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Variations and Factors Characterizing Ecological Niches of Understory Herbaceous Species in Plantation Forests

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Abstract: Plant ecological niche characteristics are powerful representations of plant survival status. Understory herbaceous species in plantation forests are sensitive to local ecological environment changes; patterns of ecological niche changes of herbaceous plants under plantation forests are of great significance for maintaining the stability and sustainable development of plantation forest ecosystems. This study aims to explore the ecological niche characteristics of understory herbaceous species in plantation forests and their influencing factors. Six different site types of *Pinus tabulaeformis* plantations were selected from a stable plantation community in the feldspathic sandstone area of the Loess Plateau (China). The relative importance value and niche breadth were used as comprehensive quantitative indices to characterize the status, role, and degree of dominance of understory herbaceous species in plantation forests. We found few dominant species of understory herbaceous species in plantation forests, mostly companion species. The niche characteristics of understory herbaceous species in plantation forests varied significantly. For understory herbaceous species, the niche width was positively correlated with slopes and the niche overlap of the sunny slopes was positively relevant with slopes, while that of the shady slopes was negatively correlated. A canonical correspondence analysis indicated that several major factors influencing the niche breadth and niche overlap of understory herbaceous species in plantation forests were different. The canopy density and slope of plantation played a major role in the niche breadth and niche overlap of understory herbaceous species in plantation forests. In summary, the species distribution of understory herbaceous species in plantation forests was determined by site type. The canopy density and geographical slope were the dominant environmental factors for different ecological niche characteristics of understory herbaceous species. The ecological niche variation of different herbaceous species was the consequence of the integrated effects of the plantation and geographical environment.

Keywords: plantation forests; niche breadth; niche overlap; environmental interpretation

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1. Introduction

The concept of a niche was first proposed by ecologist Grinnell and used for the first time to express the status of biological units in spatial environmental units, namely, spatial niches [1]. Hutchinson proposed a more modern n-dimensional niche theory from a multidimensional perspective [2]. The ecological niche theory has become a fundamental principle of modern ecology, providing a quantitative basis for the coexistence and competitive systems of species in natural communities [3]. The theory contributes to understanding species composition, determining interspecies relationships, responding to environmental changes affecting species, and clarifying the adaptation of species due to the environment [4].

The ecological niche theory provides the basis for explaining the distribution of species exposed to the environment and for understanding the status of species in a given ecosystem community [5]. Based on the in-depth study of the ecological niche theory, niches can be used to describe the status and role of species within a community [4]. The construction of artificial vegetation can have a certain impact on the vegetation characteristics of the original landform [6]. The development of understory plants depends on the status of the understory habitat; that is, the harsher the habitat stand, the stronger the selection process for species and the more pronounced the differentiation of the understory vegetation [7]. Through competitive divergence, each species only covers some parts of the total niche space available in a community, which is the basis for the coexistence of competing species and the driving force behind their evolution [8]. The restoration of understory species diversity in plantation forests has become a major objective of plantation forest management [9]. The ubiquity of the niche provides an explanation for the positive correlation between species diversity and function [10] and establishes an important method to reveal the composition, structure, and coexistence of understory species [4]. Understory vegetation is an important part of the plantation ecosystem, and it plays an important role in maintaining species diversity and ecosystem stability [11,12]. In addition, understory herbaceous species occupy a relatively small niche, where growth, development, and abundance are easily affected by the external environment; the most sensitive to changes in the ecological environment played an important role in indicating the health of the plantation forest ecosystem [13–15].

The feldspathic sandstone region of the Loess Plateau is a key and difficult area for the construction of the Three-North Shelter Forest Program. In this region, the unique diagenesis mechanism of feldspathic sandstone makes it extremely vulnerable to denudation under the interaction of hydraulic and wind power, and has been subjected to serious soil erosion. Since the 1980s, ecological management has been carried out in the feldspathic sandstone region and plantation forests have been continuously cultivated, thereby promoting local vegetation restoration, ecological environment regulation, and economic development [16]. With people's requirements for the high-quality development of an ecological economy and consensus on biodiversity conservation, maintaining the understory biodiversity of plantations has become the core content of plantation restoration and reconstruction [17]. At present, studies on understory herbaceous species mainly focus on species richness, evenness, diversity index, and biomass. However, what is the relationship between the understory herbaceous species? What are the statuses and functions of various groups? Do these issues affect the correct understanding of the understory herbaceous species diversity?

This study evaluated the niche response of understory herbaceous species to different site types in a typical stable *P. tabulaeformis* plantation on the feldspathic sandstone region of Loess Plateau. Our main research questions were: (i) What is the status and relationship of understory herbaceous species in the feldspathic sandstone region? (ii) What are the niche characteristics of understory herbaceous species on different site types of plantations? (iii) What are the factors leading to the change of niche characteristics of understory herbaceous species?

2. Materials and Methods

2.1. Research Areas

This study was conducted at the soil and water conservation demonstration area of Ordos, Inner Mongolia, China. The area is situated on the middle reach of the Yellow River and is in the east of the semiarid, *hilly gully* area of the Loess Plateau in northwest China (Figure 1). The climate is an arid and semiarid continental climate, and the temperature changes dramatically per year with an average annual temperature of 7.3 °C. The mean annual precipitation is approximately 400 mm and is mainly concentrated during the season from July to September, with a short duration of heavy rain and frequent thunderstorms. The area belongs to the key soil and water conservation demonstration area of the "Three-

North Shelter Forest Program" in China, and is affected by topography, precipitation, and temperature changes. The soil in this area is dominated by typical loess soil, which has a low soil fertilization and extreme soil erosion. The area is part of the forest-steppe zone, and plantations and grasses are widely distributed here. Typical tree species include *Pinus tabulaeformis* and *Platycladus orientalis;* the *P. tabulaeformis* plantation in the study area was planted in the same batch in 2008, and the existing density of planted forests is 833 plants per square kilometer. Typical shrubs include *Hippophae rhamnoides* and *Caragana korshinskii*. Typical grass species include *Stipa capillata*, *Thymus mongolicus*, *Cleistogenes squarrosa*, and *Heteropappus altaicus*.

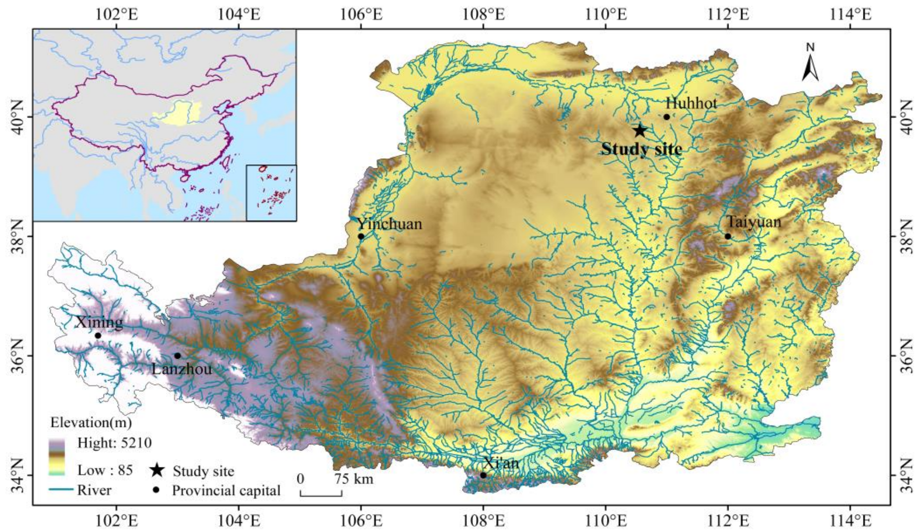

Figure 1. Geographical location of the study site.

2.2. Survey and Sampling

By collecting the quantity and ecological environment characteristics of understory herbaceous species, six different site types of *Pinus tabulaeformis* plantation forests were selected as experimental sites to explore changes and factors affecting the ecological niches of various species within the plant community. The soil under the forests was covered with secondary loess, accompanied by a feldspathic sandstone landscape and dominated by chestnut soil and aeolian sandy soil. In August 2019, large sample plots (25 m × 25 m) were established for each of the same age series of plantation stands in all six sites, giving a total of 12 plots (two replicates for each site type). Each of the 25 m × 25 m plot was divided into 25.5 m × 5 m subplots, and a small quadrat (1 m × 1 m) was set up in the center of each subplot. Field sampling was carried out in the plots from 2020 to 2021; the plantation of *P. tabulaeformis* and understory herbs of different site types were collected once in July, August, and September of each year. First, surveys were conducted (sampling plant types, coverage, height, and abundance). The sample line method was used to investigate the canopy density, which was calculated according to the ratio of the total diagonal length to the total crown length. Second, the soil physicochemical properties of each small quadrat were determined by digging 0–30 cm soil profiles (the reason for taking soil samples from 0 to 30 cm was due to the findings of previous studies that demonstrated that the grass root biomass is concentrated in the 0–30 cm soil layer [18]). A ring knife and aluminum box were used to collect soil samples after the residues and impurities on the soil surface were removed from the plot. A core of the top 10, 10–20, and 20–30 cm of soil was taken at each soil profile. The soil samples were placed in a Ziploc bag, numbered, and transferred to the laboratory to determine soil nutrient contents, such as the water content, organic matter, pH, and available nitrogen, phosphorus, and potassium.

2.3. Selection of Environmental Factors

According to the specific geographical setting and distribution characteristics of the *Pinus tabulaeformis* forests of the feldspathic sandstone area, as well as factors surrounding the soil, vegetation, and topography, we selected 11 indicators: environmental factors including altitude (AT), soil water content (SWC), soil pH (PH), soil thickness (ST), soil organic matter (SOM), slope (SL), aspect (AS), canopy density (CD), soil available nitrogen (SAN), soil available phosphorus (SAP), and soil available potassium (SAK). We determined the slope based on the standards of the slope classification of the International Geographical Union (IGU). The gradients were graded as 0–5° for flat slopes, 5–15° for gentle slopes, and 15–25° for steep slopes. The data for each indicator were expressed in terms of actual observations recorded, as well as measured values (Table 1).

Table 1. Basic condition of sample plots.

Sample Number	Site Types		Slope Aspect	Altitude (m)	Slope (°)	CD (%)	ST (m)
1	Sunny side	Flat slope	ES	1207	4	0.54 ± 0.07	0.21 ± 0.02
2		Gentle slope	ES	1228	11	0.48 ± 0.04	0.12 ± 0.01
3		Slope	WS	1210	20	0.46 ± 0.10	0.06 ± 0.01
4	Shady side	Flat slope	N	1205	3	0.49 ± 0.08	0.18 ± 0.02
5		Gentle slope	EN	1213	10	0.46 ± 0.11	0.12 ± 0.01
6		Slope	WN	1221	21	0.42 ± 0.05	0.12 ± 0.02

Notes: ES, south east; WS, south west; N, north; EN, north east; WN, north west; CD, canopy density; ST, soil thickness.

2.4. Relative Calculations and Laboratory Analyses

We used the relative importance index to quantify the status and dominance of understory herb species in the community. The relative importance index cannot only reflect the relative importance of plant species in the community, but also indirectly reflect the best habitat for plant survival. Higher values of relative importance indicated a higher importance of the species in the community and a stronger adaptability to the habitat. The relative importance value was calculated as:

$$\text{Relative importance value} = (\text{RC} + \text{RH} + \text{RA})/3 \tag{1}$$

$$\text{RC} = \frac{\text{the coverage of species}}{\text{sum of the coverage of all species}} \tag{2}$$

$$\text{RH} = \frac{\text{the height of species}}{\text{sum of the height of all species}} \tag{3}$$

$$\text{RA} = \frac{\text{the abundance of species}}{\text{sum of the abundance of all species}} \tag{4}$$

where RC is relative biomass, RH is relative height, and RA is relative abundance.

Levins' niche breadth was used as a quantitative indicator of plant species' ability to utilize environmental resources. Plant species with a higher niche breadth value could better utilize environmental resources. Levins' niche breadth was calculated as follows [19]:

$$\text{Niche breadth} = -\sum_{j=1}^{r} (P_{ij} * \log P_{ij}) \tag{5}$$

where P_{ij} represents the percentage of the jth resource utilized by the ith species in the niche of all resources and was calculated as the relative importance value of the ith species in the jth quadrat.

Pianka's econiche overlap could be used as a quantitative indicator of the degree of similarity in resource use and competition between plant species: the greater the value of econiche overlap, the greater the degree of similarity in resource use and the more intense the interspecific competition between plant species. Pianka's econiche overlap was calculated as follows [20]:

$$\text{Niche overlap} = \frac{\sum_{h=1}^{r} P_{ih} P_{jh}}{\sqrt{\sum_{h=1}^{r} {P_{ih}}^2 \sum_{h=1}^{r} {P_{jh}}^2}} \quad (6)$$

where P_{ih} and P_{jh} each represent the proportions of the importance values of the *i*th and *j*th species at the *h*th resource level to the sum of the importance values of the species at all resource levels, and r is the total number of resource sites (this paper refers to the number of sample squares). The niche overlap between species was considered meaningful at Pianka's niche overlap index of >0.3; a significant econiche overlap between species was considered at Pianka's niche overlap index of >0.6 [21].

The soil water content was determined with the oven dry method, and soil pH was measured using a pH meter. The soil organic matter content was measured using the potassium dichromate external heating method [22]. Soil available nitrogen was measured using the alkali n-proliferation method. Soil available phosphorus was measured using the 0.5 mol/L $NaHCO_3$ extraction method. Soil available potassium was measured using flame spectrophotometry with NH_4OA_C extraction [23]. The average soil physical and chemical properties in each site are shown in Table 2.

Table 2. Soil physical and chemical characteristics of different site types.

Sample Number	Site Types		SWC (%)	PH	SOM ($g \cdot kg^{-1}$)	SAN ($g \cdot kg^{-1}$)	SAP ($g \cdot kg^{-1}$)	SAK ($g \cdot kg^{-1}$)	AS
1	Sunny side	Flat slope	0.11 ± 0.03	7.52 ± 0.11	4.33 ± 0.21	4.55 ± 0.13	1.21 ± 0.08	44.05 ± 2.73	0.75
2		Gentle slope	0.08 ± 0.05	7.61 ± 0.06	3.77 ± 0.16	4.04 ± 0.12	1.09 ± 0.11	40.69 ± 1.68	0.37
3		Slope	0.07 ± 0.02	7.48 ± 0.03	3.39 ± 0.11	3.78 ± 0.14	0.99 ± 0.13	38.51 ± 5.75	0.98
4	Shady side	Flat slope	0.16 ± 0.06	7.51 ± 0.08	5.39 ± 0.31	4.75 ± 0.08	1.49 ± 0.21	48.56 ± 3.64	0.25
5		Gentle slope	0.15 ± 0.02	7.61 ± 0.12	4.82 ± 0.23	4.23 ± 0.14	1.38 ± 0.14	45.21 ± 2.78	0.02
6		Slope	0.11 ± 0.07	7.47 ± 0.04	4.45 ± 0.16	3.98 ± 0.11	1.28 ± 0.12	43.02 ± 4.21	0.63

Note: SWC, soil water content; SOM, soil organic matter; SAN, soil available nitrogen; SAP, soil available phosphorus; SAK, soil available potassium; AS, aspect.

2.5. Statistical Analyses

Quantitative conversions of slope azimuth in topographic factors were determined using the TRASP slope aspect index (numerical range 0–1). The slope aspect was determined as follows [24]:

$$TRASP = 1 - \cos[(\pi/180)(aspect - 30)]/2 \quad (7)$$

where *aspect* represents the azimuth degree of the compass measurement. The higher the TRASP value was, the more sunny the slope would be; and, conversely, the more shady.

A wider econiche of a species indicates that it is less specialized, which means it tends to be more of a generalized species (generalist species) and a broad econiche of generalist species with strong competitive abilities. A narrower econiche of a species indicates that it is more specialized, which means it tends to be more of a specialized species (specialist species); specialized species have a narrow econiche and are at a disadvantage in competition for resources [25]. Generalist species have wider fundamental niches than specialists [26]. We calculated the occurrences of species generated by simulating 1000 permutations (quasiswap permutation algorithms) performed using the EcolUtils R package. The null distribution of the niche breadth indices of these herbaceous plants was calculated through the spaaa R package. According to the simulation results, a species was considered generalist or specialist based on whether the observed occurrence exceeded the upper 95%, and the species were considered neutral taxa if the observed niche breadth was within the 95% confidence interval range [27]. A canonical correspondence analysis was used to analyze the relationship between the selected environmental factors and the ecological niche characteristics of herbaceous plants.

3. Results

3.1. Characteristics of Understory Herbaceous Species Composition in Plantation Forests

A total of 31 herbaceous species was found under different site types of a *Pinus tabulaeformis* plantation, belonging to 11 families, 24 genera (51 species, 16 families, and 32 genera less than natural control grassland), and Gramineae, Compositae, and Leguminosae accounted for a relatively large proportion, accounting for 74.19% (Gramineae 25.81%, Compositae 29.03%, and Leguminosae 19.35%) of the investigated plant species. The species of herbaceous plants found under the *P. tabulaeformis* plantation are shown in Table 3. The important species in herbaceous communities varied between different stand types, and the importance values of the same herbaceous community also differed under different stand conditions. Species, such as *Stipa capillata*, *Thymus mongolicus*, *Lespedeza davurica*, *Cleistogenes squarrosa*, and *Aster altaicus*, which play an important role in different site types, were the dominant species of herbaceous populations in the plantation forest of *P. tabulaeformis*. The life forms of understory plants were mainly semishrubs and perennial herbs, and the main types of water ecology were arid and middle arid.

Table 3. Importance values of herbaceous populations under different site types of plantation forest of *P. tabulaeformis*.

No.	Plant Species	Familia	Sunny Side			Shady Side		
			Flat Slope	Gentle Slope	Slope	Flat Slope	Gentle Slope	Slope
1	*Stipa capillata*	Gramineae	25%	20%	20%	15%	25%	-
2	*Thymus mongolicus*	Labiatae	34%	51%	17%	-	-	-
3	*Lespedeza daurica*	Leguminosae	20%	-	5%	-	17%	5%
4	*Cleistogenes squarrosa*	Gramineae	-	20%	-	25%	-	10%
5	*Heteropappus altaicus*	Compositae	-	2%	-	19%	12%	4%
6	*Gypsophila licentiana*	Caryophyllaceae	-	-	10%	15%	-	-
7	*Astragalus adsurgens*	Leguminosae	2%	-	-	7%	-	7%
8	*Artemisia argyi*	Compositae	-	-	-	-	6%	14%
9	*Hedysarum alpinum*	Leguminosae	-	-	5%	-	10%	-
10	*Artemisia gmelinii*	Compositae	-	-	-	-	-	30%
11	*Pennisetum centrasiaticum*	Gramineae	-	-	20%	-	-	-
12	*Astragalus melilotoides*	Leguminosae	-	1%	-	-	14%	-
13	*Stipa grandis*	Gramineae	-	-	-	-	-	17%
14	*Juncus effusus*	Juncaceae	-	-	16%	-	-	-
15	*Allium tenuissimum*	Liliaceae	-	-	5%	-	4%	-
16	*Echinops gmelini*	Compositae	-	-	2%	-	6%	-
17	*Polygala linarifolia*	Polygalaceae	-	1%	-	-	-	7%
18	*Gueldenstaedtia stenophylla*	Leguminosae	5%	2%	-	-	-	-
19	*Melilotus albus*	Leguminosae	-	-	-	10%	-	-
20	*Stellera chamaejasme*	Euphorbiaceae	-	-	-	10%	-	-
21	*Salsola collina*	Compositae	5%	1%	-	-	-	-

Table 3. *Cont.*

No.	Plant Species	Familia	Sunny Side			Shady Side		
			Flat Slope	Gentle Slope	Slope	Flat Slope	Gentle Slope	Slope
22	*Clematis aethusifolia*	Ranunculaceae	-	-	-	-	-	4%
23	*Cynanchum thesioides*	Asclepiadaceae	-	-	-	-	4%	-
24	*Setaria viridis*	Gramineae	1%	1%	-	-	-	-
25	*nneapogon borealis*	Gramineae	1%	-	-	-	-	-
26	*Artemisia scoparia*	Compositae	2%	-	-	-	-	-
27	*Eragrostis minor*	Gramineae	2%	-	-	-	-	-
28	*Ixeris denticulata*	Compositae	-	-	-	-	2%	-
29	*Corispermum chinganicum*	Compositae	2%	-	-	-	-	-
30	*Artemisia eriopoda*	Compositae	-	-	-	-	-	2%
31	*Tragus mongolorum*	Gramineae	1%	1%	-	-	-	-

3.2. Characteristics of Niche on Understory Herbaceous Species in Plantation Forest

We calculated the niche breadth index and niche overlap index of 31 herb species using Levins and Pianka's formulas (Figure 2). The average value of the niche breadth index of the herbaceous species under the plantation forest on the sunny side showed a gradual upward trend with an increasing slope; however, the average value of the niche breadth index of the herbaceous species on the shaded side showed a gradual decline with an increasing slope. The mean values of the niche breadth indices of the herbaceous species under the plantation forest on the shaded side were close to the median values of the niche breadth indices, but the mean value of the niche breadth index of the herbaceous species under the plantation forest on the sunny side deviated from the median of the niche breadth index. The distribution of the niche breadth of the herbaceous species under the plantation forest on the sunny sides was discontinuous and showed differentiation at both ends. Nevertheless, the niche breadth distribution of understory species in shady sides was relatively continuous and uniform. The overall niche breadth index distribution was more continuous, but the mean was smaller.

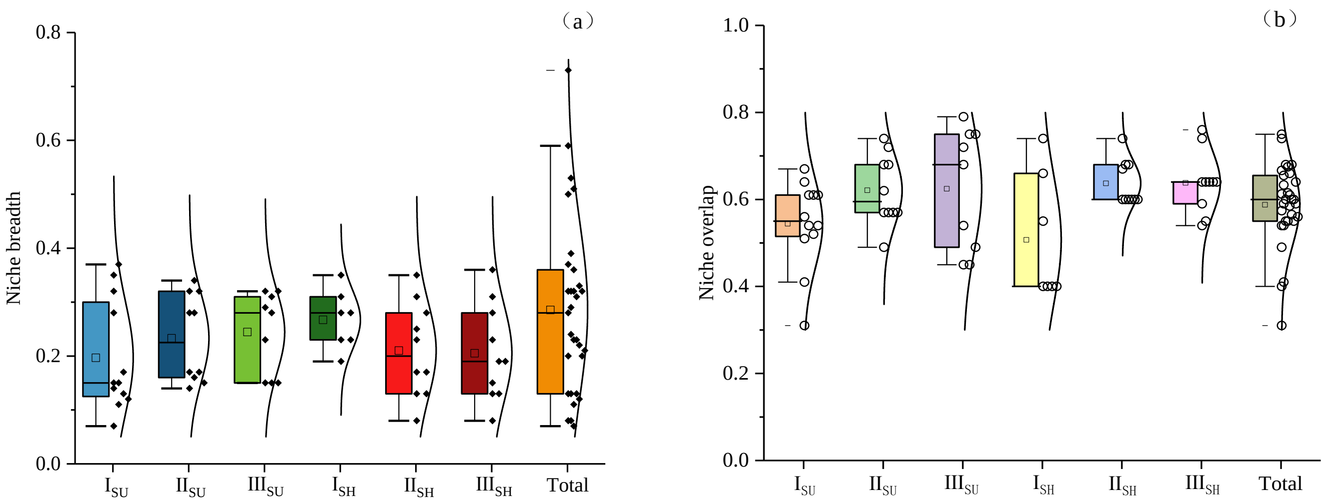

Figure 2. Niche width index (**a**) and overlap index (**b**) of understory herbaceous species in *P. tabulaeformis* plantation of different site types. Notes: I_{SU} represents flat slope of sunny side; II_{SU} represents gentle slope of sunny side; III_{SU} represents slope of sunny side. I_{SH} represents flat slope of shady side; II_{SH} represents gentle slope of shady side; III_{SH} represents slope of shady side. ♦, ○ represents species, whose distribution conforms to normal distribution.

The average value of the niche overlap index of herbaceous species under a sunny and shady plantation forest increased gradually with an increasing slope, showing symmetry. The niche overlap index distribution of species on the sunny slope was continuous and uniform. However, the niche overlap index distribution of species on the shady slope was relatively concentrated, and the two ends were graded. The average value of the niche overlap index of herbaceous species under different site types of a plantation on the sunny slope was close to the median value of the niche overlap index. However, the average value of the niche overlap index of herbaceous species under different site types of the plantation on the shady slopes deviated from the median value of the niche overlap index. The overall niche overlap index was relatively concentrated, with the mean close to 0.6 (niche overlap index greater than 0.6 was a significant niche overlap). Regardless of the shady or sunny slopes, as the slope increased, the significant niche overlap (greater than 0.6) increased significantly.

3.3. Classification of Understory Herbaceous Species in Plantation Forest

Based on the analysis of the nullity distribution of the niche width index of the understory herbaceous plants in the artificial *P. tabulaeformis* forest, the herbaceous plants with a niche breadth index above the upper limit of the 95% confidence interval for nullity distribution were *Stipa capillata*, *Lespedeza daurica*, and *Heteropappus altaicus*, and were defined as generalized species (Figure 3). Species that exceeded the lower limit of the 95% confidence interval of the nullity distribution were *Artemisia gmelinii*, *Pennisetum centrasiaticum*, *Stipa grandis*, *Juncus effusus*, *Melilotus albus*, *Clematis aethusifolia*, *Corispermum chinganicum*, and *Artemisia eriopoda*, and were defined as specialized species. Species within the 95% confidence interval of the nullity distribution were *Thymus mongolicus*, *Cleistogenes squarrosa*, *Gypsophila licentiana*, *Astragalus adsurgens*, *Artemisia argyi*, *Hedysarum alpinum*, *Astragalus melilotoides*, *Allium tenuissimum*, *Echinops gmelini*, *Polygala linarifolia*, *Gueldenstaedtia stenophylla, Stellera chamaejasme, Salsola collina*, *Cynanchum thesioides*, *Setaria viridis*, *nneapogon borealis*, *Artemisia scoparia*, *Eragrostis minor*, *Ixeris denticulata*, and *Tragus mongolorum*, and were defined as neutral species. The number of generalized species was the lowest, accounting for only 9.68% of understory herbaceous species. The number of specialized species was 8, accounting for 25.81%, and that of neutral species was 20, accounting for 64.52%.

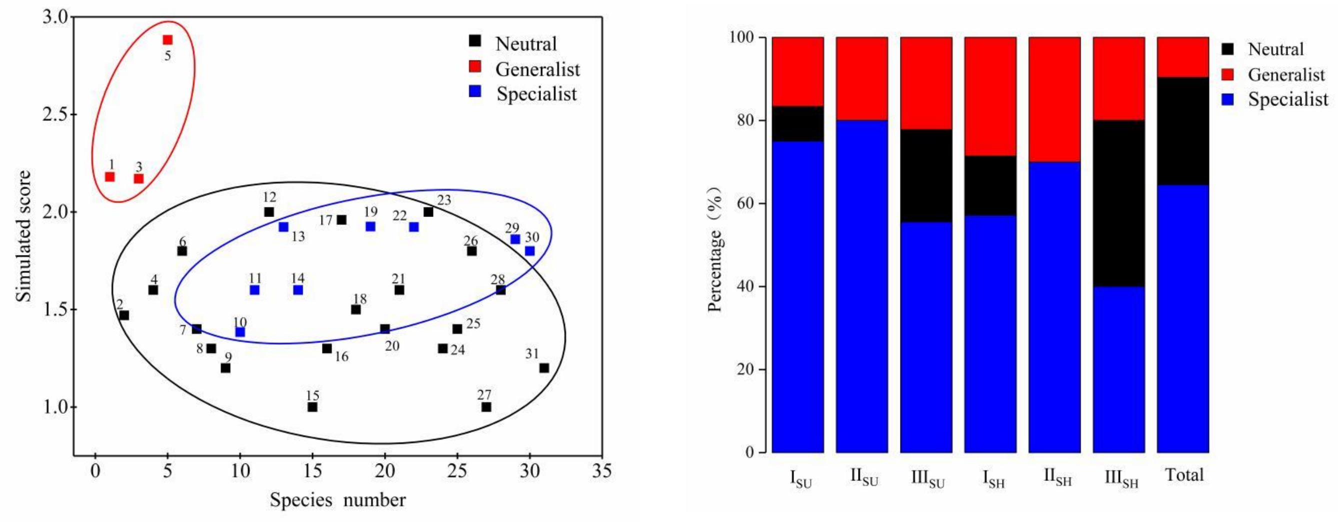

Figure 3. Classification of understory herbs in *P. tabulaeformis* plantation of different site types. Note: species numbers in the figure are consistent with those in Table 3.

3.4. Environmental Interpretation of Niche Characteristics

The CCA ordination axis of the understory herbaceous species niche width was correlated with environmental factors (Figure 4). Axes one and two were significantly correlated with environmental factors. The eigenvalues were 0.64 and 0.46, the cumulative contribution of the species environmental relationship variance was 53.98%, and the total explanation rate of the environmental variables to response variables was 93.11%. The sequence diagrams better reflect the relationship between environmental factors and the ecological niche width of species. The ranking of the contribution of each ecological factor to the effect of the population niche width was as follows: CD(24.2%) > SL(20.0%) > SAP(19.3%) > SOM(18.7%) > SWC(17.8%) > SAK(17.7%) > AS(17.4%) > SAN(17.2%) > ST(16.4%) > PH(15.7%) > AT(13.6%). Meanwhile, the responses of each environmental variable to generalized species with a higher basal niche breadth were relatively strong and concentrated, closer to the center point on the sorted map. The responses of each environmental variable to neutral species and specialized species were relatively scattered and single, farther from the center point on the sorted map.

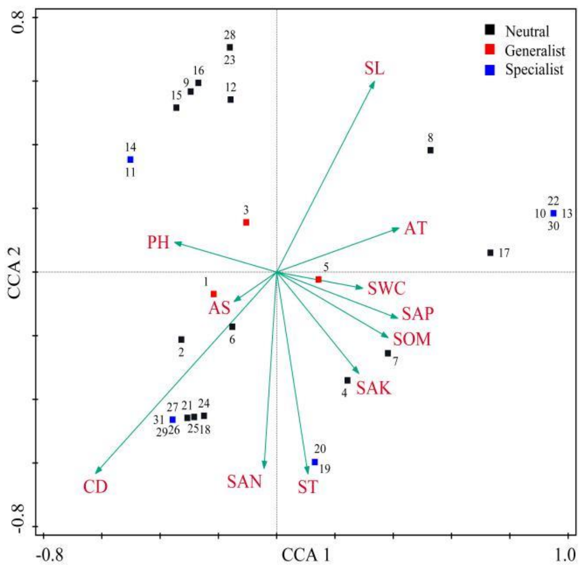

Figure 4. CCA ranking of the influencing factors of population niche width (note: species numbers in the figure are consistent with those in Table 3).

The understory herbaceous species niche overlap CCA ordination axis was correlated with environmental factors (Figure 5). The first and second axes were still significantly correlated with environmental factors. The eigenvalues were 0.63 and 0.60. The cumulative contribution rate of the species–environment relationship variance was 54.56%. The total explanation rate of the environmental variables to response variables was 89.73%. The ordination map could better reflect the relationship between the environmental factors and species niche overlap. The order of the contribution rate of each ecological factor to the overlap of the population niche was as follows: CD(25.3%) > SL(20.6%) > ST(18.9%) >SAN(17.8%) > AT(15.9%) > SAP(15.8%) > SOM(15.4%) > PH(15.2%) > AS(15.1%) > SAK(14.8%) > SWC(14.8%). Simultaneously, the responses of each environmental variable overlapping with the generalized species niche were relatively strong and concentrated, and were closer to the center point on the ordination map. However, the responses of each environmental variable to neutral species and specialized species were relatively scattered and single, and were far from the center point on the ranking map. Notably, for both the niche breadth and niche overlap, specialized species showed a high degree of overlap in the ordination map.

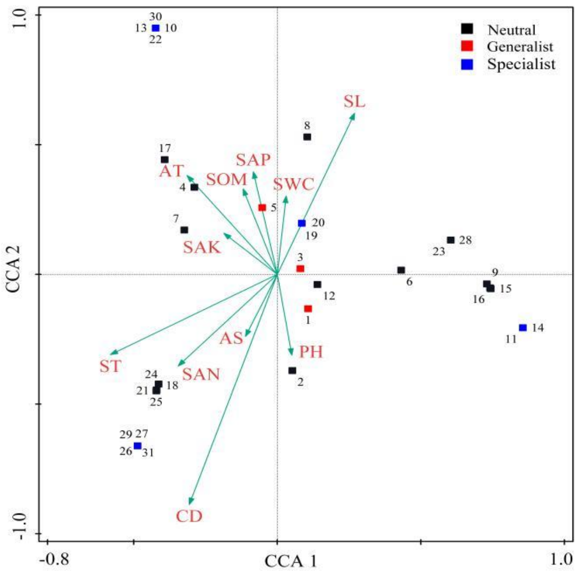

Figure 5. CCA ranking of the influencing factors of population niche overlap (note: species numbers in the figure are consistent with those in Table 3).

4. Discussion

4.1. Variation Law of Niche Breadth and Niche Overlap of Understory Herbaceous Species

In this study, the niche breadth and niche overlap were used to quantify the niche characteristics of understory herbaceous species in a plantation forest. The niche breadth can reflect the relative utilization of species relative to environmental resource sites, which exist in the mutual game between species and the environment, and their size depends on the availability of species to environmental resources [28]. This study showed that the species niche breadth of each herbal community under different types of artificial pine forests was significantly different, and the overall value was small. In general, herbs were relatively weaker in the utilization of environmental resources compared to shrubs and trees [29]. The resource utilization capacity of species varied due to the high spatial heterogeneity of resources, and the ecological adaptability of different resource spaces was also significantly different [30]. In the feldspathic sandstone area in the hilly and gully area of the Loess Plateau (characterized by drought, nutrient infertility, and severe soil erosion), the ability of species to survive was rigorously tested. Only species with strong habitat adaptability (e.g., only those able to adapt to dry conditions and poor soils) and fully utilizing environmental resources can survive and develop [31]. This study showed that the niche breadth of dominant species under a forest was relatively large or widely distributed, while the associated herb species had a smaller niche breadth or a narrower distribution. This phenomenon also suggested that the specialization of understory herbaceous species exists in plantation forests. Compared with natural grasslands, plantations have inhibitory effects on the balanced development of understory herbaceous plant communities [32].

The niche overlap was used to quantify the commonness of different community species in environmental resource allocation, assess the ecological similarity between species, and interpret the competitiveness of each other's species [3]. Some scholars believe that the niche overlap may be one of the determinants of species diversity and community structure stability [33]. This study showed that the niche overlap of herbaceous plants under a flat slope plantation was lower than that under oblique and gentle slope plantations. In general, species' use of resources was differentiated as communities continued to evolve, and the species' reproductive strategies and populations that adapted to the changes could make full use of the resources, with the niche overlap among the populations being low [34]. Herbaceous species in plantations with a flat slope stand type were significantly better at resource use zonation than herbaceous plants on gently sloping slopes. At the same time, the higher the niche overlap, the greater the interspecific competition, which was more conducive to the occurrence of community succession. By contrast, the smaller the niche overlap, the smaller the interspecific competition, and the community was in a relatively stable state [35]. This study showed that different site types had different effects on the stability of herbaceous communities under a plantation. The stability of herbaceous communities in the plantation with flat slopes was relatively better than that of herbaceous communities on gently sloping slopes. By describing the ecological niches of different plant species under the plantation forest, we improved the understanding of the status and role of understory plants in the community, and realized that the site conditions of the plantation forest played a significant role in the restoration of understory vegetation. However, species with a larger niche overlap usually had a larger niche breadth [35]. Species with a high niche overlap also occurred among species with narrower niche widths due to the high spatial heterogeneity of the resources of different species and the different capacity of each species to use the resources [36]; these species included *Gypsophila licentiana*, *Stipa grandis*, *Hedysarum alpinum*, and *Setaria viridis*. No obvious linear relationship was found between the population niche width and niche overlap.

4.2. Differentiation of Understory Herbaceous Species

A replacement method based on the EcolUtils R package was used to calculate the zero distributions of the niche width index of understory herbs, and, thus, to divide understory herbaceous species as generalized and specialized. The classification found that the total number of generalist herbaceous species under the Pinus tabulaeformis forest was much less than that of neutral and special species. Thus, the number of herbaceous species with obvious survival and development advantages in this particular environment was relatively small. Meanwhile, the canonical correspondence analysis showed that the range of the resource utilization of generalized species was significantly larger than that of neutral species and specialized species, and they had a wider ecological footprint. For neutral species, especially specialized species, the relatively homogenous and similar use of resources led to a relatively concentrated and off-center distribution. The classification of understory herbaceous species, combined with ecological niche characteristics, improved our understanding of understory species regarding differences in environmental resource uses. However, what is worth discussing is what kind of classification ratio would be best in meeting the requirements of plantation biodiversity and ecological stability.

4.3. Factors Affecting Niche Patterns of Understory Herbaceous Species

Differences in the ecological niche characteristics of populations were characterized based on the synergistic influence of multiple environmental factors; the scope of the study varied and so did its influencing factors [37]. Many studies have shown that the species distribution of understory herbaceous species communities is closely related to environmental factors such as the range of canopy, topography, and soil nutrients [38]. The present study showed that environmental factors had different effects on the ecological niche characteristics of understory herbaceous species (Figure 6). The plantation canopy density and geographic slope had significant effects on the niche breadth and niche overlap of understory herbaceous species. In general, soil erosion in the feldspathic sandstone area was serious, and the soil nutrients were poor; at the time, the soil organic matter and soil moisture content were at a low level, and the climatic conditions of small watersheds were basically the same [39]. Areas with a lower slope gradient had better resource environments than areas with a higher slope gradient [40]. At the same time, the canopy density of the plantation directly affected light transmission under the forest, rainfall penetration, stem runoff, soil temperature, and humidity, which indirectly led to changes in the original soil structure and nutrients [23,41], thereby directly affecting the distribution of herbaceous plants under the forest. The effects of soil nutrients (such as SOM, SAN, SAP, and SAK) and water content on the niche breadth of understory herbaceous species were higher than that of the niche overlap. The presence of understory herbaceous species depended on the efficient use of environmental resources, expressed as competition for soil nutrients, water, and other resources [42]; under the conditions of poor overall water and fertility, the plants would first survive and then thrive [43]. Thus, the effects of soil nutrients and soil water content on the species niche width were more direct and widespread, while the effects on the species niche overlap were relatively limited. In addition, the effects of soil pH on the niche width and niche overlap were generally consistent; that is, the effect of elevation on the niche overlap was higher than the niche width, while the effect of slope orientation was the opposite and more significant than that of elevation. The soil of typical plantation forests in the feldspathic sandstone area was mainly covered with weakly alkaline secondary loess with little variation in pH; minimal variations were found in the effect of soil acidity and alkalinity on plants. The variations in altitude and slope orientation tended to change the photic environment and have a significant impact on the distribution of species [44]. However, the effect of elevation on the niche of species was less than the slope orientation, probably due to the small difference in elevation in the study area. Soil thickness was a unique indicator of environmental factors and had a significant impact on the ecological niche characteristics of understory herbaceous species, especially the niche overlap. Soil erosion was serious in the feldspathic sandstone area, and the soil thickness in some areas was less than 5 cm, accompanied by feldspathic sandstone debris and its exposed weathering materials. When wetted by rain, the feldspathic sandstone debris was unstable and dispersed into fine gravel, easily causing the erosion of the soil cover. Clearly, soil thickness had a major influence on the water and fertility retention of the soil in this area [45], and indirectly impacted on the ecological niche of the understory herbaceous species community.

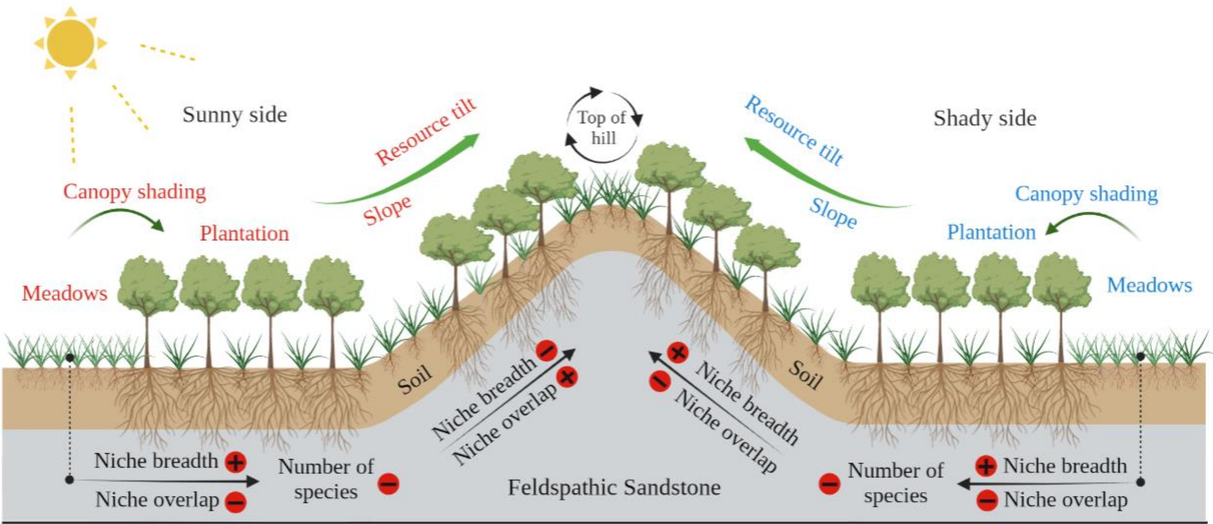

Figure 6. Schematic diagram of changes in the niche characteristics of herbaceous species under plantation.

5. Conclusions

This study showed significant differences in the distribution and interspecific relationships of understory herbaceous species in a plantation forest of different site types. Understory herbaceous species on flat slopes had a relatively uniform distribution and less interspecific competition. The canopy density and geographical slope were the main factors affecting the niche characteristics of understory herbaceous species. The results emphasized the importance of a specific geographical environment for the screening of understory plant distribution in plantations. Niche change characteristics of different herbaceous plants could be due to the comprehensive influence of the plantation and geographical environment. This work helped advance our understanding of the plantation management and restoration of understory species diversity.

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