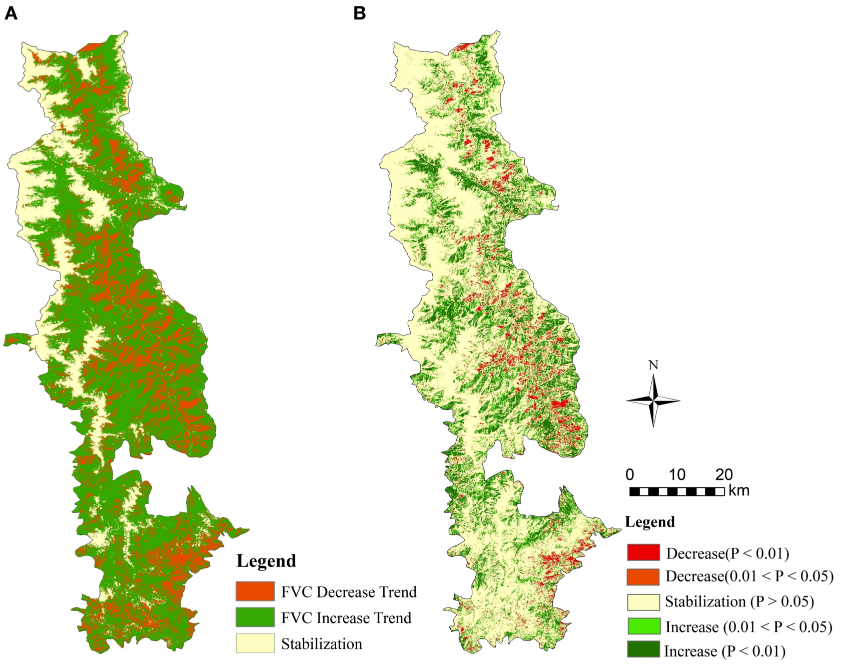

FIGURE 6
Spatial distribution of FVC 1986-2020 tendency in the BNNR; **(A)** the findings of TS analysis; **(B)** tendency in FVC 1986-2020 in the BNNR combining TS and MK.

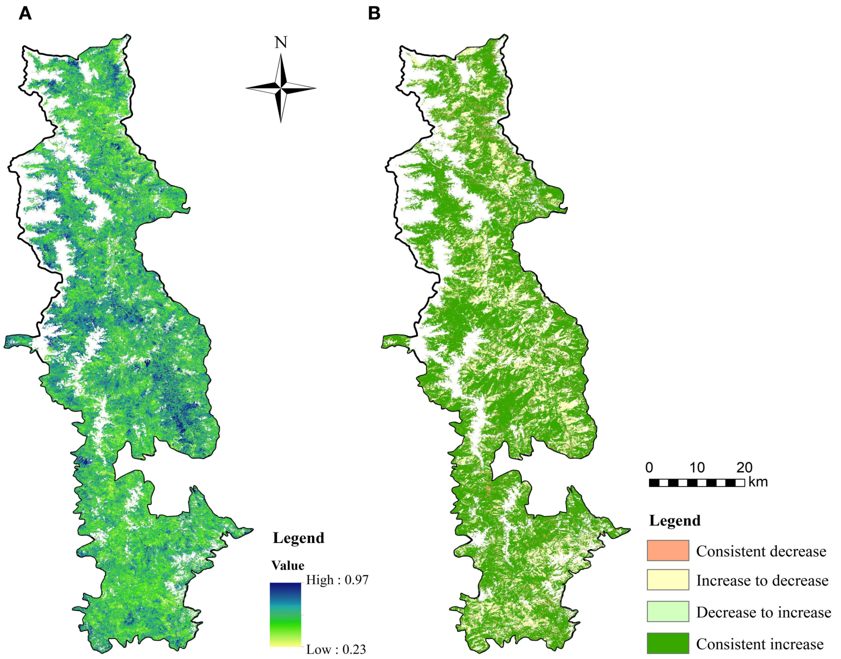

FIGURE 7
Projections of future trends in FVC in the BNNR combined the Hurst exponent with TS; **(A)** results of the Hurst exponent; **(B)** future change trend distribution of FVC.

Ultimately, at elevations greater than 4500m, vegetation is largely unchanged.

The proportion of area in class V increases with slope gradient from 46% for flat slopes to 66% for steep slopes when the slope is less than 35° (see Figure 8B). Concurrently, class IV, class III, and class II decreased by 6%, 7% and 5% respectively from flat slope to steep slope. The FVC significantly reduced proportion increases with the slope increasing, from 4% for flat slopes (<5°) to 10% for dangerous slopes (>46°) (see Figure 8E). The proportion of significant increase reaches its peak value in the slope range of 26°~45°. However, the difference in

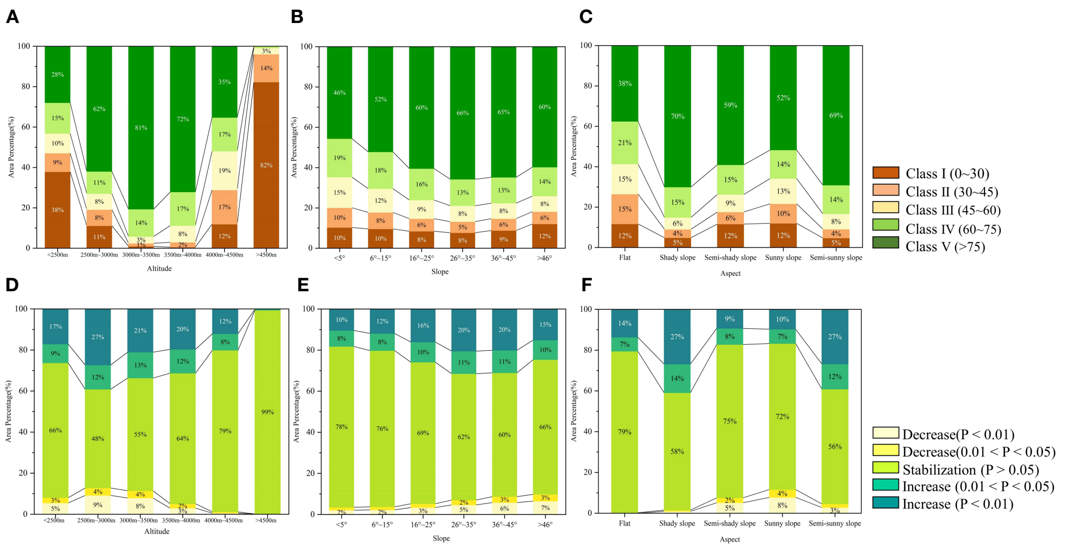

FIGURE 8
Proportion of each class FVC and FVC change trend in terrain factors; **(A)** proportion of FVC classes at various altitudes, **(B)** slopes, **(C)** and aspects; **(D)** proportion of FVC change trend at various altitudes, **(E)** slopes, **(F)** and aspects.

FVC between different slopes is relatively small compared to the difference in FVC between different altitudes and aspects.

The percentage of class V FVC in the BNNR is relatively higher on the shady slopes and semi-sunny slopes compared to other aspects (see Figure 8C). Additionally, the percentage of significant increases is higher for shady and semi-sunny slopes than for other slope orientations, while the percentage of significant decreases is relatively high for sunny and semi-sunny slopes (see Figure 8F). Specifically, shady slopes accounted for less than 2% of the area of significant FVC reductions, while sunny slopes accounted for 12% of the area of significant reductions. Conversely, the ratio of each grade of FVC does not differ much on the flats, and fewer areas with significant vegetative changes.

In summary, the distribution and changes in vegetative cover in the BNNR are likely more influenced by elevation compared to slope and aspect. Therefore, the vegetation in the BNNR with an altitude of 2500m to 3500m and located on the sunny slopes needs more attention.

4.3.2 Climate effects on FVC

The annual mean temperature of the BNNR stands at 4.2°C, displaying a fluctuating upward trend over the 35-year period. There's a notable difference of 1.6°C between the highest (5.0°C in 2009) and lowest (3.4°C in 1992) annual mean temperatures (see Figure 9). Moreover, the average annual precipitation is recorded at 733.5 mm, with a slowly declining trend but significant inter-annual fluctuations. The disparity between the highest precipitation year (939.4 mm in 1998) and the lowest year (538.9 mm in 2014) is nearly 400 mm. Overall, temperature decreases from east to northwest in the BNNR, primarily influenced by topography. The lowest mean annual temperatures occur in the snow-covered mountainous areas at high elevations, while the highest mean annual temperatures are observed in the valleys at lower elevations. The spatial distribution of annual precipitation varies widely, with areas of higher precipitation distributed only in the southern part of the BNNR and along the banks of the Zhubaluo River.

For the majority of the BNNR (62.65%), there was a positive correlation between FVC and temperature; of this, 27.90% of the region demonstrated a significant positive association ($p<0.05$) (see Figures 10A, C). The percentage of area where FVC is negatively correlated with annual mean temperature is 27.36%, with 7.63% of the negatively linked area is explained by a significant negative correlation. The southwestern and west-central sections of the BNNR are primarily home to the places where FVC and temperature have a major positive tie, while the negative correlation regions are primarily situated in the valley area of the BNNR's northern part, on both sides of the Zhubaluo River in the central part, and in the southeastern part. Combined with the topography, it can be found that the negative correlation area is mostly distributed in the area of low elevation. The correlation between FVC and precipitation is indicated in Figures 10B, D), the area with positive correlation is 52.64% of the BNNR, while the negative correlation is 37.36%. Among them, significant positive correlation and significant negative correlation made up 7.79% and 3.11% of positive and negative correlations, respectively. The southern part of the BNNR is home to the majority of the regions where FVC and precipitation have a substantial positive association. The regions of negative correlation are located primarily in the northeastern portion. The findings revealed that the correlation between FVC and temperature is stronger in the BNNR compared to annual precipitation. The findings of the significance test confirm this view as well.

5 Discussion

5.1 FVC trend analysis

The lower FVC areas in the BNNR are concentrated in the snow-covered areas of the North and Midwest, as well as in the valleys. This finding is more in accordance with the local climate,

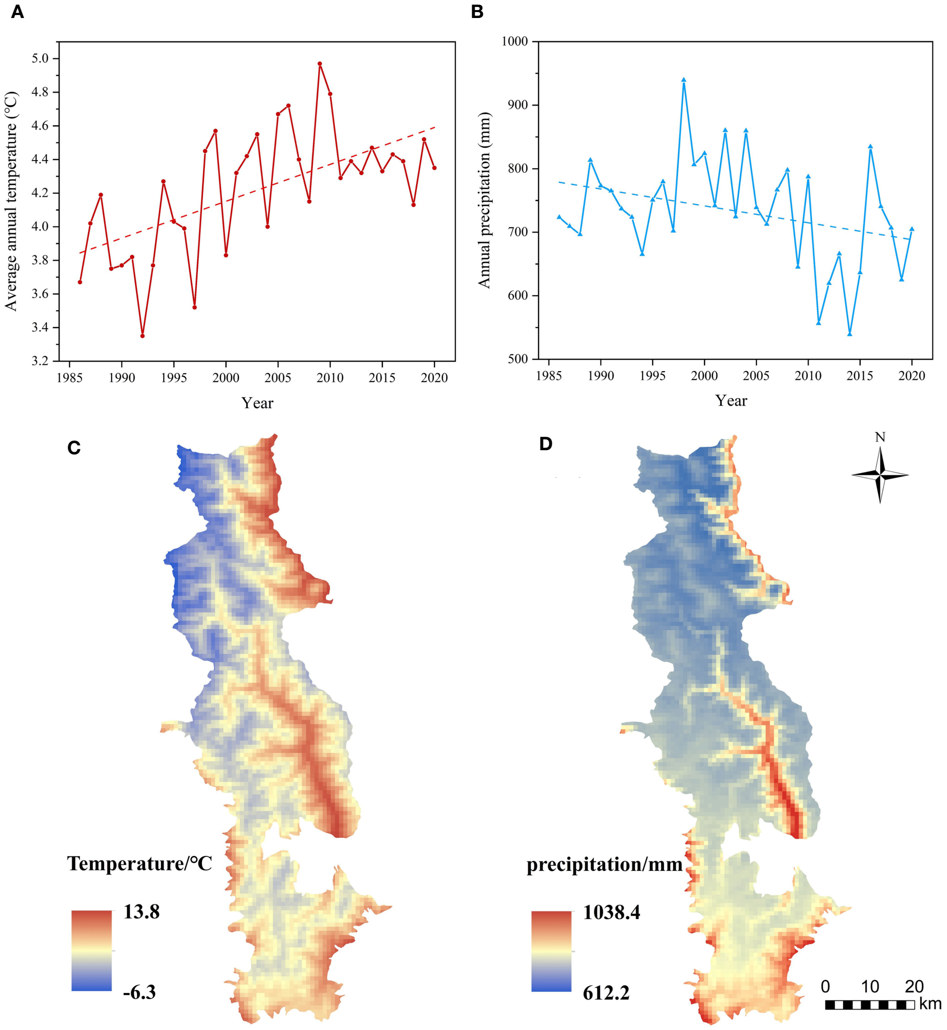

FIGURE 9
Temporal variation and distribution in space of temperature and precipitation; **(A)** temperature and **(B)** annual precipitation in the BNNR between 1986 and 2020; **(C)** differences in the space distribution of average temperature **(D)** precipitation.

the northwest part of the BNNR belongs to the Tibetan Plateau climate type, and the northeast part of the Jinsha River coast is owned by the arid river valley climate. These climatic influences render these areas more suitable for scrub and meadows, contributing to the lower FVC levels observed in the northern part of the BNNR (Chai et al., 2002). Conversely, regions around the towns of Xiaruo in the east-central part and Tacheng in the south, characterized by lower elevations and relatively higher moisture levels compared to the northern part, are more conducive to plant survival, resulting in higher vegetation cover.

Over the previous 35 years, there has been an overall upward trend in the BNNR's average annual FVC. However, the growth rate has been relatively slow, at about 2.65% per decade. This finding is consistent with the results of other researches in the south-eastern part of the QTP and the Three Parallel Rivers region (Li et al., 2016; Wang et al., 2021b). This trend is primarily beneficial due to the active response of the local government in implementing major ecological protection projects such as the Natural Forest Protection Project, and the Yangtze River Basin Forest Protection Project and so on (Yang, 2017; Li et al., 2021; Deng et al., 2022b). These initiatives have led to a reduction in anthropogenic disturbances while promoting afforestation and vegetation recovery efforts in the BNNR. The spatial distribution results of FVC trends indicate that the recovery and decline of vegetation are patchily distributed along the banks of the Zhubaluo River. The low altitude of the area, the predominant vegetation category of cultivated vegetation, as well as the frequency of agricultural activities make the vegetation changes along the river banks relatively complex (Liu et al., 2014; Wang et al., 2021a).

The Hurst exponent prediction results indicate a continued upward trend in FVC within the BNNR. However, based on the spatial distribution of tendency projections, it can be seen that the ecosystems in the eastern and southern fringes of the protected areas are relatively fragile. These regions are still subject to pressure from vegetation degradation, influenced by both natural processes and human activities.

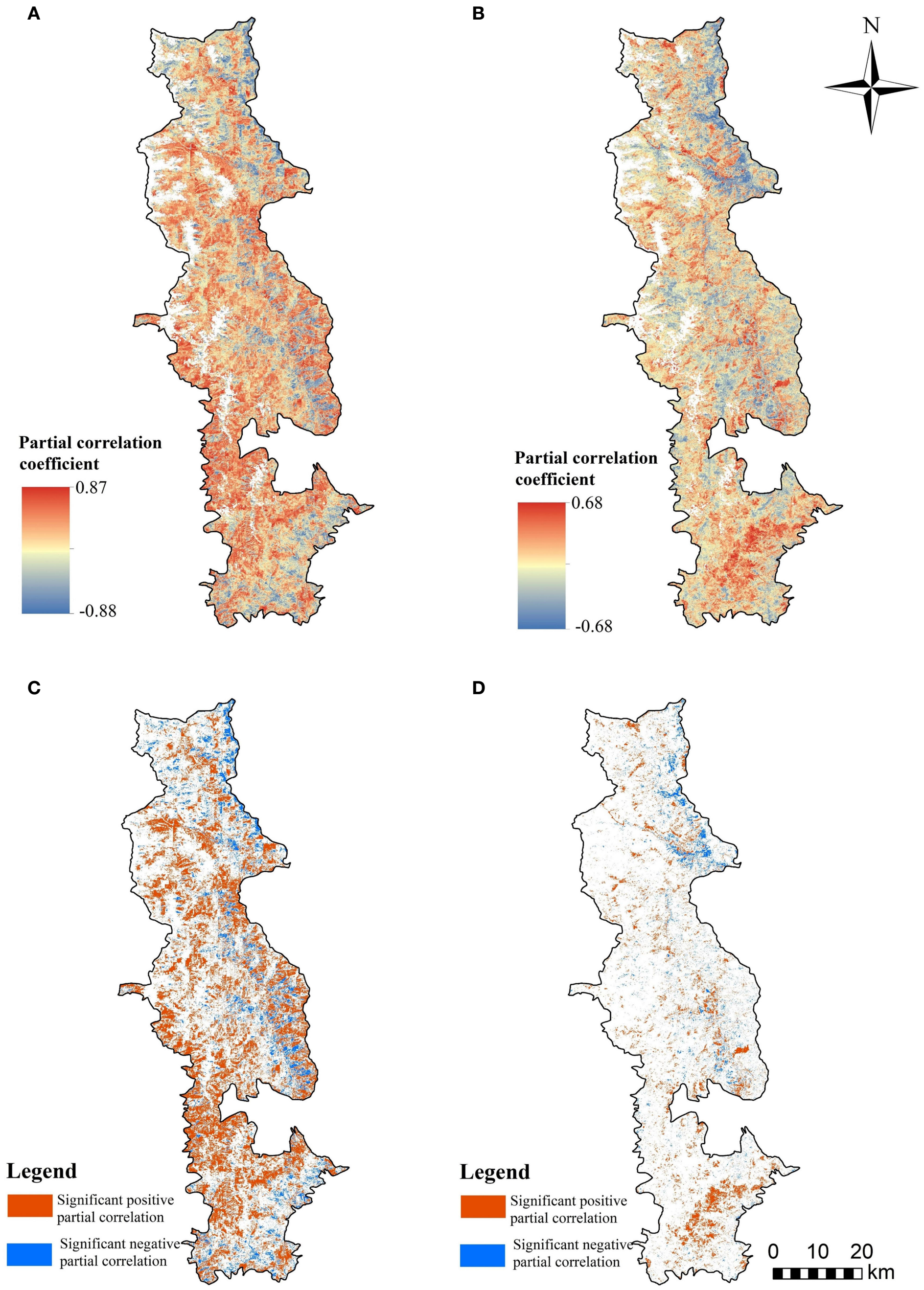

FIGURE 10
Partial correlation coefficient among FVC and climatic factors; **(A)** partial correlation among FVC and temperature **(B)** as well as precipitation; **(C)** significance test of partial correlation among FVC and annual mean temperature **(D)** as well as precipitation.

5.2 Topography and climate impact analysis on FVC

5.2.1 Effect of topography on vegetation cover

The vertical distribution of vegetative cover in the BNNR shows that the region below 3300m is cool coniferous forest, warm coniferous forest and river valley scrub; from 3300m to 4000m is cool coniferous forest, and above 4000m is scrub meadow (Fan and Bai, 2021; Shi et al., 2021a). Different categories of vegetation are strongly affected by the scale of the terrain, and therefore trends also vary (Li et al., 2016). In the altitude range from 2500m to 4000m, the distribution of class IV and class V is predominant, and the sum of the two is more than 70%. And the percentage of significant increase in FVC was also relatively high in this elevation interval. The possible reason for this is that the soil here is dominated by mountain brown loam with high soil fertility. Therefore, this elevation range has a relatively high vegetation cover ability. Conversely, the relatively low-altitude areas below 2500m and above 4500m in the reserve have low vegetation cover, with grassland and scrub dominating the vegetation. The lower areas, below 2500 m, are characterized by dry, hot river valleys with minimal precipitation and high evaporation, making them unsuitable for forests but conducive to shrubs and grasses (Chai et al., 2002; Zhang et al., 2019). Areas above 4500 m are characterized by year-round snow and ice cover, slow accumulation of organic matter, and a shortened growing season for vegetation as the altitude rises (Li et al., 2016). Vegetation degradation is primarily observed at altitudes of 2500 m to 3500 m. According to the relevant data, the areas suitable for agriculture and animal husbandry in the study region are mainly located at low altitude (Wang et al., 2023). This suggests that the incidence of vegetation degradation in some low elevation regions may be related to anthropogenic factors.

The research results revealed that the FVC of the BNNR peaked at slopes ranging from 26° to 45°, with minimal differences in FVC among different slope categories. This may be related to the fact that gently sloping areas are subject to more frequent anthropogenic disturbances, but such disturbances are decreasing as the slope increases. Moreover, the percentage of area significantly reduced of FVC increases with slope, but the change is small. Slope has a relatively limited effect on the distribution and tendency of FVC, and the difference in FVC between different slopes in the BNNR is small. This phenomenon may be due to the fact that with the increase gradually of slope, soil water and nutrients will be more easily lost, so that the percentage of vegetation decline in the higher slope area will be slightly increased (Zhang et al., 2013). Relevant studies show that vegetative coverage in the TPRR is highest at a slope of 35° (Wang et al., 2021b), and have concluded that vegetation in this region is less affected by slope (Huang et al., 2023), which is in agreement with the findings of this research.

In the BNNR, vegetative cover is lower on sunny and semi-shady slopes compared to other slopes. Vegetation degradation predominantly takes place on sunny and semi-shady slopes. Revegetation occurs mainly on shady and semi- sunny slopes. This may be due to differences in radiation, temperature and water evapotranspiration on different slopes (Zhang et al., 2022a), leading to differences in vegetation distribution and growth. Combined with the fact that the main tree species in the BNNR are trees of the *Abies* and *Picea* (Shi et al., 2021a), which are better adapted to a cooler and colder climate, the shady slopes are more suitable for growth.

In summary, the variances and shifts in vegetative cover distribution within the BNNR are likely more influenced by elevation than by other factors.

5.2.2 Impact of climate factors on vegetation cover

The QTP has long been acknowledged as a region experiencing more pronounced impacts from climate warming (Rangwala and Miller, 2012). Precipitation and temperature are the two primary climate elements that impact the growth of vegetative cover. In the BNNR, which is situated in the eastern section of the QTP, we found association between FVC and temperature was stronger than that of precipitation. This conclusion was further verified in the results of the significance test. Furthermore, this is in agreement with previous findings in the region that temperature is the leading element controlling or influencing vegetation cover increase in the region (Wang et al., 2021a; Guo et al., 2023). Owing to the relatively complicated terrain of the area, there are more pronounced spatial variations in the distribution of precipitation and temperature (Zhang et al., 2018; Guo et al., 2023), resulting in different correlations between FVC and climate elements in different areas. The relationship between temperature and elevation elements tends to have a more pronounced linear negative correlation, leading to possible differences in the response of vegetation dynamics to temperature. Wang et al. on the Tibetan Plateau showed that the correlation between vegetation and temperature varied at different altitudes, especially at altitudes above 2400 m, where temperature, instead of precipitation, played a major role in regulating the vegetation ecosystem (Wang et al., 2020).

Additionally, to some degree, the rise in temperature might encourage the development of plants (Wei et al., 2022). Several studies have shown that in the summer, temperature and tree radial growth are favorably connected (Kang et al., 2021). The growth of dominant tree species such as *Abies george* and *Picea asperata* in the BNNR was positively correlated with temperature (Shi et al., 2021a). This may also be one of the reasons for the relatively strong correlation between temperature and vegetation cover. However, it has also been suggested that raised temperature would lead to an increase in plant respiration rate (Hua et al., 2019). Rising temperatures will accelerate snowmelt, potentially yielding diverse effects on vegetation. On the one hand, early snowmelt and longer growing seasons will increase vegetation productivity, but on the other hand, early snowmelt may also lead to low temperatures in the early spring and reduced snowmelt in the summer leading to droughts and a decrease in vegetation productivity, which is mainly related to seasonal and geographic variations (Wang et al., 2013). Vegetation phenology is closely related to climate. It has been suggested that climate warming leads to a longer growing season for vegetation, which promotes plant growth and biomass accumulation (Wheeler et al., 2017). As there is a strong link between vegetation cover and biomass (Qin et al., 2022). Therefore, changes in vegetation phenology as a result of climate warming have had a relatively positive effect on vegetation cover.

Regarding the regional distribution of positive correlations with precipitation, the southern part of the BNNR exhibits a vegetation cover more susceptible to precipitation, possibly linked to variations in the distribution of vegetation categories. In the past, temperature has been more influential on vegetation than rainfall. However, as temperature continues to rise and annual precipitation tends to reduce, the association of vegetative growth with precipitation may become stronger in the future. In the context of global warming, the frequency and magnitude of climate extremes have increased. Hazards such as droughts, temperature extremes, and floods can cause varying degrees of vegetation degradation (Manoranjan et al., 2024). Therefore, the mechanism of vegetation response to global warming in high-altitude mountainous areas needs to be further investigated.

5.3 Limitations and deficiencies

This study focuses on analyzing the long time-series variation patterns of vegetation. Vegetation phenology is also a key indicator for evaluating climate impacts on vegetation, carbon cycling, and interannual changes in ecosystem productivity (Wu et al., 2021; Fu et al., 2022a). This requires high-quality images of the growing season and data on the distribution of vegetation types. However, Landsat imagery capturing the vegetation growing season in the study area is significantly impacted by clouds and cloud shadows. This challenge may necessitate the integration of other imagery sources to generate higher-quality growing season imagery. Additionally, there is currently a temporary absence of vegetation type data in the study area. This gap could be addressed in the future with the generation of spatial distribution data on vegetation types in protected areas using more advanced equipment and methods.

6 Conclusion

The spatial and temporal variations, as well as the developmental tendencies of FVC, were investigated using the TS and MK methods, while the prediction of FVC was analyzed through the Hurst exponent. Topographic effects of FVC and its trends were also analyzed. Furthermore, to examine the correlation between FVC and climatic elements at the pixel level, a partial correlation coefficient was applied. This research primarily yielded the following key findings: FVC of the BNNR exhibited an upward trend from 1986 to 2020, with the mean FVC value growing from 59.40% in 1986 to 68.67% in 2020. The proportion of class I, II, III and IV decreased, while the proportion of class V FVC increased significantly. The spatially distributed differences of FVC in the BNNR are very obvious. Higher FVC regions are mostly situated at the east-central and southern portions of the BNNR. Snow-covered regions and valleys in the northern and west-central portions of the BNNR have lower FVC. FVC trends in the BNNR reveal two distinct patterns: a declining trend that accounted for 22.13% (a significant decrease of 6.42%) and a growing trend that accounted for 59.03% (a significant rise of 28.04%) of the area, respectively. Hurst exponent analysis indicated that most regions in the BNNR will continue to have an increased trend of FVC in the future. Topographic factors significantly influence the shift in FVC trends and spatial distribution. The vegetation coverage is higher in the height range from 2500m to 4000m, and the percentage of significant increase in FVC is also higher in this region. The area of significant vegetation change decreases with elevation. Slope has a limited effect on FVC distribution and trend, with minimal differences observed between different slopes. FVC tends to be lower on sunny and semi-shady slopes compared to other slopes, with vegetation degradation predominantly occurring in these areas. The following are the primary ways that climate variables affect the vegetation in this area: the FVC of the BNNR was positively correlated with precipitation and temperature, making up 52.64% and 62.65% of the total area, correspondingly. The temperature factor has a relatively strong ability to influence the vegetation cover with high spatial correlation.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding author.

Author contributions

ZX: Formal Analysis, Investigation, Methodology, Software, Visualization, Writing – review & editing, Validation, Writing – original draft. XS: Formal Analysis, Investigation, Methodology, Software, Visualization, Writing – review & editing. SG: Investigation, Resources, Validation, Writing – review & editing. QS: Investigation, Resources, Validation, Writing – review & editing. YY: Investigation, Resources, Validation, Writing – review & editing. LC: Conceptualization, Data curation, Funding acquisition, Investigation, Resources, Supervision, Validation, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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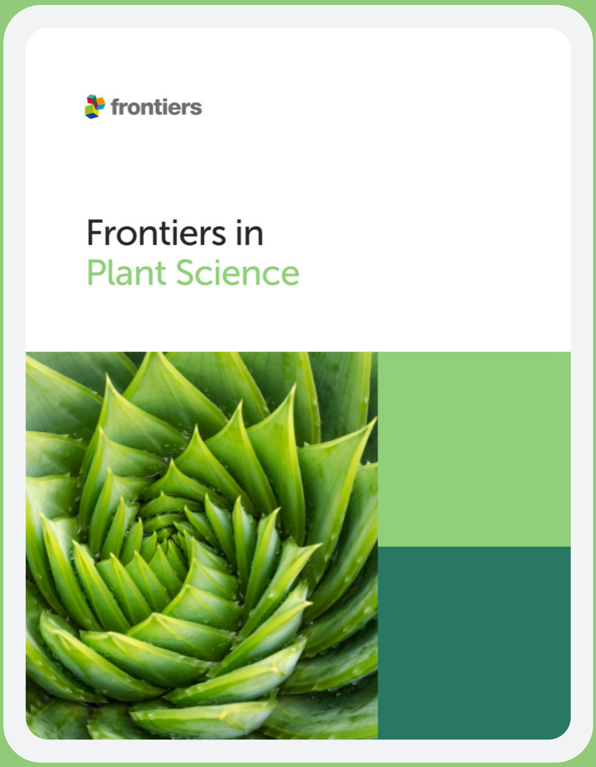

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