



Article

Plant Diversity Responses of *Ulmus pumila* L. Communities to Grazing Management in Hunshandak Sandy Land, China

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Abstract: Biodiversity is sensitive to climate change and human activity. Grazing management practices have a profound impact on plant species–genetic diversity in grassland and woodland communities. In this study, we explored the responses of species and genetic diversity to grazing in *Ulmus pumila* L. communities in the Hunshandak Sandy Land, analyzed the relationship between species and genetic diversity, and revealed the effects of climate factors on them. We found that the dominant species were *Spiraea trilobata*, *Caragana microphylla* and *Artemisia intramongolica* in *U. pumila* communities. Plant species richness in the banned grazing (BG) and seasonal grazing (SG) communities was significantly higher than that in the delayed grazing (DG) community. Plant Simpson's diversity index showed a downward trend with increasing grazing duration. There was no difference in allelic richness in nuclear DNA (*nrDNA*) of *U. pumila* and chloroplast DNA (*cpDNA*) of NU (other dominant species besides *U. pumila*) among grazing management types. The expected heterozygosity of *U* in *nrDNA* and *cpDNA* was significantly affected by grazing management, and the trend was BG > SG > DG. The genetic diversity of *U* was lower than that of NU. The genetic diversity characteristics of *U* in *cpDNA* were lower than those in *nrDNA*. The analysis of molecular variance (AMOVA) showed that 98.08% of the variation in *U* and 95.25% of the variation in NU was attributed within populations and the differences within grazing management types were 13.35% in *U* and 24.08% in NU ($p < 0.001$). The species richness of communities was positively correlated with the genetic diversity of *U*, NU and all dominant species (*U* + NU) in communities. The nineteen climatic variables together explained 94.24% and 79.08% of the total variation in *U* and NU genetic and species diversity. The mean temperature of the warmest quarter and temperature seasonality were the main factors affecting genetic diversity ($p = 0.046$; 0.01), while the maximum temperature of the warmest month was the main factor affecting species diversity ($p = 0.05$).

Keywords: species diversity; genetic diversity; climatic factors; sparse forest grassland; Inner Mongolia Plateau



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1. Introduction

Biodiversity is a frequently employed term that encompasses various tiers of biological organization, including genes, species and ecosystems [1]. Plant diversity is one of the most important elements of biodiversity [2], and is easily restricted by the environment, particularly in the formation of genetic diversity and species diversity within communities [3]. Because changes in habitat characteristics disturb the niche width and population size of dominant plant species, the level of species diversity varies [4]. Similarly, the accumulation of genetic diversity of species in response to habitat change will improve the adaptability and viability of organisms [5]. Genetic variation within species could lead to differences in resource utilization, growth rate, and reproductive strategies among different

individuals, thus affecting the structure and dynamics of the entire community. In turn, the ecological conditions of the changed community will accelerate the rate of evolution of different species to adapt to the environment [6]. Numerous studies have indicated that the relationship between species diversity and genetic diversity is intricate. This may be reflected as a parallel relationship due to drift, selection and species turnover [4,7], as genetic variation in a dominant species changes the biotic environment in the remaining species of the community and restricts community species diversity [7], or as the species diversity of communities affects the selection and genetic diversity levels of constituent populations [6–8]. The life type of the dominant species determines the composition of the community and determines the genetic diversity and species diversity within the community [7]. On the other hand, the patterns of genetic variation within species have an impact on the interactions between species and, as a result, influence community composition in diverse environments [9]. The study of species genetic diversity correlations in plant diversity is of great significance for biodiversity conservation planning. Studies on the interaction between genes in dominant species and populations of other species in the community can provide a basis for conceptual unification in biodiversity research.

Grazing is the most important and widespread land use and management practice in grassland ecosystems [10–12]. Grazing represents a multifaceted process where energy and nutrients move from the producer (plant) to the consumer (herbivore) level [13]. This intricate process involves various complicating elements, including the type of grassland, stocking rate, grazing intensity, type of livestock, and duration of the grazing season [14]. Grazing directly and indirectly affects both the structure and function of the ecosystem, as well as the biological relationship of the community, which are particularly important to the stability of grassland ecosystems [15,16]. Grasslands are lands that are extensively grazed throughout the world, including natural grasslands and savannas. These lands are not only an important source of livelihood for millions of pastoralists but also major wildlife habitats and conservation areas for plant genetic resources [13]. Optimizing grazing intensity and diversifying grazing type are key management measures for promoting grassland restoration, improving livestock production efficiency, and accomplishing grassland biodiversity conservation and sustainable development [14,16,17]. Moreover, rational grazing is beneficial for controlling understory woody vegetation and reducing forest fires, limiting the invasion of alien species and preventing declines in biodiversity [13], decreasing asymmetrical competition among plant species in the community [15,18] and protecting and utilizing animal and plant resources [16]. Improved grazing management regimes have been widely used in Inner Mongolia grasslands [12]. In view of the degradation of grassland caused by long-term overgrazing, ecological restoration measures have been implemented mainly by banning grazing, resting grazing, rotational grazing and seasonal grazing [14,17].

Hunshandak Sandy Land, situated in the eastern region of the Inner Mongolia Plateau, is one of China's four major sandy land areas [19]. It serves as the transitional zone between a typical steppe region and a dry farming area in northern China [20]. Hunshandak Sandy Land falls within the middle temperate zone and experiences a semi-arid to arid continental monsoon climate, with an area of 3.8×10^4 km² [19], altitude of 1100–1300 m, annual evaporation of 1680–2940 mm, annual average temperature of 1.8 °C and annual average rainfall of approximately 310 mm, mainly in summer, accounting for approximately 70% of the annual total [21]. The zonal soil is mainly sandy chestnut soil and aeolian sandy soil [22]. The most typical natural top-level vegetation community in Hunshandak Sandy Land is *Ulmus pumila* L. sparse forest grassland (Figure 1), which is a nonzonal hidden vegetation type [23]. The zonal vegetation of Hunshandak Sandy Land includes meadow steppe, steppe and desert steppe [24]. Vegetation growth is good, mainly *Gramineae* and *Artemisia* vegetation, and coverage is generally 30–50% [25]. The primary tree species in the region is *U. pumila*. The main shrubs are *Caragana microphylla* Lam., *Spiraea aquilegifolia* Pall. and *Ribes diacanthum* Pall. The main herbaceous plants are *Leymus chinense* (Trin.) Tzvel, *Agropyron cristatum* (L.) Beauv, *Polygonum divaricatum* L., *Potentilla chinensis* Ser., *Artemisia*

frigida Willd., *Chenopodium glaucum* L., *Setaria viridis* (L.) Beauv and *Leymus secalinus* (Georgi) Tzvel [21,26]. Since the 1960s, due to unreasonable human activities, especially overgrazing, Hunshandak Sandy Land has been seriously degraded and desertified, and it has become one of the few areas in China with a desertification development rate that exceeds 4% [19]. This has not only reduced pasture productivity significantly and restricted the healthy development of the livestock industry, but also led to it becoming one of the main dust sources in Beijing and Tianjin [19]. To restore and manage the sandy ecosystem sustainably, the Inner Mongolia Autonomous Region launched the “Returning Pasture to Grassland” project in 2003 and began to implement the “three grazing policies” system, namely banning grazing, resting grazing and rotating grazing [27].



Figure 1. The natural community of *Ulmus pumila*.

In Hunshandak Sandy Land, *U. pumila* sparse forest grassland is mainly distributed in the eastern part of Zhenglan Banner and Keshiketeng Banner. After a long period of vegetation succession, *U. pumila* sparse forest has become the top community and the most stable type of native vegetation in Hunshandak Sandy Land [28]. *U. pumila* sparse forest is a mixture of trees, shrubs and herbs with rich biodiversity and important ecological functions, providing feed for large herbivores [29]. However, in recent years, the phenomenon of overgrazing in *U. pumila* sparse forest grassland has been very common, the stocking rate has exceeded a reasonable level by 20% and the grassland has been seriously degraded [30]. Grassland degradation caused by overgrazing has prevented the natural regeneration of the *U. pumila* population, causing many shrub deaths and significantly reducing herb coverage, plant species and the proportion of perennial herbs [23].

Given the importance of these communities’ preservation and the income from grazing needed for sustaining nearby human populations, we have studied the influence of three possible grazing management practices on plant species diversity, as well as their influence on genetic diversity. Since genetic diversity and species diversity relationships can be intricate and both affected by levels of grazing, the main questions are as follows: (1) Is there a difference in the species diversity of *U. pumila* communities and the genetic diversity of *U. pumila* and dominant plant species in communities among grazing management types (banned grazing, seasonal grazing and delayed grazing)? If this is the case, what are the change trends and characteristics of species diversity and genetic diversity in Hunshandak Sandy Land? (2) Is there a correlation between the species richness and genetic diversity of *U. pumila* communities under different grazing management practices? If this is the case, how are they correlated? (3) Are the species diversity and genetic diversity (species level

and community level) of *U. pumila* communities affected by regional bioclimatic factors in Hunshandak Sandy Land? If this is the case, which climatic factor influences the plant diversity of *U. pumila* communities in Hunshandak Sandy Land? How do they relate to each other? The aim of this study was to provide additional insights into the conservation of biodiversity within *U. pumila* communities. These findings have practical implications for restoring and managing grazing ecosystems in arid and semiarid regions.

2. Materials and Methods

2.1. Experimental Design

In the main distribution area of *U. pumila* sparse forest grassland, Zhenglan Banner and Keshiketeng Banner of Hunshandak Sandy Land, we selected 3 *U. pumila* sparse forest grassland fields with different grazing management types established in 2017; banned grazing fields (BG, communities 1–5), seasonal grazing fields (SG, communities 6–9) and delayed grazing fields (DG, communities 10–12) (Figure 2a). The BG fields were fenced year-round. The SG and DG fields were grazed with intensities of 10 cattle per 7 hm² (1.4 cattle units/hm²). The SG fields were grazed in summer and autumn. The DG fields were interrupted from grazing for 45 days at the beginning of plant growth in spring (10 April to 25 May) and were grazed the remaining time. The vegetation cover of the three grazing fields was 93%, 81% and 67%, respectively. The dominant shrub in all three grazing fields was *U. pumila* seedlings, and the dominant herbs of the three grazing fields were *Setaria trilobata* L., *Leymus secalinus* (Georgi) and *Artemisia intramongolica* H. C. Fu.

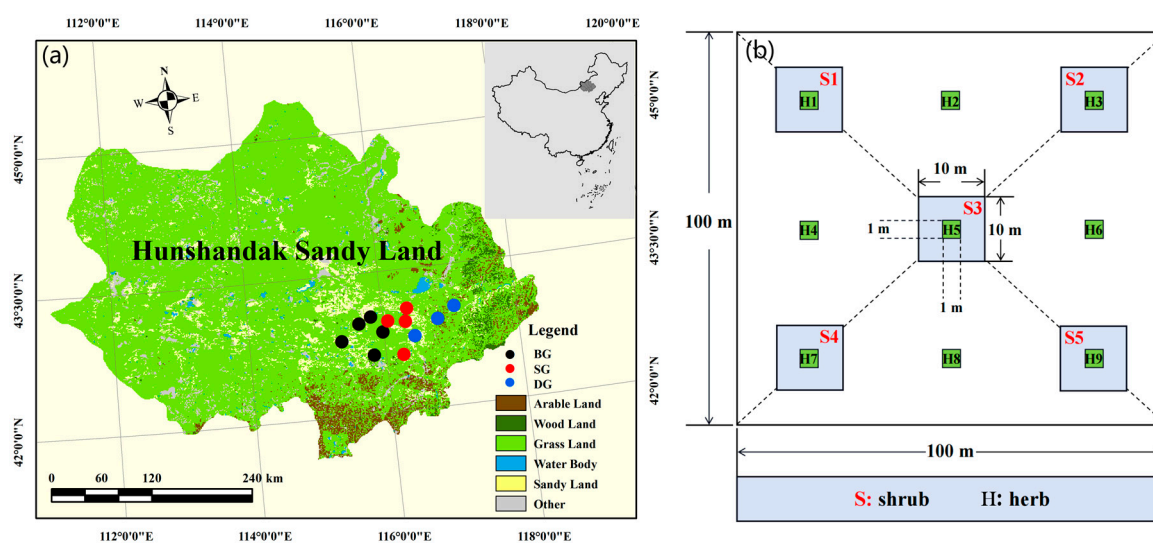


Figure 2. Sampling sites (a) and quadrat layout (b) of *Ulmus pumila* sparse forest grassland fields in Hunshandak Sandy Land.

2.2. Field Sampling and Climate Data Gathering

The *U. pumila* community consists of tree, shrub and herb layers. Although these layers are not at the same level, they influence each other, depend on each other and form an adaptation to growing space and light, water, nutrients, etc. The tree layer is the main body of the *U. pumila* community, and the shrub and herb layers belong to the understory vegetation. Each layer of the community has dominant species, namely U (*U. pumila*, tree layer) and NU (other dominant species besides *U. pumila*, shrub and herb layer).

The number of plants, vegetation cover, height and frequency of plants were determined in mid-August of 2018 and 2019. In each field type, we established a sizable quadrat measuring 100 m × 100 m to assess the species composition of all trees, shrubs and herbs. Within the large quadrat, we established five shrub quadrats measuring 10 m × 10 m and nine herb quadrats measuring 1 m × 1 m, as depicted in Figure 2b. The NU combinations of each grazing management type in this study were different, as shown

in Table 1. A total of 48 *U. pumila* samples (U) and 72 other dominant plant samples (NU) were arbitrarily sampled from their young healthy leaves and promptly stored with silica gel in zip-lock plastic bags, preserving them for future DNA extraction. The sample information used in genetic diversity for each grazing management types shown in Table 1. Climatic data spanning the years 1970 to 2000 were obtained from the WorldClim data website <https://www.worldclim.org/> (accessed on 8 November 2021). This dataset comprised 19 climatic variables, each providing insights into the region's climate characteristics. These variables included annual mean temperature (AMT), mean diurnal range (MDR), isothermality (ISO), temperature seasonality (TS), max temperature of warmest month (WMT), min temperature of coldest month (CMT), temperature annual range (ART), mean temperature of wettest quarter (WQT), mean temperature of driest quarter (DQT), mean temperature of warmest quarter (TWQ), mean temperature of coldest quarter (CQT), annual precipitation (AP), precipitation of wettest month (WMP), precipitation of driest month (DMP), precipitation seasonality (PS), precipitation of wettest quarter (WQP), precipitation of driest quarter (DQP), precipitation of warmest quarter (PWQ) and precipitation of coldest quarter (CQP). These climatic data were crucial for assessing the influence of climatic factors on plant diversity in the Hunshandak Sandy Land region, shedding light on the intricate relationship between environmental conditions and biodiversity.

Table 1. Sample list for genetic analysis of *Ulmus pumila* communities from different grazing management types.

Grazing Management Types	Number of <i>Ulmus pumila</i> Samples	Species Name and Number of Other Dominant Species Samples besides <i>U. pumila</i>
BG	20	<i>Agropyron cristatum</i> (L.) Gaertn. (2) <i>Artemisia frigida</i> Willd. (3) <i>Artemisia halodendron</i> Turcz. (4) <i>Artemisia scoparia</i> Waldst. et Kit (4) <i>Caragana korshinskii</i> Kom(2) <i>Carduus crispus</i> L. (2) <i>Cleistogenes squarrosa</i> (Trin.) Keng (2) <i>Setaria viridis</i> (L.) Beauv. (4) <i>Spiraea trilobata</i> L. (3)
SG	16	<i>Artemisia frigida</i> Willd. (2) <i>Artemisia halodendron</i> Turcz. (4) <i>Caragana microphylla</i> Lam. (4) <i>Carex duriuscula</i> C. A. Mey. (3) <i>Chenopodium acuminatum</i> Willd. (3) <i>Leymus secalinus</i> (Georgi) Tzvel. (2) <i>Setaria viridis</i> (L.) Beauv. (2) <i>Spiraea trilobata</i> L. (4)
DG	12	<i>Artemisia halodendron</i> Turcz. (8) <i>Corispermum mongolicum</i> Iliin. (4) <i>Salix cheilophila</i> Schneid. (2) <i>Salix gordejewii</i> Y. L. Chang et Skv. (8)

BG, banned grazing; SG, seasonal grazing; DG, delayed grazing.

2.3. Molecular Methods

Total genomic DNA extraction was carried out using AxyPrep genomic DNA mini kits (Axygen Inc., Beijing, China), adhering to the manufacturer's provided protocols. DNA quality assessment was performed using a 1.0% agarose gel. Referring to the Consortium for the Barcode of Life (CBOL), several pairs of chloroplast DNA (*cpDNA*) and nuclear DNA (*nrDNA*) primers were used [31–33] (Table 2). Polymerase chain reactions (PCRs) were conducted in a 25 µL reaction mixture containing 40 ng of genomic DNA, 1.0 U of Taq polymerase (Axygen Inc., Beijing, China), 3 mM MgCl₂, 500 µM of each dNTP, 20 mM Tris-HCl (pH 8.3), 100 mM KCl and 0.3 µM of each primer. Amplification involved an initial

denaturation at 94 °C for 3 min, followed by 30 cycles of 30 s at 94 °C, 30 s at an appropriate annealing temperature, 1 min at 72 °C, and a final extension step at 72 °C for 5 min. PCR products were assessed by 1.0% agarose gel electrophoresis. Subsequently, the products were purified using the AxyPrep PCR purification kit following the manufacturer's protocol (Axygen Inc., Beijing, China), and DNA sequencing was carried out by the MEIJI sequencing company in Shanghai, China, employing the PCR primers as sequencing primers.

Table 2. Primer sequences in chloroplast and nuclear DNA of the selected species.

	Primer	Sequence (5'–3')	References
cpDNA	<i>psbA-trnH</i>	F: GTTATGCATGAACGTAATGCTC R: CGCGCATGGTGGATTACAATCC	Tate et al., 2003 [31]
	<i>trnL-trnF</i>	F: CGAAATCGGTAGACGCTACG R: ATTTGAACTGGTGACACGAG	Taberlet et al., 1991 [32]
nrDNA	ITS1-ITS4	F: AGGTGACCTGCCGAAGGATCATT R: GGTAGTCCCGCCTGACCTGG	White et al., 1990 [33]

cpDNA, chloroplast DNA; nrDNA, nuclear DNA.

2.4. Data Analyses

Two diversity indices were used to estimate plant species diversity: species richness (S_R) and Simpson's diversity index (D). $D = 1 - \sum_i^S P_i^2$, where P_i represents the proportion of each category i [34]. The importance value (IV) was calculated as the average of the relative height, relative frequency and relative coverage of the plant [35]. The measures of plant genetic diversity from U (*U. pumila*) and NU (other dominant species besides *U. pumila*) (Table 1) with different grazing management types were calculated with Arlequin 3.0 [36], including allelic richness (A_R) and expected heterozygosity (H_E), gene diversity (G_d), the number of haplotypes (H) and haplotype diversity (H_d) [37,38]. Genetic differentiation among populations in the different grazing management type groups was estimated by pairwise F_{ST} values [39]. Analysis of molecular variance (AMOVA) was conducted to assess the variation in U and NU among and within populations, and to compare the differences in U and NU populations within the same grazing management type and among grazing types using Arlequin 3.0 software [37]. We examined the connections between S_R and plant genetic diversity (A_R and H_E) using Pearson correlation. Before conducting analysis of variance (ANOVA) and correlation analysis, the data underwent normality testing to confirm a normal distribution. ANOVA was conducted to determine differences between grazing management types and diversity indices. One-way (independent variables: grazing management types; dependent variable: plant species diversity indices) or two-way (independent variables: grazing management types \times species; dependent variable: plant genetic diversity indices) ANOVA followed by Tukey's post hoc test. All statistical analyses were performed using SPSS 19.0 for Windows (SPSS, Inc., Chicago, IL, USA). Redundancy analysis (RDA) was applied to assess the relative impact of the recorded climate variables on the plant diversity indices across 12 *U. pumila* communities. Initially, data underwent detrended correspondence analysis, indicating the suitability of RDA (gradient length < 3). To prevent overfitting caused by the extensive set of explanatory variables, a 'forward selection' approach was used to select the most influential variables during analysis. Prior to analysis, plant diversity indices and climate data were log-transformed ($\log(x + 1)$). The RDA was conducted using CANOCO Version 4.5 [40], and all graphical representations were generated using Origin 2018.

3. Results

3.1. Effect of Grazing Intensity on Plant Species Diversity

Sixty-seven species were recorded in all grazing sites (Table 3). Specifically, there were 55 plant taxa in the banned grazing (BG) *U. pumila* communities, 39 plant taxa in the seasonally grazed (SG) *U. pumila* communities and 29 plant taxa in the delayed

grazing (DG) *U. pumila* communities. The importance values of shrubs and herbs in the BG communities were similar, which were 49.89% and 50.11% of the total importance value, respectively, while those of the SG and DG communities were very close, and the trends were consistent, which were 61.29% and 38.71%, and 61.96% and 38.04%, for shrubs and herbs, respectively. Based on the species importance value, it was observed that *U. pumila* and its seedlings held the dominant position within all of the communities. In addition, *S. trilobata*, *C. microphylla* and *A. halodendron* were the dominant species in the BG, SG and DG communities, respectively. The results of one-way ANOVAs indicated that grazing management types had a significant impact on plant species richness (S_R) and Simpson's diversity index (D) ($p < 0.001$) (Figure 3). Specifically, the analysis revealed that the S_R in the BG and SG communities was significantly higher than that in the DG communities, with values of 23.8 ± 2.280 and 24 ± 2.944 , respectively ($p < 0.05$). The plant Simpson's diversity index (D) showed a downward trend with increasing grazing management intensity. The values of S_R and D in the DG community were the lowest (14.33 ± 2.08 ; 0.197 ± 0.002 , $p < 0.001$).

Table 3. Importance value of dominant species in elm *Ulmus pumila* communities with different grazing management types.

Species	Life-Form	Important Value (%)		
		BG	SG	DG
<i>Setaria viridis</i> (L.) Beauv.	annual	0.43	0.32	0.08
<i>Corispermum mongolicum</i> Iiin.		0.25	0.50	0.33
<i>Chenopodium aristatum</i> L.		0.24	0.19	0.09
<i>Bassia dasyphylla</i> (Fisch. et C. A. Mey.) Kuntze		0.04	0.08	0.06
<i>Salsola collina</i> Pall.		0.02	0.14	0.07
<i>Chenopodium acuminatum</i> Willd.		0.02	0.08	0.05
<i>Artemisia palustris</i> Linn.		0.05	0.01	
<i>Echinops gmelini</i> Turcz.		0.01	0.01	
<i>Cannabis sativa</i> L.		0.01	0.05	
<i>Xanthium sibiricum</i> Patr. ex Widder		0.01		
<i>Agriophyllum squarrosum</i> (Linn.) Moq.			0.07	
<i>Eragrostis pilosa</i> (Linn.) Beauv.				0.01
<i>Artemisia scoparia</i> Waldst. et Kit		biennial	0.19	0.11
<i>Artemisia sieversiana</i> Ehrhart ex Willd.	0.08		0.01	
<i>Lappula myosotis</i> V. Wolf	0.04		0.05	
<i>Sonchus oleraceus</i> L.	0.01			0.01
<i>Dontostemon dentatus</i> (Bunge) Ledeb.	0.03			0.08
<i>Carduus crispus</i> L.	0.53			
<i>Silene aprica</i> Turcz. ex Fisch. et Mey.	0.01			
<i>Agropyron cristatum</i> (L.) Gaertn.	perennial	0.46	0.28	0.19
<i>Artemisia frigida</i> Willd.		0.42	0.29	0.03
<i>Carex duriuscula</i> C. A. Mey.		0.26	0.24	0.24
<i>Cleistogenes squarrosa</i> (Trin.) Keng		0.26	0.14	0.02
<i>Potentilla acaulis</i> L.		0.10	0.01	0.01
<i>Medicago ruthenica</i> (L.) Trautv.		0.07	0.02	0.13
<i>Carex tristachya</i> Thunb.		0.02	0.11	0.03
<i>Bromus inermis</i> Leyss.		0.01	0.01	0.04
<i>Leymus secalinus</i> (Georgi) Tzvel.		0.01	0.25	0.01
<i>Allium tenuissimum</i> L.		0.05	0.01	
<i>Poa sphondylodes</i> Trin.		0.04	0.01	
<i>Potentilla bifurca</i> Linn.		0.04	0.02	
<i>Achnatherum sibiricum</i> (L.) Keng		0.02	0.09	
<i>Allium senescens</i> L.		0.02	0.04	
<i>Allium mongolicum</i> Regel.		0.01	0.02	
<i>Stipa grandis</i> P.A. Smirn.	0.05		0.01	

Table 3. Cont.

Species	Life-Form	Important Value (%)		
		BG	SG	DG
<i>Leymus chinensis</i> (Trin.) Tzvel.	perennial	0.02		0.09
<i>Phragmites australis</i> (Cav.) Trin. ex Steu.			0.08	0.01
<i>Leontopodium leontopodioides</i> (Willd.) Beauv.		0.34		
<i>Dianthus chinensis</i> L.		0.10		
<i>Ferula bungeana</i> Kitag.		0.08		
<i>Heteropappus altaicus</i> (Willd.) Novopokr.		0.04		
<i>Oxytropis racemosa</i> Turcz.		0.03		
<i>Erodium stephanianum</i> Willd.		0.02		
<i>Psammochloa villosa</i> (Trin.) Bor		0.02		
<i>Astragalus laxmannii</i> Jacquin		0.02		
<i>Allium ramosum</i> L.		0.01		
<i>Oxytropis racemosa</i> Turcz.		0.01		
<i>Calamagrostis pseudophragmites</i> (Haller f.) Koeler				0.02
<i>Chamaerhodos canescens</i> Krause				0.02
<i>Thalictrum petaloideum</i> L.				0.02
<i>Polygonum sibiricum</i> Laxm.				0.01
<i>Polygonum divaricatum</i> L.				0.09
<i>Hedysarum gmelinii</i> Ledeb.				0.04
<i>Ptilotricum canescens</i> (DC.) C. A. Mey.				0.02
<i>Ulmus pumila</i> L.		shrub	1.15	1.55
<i>Artemisia halodendron</i> Turcz.	0.42		1.08	0.78
<i>Spiraea trilobata</i> L.	2.58		0.98	
<i>Caragana microphylla</i> Lam.	0.03		1.40	
<i>Thymus mongolicus</i> Ronn.	0.01		0.02	
<i>Caragana korshinskii</i> Kom.	0.27			
<i>Lespedeza daurica</i> (Laxm.) Schindl.	0.03			
<i>Kochia prostrata</i> (L.) Schrad.	0.02			
<i>Cynanchum thesioides</i> (Frey) K. Schum.	0.01			
<i>Berberis poirerii</i> Schneid.			0.10	
<i>Salix gordejewii</i> Y. L. Chang et Skv.				0.58
<i>Salix cheilophila</i> Schneid.				0.42
<i>Hedysarum fruticosum</i> Pall.				0.04

BG, banned grazing fields; SG, seasonal grazing fields; DG, delayed grazing fields.

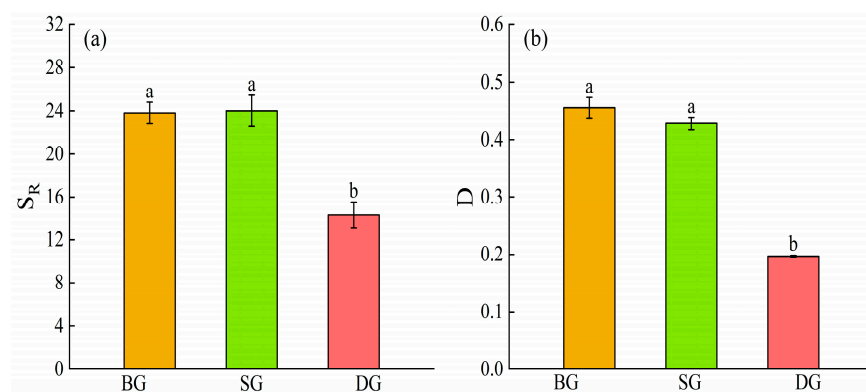


Figure 3. The plant species diversity ((a) S_R , species richness; (b) D , Simpson's diversity index) of *Ulmus pumila* sparse forest grassland fields with different grazing management types. Values are mean \pm SE. Different lowercase letters indicate significant differences ($p < 0.05$) among grazing management treatment types. BG, banned grazing fields; SG, seasonal grazing fields; DG, delayed grazing fields.

3.2. Effect of Grazing Intensity on Plant Genetic Diversity

The genetic indices (A_R and H_E) of U (*U. pumila*) and NU (other dominant species besides *U. pumila*) from grazing management types are given in Figures 4 and 5. The genetic diversity indices exhibited significant variations among different grazing management types, as indicated by two-way ANOVAs. Among the three grazing management types, the nrA_R and H_E of NU were the lowest (1.209 ± 0.084 , 0.347 ± 0.041) in the SG communities and compared to those in the BG (1.622 ± 0.202 , 0.416 ± 0.021) and DG communities (1.542 ± 0.057) (Figures 4 and 5). However, there was no difference in A_R in the *nrDNA* of U among grazing management types (Figure 4); in contrast, the H_E of U in the *nrDNA* and *cpDNA* was significantly affected by grazing management, and the trend was BG > SG > DG (Figure 5). Comparing the genetic parameters of U and NU, the cpA_R of U was noticeably lower than that of NU at all grazing management types (Figure 4). There was no marked difference in nrH_E between U and NU; however, there was no inconsistency in the cpH_E ; that is, the value for U was higher than that for NU in the BG, and the opposite was true in the DG (Figure 5).

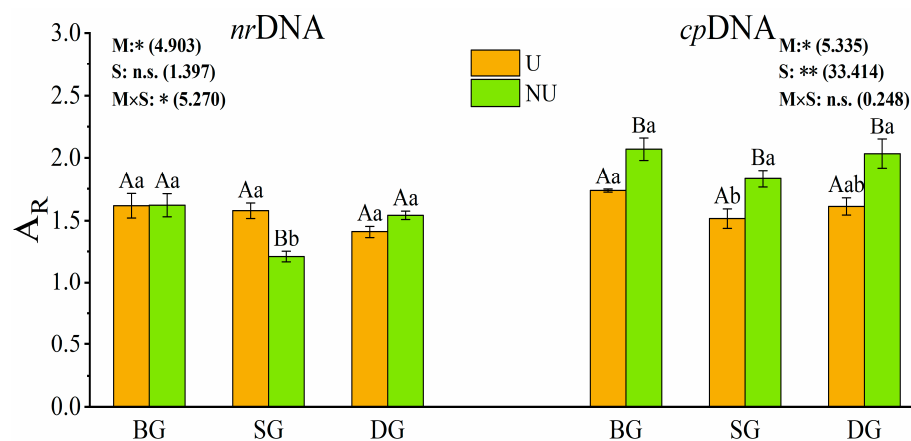


Figure 4. The plant allelic richness (A_R) of *Ulmus pumila* communities with different grazing management types. Values are expressed as mean \pm SE. Bars marked with distinct lowercase letters indicate significant differences among grazing management treatment types ($p < 0.05$). Bars marked with different capital letters signify significant variations between nuclear and chloroplast DNA genetic diversity treatments ($p < 0.05$). *nrDNA* and *cpDNA*, nuclear and chloroplast DNA. BG, banned grazing fields; SG, seasonal grazing fields; DG, delayed grazing fields; U, *Ulmus pumila*; NU, other dominant species besides *Ulmus pumila*; M, grazing management types; S, species; * and **, significant difference at $p < 0.05$ and $p < 0.01$ levels; n.s., no significant difference.

The comparative analysis results of the genetic diversity of chloroplast genes, nuclear genes and their combined genes at the species level are shown in Table 4. Data analysis showed that the genetic diversity of U was lower than that of NU. The genetic diversity characteristics of U in chloroplast genes were lower than those in nuclear genes, and most of the parameters in nuclear genes were the highest (Table 4). AMOVA showed that 1.92% of the variation in U and 4.75% of the variation in NU was attributed among populations, and within-population variation accounted for 98.08% and 95.25% of the total variation, respectively (Table 5). At the grazing management level, the differences among management types were 1.16% in U ($p < 0.001$) and 1.7% in NU ($p = 0.004$), and the differences within populations among grazing management types were 13.35% in U and 24.08% in NU ($p < 0.001$). The F_{ST} values for U and NU were 0.1219 and 0.2238 at the species level, respectively.

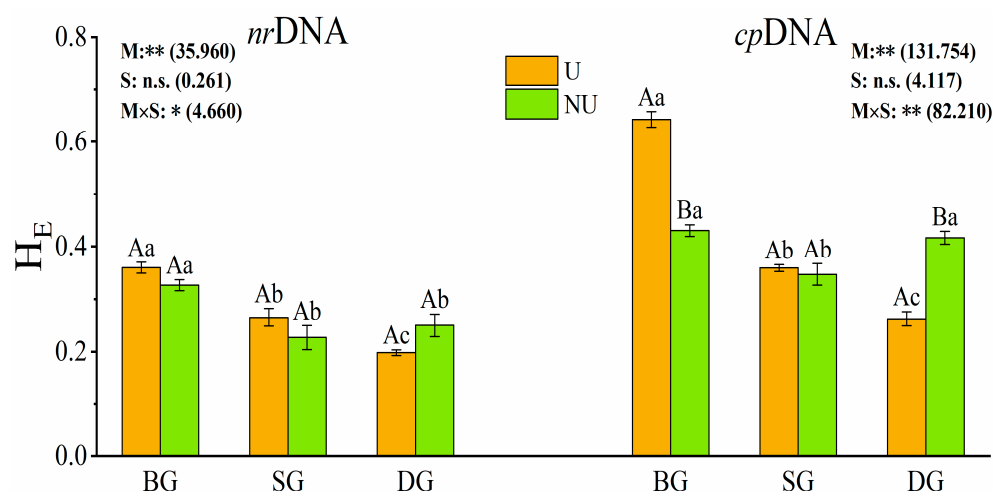


Figure 5. The plant expected heterozygosity (H_E) of *Ulmus pumila* communities with different grazing management types. The data is presented as mean \pm SE. Bars with distinct lowercase labels indicate notable disparities among the various grazing management treatment types ($p < 0.05$). Meanwhile, bars designated with different uppercase labels indicate significant distinctions between treatments involving nuclear and chloroplast DNA genetic diversity ($p < 0.05$). *nrDNA* and *cpDNA*, nuclear and chloroplast DNA. BG, banned grazing fields; SG, seasonal grazing fields; DG, delayed grazing fields; U, *Ulmus pumila*; NU, other dominant species besides *Ulmus pumila*; M, grazing management types; S, species; * and **, significant difference at $p < 0.05$ and $p < 0.01$ levels; n.s., no significant difference.

Table 4. Genetic diversity parameters at species level.

Gene	Species	H	$H_d \pm SD$	$A_R \pm SD$	$H_E \pm SD$	$G_d \pm SD$
<i>cpDNA</i>	U	20	0.497 ± 0.163	2.968 ± 0.649	0.252 ± 0.133	0.848 ± 0.079
	NU	34	0.584 ± 0.233	3.467 ± 0.639	0.435 ± 0.187	0.847 ± 0.034
<i>nrDNA</i>	U	22	0.649 ± 0.136	3.163 ± 1.02	0.281 ± 0.185	0.905 ± 0.040
	NU	38	0.754 ± 0.189	3.660 ± 1.071	0.378 ± 0.215	0.942 ± 0.034
COM	U	27	0.762 ± 0.228	3.134 ± 1.067	0.268 ± 0.184	0.865 ± 0.018
	NU	45	0.791 ± 0.272	3.332 ± 1.011	0.394 ± 0.200	0.907 ± 0.012

U, *U. pumila*; NU, other dominant species besides *Ulmus pumila*; H, the number of haplotypes; H_d , the haplotype diversity; A_R , allelic richness; H_E , expected heterozygosity; G_d , gene diversity.

Table 5. Analysis of molecular variance (AMOVA) for *Ulmus pumila* and non-*Ulmus pumila* species.

Species	Source of Variation	df	Percentage of Variation	Fixation Indices	p
U	Among populations	11	1.92	$F_{ST} = 0.0192$	$p < 0.001$
	Within population	36	98.08		
	Total	48			
	Among grazing types	2	1.16	$F_{CT} = 0.0116$	$p < 0.001$
	Within population among grazing types	9	13.35		
	Total	36	87.82		
NU	Among populations	11	4.75	$F_{ST} = 0.0475$	$p = 0.004$
	Within population	132	95.25		
	Total	144			
	Among grazing types	2	1.70	$F_{CT} = 0.0170$	$p = 0.003$
	Within population among grazing types	9	24.08		
	Total	132	77.62		

U, *U. pumila*; NU, other dominant species besides *Ulmus pumila*.

3.3. Correlations between Plant Species and Genetic Diversity

The correlation analyses revealed a positive association between species diversity and the genetic diversity of U, NU and all dominant species (U + NU) from grazing management communities, as depicted in Figure 6. The data clearly indicated a significant correlation between S_R and allelic richness of U (U_{A_R}) ($r = 0.90$, $p < 0.001$) (Figure 6a), a significant correlation between S_R and expected heterozygosity of NU (NU_{H_E}) ($r = 0.77$, $p = 0.003$) (Figure 6d), and no significant correlation between S_R and other genetic diversity parameters (U_{H_E} , NU_{A_R} , CA_R and CH_E) ($p > 0.05$) (Figure 6b,c,e,f).

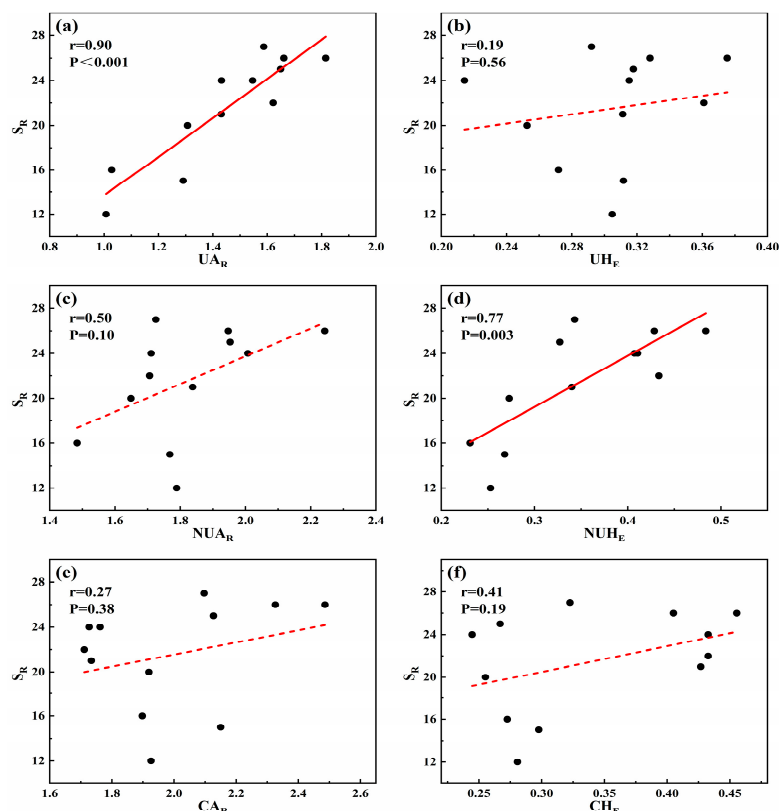


Figure 6. The correlation between species richness and genetic diversity. (between species richness (S_R) and allelic richness of *U. pumila* (U_{A_R}) (a); expected heterozygosity of *U. pumila* (U_{H_E}) (b); allelic richness of other dominant species besides *Ulmus pumila* (NU_{A_R}) (c); expected heterozygosity of other dominant species besides *Ulmus pumila* (NU_{H_E}) (d); allelic richness of community (CA_R) (e); expected heterozygosity of community (CH_E) (f).

3.4. Correlations between Climatic and Species–Genetic Diversity

The plant diversities of *U. pumila* sparse forest grassland communities in Hunshandak Sandy Land were impacted by various climatic factors, including AMT, MDR, ISO, TS, WMT, CMT, ART, WQT, DQT, TWQ, CQT, AP, WMP, DMP, PS, WQP, DQP, PWQ and CQP (Figure 7). RDA revealed that the collective influence of the nineteen climatic variables accounted for 94.24% of the overall variation in the genetic diversity of U and NU (Figure 7a). Axis 1 and Axis 2 explained 76.04% and 18.2% of the total variation, respectively. Notably, among the nineteen climatic variables, only TWQ and TS were found to be statistically significant according to the Monte Carlo permutation test ($p = 0.046$; 0.01). The remaining variables did not demonstrate significant associations (all cases, $p > 0.05$). Specifically, TWQ and TS accounted for 26.6% and 17.1% of the total explained variation, respectively (Figure 7a). Additionally, the RDA indicated that the combined influence of the nineteen climatic variables accounted for 79.08% of the total variation in the species diversity of *U. pumila* communities. Axis 1 and Axis 2 explained 56.91% and 22.17% of the total variation,

respectively (Figure 7b). Among these nineteen climatic variables, only WMT exhibited statistical significance based on the Monte Carlo permutation test ($p = 0.05$). Specifically, 20.7% of the total explained variation was attributed to WMT (Figure 7b).

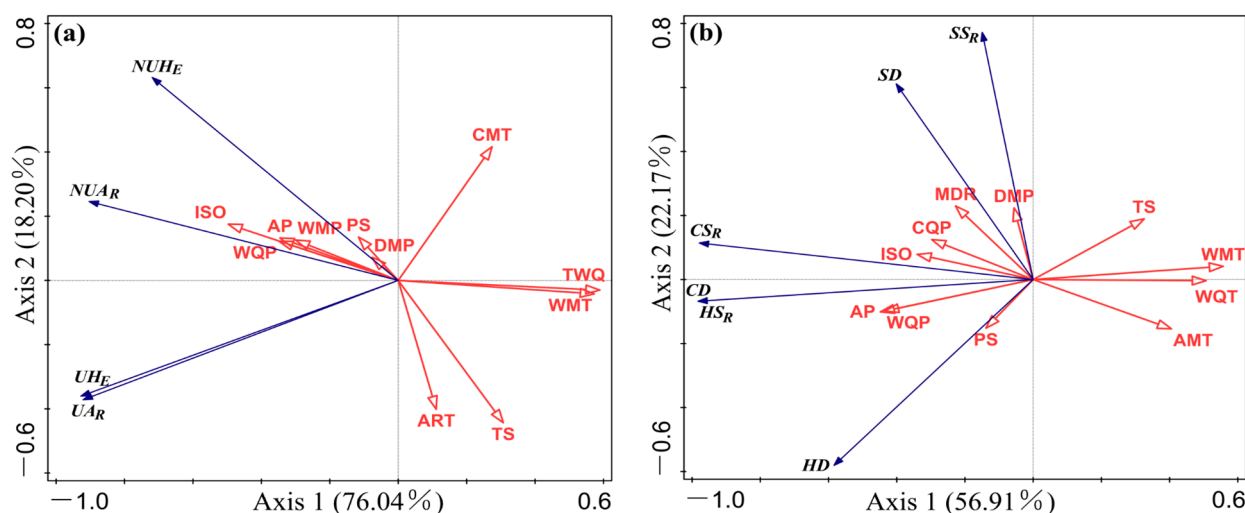


Figure 7. RDA between plant diversity ((a) species level; (b) community level) of *Ulmus pumila* communities) and bioclimatic factors. A_R, allelic richness; H_E, expected heterozygosity; U, *U. pumila*; NU, non-*U. pumila* species; SS_R, species richness of shrubs; HS_R, species richness of herbs; CS_R, species richness of communities; SD, Simpson's diversity index of shrubs; HD, Simpson's diversity index of herbs; CD, Simpson's diversity index of communities.

4. Discussion

4.1. Responses of Species Diversity to Grazing Types

The community structure and composition of the *U. pumila* sparse forest grassland were affected by grazing type in Hunshandak Sandy Land. In this study, we found that the number of species in the BG communities was the highest, and that in the DG communities was the lowest. This was consistent with the results of most studies on sparse forest grasslands and grasslands [41–43]. The species diversity parameters (S_R and D) in the DG were significantly lower than those in the BG and SG communities; nevertheless, there was no significant difference between the BG and SG communities. The reason is that the grazing time of the DG communities (continuous grazing for up to 320 days) each year is time unit longer than that of the BG and SG communities. Among the three grazing management policies implemented, the DG policy with the longest continuous grazing period reduced the species and quantity of plants and destroyed the ecological balance, indicating that the DG policy was the least beneficial for the restoration of *U. pumila* sparse forest grassland and grassland vegetation. The results of this study revealed that the species richness of the *U. pumila* sparse forest grassland community was relatively high under both non-grazed and seasonal grazing. In line with this, similar studies in grasslands found that non-grazed and seasonal grazing increased the level of species diversity in grassland communities [44–46].

4.2. Responses of Genetic Diversity and Difference to Grazing Types

Genetic data results indicated that the nuclear allelic richness (nrA_R) of U (*U. pumila*) was not different under different grazing types, and the nuclear expected heterozygosity (nrH_E) of all species was lower than the chloroplast expected heterozygosity (cpH_E), indicating that the species chloroplast gene flow rates of *U. pumila* sparse forest grassland are faster than the nuclear gene flow rates. This is because the majority of species in the community are maternally inherited (gene flow by seeds or vegetative spread) [47], which is also in line with the natural phenomenon that most angiosperms mainly rely on maternal

inheritance [48,49]. The genetic diversity parameters, including cpA_R and H_E in U and nrA_R and H_E in NU (other dominant species besides *U. pumila*), were consistently lower in the SG than in the BG. This suggests that species diversity and genetic diversity within *U. pumila* sparse forest grassland communities responded differently to various grazing types. Furthermore, at the species level, the genetic diversity of U was found to be lower than that of NU; this may be because, compared with U, the species used for genetic diversity analysis of NU came from the shrub and herb layer, which had more abundant species and larger sample size, and most of the species were dominant species in the community, with stronger environmental adaptability and more complex phylogenetic relationships, which may increase the overall genetic diversity level [1,50]. At the same time, most of the genetic diversity parameters of nuclear genes were higher than those of chloroplast genes in U and NU, indicating that the evolutionary adaptation of nuclear genes was stronger than that of chloroplast genes.

The AMOVA data revealed that the genetic differentiation of U and NU within populations in Hunshandak Sandy Land was high, both higher than 95%, explaining why the genetic differentiation of species in *U. pumila* sparse forest grassland was mainly within the populations. We discovered that the genetic differences between the U and shrub-grass layers under the same grazing management practices were larger than those between the different management practices. The overall variation rates were 13.35% and 24.08%, respectively, which indicated that grazing management easily caused genetic differentiation in the *U. pumila* sparse forest grassland community. This is consistent with some research findings, where grazing caused genetic differentiation of plant communities in *Stipa grandis* steppe (19.84%) and alpine meadow (>12%) [51,52].

4.3. Relationship between Species and Genetic Diversity

Numerous studies have investigated the relationship between plant species and genetic diversity, yielding inconsistent results. This relationship may take different forms: it could be parallel [4,53], where the genetic diversity of dominant species influences community species diversity [54], or it could be positive, where community species diversity affects the genetic diversity of dominant species [6]. In our study, species diversity at the U, NU and community levels was positively correlated with genetic diversity. The S_R of the dominant plants (U and NU) was significantly positively correlated with A_R and H_E , respectively, indicating that S_R and A_R in the tree layer and S_R and H_E in the shrub-grass layer had significant interactions. Our results are supported by theoretical [6,52] and empirical [7,55] studies of species–genetic diversity relationships. Combined with relevant research results, our study shows that grazing can cause changes in the species composition and ecological niche of the *U. pumila* sparse forest grassland community and enhance intraspecific and interspecific competition for nutrients and space in microhabitats, thus stimulating and changing the genetic variation patterns of species and indirectly promoting genetic differences among different species in the community.

4.4. Effects of Climate Factors on Plant Species and Genetic Diversity

The RDA results showed that the contribution rate of 19 climate factors to the genetic diversity of the *U. pumila* sparse forest grassland community was as high as 94.24%, indicating that the genetic diversity was mainly affected by climate factors and that other environmental factors had little effect on the genetic diversity of the species. We screened TWQ and TS as the main climatic factors restricting the genetic diversity of *U. pumila* sparse forest grassland species. This is the same as the relationship between genetic diversity and climate factors of *A. halodendron* and *C. microphylla* populations in similar regions [56,57], indicating that temperature is the key factor affecting plant genetic diversity in sandy grasslands. In this study, the total contribution of 19 climatic factors to community species diversity was 79.08%, indicating that environmental factors have a major effect on the species diversity of the community. This is also consistent with the results on the effects of climate factors on the species diversity of forests [58,59]. The data in this paper suggested

that the species diversity of *U. pumila* sparse forest grassland is significantly affected by WMT. This is consistent with the relationship between species diversity and temperature in plant communities on a large scale, where there was a significant positive correlation between plant species richness and average annual temperature in well-protected forests across four climate regions in China ($p < 0.05$) [58]. However, the results are inconsistent with similar studies on small scales, and there was a significant negative correlation between plant species richness and average annual temperature in warm temperate deciduous broad-leaved forest from Tuoliang National Nature Reserve in China ($p < 0.05$) [60]. This may be related to community type and regional microclimate.

5. Conclusions

The community structure, composition, species diversity and genetic diversity of the *U. pumila* sparse forest grassland in Hunshandak Sandy Land were all affected by grazing management type. The shrub layer was the main component of the vegetation community, and had higher species diversity and genetic diversity. Shrubs with strong resistance to grazing were *S. trilobata*, *C. microphylla* and *A. halodendron*. Grazing management easily caused genetic differentiation in the *U. pumila* sparse forest grassland community. A long continuous grazing period is not conducive to the conservation of species diversity in the *U. pumila* sparse forest grassland. The potential positive connections between species diversity and the genetic diversity of communities contributed to the substantial unification of biodiversity conservation at the gene and species levels. Both the genetic diversity and species diversity of *U. pumila* sparse forest grassland communities were easily affected by regional climate, and climate factors related to temperature played a leading role. In conclusion, we propose that the management strategy of *U. pumila* sparse forest grassland should be “conservation + utilization”. Scientific grazing management and sustainable use of grasslands are critical to maintaining the health of sandy ecosystems.

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