Clarifying the impact of interactions at the cropland-grassland interface on grassland biodiversity: A case study of the agropastoral ecotone in northern China

LI Mengyuan¹, LIU Siyu¹, DU Yixuan¹, CAO Wanyu¹, SI Wanyi¹

2026-07-16

ChinaRxiv

Abstract

The frequent conversion between cropland and grassland in agropastoral ecotones poses severe challenges to the protection of grassland biodiversity, and a systematic understanding of the relationship between these two aspects is urgently needed. In this study, the West Liaohe River Basin, which is a typical agropastoral ecotone in northern China, was chosen as an example. Using the field investigation data from 2023 and 2024, we calculated various biodiversity indices at both α and β scales for grassland vegetation and soil bacteria, and then analyzed the effects of the interactions at the cropland-grassland interface on grassland above-ground biodiversity, below-ground biodiversity, and their interrelationships. Moreover, we explored the driving factors of grassland biodiversity at the cropland-grassland interface. Notably, interactions at the cropland-grassland interface adversely affected grassland above- and below-ground biodiversity. Compared with the sampling points that were farther from the cropland-grassland interface (25 and 50 m), the sampling points located very close to the interface (5 and 10 m) had a decrease in species richness of more than 5.00%. This effect was jointly determined by various vegetation and soil attribute indicators and the regional environment. The litter and soil organic carbon played a prominent role in modulating the relationships between grassland above- and below-ground biodiversity at the cropland-grassland interface. The results suggested that intensive management of cropland and grassland should be enhanced in areas where agriculture and animal husbandry alternate, the disorderly reclamation and random abandonment of cropland should be prohibited, and the policy of returning cropland to grassland should be promoted systematically. These findings could provide referenced data for related studies and promote the protection of grassland biodiversity in agropastoral ecotones.

Full Text

Clarifying the impact of interactions at the cropland-grassland interface on grassland biodiversity: A case study of the agropastoral ecotone in northern China

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Abstract: The frequent conversion between cropland and grassland in agropastoral ecotones poses severe challenges to the protection of grassland biodiversity, and a systematic understanding of the relationship between these two aspects is urgently needed. In this study, the West Liaohe River Basin, which is a typical agropastoral ecotone in northern China, was chosen as an example. Using the field investigation data from 2023 and 2024, we calculated various biodiversity indices at both α and β scales for grassland vegetation and soil bacteria, and then analyzed the effects of the interactions at the cropland-grassland interface on grassland above-ground biodiversity, below-ground biodiversity, and their interrelationships. Moreover, we explored the driving factors of grassland biodiversity at the cropland-grassland interface. Notably, interactions at the cropland-grassland interface adversely affected grassland above- and below-ground biodiversity. Compared with the sampling points that were farther from the cropland-grassland interface (25 and 50 m), the sampling points located very close to the interface (5 and 10 m) had a decrease in species richness of more than 5.00%. This effect was jointly determined by various vegetation and soil attribute indicators and the regional environment. The litter and soil organic carbon played a prominent role in modulating the relationships between grassland above- and below-ground biodiversity at the cropland-grassland interface. The results suggested that intensive management of cropland and grassland should be enhanced in areas where agriculture and animal husbandry alternate, the disorderly reclamation and random abandonment of cropland should be prohibited, and the policy of returning cropland to grassland should be promoted systematically. These findings could provide reference data for related studies and promote the protection of grassland biodiversity in agropastoral ecotones.

Keywords: cropland-grassland interface; grassland biodiversity; α-diversity; β-diversity; agropastoral ecotone

Citation: LYU Xin, LI Xiaobing, DANG Dongliang, WANG Kai, ZHANG Chenhao, LI Mengyuan, LIU Siyu, DU Yixuan, CAO Wanyu, SI Wanyi. 2026. Clarifying the impact of interactions at the cropland-grassland interface on grassland biodiversity: A case study of the agropastoral ecotone in northern China. Journal of Arid Land, 18(7): 1099–1114. https://doi.org/10.1016/j.jaridl.2026.07.001; https://cstr.cn/32276.14.JAL.20250378

1 Introduction

Human-induced biodiversity loss poses a significant threat to global sustainable development,

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Received 2025-08-13; revised 2025-12-06; accepted 2025-12-10

http://jal.xjegi.com; https://www.keaipublishing.com/en/journals/journal-of-arid-land/

This version posted 2026-07-16.

with land use change as a principal driver (Newbold et al., 2015; Powers and Jetz, 2019; Lyu et al., 2024). The transformation between different land use types constitutes the primary manifestation of land use change and frequently substantially impacts biodiversity (Felipe-Lucia et al., 2020; Zhang et al., 2024). As two extensively distributed terrestrial ecosystems globally, the conversion between cropland and grassland is pervasive, particularly in agropastoral ecotones, posing a severe challenge to the conservation of grassland biodiversity (Huang et al., 2022). The cropland–grassland interface serves as an effective representation of the conversion between cropland and grassland in agropastoral ecotones and is frequently employed in relevant research (Guo et al., 2018; Xu et al., 2021). Currently, while numerous studies have focused on biodiversity in agropastoral ecotones, most have concentrated on biodiversity in cropland and grassland independently (Yan et al., 2023; Liu et al., 2025b). Overall, few studies have focused on biodiversity at the cropland–grassland interface, and targeted research and a systematic understanding of grassland biodiversity dynamics at the cropland–grassland interface in agropastoral ecotones are lacking.

Grassland biodiversity have been extensively investigated worldwide. Currently, species diversity is the most prevalent metric employed in biodiversity research. Nevertheless, owing to its inability to capture functional and ecological differences among species, a growing body of literature involves the integration of functional diversity into analytical frameworks (e.g., Wang et al., 2019). Biodiversity is a multidimensional concept, encompassing species diversity, functional diversity, and varying scales such as α, β, and γ. For example, Liang et al. (2021) employed a long-term experimental grazing platform in the exemplary grasslands of the Xilin Gol League, Inner Mongolia Autonomous Region, China, and reported that grazing induced changes in grassland plant community diversity, subsequently influencing the stability of grassland ecosystems across diverse spatial scales. This investigation concurrently accounted for various spatial scales (i.e., local and broader spatial extents) and organizational levels (i.e., species and community levels). In recent years, biodiversity research spanning different trophic levels from above- and below-ground perspectives has emerged as a pivotal frontier in ecosystem science (Soliveres et al., 2016; Zhang et al., 2021). Soils harbor complex communities of diverse organisms, and many soil microorganisms, such as nitrogen-fixing bacteria and mycorrhizal and pathogenic fungi, form symbioses with plant roots, thus directly influencing plant growth and performance (Van Der Heijden et al., 2008). For instance, Radujković et al. (2025) conducted an experimental system study in European grasslands to explore the relationship between soil diversity and ecosystem functions. Tong et al. (2023) analyzed soil microbial community diversity and its distribution characteristics under grassland, shrubland, and forestland vegetation types in the Qilian Mountains, China. Overall, there is a need to expand the dimensions, scales, and trophic levels of contemporary grassland biodiversity research, underscoring the imperative for more systematic investigations. Furthermore, increasing studies have shown that the type and intensity of land use usually have a systematic and significant effect on grassland biodiversity (Ye et al., 2024; Qi et al., 2025a). Therefore, it is highly important and urgent to systematically investigate the impact of interactions at the cropland-grassland interface on grassland biodiversity from dimensions, scales, and trophic levels. To the best of our knowledge, relatively few cases of grassland biodiversity research have been conducted at the cropland-grassland interface. However, the related issues in this typical regional type are receiving increased attention from researchers (Guo et al., 2018; Jian et al., 2025).

In summary, studies that focus on systematically investigating the impact of interactions at the cropland-grassland interface on grassland biodiversity within agropastoral ecotones are scarce. In this context, the West Liaohe River Basin, a quintessential agropastoral ecotone in northern China, was chosen for a case study. The dominant species in the grassland of the study area include *Leymus chinensis*, *Thymus mongolicus*, and *Cleistogenes squarrosa*. By integrating field survey data, we calculated various biodiversity indices at both α and β scales for grassland vegetation and soil bacteria to investigate the impact of interactions at the cropland-grassland interface on grassland above-ground biodiversity, below-ground biodiversity, and their interrelationships, and explored the underlying driving factors. Ultimately, the findings of this

study could offer a sound foundation for biodiversity conservation and sustainable development initiatives within agropastoral ecotones.

2 Materials and methods

2.1 Study area

The West Liaohe River Basin (41°18′–45°13′N, 116°36′–123°40′E) is located in the eastern segment of the Three-North Transition Zone, which is part of the northern agropastoral ecotone in China (Fig. 1). This basin traverses mainly the two prefecture-level cities of Chifeng and Tongliao in the Inner Mongolia Autonomous Region, encompassing 21 county-level administrative units and covering a total area of approximately 1.26×10^5 km^2. Surrounded by mountains to the north, west, and south and adjoining the Songliao Plain to the east, the terrain in this basin gradually slopes from west to east, with elevations ranging from 82 to 2054 m. The study area is characterized by a pronounced continental climate, marked by aridity and low precipitation, where annual evaporation surpasses water replenishment. The mean annual temperature gradually increases from northwest to southeast (5.0°C–6.5°C), and the annual precipitation ranges from 350 to 550 mm, with 70.00% of the total precipitation concentrated from June through August. The annual evaporation rate ranges from 1800 to 2000 mm. Recognized as a pivotal grain-producing region and a significant commodity grain base in China, the West Liaohe River Basin has earned the moniker Grain Warehouse of Inner Mongolia Autonomous Region. As urbanization, industrialization, and agricultural modernization have accelerated since 2000, both the expansion of cropland and the reversion of cropland to grassland have become pervasive phenomena, posing formidable challenges to the conservation of grassland biodiversity and in turn jeopardizing ecological security (Lyu et al., 2022). From 2000 to 2020, the conversion area between cropland and grassland in the study area accounted for approximately 8.55% of the entire study area. Among these areas, the area where cropland was converted to grassland accounted for approximately 3.89%, while the area where grassland was converted to cropland accounted for approximately 4.66%. Consequently, establishing a mutually beneficial strategy for cropland grain production and grassland biodiversity conservation within the West Liaohe River Basin is imperative for both scientific inquiry and pragmatic management decisions.

2.2 Data sources and preprocessing

Land use data in 2020 were sourced from the Resource and Environmental Science Data Platform (https://www.resdc.cn/) with a spatial resolution of 1 km, and were divided into cropland,

Fig. 1 Overview of the West Liaohe River Basin and land use types in 2020. The land use data were sourced from the Resource and Environmental Science Data Platform (https://www.resdc.cn/).

forestland, grassland, water bodies, construction land, and unused land. Digital elevation model (DEM) data in 2019 were obtained from the National Earth System Science Data Center (https://www.geodata.cn/main/) with a spatial resolution of 1 km. Annual temperature and precipitation data during 2010-2020 were also obtained from the National Earth System Science Data Center with a spatial resolution of 1 km. A monthly potential evapotranspiration dataset covering the period 2010-2020 was acquired from the National Tibetan Plateau Data Center (https://data.tpdc.ac.cn/home) with a spatial resolution of 1 km. The aridity index (AI, which is the ratio of annual precipitation to annual potential evapotranspiration) was calculated using precipitation and potential evapotranspiration data (Li et al., 2021). The administrative boundaries, road networks, and settlement distribution data in 2023 were derived from the National Catalogue Service for Geographic Information (https://www.webmap.cn/). Population density data (2010-2020) were sourced from the WorldPop Population Data website (https://www.worldpop.org/), formatted as GEOTIFF with a resolution of 30 arcsec. Gross regional production (GRP) and grain production were derived from the statistical yearbooks (Bureau of Statistics of Chifeng City, 2011-2021; Bureau of Statistics of Tongliao City, 2011-2021).

Fig. 2. Distribution of the sampling plots: panel (a) map showing the study area and sampling plots in 2023 and 2024 with legend; panel (b) schematic of transects and quadrats across the grassland-cropland interface with distances of 50, 25, 10, and 5 m; panel (c) field work photo of the cropland-grassland interface.

Figure 1: Fig. 2. Distribution of the sampling plots: panel (a) map showing the study area and sampling plots in 2023 and 2024 with legend; panel (b) schematic of transects and quadrats across the grassland-cropland interface with distances of 50, 25, 10, and 5 m; panel (c) field work photo of the cropland-grassland interface.

2.3 Experimental design

2.3.1 Plot and sampling setup

On the basis of land use maps of the study area spanning from 2000 to 2020, areas exhibiting conversion between cropland and grassland were delineated. By integrating the findings of field surveys conducted between 2021 and 2022, 21 plots were selected for investigation. These plots were all grasslands adjacent to cropland during the field survey in 2021, and the interviews with the surrounding residents indicated that this situation had persisted for the past 5 a or even 10 a, making them ideal sampling plots for this study. The selection of these plots adhered to two fundamental principles: (1) the plots should exhibit a documented absence of grazing activity for at least 3 a (which was verified through interviews with local residents and onsite examinations for evidence of faecal matter or grazing traces) to mitigate the potential influence of grazing on grassland biodiversity; and (2) the plots should occur in areas characterized by flat terrain to preclude the confounding effects of topographical variations on grassland biodiversity. Each plot was established at the interface between cropland and grassland, with three parallel transects extending into the grassland area to serve as replicates (Fig. 2). The spacing between adjacent transects was maintained at 10 m, and the sampling points were distributed unevenly along the transects at intervals of 5, 10, 25, and 50 m, with increased sampling density near the landscape interface. At each sampling point, a 1 m$×$1 m quadrat was established along each of the three parallel transects.

Fig. 2 Distribution of the sampling plots (a) for vegetation and soil survey in 2023 and 2024 and the arrangement of sampling points (b), as well as a field work photo of the cropland-grassland interface (c)

In this study, we used space-for-time substitution (Kharouba and Williams, 2024; Du et al., 2025). Specifically, compared with grassland farther from cropland, grassland closer to cropland is less affected by cropland. Therefore, the interactions at the cropland-grassland interface can be analyzed using data from sampling points at distances of 5, 10, 25, and 50 m from the cropland-grassland interface.

2.3.2 Vegetation and soil survey

This study conducted the vegetation community survey and collected soil samples for sampling plots at the zenith of vegetation growth (July–August) in both 2023 and 2024. In vegetation community surveys, we compiled detailed species lists for all sampling points in each plot, and recorded the density (plants/m^2), height (cm), and other ecological attributes of individual species. We collected the above-ground green biomass (g), standing dead material (g), litter (g), and below-ground biomass (g), subsequently oven-dried and weighed them to determine dry mass. We also measured key plant functional traits, such as plant height (cm), leaf area (cm^2), leaf dry weight (g), and specific leaf area (cm^2/g), which are extensively employed in studies of arid and semi-arid grassland ecosystems.

Soil samples were collected within the sampling points in each plot designated for the vegetation community survey with a soil auger at depths of 0–30 cm in 10 cm increments (i.e., 0–10, 10–20, and 20–30 cm). We thoroughly mixed the soil samples from the three depth layers in each quadrat and removed stones and roots. A portion of each sample was dried naturally and sieved, and conventional laboratory methods, including methods for analyzing the soil moisture content (SMC; %) and soil organic carbon (SOC; g/kg), were employed to determine its physical and chemical properties. The remaining portion of each sample was preserved at low temperatures in liquid nitrogen tanks for subsequent analysis of the soil microbial community. Given the significant proportion of bacteria among soil microorganisms and their pivotal role in sustaining soil functions (Jia et al., 2023; Peng et al., 2025), we adopted the Illumina MiSeq high-throughput sequencing platform (Illumina, San Diego, USA) to assess soil bacterial diversity.

2.4 Modelling and analysis

2.4.1 Calculation of biodiversity indices

On the basis of the field survey data, we calculated the species diversity (α and β scales) and functional diversity (α scale only) for grassland vegetation and soil bacteria (Table 1). Species α-diversity was assessed using the Shannon-Wiener index (Shannon index; indicative of species richness), Pielou’ s evenness index (Pielou index; reflective of species evenness), and Simpson’ s diversity index (Simpson index) (Wang et al., 2020; Liu et al., 2025b). Species β-diversity was quantified using Bray–Curtis dissimilarity and Jaccard distance (Thiele et al., 2018; Ricotta and Pavoine, 2022). Functional α-diversity was assessed using functional dispersion (FDis) and Rao’ s quadratic entropy (FDQ). By capturing the abundance-weighted spread of species in a multidimensional trait space, FDis is a measure of functional richness that accounts for the relative abundance of species (Laliberté and Legendre, 2010; Braschler et al., 2022). FDQ was chosen to estimate functional diversity because it reflects the dispersion of species in trait space and allows the use of relative abundance data (Botta-Dukát, 2005; Wang et al., 2020).

Table 1 Biodiversity indices in this study

Survey subject	Diversity type	Index
Vegetation	Species α-diversity	Shannon-Wiener index (Shannon index) and Pielou' s evenness index (Pielou index)
Vegetation	Functional α-diversity	Functional dispersion (FDis) and Rao' s quadratic entropy (FDQ)
Vegetation	Species β-diversity	Bray-Curtis dissimilarity and Jaccard distance
Soil bacteria	Species α-diversity	Shannon index and Simpson' s diversity index (Simpson index)
Soil bacteria	Species β-diversity	Bray-Curtis dissimilarity

2.4.2 Driver analysis

This study conducted the driver analysis at both the plot scale and the regional scale. At the plot

scale, we analyzed the biodiversity and driving factors based on data from the sampling points at different distances from the cropland-grassland interface within each plot, resulting in a total of 84 samples. At the regional scale, each plot was treated as a single sample without distinguishing distances, and the relationship between overall biodiversity and environmental factors was examined across plots, resulting in a total of 21 samples.

At the plot scale, multiple linear regression analysis was employed to assess the contributions of six environmental variables—fractional vegetation cover (FVC), above-ground biomass (AGB; g), litter (g), SMC (%), soil bulk density (SBD; g/cm^3), and SOC (g/kg)—to the grassland above- and below-ground biodiversity. The objective was to elucidate the drivers of grassland biodiversity at the cropland-grassland interface. Multicollinearity analysis of these six environmental variables (independent variables) revealed that all variance inflation factor (VIF) values were less than 5, indicating the absence of significant multicollinearity. This analytical process was implemented via IBM SPSS Statistics v.20.

Furthermore, at the regional scale, Pearson' s correlation analysis was conducted to investigate the effects of regional natural and human activity factors on the grassland above- and below-ground biodiversity. The natural factors included four primary indicators: temperature (°C), precipitation (mm), AI, and DEM (m). The human activity factors included five main indicators: population density (PD; persons/km^2), distance to the nearest road (DNR; km), distance to the nearest settlement (DNS; km), gross regional production (GRP; 10^4 CNY), and grain production (GP; t/km^2).

3 Results

3.1 Variations in grassland above- and below-ground biodiversity at the cropland-grassland interface

In this study, variations in the biodiversity of grassland vegetation and soil bacteria were examined along a distance gradient from the cropland-grassland interface to grassland (Fig. 3). With respect to vegetation, and specifically considering species α-diversity, grassland situated at greater distances from the cropland-grassland interface presented higher Shannon index and lower Pielou index values (Fig. 3a and b). In terms of functional α-diversity, grassland farther from the interface presented higher FDis and FDQ values (Fig. 3c and d). For species β-diversity, grassland at greater distances from the interface presented higher Bray-Curtis dissimilarity and Jaccard distance values (Fig. 3e and f). Collectively, these findings suggested that the interactions at the cropland-grassland interface adversely affect the above-ground biodiversity of grassland adjacent to cropland. With respect to soil bacteria, and specifically considering species α-diversity, grasslands located farther from the interface exhibited minimal changes in Shannon index and Simpson index (Fig. 3g and h). For species β-diversity, the soils in grassland at greater distances from the interface presented higher Bray-Curtis dissimilarity values (Fig. 3i). These observations suggested that the interactions at the cropland-grassland interface impose a negligible effect on the species α-diversity of below-ground microbial communities adjacent to cropland but result in a reduction in species β-diversity. Overall, interactions at the cropland-grassland interface adversely affected grassland above- and below-ground biodiversity. Compared with the sampling points that were farther from the cropland-grassland interface (25 and 50 m), the points located very close to the interface (5 and 10 m) had a decrease in species richness of more than 5.00%.

3.2 Variations in the relationships between above- and below-ground biodiversity at the cropland-grassland interface

First, the correlation between above- and below-ground biodiversity was examined along a distance gradient from the cropland-grassland interface to grassland via α-scale analysis (Fig. 4). Along the gradient extending from cropland to grassland, the correlation between grassland vegetation biodiversity indices and soil Simpson index changed. Specifically, from 5 to 50 m away from the cropland-grassland interface, the strength of the correlation between the four

Fig. 3 Variations in biodiversity indices of grassland vegetation (a–f) and soil

Fig. 3

Figure 2: Fig. 3

bacteria (g-i) along a distance gradient from the cropland-grassland interface to grassland. Veg_Shannon, vegetation Shannon-Wiener index; Veg_Pielou, vegetation Pielou' s evenness index; Veg_FDis, vegetation functional dispersion; Veg_FDQ, Rao' s quadratic entropy; Veg_Bray-Curtis, vegetation Bray-Curtis dissimilarity; Veg_Jaccard, vegetation Jaccard distance; Soil_Shannon, soil Shannon-Wiener index; Soil_Simpson, soil Simpson' s diversity index; Soil_Bray, soil Bray-Curtis dissimilarity. For α-diversity, L1, L2, L3, and L4 denote the analyses of sampling points located 5, 10, 25, and 50 m from the cropland-grassland interface, respectively. For β-diversity, LA, LB, and LC denote comparisons of sampling points located 5 and 10, 10 and 25, and 25 and 50 m from the cropland-grassland interface, respectively. The boxes indicate the IQR (interquartile range, 25th to 75th percentiles); lines within the boxes indicate the median (50th percentile); squares within the boxes indicate the mean. Whiskers extend to the most extreme values within 1.5×IQR. The data distribution is represented by black diamonds and normal fit curves. Slope indicates the trend in mean values: positive for an increase, negative for a decrease.

vegetation biodiversity indices and soil Simpson index increased. At a distance of 50 m from the cropland-grassland interface, a significant positive correlation was observed between the vegetation Shannon index and soil Simpson index ($P < 0.05$). These findings suggested that the interactions at the cropland-grassland interface cause a reduction in the correlation between above- and below-ground biodiversity at the α scale in grassland adjacent to cropland. The correlation between above- and below-ground biodiversity was subsequently analyzed at the β scale (Fig. 5). Compared with the sampling points at 5 and 10 m, the positive correlation between the Bray-Curtis dissimilarity of vegetation and that of soil enhanced between the points at 10 and 25 m, as well as between those at 25 and 50 m. Overall, along the distance gradient, the correlation between the above- and below-ground biodiversity in grassland at the β scale did not vary significantly.

3.3 Analysis of factors influencing grassland biodiversity at the cropland-grassland interface

This study employed the multiple linear regression method to analyze the driving factors of grassland above- and below-ground biodiversity at the plot scale (Table 2). Overall, grassland

Fig. 4 Visible heatmap panels. In each panel, the row and column labels are `Veg_Shannon`, `Veg_Pielou`, `Veg_FDis`, `Veg_FDQ`, `Soil_Shannon`, and `Soil_Simpson`; the colorbar is labeled "Correlation coefficient" and ranges from −1.00 to 1.00.

- **(a) 5 m**
  - `Veg_Shannon`: 1.00
  - `Veg_Pielou`: 0.55**, 1.00
  - `Veg_FDis`: 0.52*, 0.40, 1.00
  - `Veg_FDQ`: 0.42, 0.34, 0.96***, 1.00
  - `Soil_Shannon`: −0.23, 0.16, −0.18, −0.19, 1.00
  - `Soil_Simpson`: −0.15, −0.06, 0.10, 0.05, 0.52*, 1.00
- **(b) 10 m**
  - `Veg_Shannon`: 1.00
  - `Veg_Pielou`: 0.78***, 1.00
  - `Veg_FDis`: 0.67***, 0.52*, 1.00
  - `Veg_FDQ`: 0.56**, 0.41, 0.95***, 1.00
  - `Soil_Shannon`: −0.23, −0.01, −0.32, −0.31, 1.00
  - `Soil_Simpson`: 0.09, 0.22, −0.15, −0.13, 0.67***, 1.00
- **(c) 25 m**
  - `Veg_Shannon`: 1.00
  - `Veg_Pielou`: 0.70***, 1.00
  - `Veg_FDis`: 0.61**, 0.34, 1.00
  - `Veg_FDQ`: 0.53*, 0.25, 0.95***, 1.00
  - `Soil_Shannon`: −0.27, 0.09, −0.41, −0.39, 1.00
  - `Soil_Simpson`: 0.05, −0.20, −0.06, −0.02, 0.32, 1.00
- **(d) 50 m**
  - `Veg_Shannon`: 1.00
  - `Veg_Pielou`: 0.70***, 1.00
  - `Veg_FDis`: 0.27, −0.06, 1.00
  - `Veg_FDQ`: 0.17, 0.01, 0.93***, 1.00
  - `Soil_Shannon`: −0.05, 0.36, −0.16, −0.04, 1.00
  - `Soil_Simpson`: 0.51*, 0.26, 0.38, 0.24, 0.19, 1.00

Fig. 4 Variations in the correlation between different biodiversity indices at the α scale along a distance gradient of 5 m (a), 10 m (b), 25 m (c), and 50 m (d) from the cropland-grassland interface to grassland. The correlation between the above- and below-ground biodiversity indices can be found within the green border. *, $P < 0.050$ level; **, $P < 0.010$ level; ***, $P < 0.001$ level.

Fig. 5 Visible heatmap panels. In each panel, the row and column labels are `Veg_Bray-Curtis`, `Veg_Jaccard`, and `Soil_Bray-Curtis`; the colorbar is labeled "Correlation coefficient" and ranges from −1.00 to 1.00.

- **(a)**
  - `Veg_Bray-Curtis`: 1.00
  - `Veg_Jaccard`: 0.45*, 1.00
  - `Soil_Bray-Curtis`: 0.15, −0.03, 1.00
- **(b)**
  - `Veg_Bray-Curtis`: 1.00
  - `Veg_Jaccard`: 0.46*, 1.00
  - `Soil_Bray-Curtis`: 0.35, 0.18, 1.00

- **(c)**
  - `Veg_Bray-Curtis`: 1.00
  - `Veg_Jaccard`: 0.66**, 1.00
  - `Soil_Bray-Curtis`: 0.31, 0.05, 1.00

Fig. 5 Variations in the correlation between different biodiversity indices at the β scale between sampling points located 5 and 10 m (a), 10 and 25 m (b), and 25 and 50 m (c) from the cropland-grassland interface. The correlation between the above- and below-ground biodiversity indices can be found within the green border. *, $P < 0.050$ level; **, $P < 0.010$ level.

Table 2 Effects of environmental factors on grassland biodiversity at the plot scale

Scale	Index	Factor	Coefficient	P value
α	Veg_Shannon	SMC	-3.235^{*}	0.018
α	Veg_Shannon	SOC	0.039^{*}	0.046
α	Veg_Pielou	FVC	-0.165^{*}	0.031
α	Veg_Pielou	SMC	-0.606^{*}	0.027
α	Veg_FDis	Litter	0.002^{*}	0.014
α	Veg_FDis	SOC	0.024^{**}	0.002
α	Veg_FDQ	Litter	0.003^{**}	0.002
α	Veg_FDQ	SOC	0.040^{***}	0.000
α	Soil_Shannon	AGB	-0.005^{**}	0.003
α	Soil_Shannon	Litter	-0.030^{***}	0.000
α	Soil_Shannon	SBD	3.536^{*}	0.022
α	Soil_Shannon	SOC	0.136^{**}	0.009
α	Soil_Simpson	Litter	-0.000^{**}	0.001
α	Soil_Simpson	SOC	0.000^{*}	0.020
β	Veg_Bray-Curtis	Litter	0.002^{*}	0.038
β	Veg_Jaccard	Litter	0.001^{*}	0.029
β	Veg_Jaccard	SBD	-0.386^{*}	0.036
β	Soil_Bray-Curtis	Litter	0.004^{***}	0.000
β	Soil_Bray-Curtis	SBD	-0.409^{*}	0.021
β	Soil_Bray-Curtis	SOC	-0.022^{***}	0.000

Note: Veg_Shannon, vegetation Shannon-Wiener index; Veg_Pielou, vegetation Pielou' s evenness index; Veg_FDis, vegetation functional dispersion; Veg_FDQ, Rao' s quadratic entropy; Veg_Bray-Curtis, vegetation Bray-Curtis dissimilarity; Veg_Jaccard, vegetation Jaccard distance; Soil_Shannon, soil Shannon-Wiener index; Soil_Simpson, soil Simpson' s diversity index; Soil_Bray, soil Bray-Curtis dissimilarity; FVC, fractional vegetation cover; AGB, above-ground biomass; SMC, soil moisture content; SBD, soil bulk density; SOC, soil organic carbon. *, $P < 0.050$ level; **, $P < 0.010$ level; ***, $P < 0.001$ level.

above- and below-ground biodiversity at the cropland–grassland interface was collectively influenced by multiple vegetation and soil attribute indicators. Compared with FVC and AGB, litter, SMC, SBD, and SOC more notably affected the grassland above- and below-ground biodiversity. Among these factors, litter significantly positively influenced the functional α-diversity of vegetation, significantly negatively influenced the species α-diversity of soil bacteria, and significantly positively influenced the species β-diversity of both vegetation and soil bacteria. SMC significantly negatively affected the species α-diversity of vegetation. In contrast, SBD significantly positively influenced the species α-diversity of soil bacteria and significantly negatively influenced the species β-diversity of both vegetation and soil bacteria. Moreover, SOC significantly positively affected the species α-diversity and functional α-diversity of vegetation and the species α-diversity of soil bacteria but significantly negatively influenced the species β-diversity of soil bacteria. Furthermore, grassland located farther from the cropland–grassland interface exhibited increased correlations between above- and below-ground biodiversity at both α and β scales. Grasslands situated farther from the interface presented relatively high litter weights and low SOC contents (Fig. S1). These observations suggested that the relationships between grassland above- and below-ground biodiversity at the cropland–grassland interface may be jointly modulated by litter and SOC.

At the regional scale, Pearson’ s correlation analysis was employed to examine the effects of natural and human activity factors on grassland above- and below-ground biodiversity (Table 3). Overall, grassland biodiversity at the cropland–grassland interface was influenced by both natural and human activity factors, with natural factors having greater effects than human activity factors.

did. Temperature, precipitation, and AI significantly negatively influenced grassland biodiversity at both α and β scales. DEM significantly positively affected grassland above-ground biodiversity at the α scale, whereas DNS and PD had significant positive and negative effects, respectively, on grassland below-ground biodiversity at the α scale. Compared with above-ground biodiversity, below-ground biodiversity was less notably influenced by the four natural factors; temperature significantly negatively influenced the below-ground biodiversity only at the β scale. The four natural factors more strongly impacted above-ground biodiversity at the α scale than at the β scale. At the α scale, all four above-ground biodiversity indices were influenced to varying degrees by the four natural factors, whereas at the β scale, only the Jaccard distance was significantly affected by precipitation and AI. Human activity factors significantly influenced only the grassland below-ground biodiversity at the α scale.

Table 3 Effects of environmental factors on grassland biodiversity at the regional scale

Scale	Index	Tem	Pre	AI	DEM	DNR	DNS	GP	GRP	PD
α	Veg_Shannon	−0.52*	−0.61**	−0.59**	0.39	−0.09	−0.14	−0.37	−0.34	0.13

Scale	Index	Tem	Pre	AI	DEM	DNR	DNS	GP	GRP	PD
α	Veg_Pielou	−0.53*	−0.54*	−0.54*	0.47*	0.03	0.15	−0.26	−0.08	−0.01
α	Veg_FDis	−0.31	−0.59**	−0.59**	0.47*	−0.34	−0.36	−0.41	−0.13	0.12
α	Veg_FDQ	−0.18	−0.47*	−0.47*	0.36	−0.18	−0.35	−0.33	−0.11	0.09
α	Soil_Shannon	0.36	0.06	0.03	0.00	0.17	0.45*	−0.00	0.13	−0.55**
α	Soil_Simpson	0.19	−0.16	−0.19	0.12	−0.26	−0.07	−0.20	−0.04	−0.25
β	Veg_Bray-Curtis	−0.42	−0.42	−0.42	0.19	−0.21	0.27	0.06	0.16	−0.08
β	Veg_Jaccard	−0.27	−0.49*	−0.46*	0.33	−0.09	0.39	−0.30	−0.38	−0.17
β	Soil_Bray-Curtis	−0.61**	−0.21	−0.19	0.21	−0.04	−0.17	0.03	−0.03	0.42

Note: Tem, temperature; Pre, precipitation; AI, aridity index; DEM, digital elevation model; DNR, distance to the nearest road; DNS, distance to the nearest settlement; GRP, gross regional production; GP, grain production; PD, population density. Values are Pearson' s correlation coefficients. *, $P < 0.050$ level; **, $P < 0.010$ level.

4 Discussion

4.1 Impact of interactions at the cropland-grassland interface on grassland biodiversity

Numerous studies have focused on investigating cropland or grassland biodiversity (Meier et al., 2022; Zhao et al., 2024; Liu et al., 2025a); however, research focusing on biodiversity at the cropland–grassland interface remains relatively scarce (Guo et al., 2018). While scholars have investigated the effects of agricultural management practices on grassland biodiversity (van Eekeren et al., 2025) and the conservation of grassland biodiversity within agropastoral ecotones (Su et al., 2022), these studies often focus on a single dimension, scale, or trophic level. This study systematically revealed the impact of interactions at the cropland–grassland interface on grassland above-ground biodiversity, below-ground biodiversity, and their interrelationships, thereby providing a robust foundation for grassland biodiversity management in agropastoral ecotones.

Interactions at the cropland–grassland interface adversely affected the biodiversity of grassland vegetation adjacent to cropland, likely because of human disturbances such as routine farming activities and pesticide applications, which affect adjacent grassland. Furthermore, the interactions led to an increase in species α-diversity but a decrease in species β-diversity for the soil bacteria of grassland adjacent to cropland. This phenomenon may be attributed to the application of organic fertilizers in cropland, which promotes bacterial proliferation and induces changes in the abundance, composition, and structure of soil microorganisms. Given the relatively uniform management practices in cropland, grassland adjacent to cropland is more susceptible to lateral nutrient migration, resulting in heightened bacterial diversity but decreased interbacterial differences. Additionally, interactions at the cropland–grassland interface influences the coupling

relationship between above- and below-ground biodiversity in grassland. Grassland located farther from the cropland–grassland interface exhibited a significant increase in the correlation between above- and below-ground biodiversity at the α scale, whereas the correlation at the β scale increased but did not reach statistical significance. Notably, vegetation–soil feedback synergy in grassland ecosystems located away from cropland could enhance grassland ecological functions and facilitate the restoration of degraded grassland. Previous research has demonstrated that increasing the diversity of grassland plants, soil microorganisms, and their interactions enhances ecosystem multifunctionality (Guo et al., 2021; Zhang et al., 2023), thereby supporting the findings of this study.

The grassland above-ground biodiversity, below-ground biodiversity and their interrelationships at the cropland–grassland interface were collectively influenced by various vegetation and soil attribute indicators. Compared with FVC and AGB, litter, SMC, SBD, and SOC more notably influenced the grassland biodiversity indices (Table 1). The pivotal role of soil physicochemical properties in shaping grassland vegetation distribution and diversity has been substantiated in prior research (Qi et al., 2025b). Notably, studies conducted in grassland generally suggested that soil moisture significantly and positively influences vegetation species diversity (Liu et al., 2025b). However, in this study, SMC and SOC significantly negatively influenced both the vegetation Shannon index and Pielou index. This discrepancy may stem from the focus of this study on the drivers of grassland vegetation diversity at the cropland–grassland interface. Owing to irrigation practices in adjacent cropland, grassland near these areas often demonstrates elevated SMC levels. However, this interface influence paradoxically reduces vegetation species diversity. Furthermore, the relationships between above- and below-ground biodiversity at the cropland–grassland interface were influenced by both litter and SOC. These findings further underscored the necessity of enhancing the coordinated management of cropland and grassland in agropastoral ecotones.

At the regional scale, natural factors exerted a greater influence on grassland biodiversity than human activity factors did (Table 3). This observation is plausible, as natural conditions frequently dictate the spatial distribution patterns of grassland biodiversity (Bhat et al., 2023). Nevertheless, stringent management of human activities is vital, given their propensity to serve as the primary drivers of biodiversity loss. Compared with below-ground biodiversity, grassland above-ground biodiversity was more profoundly affected by the four natural factors (Table 3). A study of alpine grasslands on the Qinghai–Xizang Plateau revealed that above-ground plant diversity and below-ground soil microbial diversity respond asynchronously to climate warming and human activities, with plant diversity exhibiting heightened sensitivity (Shangguan et al., 2024), thereby supporting this observation. Additionally, this study revealed that temperature, precipitation, and AI collectively negatively impact grassland biodiversity, whereas DEM shows positive influence (Table 3). The positive correlation between DEM and biodiversity indices conforms with the findings of previous studies (Bai et al., 2024). Positive relationships typically exist among temperature, precipitation, and biodiversity (Yang et al., 2024). Moreover, relatively high AI values suggest increased moisture levels, which are generally conducive to biodiversity maintenance. In this study, regions characterized by higher temperatures, precipitation levels, and AI values may coincide with areas of concentrated cropland, where agricultural activities strongly negatively impact grassland biodiversity. These findings underscored the critical importance of enhancing the protection of grassland biodiversity in agropastoral ecotones.

4.2 Challenges and strategies for the conservation of grassland biodiversity in agropastoral ecotones

Against the backdrop of agricultural expansion, extensive grassland areas have been converted into cropland, resulting in the loss of habitats for animals, plants, and microorganisms that have adapted to the grassland environment, consequently leading to a decrease in species richness. In contrast to cropland ecosystems, which represent monoculture systems, grassland ecosystems typically exhibit complex hierarchical structures, encompassing plants of varying heights, diverse

animal communities, and abundant microbial communities. Consequently, the conversion of grassland into cropland leads to a simplification of the regional ecosystem structure. This study demonstrated that interactions at the cropland-grassland interface have detrimental effects on the above- and below-ground biodiversity of grassland adjacent to cropland as well as on their interrelationships (Figs. 3 and 4). Overall, cropland expansion contributes to a reduction in biodiversity, which in turn undermines the stability and resilience of ecosystems, increasing their susceptibility to external disturbances and damage.

In addition to cropland expansion, cropland abandonment and the conversion of cropland back to grassland (grassland restoration) are significant manifestations of changes at the cropland-grassland interface in agropastoral ecotones. While both cropland abandonment and grassland restoration involve the transition of cropland to grassland, cropland abandonment directly affects the quantity and quality of cropland, thereby posing a threat to national food security and social stability. Although both cropland abandonment and afforestation (or, more accurately, grassland restoration) efforts contribute to the recovery of grassland biodiversity, the restoration process is protracted, often spanning over two decades (Chen et al., 2021; Zheng et al., 2023). This highlights the necessity of integrating the coordinated management of cropland and grassland into preliminary planning for the protection of grassland biodiversity in agropastoral ecotones, and advocating proactive management strategies rather than reactive governance measures. Prior research has also advocated for the prohibition of cropland abandonment and disorderly cultivation, emphasizing the importance of strengthening the management of cropland-grassland conversion (Tian et al., 2023).

Grazing constitutes another pivotal factor influencing the conservation of grassland biodiversity within agropastoral ecotones. However, the complete prohibition of grazing activities in these zones adversely affects the livelihoods of residents and undermines regional sustainable development. Indeed, previous studies have revealed the constructive role of moderate-intensity grazing in sustaining grassland biodiversity, particularly species richness (Borer et al., 2014; Song et al., 2024). Consequently, enhancing grazing management has emerged as a critical strategy for ensuring grassland biodiversity in agropastoral ecotones. Overall, it is vital to intensify the management of both cropland and grassland in these zones to mitigate biodiversity loss stemming from landscape fragmentation (Yu et al., 2024). This endeavour aims to achieve structural equilibrium between crop cultivation and livestock husbandry, thereby fostering a synergistic outcome that benefits both regional cropland grain production and the preservation of grassland biodiversity.

4.3 Limitations and prospects

This study has several limitations. First, constrained by human and financial resources, only 21 plots were surveyed. In future work, more in-depth research should be prioritized, with the goal of increasing the number of sampling points along each transect and establishing a certain number of sampling points in cropland. During field surveys, plots devoid of grazing traces were selected through interviews and onsite inspections (e.g., examining cattle and sheep droppings and signs of plant browsing). Nevertheless, excluding only human activities unrelated to crop land management remains challenging and may introduce uncertainty into the results. Although field surveys constitute an indispensable cornerstone of scientific research, they are resource intensive and costly and often struggle to provide large-scale, long-term observational data. Hence, in the future, it will be crucial to integrate sky-ground integrated remote sensing technology to enhance biodiversity monitoring capabilities (Lyu et al., 2024), thereby promoting the protection of grassland biodiversity in agropastoral ecotones.

5 Conclusions

This study systematically revealed the impact of interactions at the cropland-grassland interface on grassland biodiversity while also investigating the underlying driving factors. Interactions at

the cropland-grassland interface caused notable decreases in grassland above-ground biodiversity at both the α and β scales, in grassland below-ground biodiversity at the β scale, and in the correlation between grassland above- and below-ground biodiversity at the α scale. This interface adversely influenced grassland above-ground biodiversity and its relationship with below-ground biodiversity, an influence that was compounded by various vegetation and soil attribute indicators and regional environmental conditions. Compared with those in pure grassland ecosystems, grassland biodiversity in agropastoral ecotones exhibited distinct response patterns to climate change and human activities, indicating more notable challenges. This study advocates the strengthening of intensive management practices for cropland and grassland in agropastoral ecotones, aiming to achieve a balance between regional grain production and grassland biodiversity conservation. These findings offer a robust theoretical foundation for grassland biodiversity conservation initiatives in agropastoral ecotones, promoting regional sustainable development.

Conflict of interest

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

Acknowledgements

This research was supported by the National Natural Science Foundation of China (32201345, 42271291).

Author contributions

Conceptualization: LYU Xin; Methodology: LYU Xin; Formal analysis: LYU Xin, DANG Dongliang; Investigation and data curation: LYU Xin, DANG Dongliang, WANG Kai, ZHANG Chenhao, LI Mengyuan, LIU Siyu, DU Yixuan, CAO Wanyu; Writing - original draft preparation: LYU Xin, DANG Dongliang, SI Wanyi; Writing - review and editing: LYU Xin, LI Xiaobing; Funding acquisition: LYU Xin, LI Xiaobing; Resources: LI Xiaobing; Supervision: LI Xiaobing. All authors approved the manuscript.

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Appendix

Fig. S1 Variations in vegetation and soil properties along a distance gradient from the cropland-grassland interface to grassland. (a), fractional vegetation cover (FVC); (b), above-ground biomass (AGB); (c), litter; (d), soil moisture content (SMC); (e), soil bulk density (SBD); (f), soil organic carbon (SOC). L1, L2, L3, and L4 denote sampling points located 5, 10, 25, and 50 m from the farmland-grassland interface, respectively. The boxes indicate the IQR (interquartile range, 25^{th} to 75^{th} percentiles); lines within the boxes indicate the median (50^{th} percentile); squares within the boxes indicate the mean. Whiskers extend to the most extreme values within 1.5×IQR. The data distribution is represented by black diamonds and normal fit curves. Slope indicates the trend in mean values: positive for an increase and negative for a decrease.

Note: Figure translations are in progress. See original paper for figures.