


## Article

# Species-Abundance Distribution Patterns of Plant Communities in the Gurbantünggüt Desert, China

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**Abstract:** It is important to study the species-abundance distribution pattern in a community to reveal the mechanism of community assembly. Six abundance models (log-normal distribution model, Zipf model, Zipf–Mandelbrot model, broken stick model, niche preemption model, and Volkov model) were used to fit the species-abundance distribution pattern of six scales (10 m × 10 m, 20 m × 20 m, 40 m × 40 m, 60 m × 60 m, 80 m × 80 m, 100 m × 100 m) in fixed, semifixed, and mobile sand dunes in the Gurbantünggüt Desert, respectively. The best-fitting model was determined using the K-S test, the Chi-square test, and the Akaike information criterion. The results showed that the values of soil salinity, nutrients, water content, Shannon–Wiener diversity index ( $H'$ ), Pielou evenness index ( $E$ ), and Simpson index ( $D$ ) were ranked in all three habitats as fixed dunes > semifixed dunes > mobile dunes. The rank curves span a narrow range on the horizontal axis at scales of 10 m × 10 m and 20 m × 20 m, and species richness is minimal. As the scale increases, the span range of the curve gradually increases, and species richness becomes higher at scales of 40 m × 40 m, 60 m × 60 m, 80 m × 80 m, and 100 m × 100 m. At the 10 m × 10 m and 20 m × 20 m scales, the broken stick model fits best in the three dune habitats. At the 40 m × 40 m and 60 m × 60 m scales, the niche preemption model fits best in the three dune habitats. At the 80 m × 80 m and 100 m × 100 m scales, the Volkov neutral model fits best in the fixed and semifixed dune habitats, and the niche preemption model fits best in the mobile dune habitats. In fixed, semifixed, and mobile dunes, both niche and neutral processes played important roles in community construction, reflecting the manifestation of the community niche-neutral continuum.

**Keywords:** species-abundance distribution; scale effect; species-abundance model; the Gurbantünggüt Desert

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## 1. Introduction

In the context of global change, to predict the impact of different environmental change scenarios on future habitat suitability and to describe the relationship between species occurrence and environmental variables, the study of species abundance has become of high interest in ecological research [1]. Abundance refers to the number of species or population density, or a measure of dominance and evenness, which reveals the ability of a species to occupy resources [2,3]. Typically, the species-abundance distribution (SAD) and the histogram of the number of species with a given number of individuals are used to communicate information about the relative abundances of species. SAD can characterize the aspects of a community's structure, such as the proportion of uncommon and common species and the process by which dominating species evolve ecologically and can be compared among different ecological communities [4–7]. Community structure is closely related to niche models in which different species coexist: most species inhabit their own

niche, and their species abundance fluctuates around the peak of the SAD [8]. It has become a powerful tool in community assembly.

Arid regions are one of the most vulnerable ecosystems, accounting for about 45% of the earth's surface, and arid environments are very fragile, so they are key areas for studying the multiple distribution patterns of species [9]. In studying the species-abundance patterns of perennial vascular plants in global dryland communities, Ulrich et al. [10] found that most dryland plant communities worldwide were most suitable for the log-normal distribution. Zhang et al. [11] found that the species-abundance distribution of desert plants showed a log-normal model under high water salt habitat and met the Zipf model under low water salt conditions. In the Edicalera strata, Mitchell et al. [12] used ecological model fitting to find that neutral processes dominated early palaeontological biomes, while niche processes had limited impact. Several authors (e.g., Vergnon et al. [13]; Matthews and Whittaker [14]; Leibold et al. [8]) have worked to integrate the aspects of niche and neutrality theories that have been used to predict and explain patterns of species-abundance distribution (SAD). In the future, it is important to study the distribution patterns of species abundance in arid areas based on niche theory and neutral theory and combine the method of species-abundance distribution model fitting [15].

Since Motomura (1932) first proposed the geometric series model (GSM) for fitting species-abundance distribution curves, various new models have emerged, and, for the examination of species-abundance patterns, more than 30 models have been employed to date [16]. Statistical models, niche models, and neutral models are the three categories of models that are now available [17]. The earliest applied theoretical model is the statistical model, the most typical of which are the log-series distribution model of the multidegree curve proposed by Fisher et al. [18] and the logarithmic distribution model proposed by Preston et al. [19]. Although Fisher's and Preston's models can better reflect the species-abundance distribution pattern, they do not truly connect the statistical theory with the statistical population model, and they are inappropriate to analyze the variability of the community [20,21]. In their study of ancient Egyptian steppe vegetation, Werner et al. [22] found that log-normal SAD tended to prevail in a wider range of environmental conditions, including more extreme habitats such as arid environments. The niche model can predict species survival according to the actual distribution range and environmental variables, which is suitable for the study of simple communities and complex community structures [23]. For instance, the niche preemption model (NPM) established by Motomura [24] and the broken stick model (BSM) based on the niche theory proposed by MacArthur [25] have been extensively employed and have more extensive ecological importance. Hubbell [26] used the neutral theoretical model to examine the species abundance in communities. The neutral theory stands in opposition to the niche theory: dispersal limitation is an important inference of the neutral theory, which emphasizes the impact of distance effects on community structure and explains the species-abundance distribution pattern of the community from a biological point of view [27,28], such as the metacommunity zero-sum multinomial distribution model. Niche theory mainly emphasizes the concept of a spatial niche, where coexisting species produce niche differentiation due to competition [29]. Chen et al. [30] summarized recent advances in the biogeography of arbuscular mycorrhizal fungi (AMF) and proposed that, at global and regional scales, AMF community construction is consistent with the niche-neutral continuum hypothesis, but the relative importance of these drivers varies at different scales.

The species-abundance pattern has a scale effect. When the sampling scale changes, the number of common and rare species will change, and the species composition, environment, and interspecific relationships of plant communities will also change, which will lead to changes in species-abundance distribution patterns [31]. For example, Cheng et al. [32] and Tan et al. (2020) [33] found that neutral models fit well at all scales in temperate coniferous forests and subtropical Gutianshan forests in northeast China. Wu et al. [34] found that, with the increase in sampling scale, neutral processes gradually replaced niche processes and became the main mechanism in maintaining the species-abundance

distribution in subtropical broad-leaved mixed forests; Zhu et al. [35] found that neutral processes explained species-abundance patterns more strongly than niche processes at large scales in the Seven Sisters Nature Reserve; Rebecca et al. [36] demonstrated the challenges of detecting scale dependence in cross-sectional research syntheses using multilevel models in a full data analysis of simulation data from a large range of old-growth and secondary forests across the globe; Gabrielsen et al. [37] combined wetland permanence predictions from remotely sensed imagery with eDNA to assess the occurrence and abundance of three amphibian species in plains and grassland potholes in the United States and found that habitat variability at spatial and temporal scales contributed to species occurrence and abundance. Therefore, scale effects must be considered when analyzing patterns of species-abundance distribution.

Species-abundance patterns and environmental variables have nonrandom correlations [38]. Recent studies have shown that regional topography characteristics, such as aspect and slope, and edaphic elements, such as those of chemical and physical qualities, are frequently associated with ecological influences on vegetation patterns [39–41]. Soil factors play an important role in plant production, growth, and development, bringing certain species to the top of the abundance pyramid [42,43]. For example, Bohlman et al. [44] found that soil fertility and pH had a strong influence on species richness in forest communities. Hu et al. [45] found that soil salinity, organic matter, and water content had significant effects on community stability under suitable conditions in desert plant communities in the Ebinur Lake basin ( $p < 0.01$ ). Amjad et al. [46] found that species abundance was significantly correlated with soil nutrients and slope orientation by using multiple linear regression and structural equation models in wet forest ecosystems in the Western Himalayas. Djordjević et al. [47] found that environmental factors had a significant impact on the distribution, richness, and abundance of terrestrial orchids, with variations in the availability of soil resources (water and nutrients) on geological substrates significantly affecting the richness and composition of orchid species. Therefore, community species-abundance models need to consider soil factors and microtopography [10].

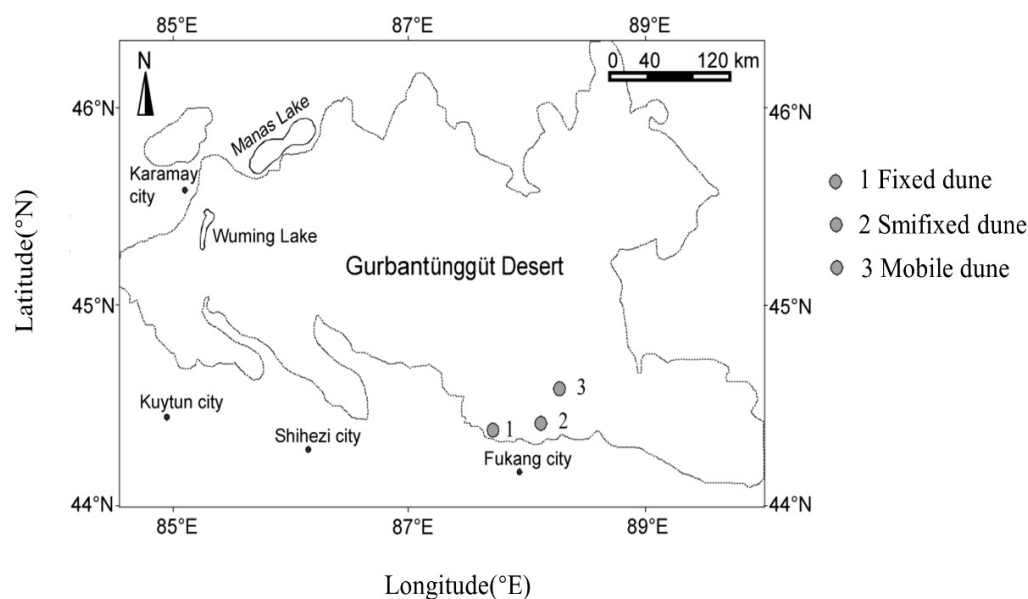
The Gurbantünggüt Desert is a temperate desert, with vegetation dominated by dry and drought-avoidant plants, of which short-lived and short-lived-like plants are widely distributed, and is an important resource base for heat-resistant, salinity-resistant, and drought-resistant species in China [48]. Desert habitats have been destroyed due to human activities and natural disturbances, with the significant localized degradation of vegetation, the loss of species diversity, and the severe degradation of ecosystem functions [49]. To protect and restore desert vegetation, scholars have conducted numerous studies on the species composition and diversity characteristics of desert plants. For example, Duan et al. [50] found that ephemeral plants exhibited an overall simple community composition, high dominance, low diversity, and low cover. Jia et al. [49] found that slope orientation and slope position were the main factors affecting herbaceous plant  $\alpha$ -diversity and  $\beta$ -diversity. Li et al. [51] found that the population of *Haloxylonammmodendron* was degraded in fixed dunes, and the populations of *Haloxylonpersicum* were stable in semifixed and mobile dunes. However, little research has been reported on the species-abundance distribution patterns of plant communities.

Currently, studies on community species-abundance distribution patterns are mainly focused on forest and grassland ecosystems, and research on species-abundance distribution patterns in temperate arid zone desert communities needs to be strengthened [52]. Six abundance models (log-normal distribution model, Zipf model, Zipf–Mandelbrot model, broken stick model, niche preemption model, and Volkov model) were used to fit different dune habitats (fixed, semifixed, and mobile dunes) at six scales (10 m  $\times$  10 m, 20 m  $\times$  20 m, 40 m  $\times$  40 m, 60 m  $\times$  60 m, 80 m  $\times$  80 m, 100 m  $\times$  100 m). In order to explore the following scientific issues: (1) the pattern of species-abundance distribution in the Gurbantünggüt Desert at different scales with respect to habitat, (2) the ecological processes and community-building mechanisms that dominate the distribution of species abundance in different dunes of the Gurbantünggüt Desert, and (3) the embodiment of the niche-neutral

continuum hypothesis in the distribution of species abundance in the plant communities of the Gurbantünggüt Desert. This study not only lays the foundation for exploring the mechanisms of desert-plant-community construction in arid zones but also has important implications for the conservation and restoration of desert vegetation.

## 2. Study Areas

The Gurbantünggüt Desert (Figure 1), located in the semienclosed Junggar Basin, is China's largest fixed and semifixed desert (44.11°–46.20° N, 84.31°–90.00° E), covering an area of approximately  $4.8 \times 10^4$  km<sup>2</sup>, with the majority of fixed and semifixed sand dunes in the interior of the desert, accounting for 97% of the total desert area. The climate of the region is typical of a temperate arid-desert climate, which is hot and dry in summers and cold and wet in winters. The total annual solar radiation is 5692–6360 MJm<sup>-2</sup>; the cumulative sunshine hours are 2780–22,980 h; the annual mean temperature is 5.7 °C; the annual temperature difference is greater than 40 °C; the extreme maximum temperature is 41.5 °C, and the extreme minimum temperature is −37.0 °C [51,53]. In the arid hinterland, the annual precipitation ranges from 70 to 120 mm; the potential evaporation exceeds 2000 mm, and the groundwater depth exceeds 30 m. The soils are predominantly sandy and windy, accounting for 80% of the desert area. Sandy and dry plants are rich. The dominant species are *Haloxylonammmodendron*, *Haloxylonpersicum*, and *Tamarix ramosissima* [54].



**Figure 1.** The study area and sample plots in the Gurbantünggüt Desert.

## 3. Research Methods

### 3.1. Sampling Setting and Sampling Method

Three typical sand dunes were selected in the Gurbantünggüt Desert: a fixed dune (44°22'34" N, 87°52'45" E), a semifixed dune (44°36'9.6" N, 88°14'17.38" E), a mobile dune (44°56'52.01" N, 88°33'29.91" E), and three large sample plots with an area of 100 m × 100 m. Each large sample plot was divided into 6 scales (10 m × 10 m, 20 m × 20 m, 40 m × 40 m, 60 m × 60 m, 80 m × 80 m, 100 m × 100 m). Plant name, density, height, width, and species coordinates (X, Y) were recorded in each sample plot (10 m × 10 m). All dunes were located using GPS.

### 3.2. Soil Collection and Analysis

In fixed, semifixed, and mobile dune habitats, soil samples of 0–20 cm were collected from different slope positions (bottom, low, middle, up, and top) of each habitat, mixed well, and brought back to the laboratory for testing. Soil water content, electrical conductivity, pH, organic carbon, CO<sub>3</sub><sup>2-</sup>, HCO<sub>3</sub><sup>-</sup>, Cl<sup>-</sup>, SO<sub>4</sub><sup>2-</sup>, Ca<sup>2+</sup>, Mg<sup>2+</sup>, K<sup>+</sup>, Na<sup>+</sup>, and total salt were

all determined. To determine soil organic carbon, soil samples were cleared of visible plant roots, animal droppings, and other debris. They were then mixed, sieved through a 0.25 mm sieve, and then passed through a 1 mm screen to determine the soil pH and conductivity. The soil organic carbon content was determined by external heating with potassium dichromate. The drying and weighing method is used to assess the soil moisture content. An experimental soil sample was dried to a constant weight and 105 °C in an oven at a constant temperature. The measurement is then performed three times, and the average value is obtained [55]. Soil pH was determined by the water–soil ratio 5:1 acidity meter method; conductivity by the water–soil ratio 5:1 conductivity method; Na<sup>+</sup> and K<sup>+</sup> by the flame photometric method; CO<sub>3</sub><sup>2-</sup> and HCO<sub>3</sub><sup>-</sup> by standard HCl titration; Mg<sup>2+</sup>, Ca<sup>2+</sup>, and SO<sub>4</sub><sup>2-</sup> by EDTA complex titration; and Cl<sup>-</sup> by standard AgNO<sub>3</sub> titration [56].

### 3.3. Important Value

A species' importance value (IV), which is a composite indicator of its status and contribution to a community, is computed as [57,58]:

$$IV = (RB + RC + RF)/3 \times 100\% \quad (1)$$

In the equation, *RB* stands for relative abundance, which is the ratio of a plant's population to all of the other plants in the dune. *RC* is the relative coverage, that is, the coverage of a plant accounts for the total number of plants in the dune. The ratio of cover: the term "relative frequency" (*RF*) refers to the ratio of the number of quadrats belonging to one species to all of the other species' quadrats, with the frequency of a species accounting for the sum of the frequencies of all plants.

### 3.4. Species Diversity Indices

The species richness index (*SP*), Shannon–Wiener diversity index (*H'*), Pielou evenness index (*E*), and Simpson dominance index (*D*) were calculated as follows [17,59,60]:

$$SP = S \quad (2)$$

$$H' = -\sum P_i \ln P_i \quad (3)$$

$$E = H' / \ln S \quad (4)$$

$$D = 1 - \sum P_i^2 \quad (5)$$

In the formula, *P<sub>i</sub>* is the proportion of the important value of the *i*th species to the total importance value, where *S* is the number of species in the quadrat.

### 3.5. Abundance-Fitting Model Selection

As a single model cannot provide accurate estimates of communities, we used six abundance models to fit species-abundance distribution patterns of fixed, semifixed, and mobile dune habitats at six different scales. These include one statistical model (log-normal distribution model), four niche models (Zipf model, Zipf–Mandelbrot model, broken stick model, niche preemption model), and one neutral model (Volkov model). The introduction of each model is as follows:

#### 3.5.1. Statistical Model

- Log-normal distribution model

The model, which was first put forth by [19], assumes that a normal distribution is confirmed by the logarithm of the number of species in the population. The number of members of each species is the variable, and the number of individuals who have an impact



on the community's makeup is the factor in regard to the distribution of species abundance. In this process [61], the formula is expressed as:

$$A_i = e^{\log(\mu) + \log(\delta)\Phi} (i = 1, 2, 3, \dots, S) \quad (6)$$

In the formula, the normal distribution's mean is  $\mu$ , its variance is  $\delta$ , and its standard deviation is  $\Phi$ .

### 3.5.2. Niche Model

- Niche preemption model

Model is predicated on the assumption that the first species in the community occupies  $k$  of the entire ecological niche; the second species occupies  $k$  of the remaining ecological niche, or  $k(1 - k)$ , and, similarly, the third species occupies  $k(1 - k)^2$  of the remaining resources, until the remaining resources are not sufficient to maintain the survival of one species [19]. The formula is expressed as:

$$A_i = A_1(1 - k)^{i-1}, i = 1, 2, 3, \dots, S \quad (7)$$

where  $A_i$  stands for the abundance of the  $i$ th species, and  $A_1$  stands for the abundance of the species projected by the model to be the most dominant.

- Broken stick model

The model assumes that the total amount of environmental resources in the entire community is a long stick and that the number of species in the community is  $n$ . It then randomly places  $n - 1$  points on the long stick and divides it into  $n$  segments, the length of each segment corresponding to the "abundance" of a species, which is expressed by  $J$  as the sum of the number of individuals of a species in the community [25], and the abundance  $A_i$  of the  $i$ th species is:

$$A_i = \frac{J}{n} \sum_{x=i}^n \frac{1}{x} \quad (i = 1, 2, 3, \dots, n) \quad (8)$$

- Zipf model

The model assumes that the emergence of a species is dependent on the physical conditions and species already present. Species that enter the community first need few prerequisites and have low invasion costs; species that enter the community later have to pay a higher price to invade [62]. Later succeeding species must pay a greater price to invade since pioneer species incur lower costs and have fewer requirements [63]. The abundance  $A_i$  of the  $i$ th species in the community is therefore stated as:

$$A_i = Jp_1 i^{-\gamma} \quad (i = 1, 2, 3, \dots) \quad (9)$$

In the formula,  $J$  is the total population of the community,  $p_1$  is the fitting's percentage of the most numerous species, and  $\gamma$  is a constant denoting the typical probability of a species emerging.

- Zipf–Mandelbrot model

The predecessor of the Zipf–Mandelbrot model is the generalized Zipf's law, which has a nonsensical parameter  $c$  replacing  $P_1$  in the Zipf model and a parameter  $\beta$  that depends on the average selectivity per class of conditions, which ecologically can be considered as the potential diversity of the environment, such as ecological niche diversity [32]. The abundance  $A_i$  of the  $i$ th species in the community is therefore stated as:

$$A_i = Jc(i + \beta)^{-\gamma} \quad (i = 1, 2, 3, \dots) \quad (10)$$

### 3.5.3. Volkov Neutral Model

The model assumes that, in a community after any individual dies, its probability of being replaced by a new species is  $v$ , and the probability of being replaced by the offspring of any remaining individual is  $1 - v$ ; then,  $\theta = 2Jv$ . The calculation is as follows to determine the number of species  $S$  with abundance  $n$  in the community:

$$S(n) = \theta \frac{J!}{n!(J-n)!} \frac{\Gamma(\gamma)}{\Gamma(J+\gamma)} \int_0^\gamma \frac{\Gamma(n+y)}{\Gamma(1+y)} dy \quad (11)$$

$$\Gamma(z) = \int_0^\infty t^{z-1} e^{-t} dt \quad (12)$$

$$\gamma = \frac{m(J-1)}{1-m} \quad (13)$$

In the formula,  $J$  is the sample size of the community,  $(z)$  is the function of  $z$ ,  $m$  is the migration coefficient of species from the composite community to the local community, and it is assumed that  $m$  is fixed.  $\gamma$  is the number of individuals moving to the local community.

## 3.6. Model Fit Test

### 3.6.1. Statistical Tests

As a single test of a model, goodness of fit does not accurately describe the model fit; the Kolmogorov–Smirnov (K–S) test and  $\chi^2$  test were used to test the model for species-abundance patterns. Based on the results, if  $p > 0.05$ , the model was accepted and suitable for describing the species-abundance distribution pattern of the habitat; if  $p < 0.05$ , the model was rejected and not suitable for describing the species-abundance distribution pattern of the habitat.

The K–S test is based on the cumulative distribution function and is used to test whether a cumulative distribution conforms to a theoretical distribution or to compare whether two cumulative distributions are significantly different. The formula is expressed as:

$$D = \max |F_n(x) - F(x)| \quad (14)$$

In the formula,  $F_n(x)$  is the observed series value, and  $F(x)$  is the theoretical series value or another observed series value.

### 3.6.2. AIC

The Japanese statistician Hiroji Akaike invented and developed Akaike's information criteria (AIC), also known as the AIC, which is a measure of the goodness of fit of a statistical model [64]. The smaller the AIC value is, the better the model fit. In general, the expression formula is:

$$L(\theta|x) = P(X = x|\theta) \quad (15)$$

$$AIC = -2 \ln(L) + 2k \quad (16)$$

In the formula, the model's error is assumed to follow an independent normal distribution, where  $k$  denotes the number of parameters, and  $L$  denotes the likelihood function.

## 3.7. 95% Confidence Interval Test

Through the 95% confidence interval test, the fitting effect of the Volkov neutral model to the actual observations was further tested. The prediction distribution was performed 600 times on the actual observation data, and after sorting according to the size of the predicted abundance value of the model, the 15th (2.5%) and 585th was taken as the upper and lower bounds of the 95% confidence interval [65].

### 3.8. Data Processing

In this study, abundance-rank curves were chosen to represent species abundance. The vertical axis in the abundance level curve shows the number of species at each corresponding species level, while the horizontal axis represents the species level; that is, the abundance of all species in the community is ranked from high to low [66]. Finally, Origin 2018 was used to draw the corresponding abundance-rank curve. The species abundance-distribution curves, model fitting test, and species-diversity calculation were completed by the *sads* package and *vegan* package in R 4.1.1; the K-S test and the Chi-square test of each model were completed by SPSS software.

## 4. Results

### 4.1. Soil Salinity and Water Content in Different Dune Habitats

The soil water content and salinity were significantly different in fixed, semifixed, and mobile dune habitats (Table 1). Soil water content, electrical conductivity, soil pH, soil organic carbon,  $\text{CO}_3^{2-}$ ,  $\text{HCO}_3^-$ ,  $\text{Cl}^-$ ,  $\text{K}^+$ ,  $\text{Na}^+$ , and total salt in the three habitats were ranked as fixed dune > semifixed dune > mobile dune;  $\text{Ca}^{2+}$  and  $\text{Mg}^{2+}$  were ranked as mobile dune > semifixed dune > fixed dune.

**Table 1.** Soil characteristics of the three different habitats in the Gurbantünggüt Desert (mean  $\pm$  SD).

	Fixed Dune	Semifixed Dune	Mobile Dune	<i>p</i>
Soil water content (%)	1.403 $\pm$ 0.623 <sup>a</sup>	0.988 $\pm$ 0.318 <sup>a</sup>	0.463 $\pm$ 0.134 <sup>b</sup>	<0.01
Electrical conductivity (ms/cm)	1.049 $\pm$ 0.730 <sup>a</sup>	0.499 $\pm$ 0.385 <sup>a</sup>	0.155 $\pm$ 0.033 <sup>a</sup>	0.04
Soil pH	8.573 $\pm$ 0.190 <sup>a</sup>	8.492 $\pm$ 0.1824 <sup>a</sup>	8.450 $\pm$ 0.190 <sup>a</sup>	0.80
Soil organic carbon (g/kg)	1.439 $\pm$ 0.735 <sup>a</sup>	1.117 $\pm$ 0.364 <sup>ab</sup>	0.640 $\pm$ 0.279 <sup>b</sup>	0.01
$\text{CO}_3^{2-}$ (g/kg)	0.017 $\pm$ 0.007 <sup>a</sup>	0.009 $\pm$ 0.003 <sup>b</sup>	0.008 $\pm$ 0.002 <sup>b</sup>	<0.01
$\text{HCO}_3^-$ (g/kg)	0.115 $\pm$ 0.111 <sup>a</sup>	0.087 $\pm$ 0.070 <sup>a</sup>	0.063 $\pm$ 0.033 <sup>a</sup>	0.25
$\text{Cl}^-$ (g/kg)	0.070 $\pm$ 0.039 <sup>a</sup>	0.061 $\pm$ 0.029 <sup>a</sup>	0.058 $\pm$ 0.031 <sup>a</sup>	0.53
$\text{SO}_4^{2-}$ (g/kg)	0.022 $\pm$ 0.006 <sup>a</sup>	0.020 $\pm$ 0.003 <sup>a</sup>	0.022 $\pm$ 0.013 <sup>a</sup>	0.96
$\text{Ca}^{2+}$ (g/kg)	0.034 $\pm$ 0.021 <sup>a</sup>	0.026 $\pm$ 0.022 <sup>a</sup>	0.047 $\pm$ 0.048 <sup>a</sup>	0.51
$\text{Mg}^{2+}$ (g/kg)	0.032 $\pm$ 0.023 <sup>a</sup>	0.030 $\pm$ 0.017 <sup>a</sup>	0.038 $\pm$ 0.019 <sup>a</sup>	0.60
$\text{K}^+$ (g/kg)	0.004 $\pm$ 0.002 <sup>a</sup>	0.003 $\pm$ 0.001 <sup>a</sup>	0.003 $\pm$ 0.002 <sup>a</sup>	0.10
$\text{Na}^+$ (g/kg)	0.002 $\pm$ 0.002 <sup>a</sup>	0.002 $\pm$ 0.001 <sup>a</sup>	0.001 $\pm$ 0.001 <sup>a</sup>	0.24
Total salt (g/kg)	0.296 $\pm$ 0.129 <sup>a</sup>	0.238 $\pm$ 0.097 <sup>a</sup>	0.221 $\pm$ 0.063 <sup>a</sup>	0.20

Different lowercase letters in the same row indicate extremely significant differences ( $p < 0.01$ ).

### 4.2. Species-Abundance Distribution by Habitat

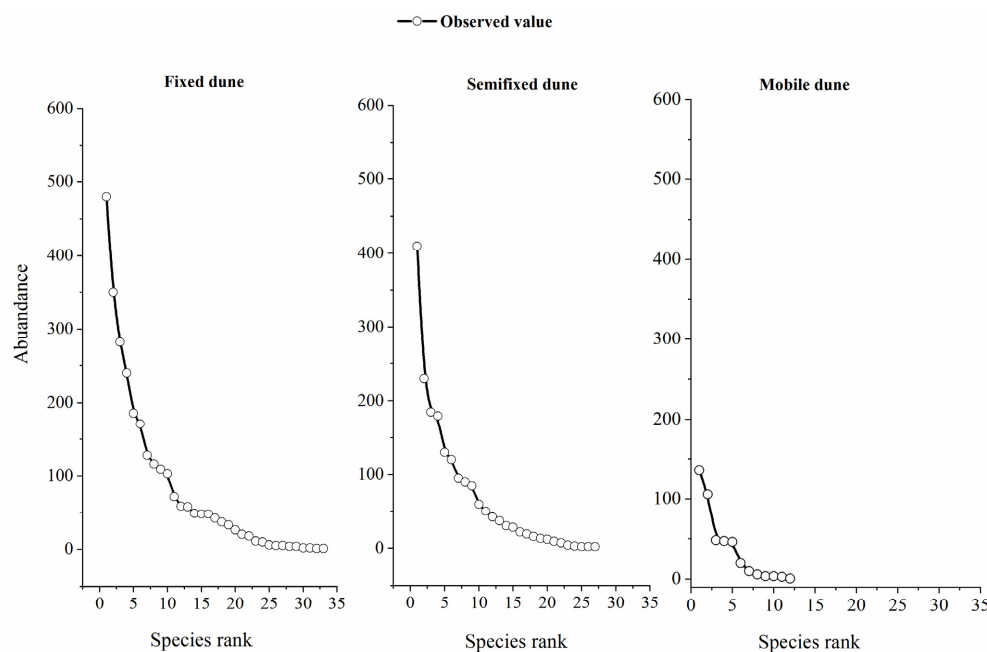
There are 13 families, 36 genera, and 38 species in fixed dunes, semifixed dunes, and mobile dunes (Table 2) and 4 common species (relative frequency and importance value > 25%) and 12 rare species (relative frequency and importance value < 5%). The species-abundance distribution shows that the number of species in the three habitats is ranked as fixed dunes > semifixed dunes > mobile dunes, with semifixed dunes having the highest number of individual species (Figure 2).

The species-abundance-rank curves for the three dune habitats showed the same trend; that is, the abundance-rank curves spanned the range on the horizontal axis in the following order: fixed dunes > semifixed dunes > mobile dunes (Figure 2). The span of the curve on the horizontal axis is larger, and the species richness is greater. Therefore, the species richness of the three dune habitats is fixed dune > semifixed dune > mobile dune (Figure 2).



**Table 2.** Family and genera of plant species and their relative frequency (*rf*) and importance value (*IV*).

Family	Genus	Species	RF (%)	IV (%)	
Chenopodiaceae	<i>Haloxylon</i>	<i>Haloxylon ammodendron</i>	33.00	48.81	
		<i>Haloxylon persicum</i>	30.00	28.07	
	<i>Salsola</i>	<i>Salsola praecox</i>	13.33	10.42	
		<i>Salsola nitrraria</i>	3.67	0.32	
	<i>Horaninovia</i>	<i>Horaninovia ulicina</i>	25.33	15.05	
	<i>Ceratocarpus</i>	<i>Ceratocarpus arenarius</i>	25.33	27.45	
	<i>Agriophyllum</i>	<i>Agriophyllum squarrosum</i>	13.33	15.23	
	<i>Corispermum</i>	<i>Corispermum lehmannianum</i>	16.00	18.69	
	<i>Calligonum</i>	<i>Calligonum leucocladum</i>	26.33	7.3	
	<i>Suaeda</i>	<i>Suaeda glauca</i>	13.33	14.12	
	<i>Grubovia</i>	<i>Bassia dasyphylla</i>	14.00	12.17	
	<i>Atriplex</i>	<i>Atriplex dimorphostegia</i>	8.33	1.23	
	<i>Chenopodium</i>	<i>Chenopodium glaucum</i>	2.33	0.46	
	<i>Kochia</i>	<i>Kochia iranica</i>	0.33	0.26	
	<i>Peganum</i>	<i>Peganum harmala</i>	2.33	0.23	
	Gramineae	<i>Stipagrostis</i>	<i>Stipagrostis pennata</i>	3.33	0.49
		<i>Eremopyrum</i>	<i>Eremopyrum orientale</i>	17.33	12.23
Brassicaceae	<i>Alyssum</i>	<i>Alyssum desertorum</i>	5.67	3.5	
	<i>Isatis</i>	<i>Isatis violascens</i>	12.67	2.2	
	<i>Tetracme</i>	<i>Tetracme quadricornis</i>	13.33	7.2	
Compositae	<i>Malcolmia</i>	<i>Malcolmia africana</i>	3.33	0.42	
	<i>Echinops</i>	<i>Echinops sphaerocephalus</i>	5.67	6.53	
	<i>Cancrinia</i>	<i>Cancrinia discoidea</i>	1.67	0.14	
	<i>Seriphidium</i>	<i>Seriphidium terraealbae</i>	25.33	37.19	
	<i>Hyalea</i>	<i>Hyalea pulchella</i>	11.33	1.1	
	<i>Amberboa</i>	<i>Amberboa turanica</i>	1.00	0.58	
	<i>Chondrilla</i>	<i>Chondrilla ambigua</i>	19.00	1.37	
Boraginaceae	<i>Lappula</i>	<i>Lappula semiglabra</i>	13.67	1.73	
	<i>Arnebia</i>	<i>Arnebia decumbens</i>	0.67	4.11	
Asphodelaceae	<i>Eremurus</i>	<i>Eremurus inderiensis</i>	5.67	4.74	
Liliaceae	<i>Gagea</i>	<i>Gagea nakaiana</i>	9.67	1.67	
Fabaceae	<i>Alhagi</i>	<i>Alhagi sparsifolia</i>	13.67	9.74	
	<i>Eremosparton</i>	<i>Eremosparton songoricum</i>	4.00	0.64	
Umbelliferae	<i>Soranthus</i>	<i>Soranthus meyeri</i>	13.67	2.91	
Plumbaginaceae	<i>Limonium</i>	<i>Limonium sinense</i>	1.00	0.28	
Lamiaceae	<i>Nepeta</i>	<i>Nepeta micrantha</i>	1.00	0.12	
Tamaricaceae	<i>Tamarix</i>	<i>Tamarix chinensis</i>	5.33	1.32	
Salicaceae	<i>Populus</i>	<i>Populus euphratica</i>	5.67	2.59	



**Figure 2.** Species-rank-abundance curves in fixed, semifixed and mobile dunes.

#### 4.3. Species-Abundance Distribution at Different Scales

The species richness curve spans a small range on the horizontal axis on scales of  $10\text{ m} \times 10\text{ m}$  and  $20\text{ m} \times 20\text{ m}$  (Figures 3–5). As the scale increases, with scales of  $40\text{ m} \times 40\text{ m}$ ,  $60\text{ m} \times 60\text{ m}$ , and  $80\text{ m} \times 80\text{ m}$ , the span of the curve increases, and the species richness becomes higher in fixed, semifixed, and mobile dunes.

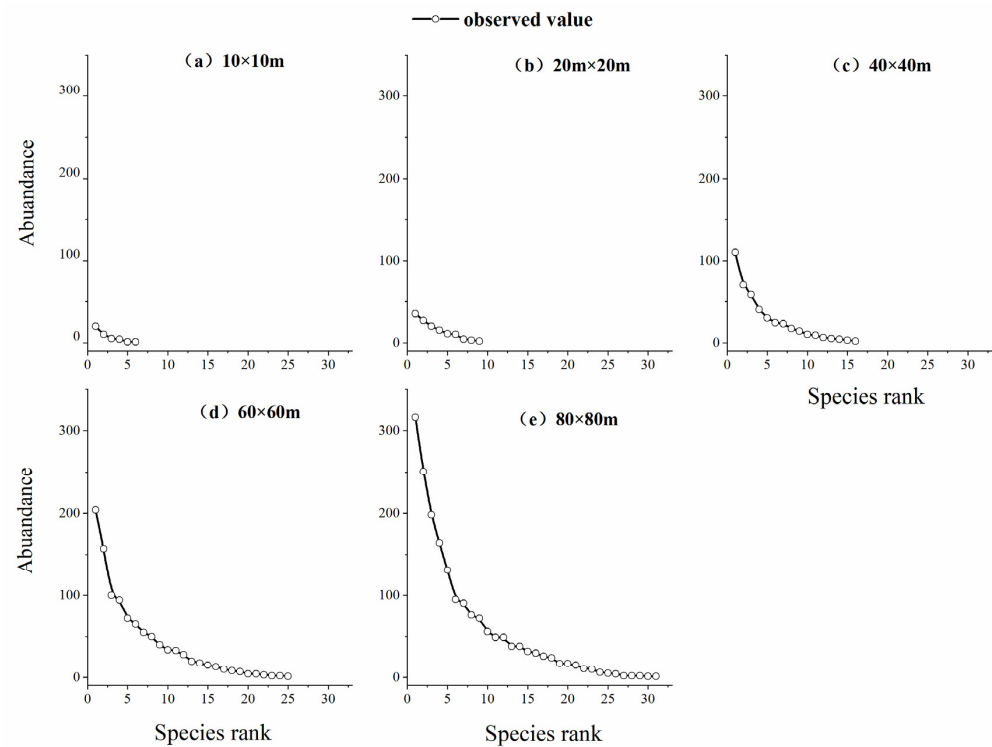


Figure 3. Species-rank-abundance curves at different scales in fixed dunes.

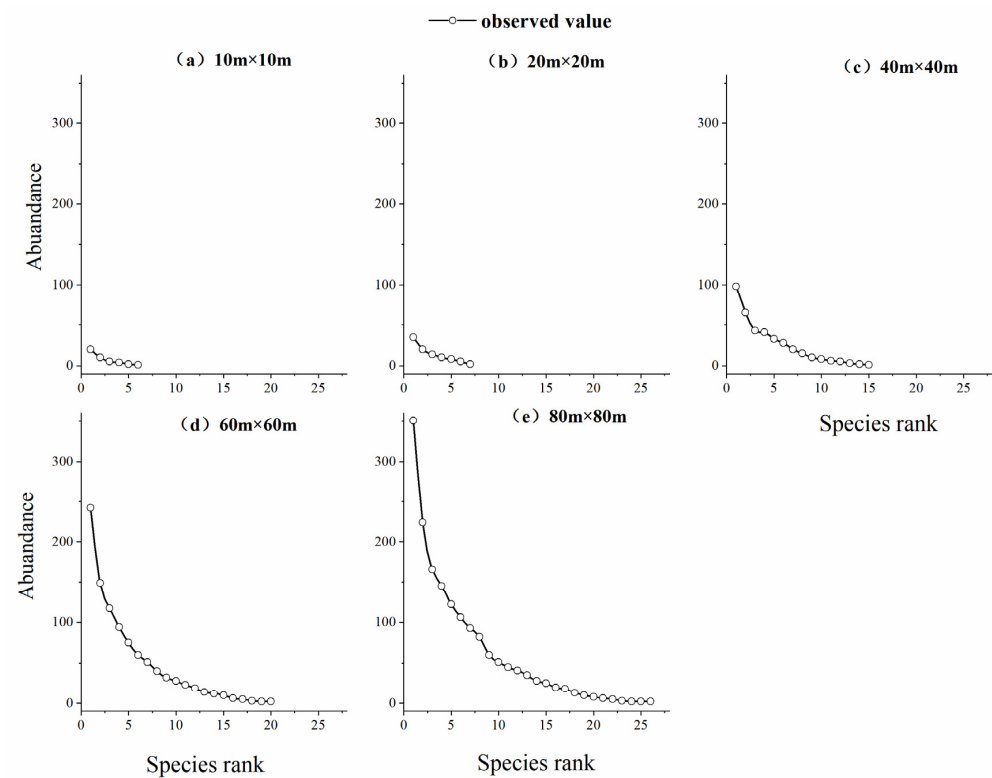


Figure 4. Species-rank-abundance curves at different scales in semifixed dunes.

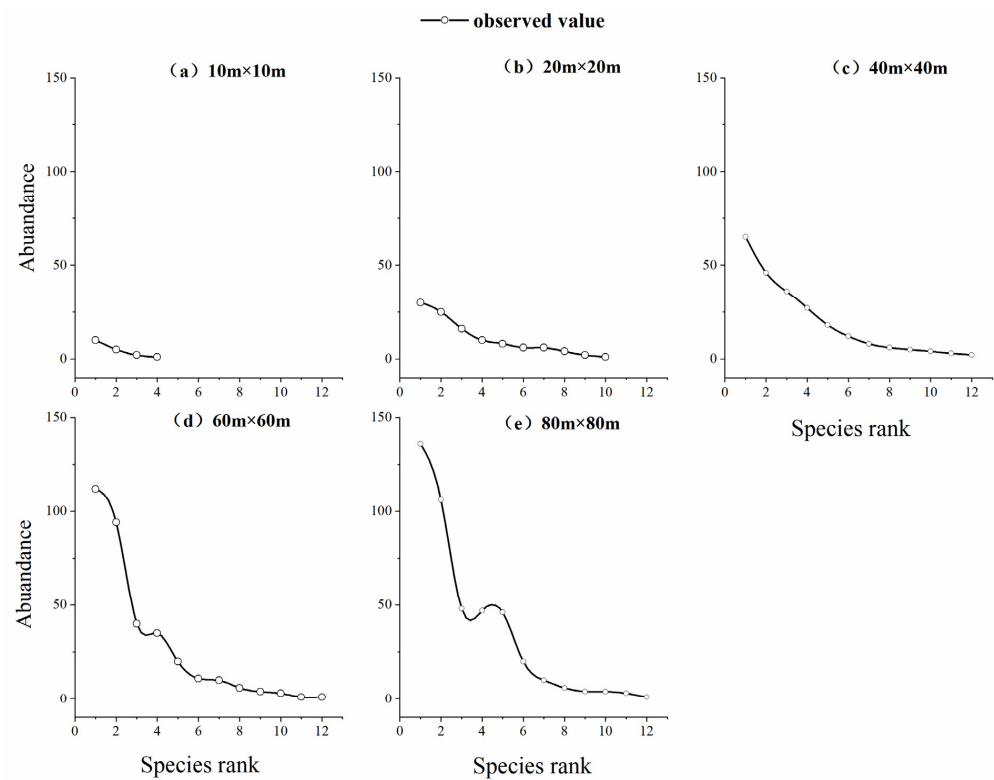


Figure 5. Species-rank-abundance curves at different scales in mobile dunes.

4.4. Species-Abundance Distribution Pattern Curve Fitting in Different Habitats

In fixed dunes, the broken stick model, log-normal distribution model, and Zipf model were all rejected by the  $\chi^2$  test ( $p < 0.01$ ), and Zipf was also significantly rejected by the K-S test ( $p < 0.05$ ). Only the niche preemption model and the Zipf–Mandelbrot model were able to fit the species-abundance distribution of this habitat better (Figure 6; Table 3). In terms of the magnitude of the AIC value, the niche preemption model is the optimal model.

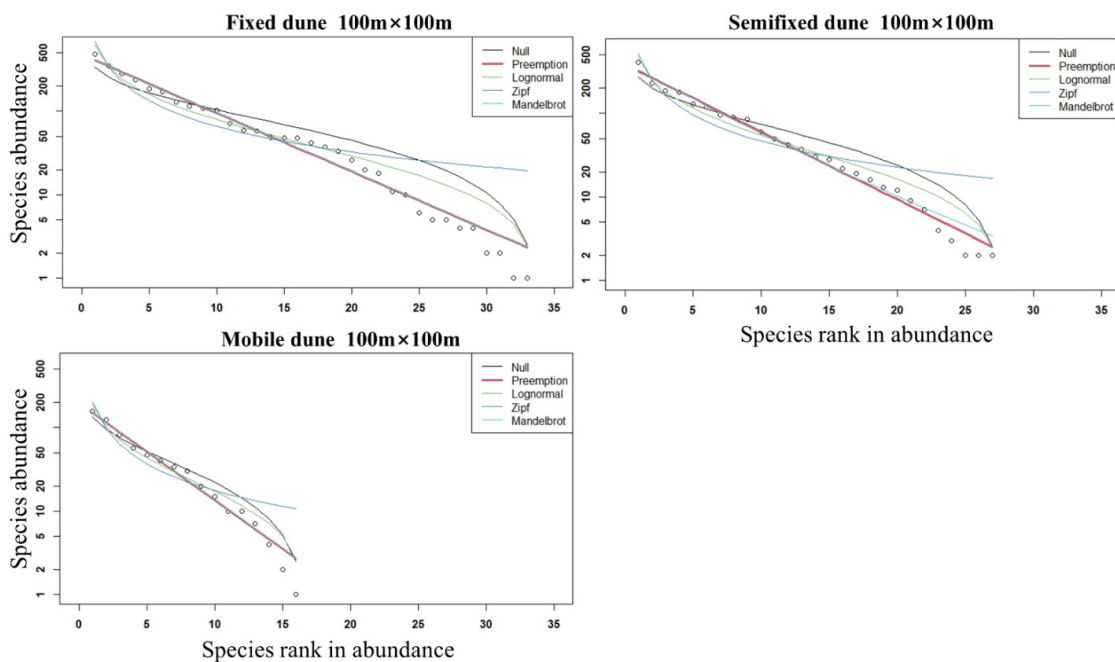


Figure 6. Species-abundance distributions and model fit in fixed, semifixed, and mobile dunes. Observations are represented by dots, and the bold line represents the best-fit model.

**Table 3.** Goodness-of-fit test of species-abundance distribution models in different habitats in the Gurbantünggüt Desert.

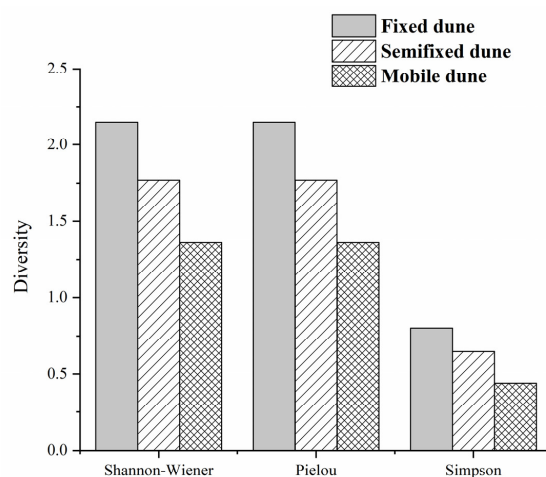
Habitat	Test Way	Model				
		Broken-Stick Model	Preemption Model	Log-Normal Model	Zipf Model	Zipf–Mandelbrot Model
Fixed dune	AIC	533.14	228.44	322.16	670.19	232.37
	D	0.86	0.49	0.49	1.48 *	0.49
	$\chi^2$	321.56 **	55.87	514.75 **	411.09 **	52.01
Semifixed dune	AIC	497.12	195.46	271.07	573.17	199.39
	D	0.82	0.41	0.86	1.87 *	1.29
	$\chi^2$	317.7 **	47.41	367.71 **	349.33 **	43.53
Mobile dune	AIC	115.93	85.36	100.34	155.93	89.27
	D	0.53	0.35	0.35	1.06	0.35
	$\chi^2$	29.29	8.66	49.12 *	66.79 **	8.95

\*  $p < 0.05$ , \*\*  $p < 0.01$ .

In semifixed dunes, the  $\chi^2$  test showed that the fit results of the three models (broken stick model, log-normal distribution model, Zipf model) still differed significantly ( $p < 0.01$ ) from the actual species-abundance distribution, but, compared to the fixed dunes, there was a diminishing discrepancy between the fit results and the actual species-abundance distribution, and the K–S test indicated that the Zipf model was still significantly rejected ( $p < 0.05$ ). Both the niche preemption model and the Zipf–Mandelbrot model predict the species-abundance distribution under this habitat condition. Based on the results of the AIC test, the niche preemption model was the best fit.

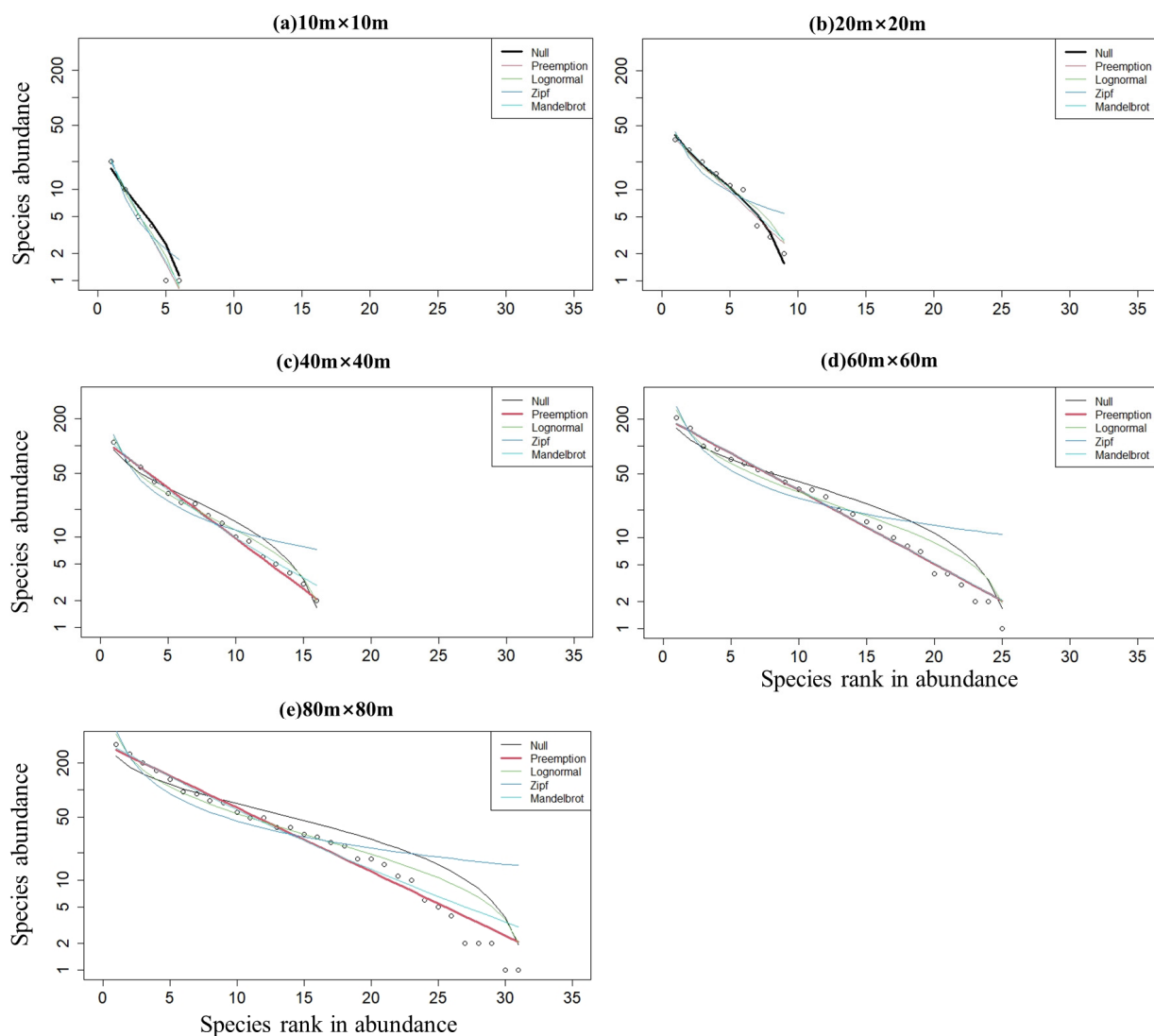
In mobile dunes, although all five models (niche preemption model, Zipf–Mandelbrot model, log-normal distribution model, broken stick model, Zipf model) were accepted by the K–S test ( $p > 0.05$ ), the  $\chi^2$  test showed that the log-normal distribution model and the Zipf model were rejected. Among the five models, the niche preemption model, the Zipf–Mandelbrot model, and the broken stick model can all predict the species-abundance distribution of the mobile dune habitat. However, the AIC value and the  $\chi^2$  test results of the niche preemption model were better than those of the Zipf–Mandelbrot model and the broken stick model, so the niche preemption model was the optimal model in the mobile dune habitat.

According to the AIC fitting results, the model fits for fixed, semifixed, and mobile dunes show the same pattern, in order: the niche preemption model > Zipf–Mandelbrot model > log-normal distribution model > broken stick model > Zipf model. The Shannon–Wiener index, Pielou index, and Simpson index of the three dune habitats are ranked as follows: fixed dunes > semifixed dunes > mobile dunes (Figure 7).

**Figure 7.** Plant diversity index of different dune habitats.

#### 4.5. Fitting Species-Abundance Distribution Curves at Different Scales

All five models were accepted in the fixed dune with scales of 10 m × 10 m and 20 m × 20 m in the K–S test and  $\chi^2$  test ( $p > 0.05$ ), but the broken stick model had the lowest AIC value and was the best model (Figure 8; Table 4). On the scale of 40 m × 40 m, all five models can fit the species-abundance distribution, but according to the AIC value, the niche preemption model becomes the optimal model for this scale. With increasing scale, at large scales of 60 m × 60 m and 80 m × 80 m, although all five models were accepted by the K–S test, the findings of the  $\chi^2$  test revealed that the predictions of the broken stick model were highly significant ( $p < 0.05$ ) from the actual species-abundance distribution, and the predictions of the log-normal and Zipf models were highly significant ( $p < 0.01$ ) compared to the actual results. The Zipf–Mandelbrot model is the best model at the 80 m × 80 m scale, according to the findings of the AIC test, while the preemption model fits best at the 60 m × 60 m scale.



**Figure 8.** Species-abundance distribution and the model fitting of fixed dunes at different spatial scales. Observations are represented by dots, and the bold line represents the best fit model.

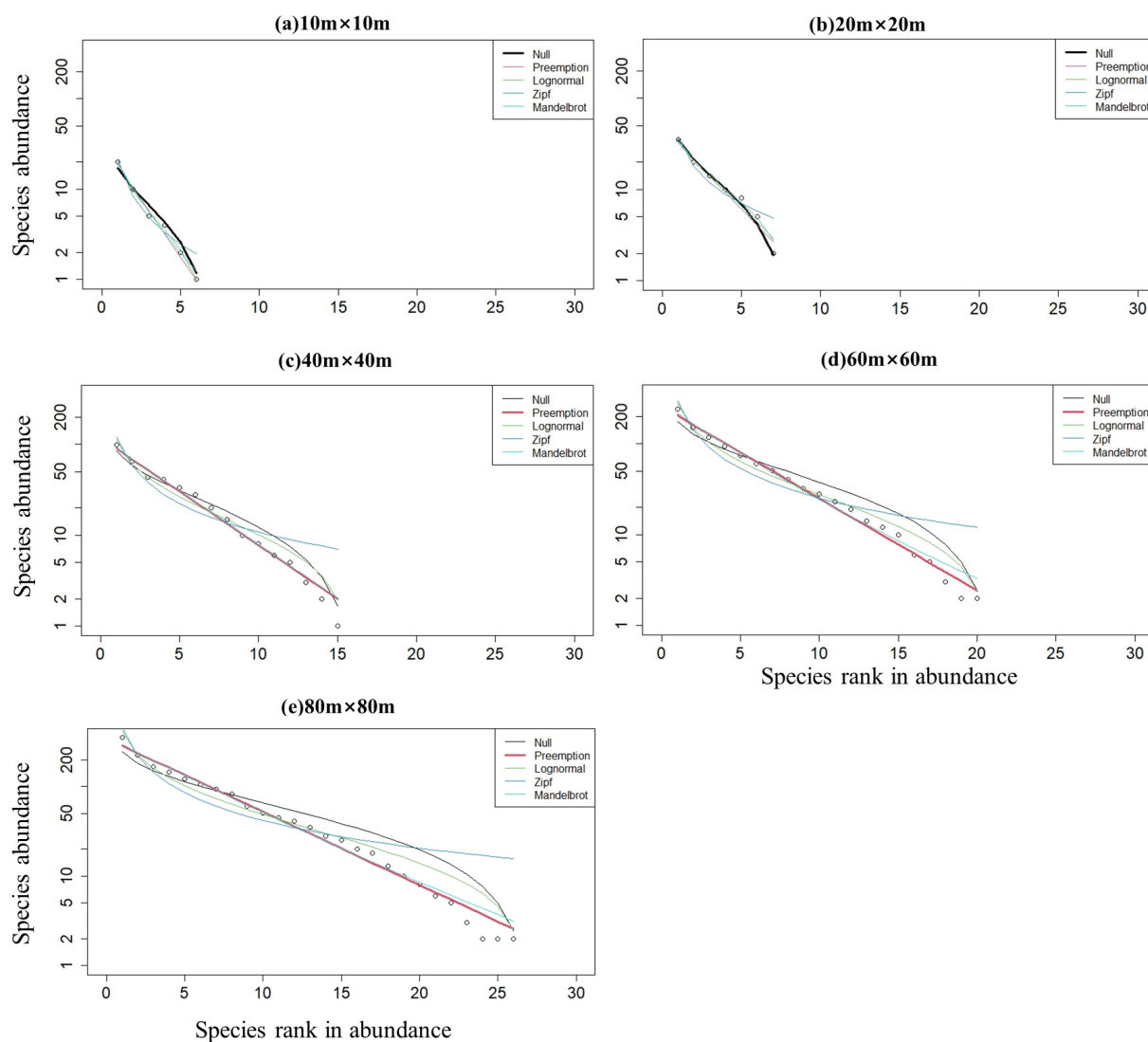
**Table 4.** AIC values of different models and the  $\chi^2$  fitting test at different sample scales.

Habitat	Scale(m)	Test Way	Model				
			Broken STICK Model	Preemptio Model	Log-Normal Model	Zipf Model	Zipf–Mandelbrot Model
Fixed dune	10 × 10	AIC	21.92	22.45	24.52	25.79	26.42
		D	0.58	0.29	0.29	0.58	0.29
		$\chi^2$	1.91	0.69	1.90	1.88	0.67
	20 × 20	AIC	39.21	41.52	44.88	52.81	45.15
		D	0.24	0.24	0.47	0.71	0.24
		$\chi^2$	2.00	1.95	4.12	10.59	2.81
	40 × 40	AIC	86.56	80.25	82.40	108.34	82.23
		D	0.35	0.18	0.35	0.88	0.35
		$\chi^2$	14.40	4.57	6.41	29.87	2.98
	60 × 60	AIC	190.66	137.90	160.09	268.43	141.80
		D	0.57	0.42	0.28	1.27	0.42
		$\chi^2$	66.27 *	16.31	80.67 **	124.52 **	15.88
	80 × 80	AIC	350.31	228.44	241.69	455.36	189.49
		D	0.76	0.64	0.38	1.27	0.64
		$\chi^2$	178.46 *	55.87	249.36 **	246.78 **	29.67
Semifixed dune	10 × 10	AIC	21.44	22.78	24.53	25.49	26.64
		D	0.29	0.29	0.29	0.29	0.29
		$\chi^2$	1.06	1.61	0.39	1.06	0.33
	20 × 20	AIC	29.40	32.29	33.27	36.25	35.97
		D	0.51	0.51	0.47	0.47	0.51
		$\chi^2$	0.50	1.04	0.96	2.87	1.02
	40 × 40	AIC	79.71	73.59	82.30	114.54	77.48
		D	0.37	0.37	0.37	0.91	0.37
		$\chi^2$	12.30	4.92	20.98	39.76	5.51
	60 × 60	AIC	170.40	114.26	124.94	211.80	116.59
		D	0.47	0.32	0.32	0.95	0.47
		$\chi^2$	67.19 **	13.27	41.19	94.37 **	11.12
	80 × 80	AIC	284.64	165.51	193.7	373.34	168.52
		D	0.69	0.42	0.28	1.25	0.56
		$\chi^2$	138.97 **	30.74	144.76 **	203.20 **	28.98
Mobile dune	10 × 10	AIC	12.47	14.32	16.36	16.73	18.29
		D	0.35	0.35	0.35	0.35	0.35
		$\chi^2$	0.20	0.03	0.86	0.49	0.05
	20 × 20	AIC	39.90	42.05	44.93	51.10	45.88
		D	0.22	0.22	0.22	0.45	0.22
		$\chi^2$	1.71	1.68	3.13	8.08	1.74
	40 × 40	AIC	59.64	54.21	63.27	77.76	58.11
		D	0.41	0.20	0.41	0.82	0.20
		$\chi^2$	7.73	0.84	8.94	22.16	0.93
	60 × 60	AIC	112.12	60.39	80.82	107.78	64.38
		D	0.61	0.20	0.20	0.82	0.41
		$\chi^2$	56.89 **	7.38	32.07	51.37 **	7.66
	80 × 80	AIC	117.09	74.15	98.02	137.16	78.12
		D	0.82	0.41	0.41	1.02	0.41
		$\chi^2$	54.26 **	18.42	56.09 **	76.63 **	19.90

\*  $p < 0.05$ , \*\*  $p < 0.01$ .

In semifixed dunes, all five models fit species-abundance distribution patterns at 10 m × 10 m and 20 m × 20 m scales, and the best fit was achieved by comparing AIC values with the broken stick model (Figure 9; Table 4). The K–S test continued to accept the five models at the scales of 40 m × 40 m and 60 m × 60 m ( $p > 0.05$ ), but the fit of the broken stick model was found to become progressively worse as the scale increased by the  $\chi^2$  test, and the broken stick and Zipf models were rejected as highly significant at the 60 m × 60 m scale ( $p < 0.01$ ). The AIC test findings demonstrate that the preemption model is the best model on the scales of 40 m × 40 m and 60 m × 60 m. At the large scale of 80 m × 80 m, the niche preemption model and the Zipf–Mandelbrot model were both able to fit the species-abundance distribution pattern at this scale, but the broken stick model, the log-normal distribution model, and the Zipf model were all rejected by the  $\chi^2$  test ( $p < 0.01$ ).

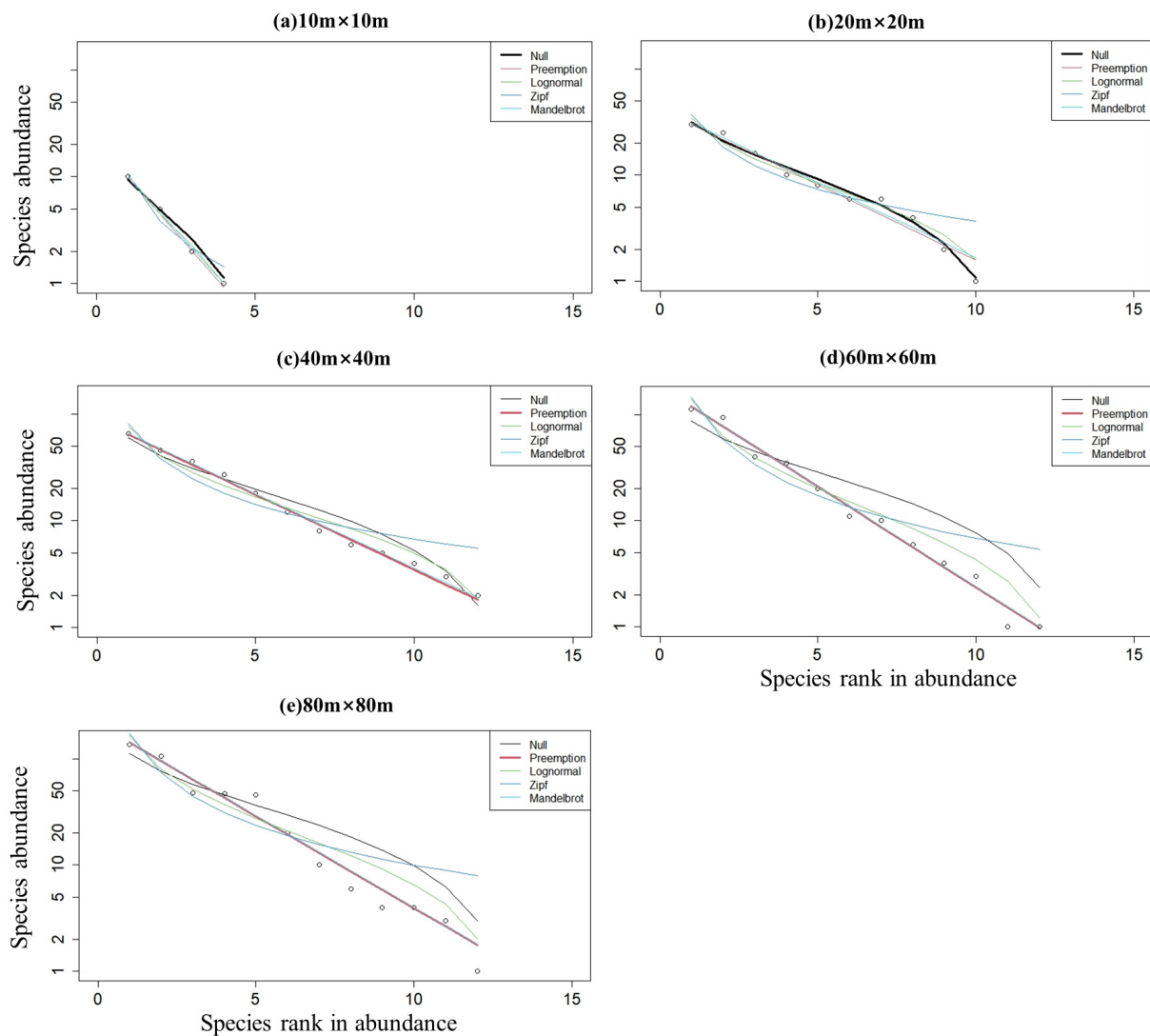




**Figure 9.** Species-abundance distribution and the model fitting of semifixed dunes at different spatial scales. Observations are represented by dots, and the bold line represents the best fit model.

In mobile dunes, at scales of  $10\text{ m} \times 10\text{ m}$ ,  $20\text{ m} \times 20\text{ m}$ , and  $40\text{ m} \times 40\text{ m}$ , all five models were accepted by the K–S test and  $\chi^2$  test. The broken stick model and the Zipf model were rejected by the  $\chi^2$  test at  $60\text{ m} \times 60\text{ m}$  and  $80\text{ m} \times 80\text{ m}$  ( $p < 0.01$ ), and the log-normal distribution model was rejected at the  $80\text{ m} \times 80\text{ m}$  scale ( $p < 0.01$ ) (Figure 10; Table 4). The species-abundance distribution pattern can be fit at five scales only by the niche preemption model and the Zipf–Mandelbrot model, and as the scale increases, the AIC difference between the models also increases. Based on the magnitude of the AIC values, the broken stick model is the optimal model at the  $10\text{ m} \times 10\text{ m}$  and  $20\text{ m} \times 20\text{ m}$  scales, and the niche preemption model is the optimal model at the  $40\text{ m} \times 40\text{ m}$ ,  $60\text{ m} \times 60\text{ m}$ , and  $80\text{ m} \times 80\text{ m}$  scales.

The Shannon–Wiener diversity index, Pielou evenness index, and Simpson diversity index at different scales are all ranked as fixed dunes > semifixed dunes > mobile dunes (Figure 11; Table 4).



**Figure 10.** Species-abundance distribution and the model fitting of mobile dunes at different spatial scales. Observations are represented by dots, and the bold line represents the best fit model.

#### 4.6. Neutral Theory Test

The Volkov neutral model was used to fit species-abundance distributions in fixed, semifixed, and mobile dunes (Figures 12–14 and Table 5). The fundamental diversity  $\theta$  is largest for fixed dunes, followed by semifixed dunes and smallest for mobile dunes, and the relationship between the magnitude of the migration rate  $m$  in the three dunes is mobile dunes > semifixed dunes > fixed dunes; except for mobile dune habitats, the fundamental diversity  $\theta$  increases with increasing sampling scale in both fixed and semifixed dune habitats, while the migration rate  $m$  gradually decreases. The Volkov neutral models of the three dunes at different scales all passed the K–S test and the  $\chi^2$  test, and the  $\chi^2$  test value of the mobile dune habitat was better than that of the semifixed dune habitat and mobile dune habitat (Table 4).

A comparison of Chi-square values for the Volkov neutral model (Table 5) and  $\chi^2$  values for five models (niche preemption model, Zipf–Mandelbrot model, log-normal distribution model, broken stick model, Zipf model) (Tables 3 and 4) shows that the fitting results of the Volkov neutral model are slightly worse than those of the broken stick model, the niche preemption model, and the Zipf–Mandelbrot model on the scales of 10 m × 10 m and 20 m × 20 m, but on the large scale of 100 m × 100 m, the fitting results of the Volkov model for the fixed dune and semifixed dune habitats are better than the other five

models; in mobile dune habitats, the Volkov model fits worse than the niche preemption model and the Zipf–Mandelbrot model for 40 m × 40 m, 60 m × 60 m, 80 m × 80 m, and 100 m × 100 m. The actually observed abundance curves at the 10 m × 10 m, 20 m × 20 m, 40 m × 40 m, 60 m × 60 m, 80 m × 80 m, and 100 m × 100 m scales fell almost exactly within the 95% confidence interval predicted by neutral theory (Figures 12–14), indicating that the Volkov neutral model could fit the species-abundance distribution patterns of the three dune habitats at different scales.

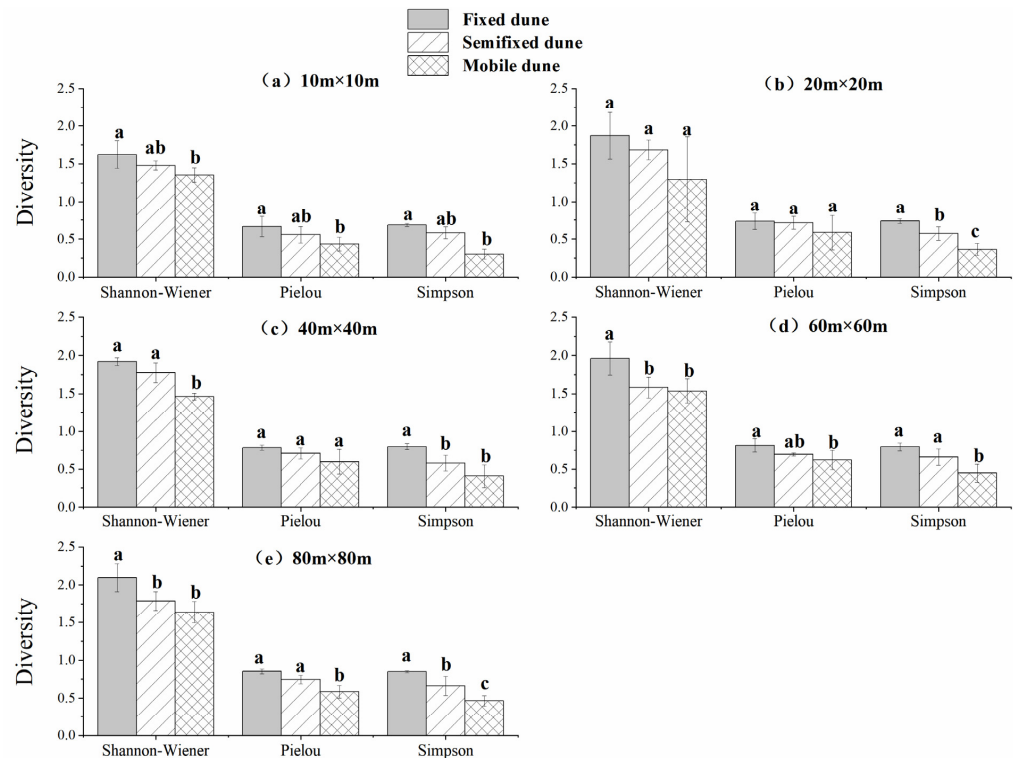
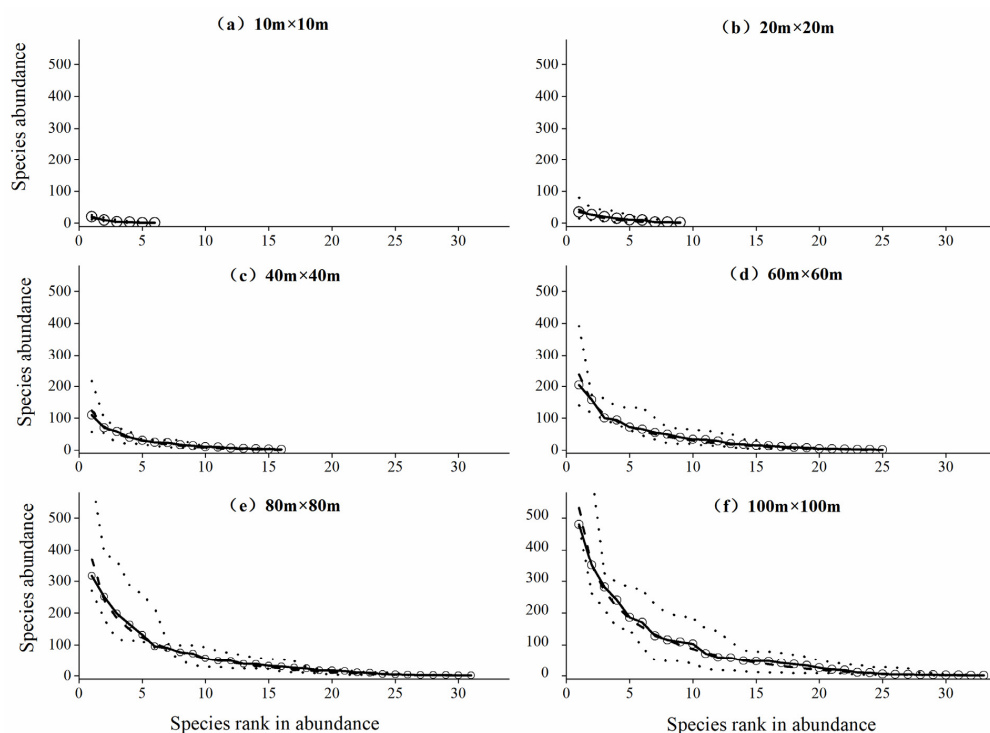


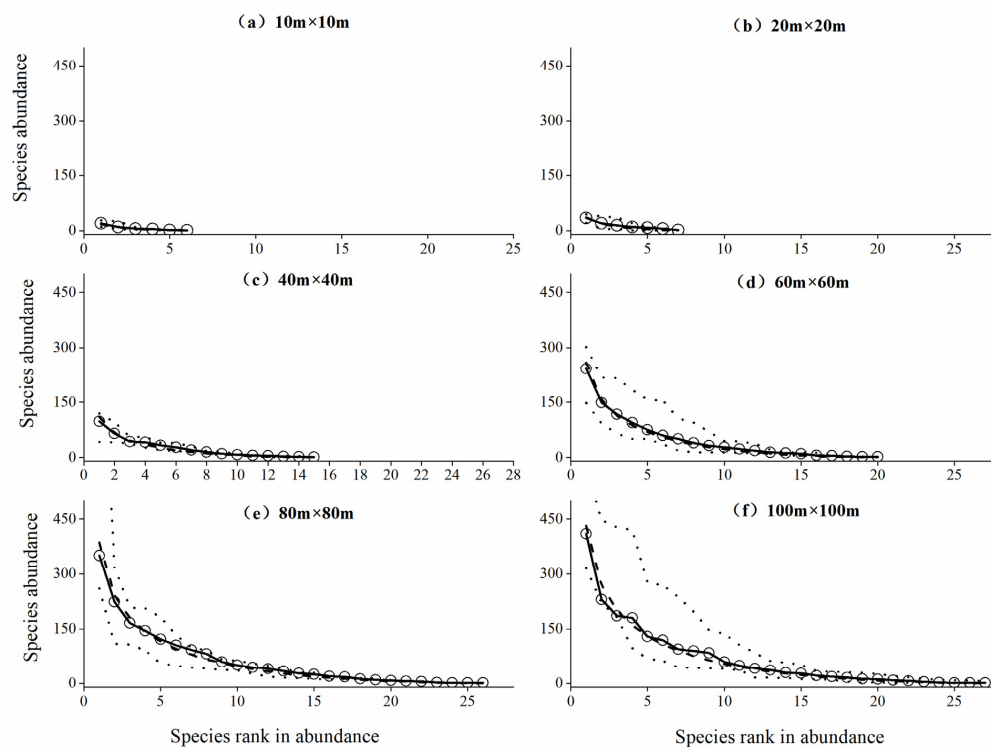
Figure 11. Species diversity index of different scales in fixed dunes, semifixed dunes, and mobile dunes.

Table 5. Prediction parameters of the neutral model and the  $\chi^2$  fitting test at different sample scales.

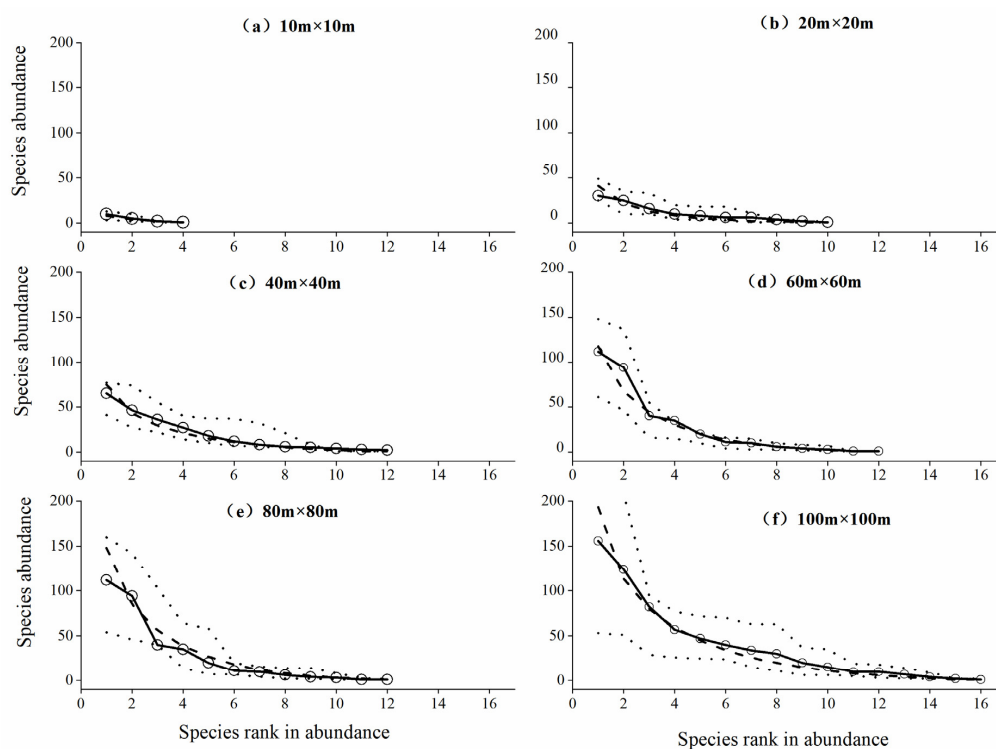
Habitat	Scale (m)	Species Number	Individual Number	Fundamental Diversity $\theta$	Migration Rate $m$	$\chi^2$	D
Fixed dune	10 × 10	6	41	9.88	0.07	1.47	0.29
	20 × 20	9	127	5.14	0.07	13.44	0.47
	40 × 40	16	425	6.76	0.05	17.54	0.35
	60 × 60	25	1039	10.26	0.03	22.09	0.28
	80 × 80	31	1828	12.44	0.02	31.80	0.38
	100 × 100	33	2726	13.79	0.01	38.00	0.37
Semifixed dune	10 × 10	6	42	5.84	0.01	0.97	0.30
	20 × 20	7	94	3.79	0.08	11.68	0.54
	40 × 40	15	378	7.59	0.04	15.37	0.37
	60 × 60	20	984	7.80	0.03	20.18	0.32
	80 × 80	26	1663	9.60	0.02	28.51	0.28
	100 × 100	27	1883	10.12	0.01	34.15	0.21
Mobile dune	10 × 10	4	18	6.69	0.13	0.75	0.35
	20 × 20	10	108	6.31	0.09	8.35	0.45
	40 × 40	12	232	6.17	0.05	13.09	0.41
	60 × 60	12	337	11.27	0.02	13.64	0.20
	80 × 80	12	431	7.57	0.02	24.40	0.41
	100 × 100	16	639	6.55	0.03	28.15	0.35



**Figure 12.** Confidence interval test results of the Volkov neutral model for simulated communities in a fixed dune habitat. The solid line indicates the actual observed abundance distribution curves; the underlined line indicates the Volkov-neutral-model-predicted abundance distribution; the dotted line indicates the abundance distribution, with 95% confidence intervals for the neutral-predicted distribution.



**Figure 13.** Confidence interval test results of the Volkov neutral model for simulated communities in a semifixed dune habitat. The solid line indicates the actual observed abundance distribution curves; the underlined line indicates the Volkov-neutral-model-predicted abundance distribution; the dotted line indicates the abundance distribution, with 95% confidence intervals for the neutral-predicted distribution.



**Figure 14.** Confidence interval test results of the Volkov neutral model for simulated communities in a mobile dune habitat. The solid line indicates the actual observed abundance distribution curves; the underlined line indicates the Volkov-neutral-model-predicted abundance distribution; the dotted line indicates the abundance distribution, with 95% confidence intervals for the neutral-predicted distribution.

## 5. Discussion

### 5.1. Species-Abundance Distribution Patterns

The extremely dry climate conditions and abundant dust-source environment render the vegetation growth conditions in the region relatively harsh in the Gurbantünggüt Desert [67]. Plant convergence adaptation and resource competition are the driving forces for plant community succession and the coexistence of restricted species [68]. In this study, histograms of species-abundance distribution and abundance-ranking curves were used to compare rare and common species in the community, and it was found that the abundance values and number of species were better in fixed dunes than in semifixed and mobile dunes, and the number of common and rare species increased with increasing scale. This may be due to the larger scales of common species occupying larger ecological niches and taking up more resources than other species that use less [69], combined with the influence of habitat heterogeneity on species distribution patterns formed by the patchy distribution of moisture, soil nutrients, etc. [70]. The study found that the Shannon–Wiener index, Pielou evenness index, and Simpson index showed an increasing trend with increasing scale, indicating that species diversity has different variation laws in space [71]. Therefore, plant communities have obvious scale effects.

Soil is a major factor influencing plant-species distribution patterns in the Gurbantünggüt Desert [72]. In this study, the soil water content, organic carbon, and salt content were found to be fixed dune > semifixed dune > mobile dune, with the same pattern of variation in the Shannon–Wiener index, Pielou evenness index, and Simpson index. This may be because the geomorphology of the Gurbantünggüt Desert landscape varies significantly horizontally and vertically, and the variety of herbaceous patches of desert plants is significantly impacted by the complexity of topography and the physical and chemical qualities of the soil in microhabitats [73]. Numerous studies have shown that, under certain drought stresses, soil moisture and soil organic matter content are important factors driving the

overall abundance of plants in the community: the important constraint of soil variables on the abundance distribution of different size classes was revealed in a study by Antunes et al. [74], and increasing soil temperature limits the abundance of smaller species by reducing the carbon content in the soil. Soil moisture is the main source of photosynthesis and transpiration for *Tamarix chinensis*, and the Gurbantünggüt Desert is an extremely arid area where *T. chinensis* and other vegetation need to absorb groundwater to maintain their normal life activities [75]. Therefore, the species diversity values and species numbers of the three different dunes in this study remained consistent with the variation in soil factors, and the species diversity index of the fixed dune habitat was significantly greater than that of the mobile dune (Figure 7). According to a field survey by Qian et al. [76], under the conditions of poorly sorted desert soils with a certain amount of moisture and organic matter, short-lived plants (such as salinity-tolerant *Haloxylon ammodendron* and *Anabasis aphylla*) mainly grow, and the plant bed and stand environment created by the dynamics of the sand surface results in the sorting of community species, making it difficult for plants on the flowing sand surface with significant wind erosion to successfully bed and stand, resulting in the longitudinal and horizontal differentiation of plant species that are more dependent on microhabitats such as topography and soil texture, forming a spatially variable trend in the species diversity of vegetation communities. According to the  $\chi^2$  test, the Volkov neutral model fits better (100 m  $\times$  100 m) than the niche preemption model for fixed and semifixed dunes, making it the optimal model. In mobile dunes, the niche preemption model is significantly better than the Volkov neutral model. This differs from the findings of Kang et al. [15] in the riparian forests of the Tarim Desert, who found that neutral processes in different habitats were always the main mechanism dominating species-abundance distribution patterns in desert riparian forest communities. The possible reason is that the soil coverage of fixed dunes is relatively good, and the accumulation of soil nutrients in mobile dunes is weak, while the aggregation of semifixed dunes and fixed dunes is strong, and the characteristics of soil factors and soil nutrients are not affected. The spatial structure and spatial autocorrelation are both good (Ma et al., 2016) [77]. Species can effectively obtain living resources and weaken the role of niche differentiation among species. Mobile dune sands are constantly transported from windward to leeward slopes and accumulate under the action of gravity; dune fixation time is relatively short; habitat heterogeneity increases; intraspecies competition is greater than interspecies competition. Typical annual plant species such as *Agriophyllum squarrosum* tend to mutually benefit in order to survive and synergistically resist harsh habitats, aggregating growth, bearing large amounts of fruit, rapid seed germination, and rapid rooting and grabbing resource space, and species achieve coexistence through the complementary effect of ecological niches [78,79]. Differences in resource use by different plants, interspecific competitive effects, and resource constraints lead to a negative correlation between species diversity and available resources [80,81]. Thus, both the neutral and niche models fit well under different habitat conditions.

### 5.2. Ecological Processes in Dune Habitats at Different Scales

Wu et al. [82] showed that the choice of sampling scale affects the assessment of community species diversity. Unlike most studies of scale effects on species-abundance distribution, this study explores the response of species-abundance patterns to scale effects under different habitat conditions. We found that both niche processes and neutral processes explain the distribution patterns of species abundance at different scales in the three dunes, suggesting that, in addition to the distribution of species at each scale being dependent on the distribution of available resources, species colonization due to local stochastic dispersal also influences the composition and distribution of species in the community [83]. At small scales of 10 m  $\times$  10 m and 20 m  $\times$  20 m, the optimal model for all three dunes is the broken stick model, which indicates that there is certainty in the allocation of resources during the development of the three dune communities at small scales. At the 40 m  $\times$  40 m



and 60 m × 60 m mid-scale, the preemption model and the niche processes represented by the Zipf–Mandelbrot model gradually dominate in the three dunes.

However, as the scale increases, at large scales of 80 m × 80 m and 100 m × 100 m, neutral processes become the main ecological processes determining the distribution patterns of species in fixed and semifixed sand dune communities. Liu et al. [84] found in their investigation of the spatial scale of forest communities that the migration rate  $m$  of the neutral model increases and then slowly stabilizes with increasing scale. This study came to a different conclusion: all dunes' migration rate  $m$  decreased with increasing scale, with the largest difference in the migration rate  $m$  of the mobile dunes. Wei et al. [83] suggest that this may be due to differences in resources such as light, temperature, and water at different scales, resulting in asymmetric competition for resource use by different individuals. In both fixed and mobile dunes, fundamental diversity  $\theta$  increases as new habitats emerge in the community as the sampling range increases; the effect of dispersal limitation on community species composition increases with scale and the community is gradually driven by neutral processes [85]. In contrast, the migration rate  $m$  difference for mobile dunes is larger; fundamental diversity  $\theta$  does not change significantly from small to large scales, and habitat heterogeneity is lower, resulting in no enhancement of dispersal at large scales. The effect of the Volkov neutral model is significantly worse than that of the preemption model for mobile dunes at large scales (80 m × 80 m and 100 m × 100 m).

### 5.3. Ecological Processes in Different Dune Habitats

Patterns of species diversity and species-abundance distribution change in response to habitat heterogeneity in the Gurbantünggüt Desert. Neutral theory processes have a strong effect on the abundance distribution of relatively species-rich communities, while they may not affect low-diversity communities [86]. This study found that the Volkov neutral model at scales of 10 m × 10 m, 20 m × 20 m, 40 m × 40 m, 60 m × 60 m, 80 m × 80 m, and 100 m × 100 m all fell within the 95% confidence interval within fixed, semifixed, and mobile dunes. Neutral processes act more on fixed and semifixed dunes than on mobile dunes and are the main factor influencing species-abundance distribution. In contrast to the traditional niche-theory explanation, community neutrality theory suggests that ecologically identical species can coexist, that changes in species abundance are stochastic, and that the number of species coexisting in a particular community is determined by a dynamic balance of migration and stochastic extinction [87]. Fixed dune habitats and semifixed habitats are subject to perennial drought and water scarcity, which limits the growth, development, and migration of species and reduces the rate of species migration [66], and the adaptive capacity of species to the drought environment is similar, each occupying the required ecological niche and forming a stable coexistence pattern, resulting in a weakening of niche processes and an increase in neutral processes [88].

In addition, species survival and reproduction depend on a combination of ecological factors, and niche processes play a dominant role in community species-abundance patterns in mobile dune habitats. In this study, the soil organic carbon content and soil water content of mobile dunes differed significantly from those of fixed and semifixed dunes compared to those of fixed and semifixed dunes, which have strong solar and wind erosion and poorer moisture conditions [89] and soil nutrient differences between dune slopes with scale effects, further enhancing interspecific competition and habitat filtering, making the Volkov neutral model, although accepted in mobile dunes, significantly less effective than the niche preemption model at large scales. Wang et al. [90] also found a greater contribution of niche differentiation in the northwest desert region but did not consider factors such as soil, topography, and anthropogenic disturbance. The niche theory of environmental filtering emphasizes the process of habitat selection for species with specific traits, such as soil nutrients, topography, and light, as filters to influence species colonization, survival, development, and environmental screening for species with similar functional traits [91]. In the environment, various characteristics, such as soil factors and topographic factors, influence the distribution and combination of survival conditions, such

as light, temperature, water, and nutrients. Zhang et al. [11] found that the plant diversity index was significantly higher in high water-salinity habitats than in low water-salinity habitats in the zone. Yang et al. [92] found that the aboveground biomass of meadow plant communities was significantly positively correlated with soil organic carbon, total nitrogen, total phosphorus, and soil water content and negatively correlated with soil pH. Soil water content and total salt content are lower in mobile dunes than in fixed and semifixed dunes, and due to various species' ecological adaptations to salinity and drought, soil nutrient and water availability support vegetation growth and abundance [93]. The number of species available for sieving into the species pool in areas under low water-salinity habitats with very low soil moisture limits (mobile dunes) is reduced, resulting in lower species diversity [94]. From fixed to mobile dune habitats, plant diversity decreases as soil nutrients and organic matter decrease, habitat conditions become more hostile, and habitat filtering and interspecific interactions are strong, leading to a stronger effect of niche effects on species richness in mobile dune habitats.

#### 5.4. The Embodiment of the Community Niche-Neutral Continuum

In 2006, Gravel et al. proposed a niche-neutral continuum based on the integration of community neutrality theory and niche theory, suggesting that competition and stochastic drift can act simultaneously in community construction and community dynamics and that the relative magnitude of their effects determines community construction as a continuum from pure ecotone construction to pure neutral construction [94,95]. Numerous studies have provided strong support for the niche-neutral continuum: Hubbell [26] pointed out that the community dynamics of temperate-tropical forests represent this continuum; Chu et al. [96] studied the relative contributions of deterministic and stochastic processes in the succession of plant communities in alpine meadows on the Qinghai-Tibet Plateau; Wang [97] once again confirmed that the subalpine meadow community is a combination of niche and neutrality construction mechanisms, and the large-scale species pool surrounding it has a log-normal distribution for species abundance; Kim et al. [98] classified microbial colonization types based on an abundance-based regression model and observed that temporal colonization patterns are affected by niche change and neutrality, providing ecological mechanisms and dynamics of bacterial and fungal communities as an ecological continuum during seed-to-seed transmission.

In this study, to verify that the plant community-building mechanism of the Gurbantünggüt Desert is influenced by the niche-neutral continuum, multiple model-testing techniques revealed that both the niche model and the neutral model fit the species-abundance distribution patterns of various dunes, with distinct strengths at different sampling scales. When the activity of one ecological process was weakened, the effect of the other was enhanced, and the two processes were not independent of each other. This result is consistent with Adler et al. [99], who suggests that community neutrality is similar to multispecies coexistence, while niche-based community construction is similar to stabilizing multispecies coexistence, and that these two processes complement each other and interact to determine species coexistence and biodiversity maintenance [100,101]. For example, at 10 m × 10 m and 20 m × 20 m scales, the broken stick model is always the optimal model for fixing dune habitats, but the Volkov neutral model's mechanism increasingly replaces the broken stick model as the primary factor affecting the distribution of species abundance as the scale increases. At the 80 m × 80 m and 100 m × 100 m scales of mobile dunes, the higher habitat heterogeneity in the community leads to enhanced dispersal limitation, and the distribution of species is mainly influenced by niche processes. The interplay of niche overlap and dispersal limitation is an essential feature of the neutral-niche continuum. Ecological niche differentiation is only evident in mobile dune communities with low species diversity, when the ecological niche overlap of species is largely absent, and the relative abundance of species is largely determined by the distribution of environmental resources. In the fixed and semifixed dune communities with high species diversity, an extremely large overlap in ecological niches between species and the high rate of immigration increase

community restriction and similarity, which also inhibits the increase in species richness, and community dynamics are dominated by stochastic exclusion, resulting in a neutral community process [101]. These findings are consistent with Gravel et al. [94]’s prediction that increased ecotone overlap and community neutrality would contribute to increased species richness along the neutral–ecotone continuum. Fisher and Mehta [102] showed that, between selection-dominated institutions (niche process) and random-dominated institutions (neutral process), different ecological communities have transitional stages, and the relationship between species and habitats increases with succession. It becomes more complex as it progresses, with intense interspecific competition in the community at the beginning of succession, and the interspecific competition gradually weakens as succession progresses [103]. This study analyzed the species-abundance distribution pattern in terms of habitat heterogeneity and scale effects and found that neutral and niche processes are equally important. Plant community construction in the three habitats is consistent with the niche-neutral continuum hypothesis, but the relative importance of ecological processes differs between habitats: neutral processes play a dominant role in the formation of the species-abundance distribution in fixed and semifixed dunes, while the community construction mechanism of mobile dunes is more in line with the theoretical mechanism represented by niche processes.

From the findings of this research, it is clear that the study of species-abundance distribution patterns in the Gurbantünggüt Desert based on the statistical, niche, and neutral abundance models are successful and that the niche-neutral continuum theory can explain the ecological processes in three typical dunes. In agreement with many ecologists worldwide, niche and neutral theories should be compatible and complementary rather than contradictory, with species-abundance patterns shifting from one model to the other [104], unlike studies by Ulrich et al. [10], Zhang et al. [11], and Villa et al. [105], who found that species-abundance distributions (SAD) conform to log-normal distributions in most desert habitats and tropical forests worldwide. Our study found that by varying from the spatial scale, the log-normal distribution was significantly rejected ( $p < 0.01$ ), and the Volkov neutral model fit was better for the three dune species at large scales as habitat filtering intensified with increasing sampling extent. It can be seen that the use of species-abundance models to fit abundance patterns in terms of scale effects and habitat heterogeneity is an effective means of understanding the ecological processes in desert-plant communities and can provide a basis for curbing ecological degradation and promoting the rehabilitation of desert vegetation globally.

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