

Article

Scale Effects on Plant Diversity in the Gurbantunggut Desert

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Abstract

Revealing scale effects and the mechanisms underlying the relationships between plant species and functional diversity is crucial for understanding the stability of desert ecosystems and formulating multiscale conservation strategies. In this study, the spatial patterns of plant species and functional diversity in the Gurbantunggut Desert were analysed via multiscale grid sampling. The results indicated that (1) both species diversity and functional diversity indices exhibited high spatial heterogeneity. At the small scale (10 m × 10 m), the values of the Shannon–Wiener and Pielou indices for fixed dunes were higher in the south than in the north. At the medium and large scales (20 m × 20 m and 50 m × 50 m, respectively), the index values were highest in the southwest, with generally greater values in the south than in the north. For semifixed and mobile dunes, the Shannon–Wiener and Pielou index values exhibited an east-high–west-low pattern at the 10 m × 10 m scale. This differentiation decreased with increasing scale, with the highest values observed in the northeast and southwest at the 50 m × 50 m scale. The spatial differentiation in functional diversity indices (Rao’s second-order entropy index and functional evenness index) exhibited distinct characteristics across the different dune types. (2) The spatial variation in all the diversity indices monotonically decreased with increasing scale, with the variance in the species diversity indices indicating the following order: Shannon–Wiener index > Pielou index > Simpson index. (3) The relationships between species richness and diversity indices exhibited significant scale dependence. At the small and medium scales, species richness was significantly positively correlated with the Shannon–Wiener index, Simpson index, and Rao’s quadratic entropy index and significantly negatively correlated with the Pielou evenness index and functional evenness index. However, at the large scale, none of these correlations were significant. (4) The species diversity indices and Rao’s quadratic entropy index were significantly positively correlated at the small and medium scales ($p < 0.01$), whereas a significant positive correlation with the functional evenness index was observed only at the 10 m × 10 m scale ($p < 0.01$). At the larger scale, these correlations became insignificant. In fixed dunes, areas of high Simpson index values exhibited a spatially complementary distribution with areas of high Shannon–Wiener index and Pielou index values, providing evidence for the combined effect of local processes such as competitive exclusion and dispersal limitation. Through comprehensive multiscale analysis, this study revealed the mechanisms underlying the scale-dependent relationships between plant species and functional diversity, thereby providing a theoretical basis for protecting and restoring desert biodiversity.



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1. Introduction

Species diversity and functional diversity constitute key dimensions for understanding ecosystem structure and function. Species diversity reflects the compositional characteristics of a given community and serves as a fundamental indicator of ecosystem complexity and stability [1–3]; functional diversity reveals the resource utilization efficiency and niche mechanisms of a community by reflecting differences in functional traits [4–6]. These two indices are interrelated and jointly maintain ecosystem stability [7–9]. Notably, both species diversity and functional diversity greatly depend on their inherent patterns and formation mechanisms [10,11]; therefore, the analysis of the relationship between the two from a multiscale perspective has become a focal point of research.

Scale effects notably influence our understanding of diversity patterns. Extensive research has revealed that species diversity patterns and their relationships with environmental factors notably depend on the observation scale. For example, the Junggar leafless bean influences neighbouring communities by altering soil factors [12], and both species richness and its formation processes vary across different scales in the Lake Aibi watershed [13]; furthermore, studies in karst forests in northwestern Guangxi [1] and Inner Mongolian grasslands [14] have confirmed similar patterns. Functional diversity also exhibits significant scale dependence; its explanatory power for community productivity often exceeds that of species diversity and varies with functional indicators and the observation scale [15]. Both changes in plant functional traits along environmental gradients [16] and the cross-scale effects of tree functional diversity on the understorey [17] demonstrate scale-specific characteristics. The unique seed dormancy strategies of ephemeral plants in the Gurbantunggut Desert [18] and the scale-dependent patterns of plant diversity and productivity [19] in turn highlight the importance of the functional dimension in shaping cross-scale processes. Although previous studies have focused on stochastic processes in desert communities [13] or the scale-dependent regulation of functional traits [20], most remain confined to a single dimension, thus making it difficult to elucidate the complete cross-scale relationships among multiple dimensions and their synergistic effects on ecosystem function [21,22]. Emphasizing species diversity alone may obscure the direct role of functional traits, whereas focusing solely on functional diversity risks neglecting the foundational role of the species composition [5,22]. Therefore, in this study, species diversity and functional diversity were integrated across multiple scales [8,23], which helps to systematically elucidate the mechanisms underlying community assembly and diversity maintenance [24]. This approach is also important for predicting ecosystem functional responses under global change and for formulating effective conservation and restoration strategies [25,26].

The Gurbantunggut Desert is the largest fixed–semifixed desert in China and represents a typical temperate desert ecosystem. Its vegetation pattern is influenced by dune landforms and soil water–salt heterogeneity, resulting in significant habitat fragmentation [27]. Recent research in this region has focused primarily on the spatial patterns and scale characteristics of species diversity. For example, the number and importance of ephemeral plants increase gradually from east to west but decrease from north to south [28]. The diversity index of understorey vegetation in *Haloxylon persicum* forests increases with increasing sampling scale and exhibits a “first decrease, then increase” pattern within the transition zone from the southern edge to the interior of the desert [29]. However, research on the multiscale patterns of plant species diversity in this desert remains nonsystematic, and studies on the scale effects of functional diversity are even more scarce. Therefore, by integrating species diversity and functional diversity across multiple spatial scales, this study aims to reveal how the relationship between these two fundamental dimensions of biodiversity changes with increasing observation scale in the heterogeneous desert landscape. This

approach is important for understanding the mechanisms underlying desert biodiversity maintenance and for formulating differentiated conservation strategies [30].

Unlike relatively stable ecosystems such as forests, the Gurbantunggut Desert is a typical temperate desert ecosystem whose vegetation exhibits unique dynamic characteristics. First, the spring layer of ephemeral and quasi-ephemeral plants is highly developed, allowing these plants to complete germination, flowering, and fruiting within a short period following precipitation, demonstrating high phenological plasticity and rapid community turnover rates [18,31]. Second, due to dune mobility and spatial–temporal heterogeneity in soil moisture, the distribution patterns and species composition of dominant plant populations (e.g., *Haloxylon ammodendron* and *Haloxylon persicum*) exhibit considerable interannual fluctuations [27,29]. These characteristics of rapid succession and high dynamics make this desert an ideal system for studying the scale effects of plant diversity—because within a relatively small spatial and temporal window, researchers can observe a wide range of species assemblages and community states. This habitat advantage is not shared by more stable ecosystems such as forests. Therefore, in this study, we take advantage of the dynamic and rapidly successional vegetation of this desert to systematically reveal the scale-effect patterns of species and functional diversity through multi-scale grid sampling.

2. Materials and Methods

2.1. Overview of the Study Area

The Gurbantunggut Desert (44°11′–46°20′ N, 84°31′–90°00′ E) is located at the centre of the Junggar Basin in Xinjiang and is the largest fixed–semifixed desert in China [32] (Figure 1). The region exhibits a temperate arid desert climate, with average annual precipitation amounts ranging from 70–150 mm, evaporation exceeding 2000 mm, and an aridity index > 10. The landforms are dominated by ridge-like fixed and semifixed dunes, with flat interdune areas, thus forming a composite landscape of sand ridges and interdune terrain [27,33]. The main soil type is aeolian soil, with desert grey-brown soil sporadically distributed in interdune areas [34]. The vegetation comprises mainly hyperxeric and xeric shrubs and subshrubs, with the dominant species including *Haloxylon persicum*, *Haloxylon ammodendron*, and *Calligonum* spp. [35]. The spring layer of ephemeral and quasi-ephemeral plants develops characteristically, resulting in distinct seasonal peaks in biodiversity [31]. This desert habitat is characterized by high heterogeneity and significant spatial fragmentation of vegetation, rendering it an ideal region for studying the multiscale patterns of plant species diversity and functional diversity, as well as their underlying mechanisms [27].

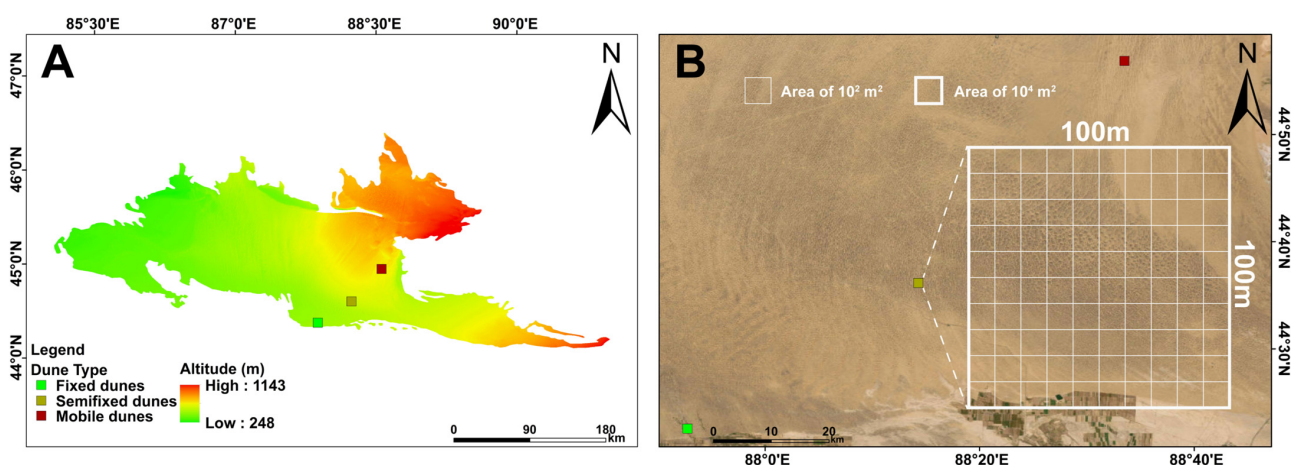


Figure 1. Study area map showing the sampling sites in the Gurbantunggut Desert region. (A) Location of the study area in China; (B) Distribution of the three sampling sites.

2.2. Site Setup

Field surveys were conducted from late April to July 2025 in a representative area of the Gurbantunggut Desert. Building upon long-term monitoring data, a large 1-ha plot was established at each of three fixed sites (Site A: 44°22'34" N, 87°52'45" E; Site B: 44°36'9.6" N, 88°14'17.38" E; C: 44°56'52.01" N, 88°33'29.91" E), with each large plot further subdivided into 100 contiguous 10 m × 10 m units. During the surveys, the species, plant height, crown spread, density, coordinates, and substrate type (fixed, semifixed, or shifting dunes) of all woody and herbaceous plants within each unit were recorded. All the plant samples were identified in the field, and specimens of uncertain identification were collected and re-examined in the laboratory. In this study, a detailed vegetation survey covering a total of 3 ha (comprising 300 10 m × 10 m units) was conducted to reveal the distribution patterns of plant diversity and its environmental drivers across multiple scales.

2.3. Data Processing and Analysis

To systematically reveal the multiscale characteristics of plant diversity in the Gurbantunggut Desert, three representative subscales (based on 1-ha plots and 10 m × 10 m basic units), whose dimensions are divisible by the plot side length, were selected for analysis, namely, 0.01 ha (10 m × 10 m), 0.04 ha (20 m × 20 m), and 0.25 ha (50 m × 50 m).

At each scale, species diversity indices (Shannon–Wiener H' , Simpson D , and Pielou E indices) and functional diversity indices (Rao's quadratic entropy Q and functional evenness $FEve$ indices) were calculated in each plot. To quantify the scale dependence of these patterns, the variance and coefficient of variation of each index were calculated at the different scales, and characteristic scales were identified through curves capturing their variation against the logarithm of the sampling area. Additionally, Pearson's correlation analysis was employed to examine the relationships between species richness and each diversity index, as well as between species diversity and functional diversity indices, and their variation across scales.

The Shannon–Wiener index, Simpson index, Pielou evenness index, Rao's quadratic entropy index, functional evenness index ($FEve$), variance, and coefficient of variation were calculated using standard formulas. Detailed mathematical derivations and variable definitions are provided in Appendix A.

Statistical data analysis was conducted in Microsoft Excel 2021 (Microsoft Corp., Redmond, WA, USA), R version 4.4.3 (R Core Team, Vienna, Austria; <https://www.r-project.org>, accessed on 1 June 2026), Python 3.12.7 (Python Software Foundation, Wilmington, DE, USA; <https://www.python.org>, accessed on 1 June 2026), and PAST 4.17 (University of Oslo, Oslo, Norway; <https://www.nhm.uio.no/english/research/infrastructure/past>, accessed on 1 June 2026). Maps of the spatial distribution patterns were generated using R version 4.4.3 (<https://www.r-project.org>, accessed on 1 June 2026). Pearson's correlation analysis was conducted in SPSS Statistics 27.0.1 (IBM Corp., Armonk, NY, USA; <https://www.ibm.com/spss>, accessed on 1 June 2026). Maps of the spatial variation were created in OriginPro 2024b (OriginLab Corp., Northampton, MA, USA; <https://www.originlab.com>, accessed on 1 June 2026).

To comprehensively characterize the species diversity of the study area, this study selected the Shannon–Wiener index, the Simpson index, and the Pielou evenness index. These three indices assess community structure from different perspectives: the Shannon–Wiener index is more sensitive to rare species and integrates both species richness and evenness [36]; the Simpson index is more sensitive to changes in dominant species, focusing on community dominance [37]; and the Pielou evenness index independently reflects the evenness of species abundance distribution [36]. These three indices complement each other, providing a more complete picture of the multi-scale characteristics of plant diversity in the Gurbantunggut Desert.

The plant functional traits used to calculate functional diversity indices and their corresponding data sources are listed in Table 1.

Table 1. Plant functional traits selected in this study and their data sources.

Traits	Trait Type	Trait State	Data Sources
Plant height	Numerical data	in metres	Field survey
Width	Numerical data	in square metres	Field survey
Life form	Name data	1 Annual herbs; 2 perennial herbs; 3 vines; 4 shrubs; 5 trees	Flora of China
Origin	Name data	1 Native plants; 2 introduced plants; 3 exotic plants; 4 invasive plants	Flora of China
Floristic zone	Name data	1 Global distribution; 2 tropical distribution; 3 temperate distribution; 4 endemic to China	Flora of China
Leaf level	Name data	1 Scale-like leaves (0–0.25 cm ²); 2 microscopic leaves (0.25–2.25 cm ²); 3 Small leaves (2.25–20.25 cm ²); 4 medium leaves (20.25–182.25 cm ²); 5 large leaves (182.25–1642.25 cm ²)	Flora of China
Leaf texture	Name data	1. Papery; 2. herbaceous; 3. leathery; 4. fleshy; 5. membranous	Flora of China
Flower colour	Name data	1. Perianth not distinct; 2. green; 3. white; 4. blue–violet; 5. yellow; 6. red; 7. two or more flower colours	Flora of China
Initial flowering stage	Numerical data	Months when plants begin to bloom, 1–12	Flora of China
Florescence	Numerical data	From the beginning of the flowering period to the end of the flowering period, 1–12	Flora of China
Pollination mode	Name data	1. Wind pollination; 2. insect pollination	Flora of China
Fruit ripening period	Numerical data	Months when plants begin to bear fruit: January–December	Flora of China
Dispersal mode	Name data	1. Autochthonous dispersal; 2. wind dispersal; 3. animal dispersal; 4. water dispersal	Flora of China
Prickly	Name data	1 Yes; 2 no	Flora of China

3. Results

3.1. Composition of Plant Communities in Different Dune Types

Based on vegetation survey data from 300 10 m × 10 m units within three 1-ha plots, the importance values (IV%) of each species in different dune types were calculated, and the results are presented in Table 2. The table shows that the composition of plant communities differs significantly among fixed, semi-fixed and mobile dunes, with each dune type exhibiting a distinct assemblage of dominant species. In fixed dunes, the dominant species are *Corispermum lehmannianum*, *Tamarix chinensis*, *Nitraria tangutorum* and *Euphorbia turczaninowii*; this community is characterised by a mixture of shrubs and herbs, relatively stable structure and high species diversity. In semi-fixed dunes, *Eremopyrum orientale* is the most dominant species, followed by *Bassia dasyphylla*, *Suaeda glauca* and *Haloxylon ammodendron*, with herbaceous plants dominating and reflecting the instability of the semi-fixed dune habitat. In mobile dunes, *H. ammodendron* is the absolute dominant species, accompanied by *Haloxylon persicum*, *Horaninowia ulicina* and *Eremopyrum orientale*; the community has a simple composition and consists mainly of shrubs and herbs that are tolerant to wind erosion and sand burial.

Table 2. Plant species list.

Family	Species	Life Form	Reproduction Mode	IV%		
				Fixed Dunes	Semifixed and Mobile Dunes	Mobile Dunes
Chenopodiaceae	<i>Haloxylon ammodendron</i> (C. A. Mey.) Bunge	Shrub	Seed propagation	7.96	12.65	28.07
	<i>Haloxylon persicum</i> Bunge ex Boiss. & Buhse	Shrub	Seed propagation	9.13	11.28	17.62

Table 2. Cont.

Family	Species	Life Form	Reproduction Mode	IV%		
				Fixed Dunes	Semifixed and Mobile Dunes	Mobile Dunes
Chenopodiaceae	<i>Agriophyllum squarrosum</i> (L.) Moq.	Herb	Seed propagation	2.79	3.84	8.54
	<i>Salsola nitraria</i> Pall.	Herb	Seed propagation	2.08	1.46	8.70
	<i>Salsola paulsenii</i> Litv.	Herb	Seed propagation	5.95	3.32	1.84
	<i>Salsola praecox</i> (Litv.) Iljin	Herb	Seed propagation	2.55	3.47	4.44
	<i>Salsola ruthenica</i> Iljin	Herb	Seed propagation	2.34	1.66	1.86
	<i>Suaeda glauca</i> (Bunge) Bunge	Herb	Seed propagation	5.76	14.09	12.32
	<i>Suaeda microphylla</i> (C. A. Mey.) Pall.	Shrub	Seed propagation	1.30	1.47	0.38
	<i>Horaninowia ulicina</i> Fisch. et Mey.	Herb	Seed propagation	7.06	7.90	16.44
	<i>Petrosimonia sibirica</i> (Pall.) Bunge	Herb	Seed propagation	1.17	0.56	2.85
	<i>Chenopodium glaucum</i> L.	Herb	Seed propagation	0.74	0.14	0.54
	<i>Kochia odontoptera</i> Schrenk	Herb	Seed propagation	0.86	-	-
	<i>Kochia iranica</i> (Moq.) Bornm.	Herb	Seed propagation	1.46	1.91	0.37
	<i>Ceratocarpus arenarius</i> L.	Herb	Seed propagation	1.73	2.24	11.25
	<i>Atriplex dimorphostegia</i> Kar. & Kir.	Herb	Seed propagation	0.84	1.48	1.67
	<i>Bassia dasyphylla</i> (Fisch. & C. A. Mey.) Kuntze	Herb	Seed propagation	3.81	14.45	2.04
Asteraceae	<i>Corispermum lehmannianum</i> Bunge	Herb	Seed propagation	26.17	5.03	12.81
	<i>Anabasis aphylla</i> L.	Shrub	Seed propagation	-	-	0.11
	<i>Seriphidium terrae-albae</i> (Krasch.) Poljakov	Herb	Seed propagation	1.38	7.56	5.13
	<i>Amberboa turanica</i> Iljin	Herb	Seed propagation	2.93	8.07	2.38
	<i>Echinops sphaerocephalus</i> L.	Herb	Seed propagation/root cutting	1.07	0.13	0.85
	<i>Hyalea pulchella</i> (Ledeb.) K. Koch	Herb	Seed propagation	1.28	0.69	2.34
	<i>Chondrilla ambigua</i> Fisch. ex Kar. & Kir.	Herb	Seed propagation	-	0.73	1.24
	<i>Artemisia desertorum</i> Spreng.	Herb	Seed propagation	1.01	1.37	0.97
	<i>Tragopogon ruber</i> S. G. Gmel.	Herb	Seed propagation	1.10	-	-
	<i>Scorzonera pusilla</i> Pall.	Herb	Seed propagation	-	-	0.37
	<i>Carlina biebersteinii</i> Bernh. ex Hornem.	Herb	Seed propagation	0.89	1.88	0.00
Brassicaceae	<i>Malcolmia scorpioides</i> (Bunge) Boiss.	Herb	Seed propagation	0.61	0.11	0.42
	<i>Malcolmia africana</i> (L.) R. Br.	Herb	Seed propagation	0.84	0.44	0.89
	<i>Isatis violascens</i> Bunge	Herb	Seed propagation	1.17	0.13	0.33
	<i>Isatis minima</i> Bunge	Herb	Seed propagation	0.68	-	-
	<i>Alyssum desertorum</i> Stapf	Herb	Seed propagation	-	0.31	0.44
	<i>Alyssum linifolium</i> Stephan ex Willd.	Herb	Seed propagation	15.74	0.28	-
	<i>Matthiola stoddarti</i> Bunge	Herb	Seed propagation	0.61	0.10	-
	<i>Goldbachia laevigata</i> (M. Bieb.) DC.	Herb	Seed propagation	1.57	-	-
Fabaceae	<i>Tetracme recurvata</i> Bunge	Herb	Seed propagation	3.86	3.12	2.13
	<i>Astragalus oxyglottis</i> Steven	Herb	Seed propagation	1.09	0.43	0.48
	<i>Astragalus cognatus</i> C. A. Mey.	Shrub	Seed propagation	-	0.75	-
	<i>Astragalus flexus</i> Fisch.	Herb	Seed propagation	3.49	-	-
	<i>Astragalus arpilobus</i> Kar. & Kir.	Herb	Seed propagation	-	-	0.27
	<i>Eremosparton songoricum</i> (Litv.) Vassilcz.	Herb	Seed propagation	0.90	-	0.25
	<i>Alhagi sparsifolia</i> Shap.	Herb	Seed propagation/root suckering	2.49	7.83	7.68
Poaceae	<i>Bromus tectorum</i> L.	Herb	Seed propagation	3.76	0.61	-
	<i>Schismus arabicus</i> Nees	Herb	Seed propagation	1.93	-	0.11
	<i>Stipagrostis pennata</i> (Trin.) De Winter	Herb	Seed propagation	1.33	-	0.45
	<i>Eremopyrum orientale</i> (L.) Jaubert & Spach	Herb	Seed propagation	6.73	29.36	14.99
Boraginaceae	<i>Lepechiniella lasiocarpa</i> W. T. Wang	Herb	Seed propagation	5.14	3.51	3.19
	<i>Arnebia decumbens</i> (Vent.) Coss. & Kralik	Herb	Seed propagation	6.21	0.20	2.49
	<i>Heliotropium acutiflorum</i> Kar. & Kir.	Herb	Seed propagation	0.79	0.05	-
	<i>Heliotropium ellipticum</i> Ledeb.	Herb	Seed propagation	0.91	-	-
Lamiaceae	<i>Chamaesphacos ilicifolius</i> Schrenk ex Fisch. & C. A. Mey.	Herb	Seed propagation	1.06	-	-
	<i>Nepeta micrantha</i> Bunge	Herb	Seed propagation	0.64	-	-
Caryophyllaceae	<i>Silene olgiana</i> B. Fedtsch.	Herb	Seed propagation	0.91	0.05	0.11
Liliaceae	<i>Gagea divaricata</i> Regel	Herb	Seed propagation/bulb propagation	0.60	0.18	-
	<i>Eremurus inderiensis</i> (Steven) Regel	Herb	Seed propagation/division	0.66	0.66	2.35
	<i>Eremurus anisopterus</i> (Kar. & Kir.) Regel	Herb	Seed propagation/division	1.07	-	1.24
	<i>Allium polyrhizum</i> Turcz. ex Regel	Herb	Seed propagation/division	1.62	0.34	-

Table 2. Cont.

Family	Species	Life Form	Reproduction Mode	IV%		
				Fixed Dunes	Semifixed and Mobile Dunes	Mobile Dunes
Tamaricaceae	<i>Tamarix chinensis</i> Lour.	Shrub	Seed propagation/cutting	23.25	4.29	8.34
	<i>Reaumuria songarica</i> (Pall.) Maxim.	Shrub	Asexual reproduction/seed propagation	0.84	0.89	-
Zygophyllaceae	<i>Nitraria tangutorum</i> Bobrov	Shrub	Seed propagation	16.82	1.87	1.02
Euphorbiaceae	<i>Euphorbia turczaninowii</i> Kar. & Kir.	Herb	Seed propagation	13.28	-	0.16
	<i>Chrozophora sabulosa</i> Kar. & Kir.	Herb	Seed propagation	1.32	-	1.61
Polygonaceae	<i>Atraphaxis pungens</i> (M. Bieb.) Jaub. & Spach	Shrub	Seed propagation	1.05	0.05	-
	<i>Calligonum junceum</i> (Fisch. & C. A. Mey.) Litv.	Shrub	Seed propagation	0.90	0.35	0.96
	<i>Calligonum leucocladum</i> (Schrenk) Bunge	Shrub	Seed propagation/layering	3.71	2.17	2.97
Papaveraceae	<i>Hypecoum parviflorum</i> Kar. & Kir.	Herb	Seed propagation	-	-	0.28
Iridaceae	<i>Iris tenuifolia</i> Pall.	Herb	Seed propagation/division	7.65	-	-
Plumbaginaceae	<i>Limonium sinense</i> (Girard) Kuntze	Herb	Seed propagation	2.16	0.44	0.31
Plantaginaceae	<i>Plantago minuta</i> Pall.	Herb	Seed propagation	1.62	0.97	3.42
Orobanchaceae	<i>Orobanche coerulescens</i> Steph.	Herb	Seed propagation	1.19	0.38	-

3.2. Spatial Distribution of Plant Species Diversity and Functional Diversity Indices in the Gurbantunggut Desert

Among the three dune types, both the plant species diversity and functional diversity indices exhibited significant spatial variation, and their patterns changed with scale (Figure 2). Overall, the distribution patterns of the Shannon–Wiener and Pielou indices were similar, revealing an increasing trend with increasing scale, whereas the pattern of the Simpson index differed. The distributions of the two functional diversity indices (Rao’s quadratic entropy index and the functional evenness index) also exhibited distinct characteristics.

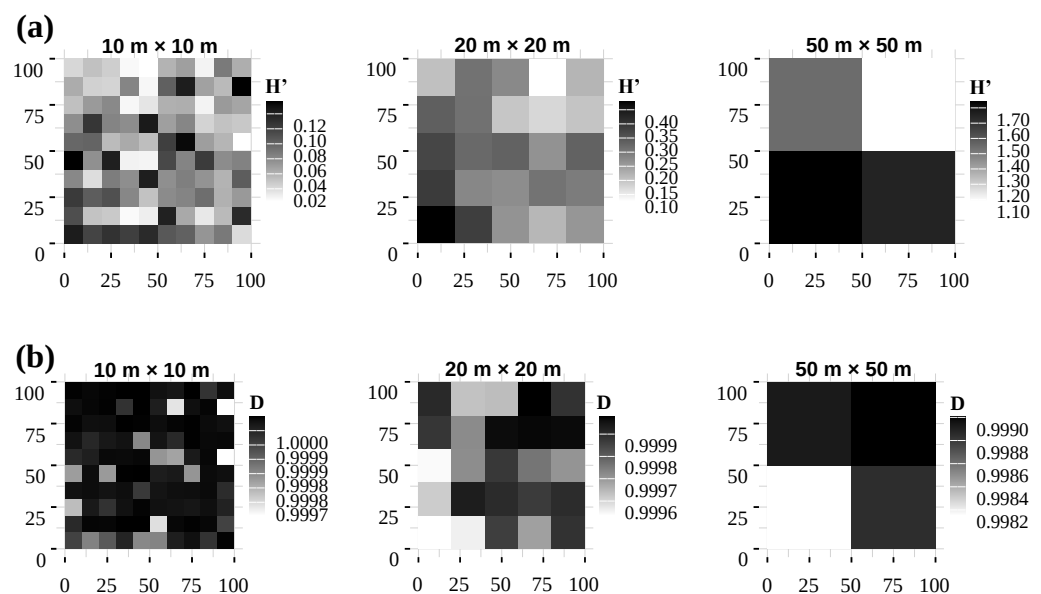


Figure 2. Cont.

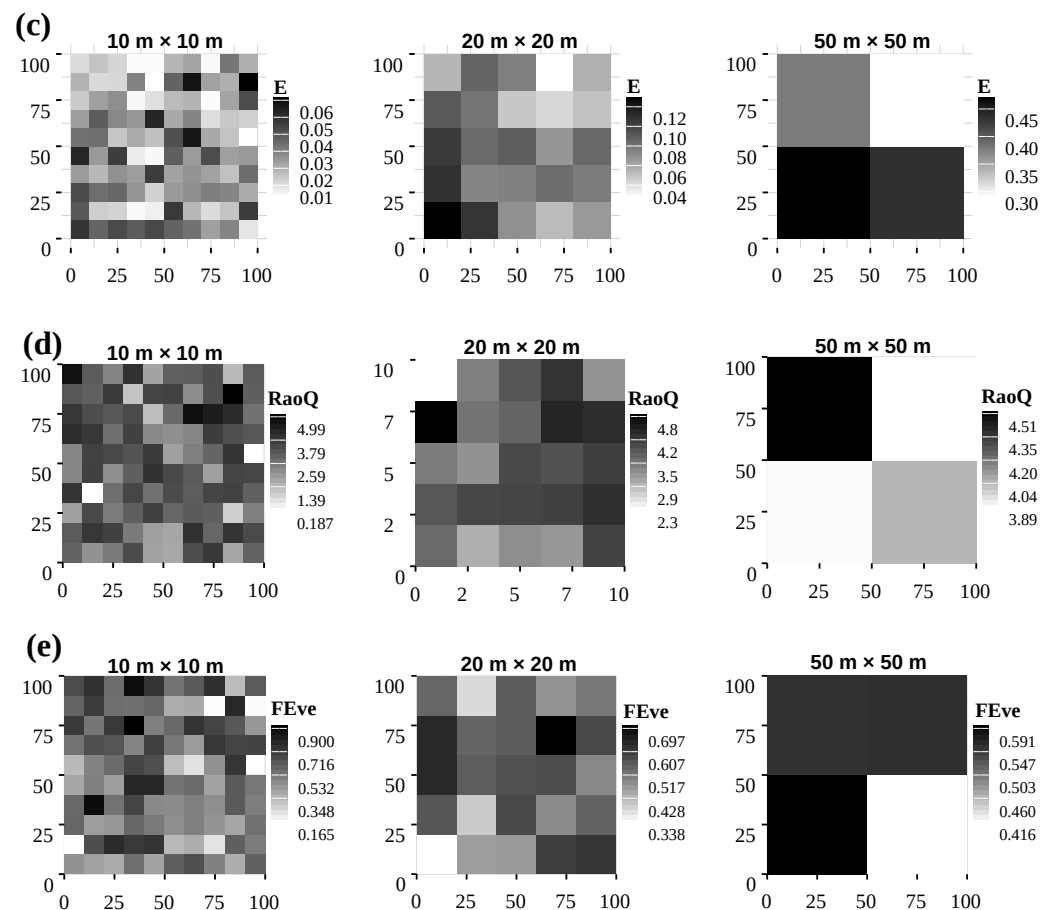


Figure 2. Spatial distributions of (a) Shannon–Wiener index (H'), (b) Simpson's diversity index (D), (c) Pielou's evenness index (E), (d) Rao's quadratic entropy ($RaoQ$), and (e) functional evenness index ($FEve$) within fixed dunes at the three sampling scales (10 m × 10 m, 20 m × 20 m, and 50 m × 50 m). The color gradient from white to black represents increasing index values.

Choosing fixed dunes as an example, the Shannon–Wiener and Pielou index values were higher on the southern side than on the northern side at the small scale (10 m × 10 m), while at the medium and large scales (20 m × 20 m and 50 m × 50 m), the index values were highest in the southwest, with generally higher index values in the southern region than in the northern region. The pattern of the Simpson index values was the opposite: at the small scale, the values on the northern side were higher than those on the southern side, whereas at the medium and large scales, the values in the northeast were highest. The functional diversity index values revealed no significant regional differentiation at the small and medium scales. At the large scale, the values of Rao's quadratic entropy index were highest in the northwest and lowest in the northeast, whereas the functional evenness index values were highest in the southwest and lowest in the southeast.

In semifixed dunes (Figure 3), the diversity pattern also significantly depended on the scale. The Shannon–Wiener and Pielou index values indicated an east-high–west-low pattern at the 10 m × 10 m scale. This differentiation weakened with increasing scale, with the highest index values observed in the northeast and southwest at the 50 m × 50 m scale. The Simpson index values, however, shifted from a pattern encompassing higher values in the west and lower values in the east at the small scale to a pattern encompassing the highest values in the northwest at the large scale. With respect to functional diversity, the Rao quadratic entropy index values indicated limited variation at the small and medium scales, but at the large scale, the values were higher in the west than in the east (with the highest values observed in the northwest). Moreover, the functional evenness index values,

in the north and south gradually increased with increasing scale. These differences indicate that large-scale divisions tend to reduce the local heterogeneity observed at smaller scales.

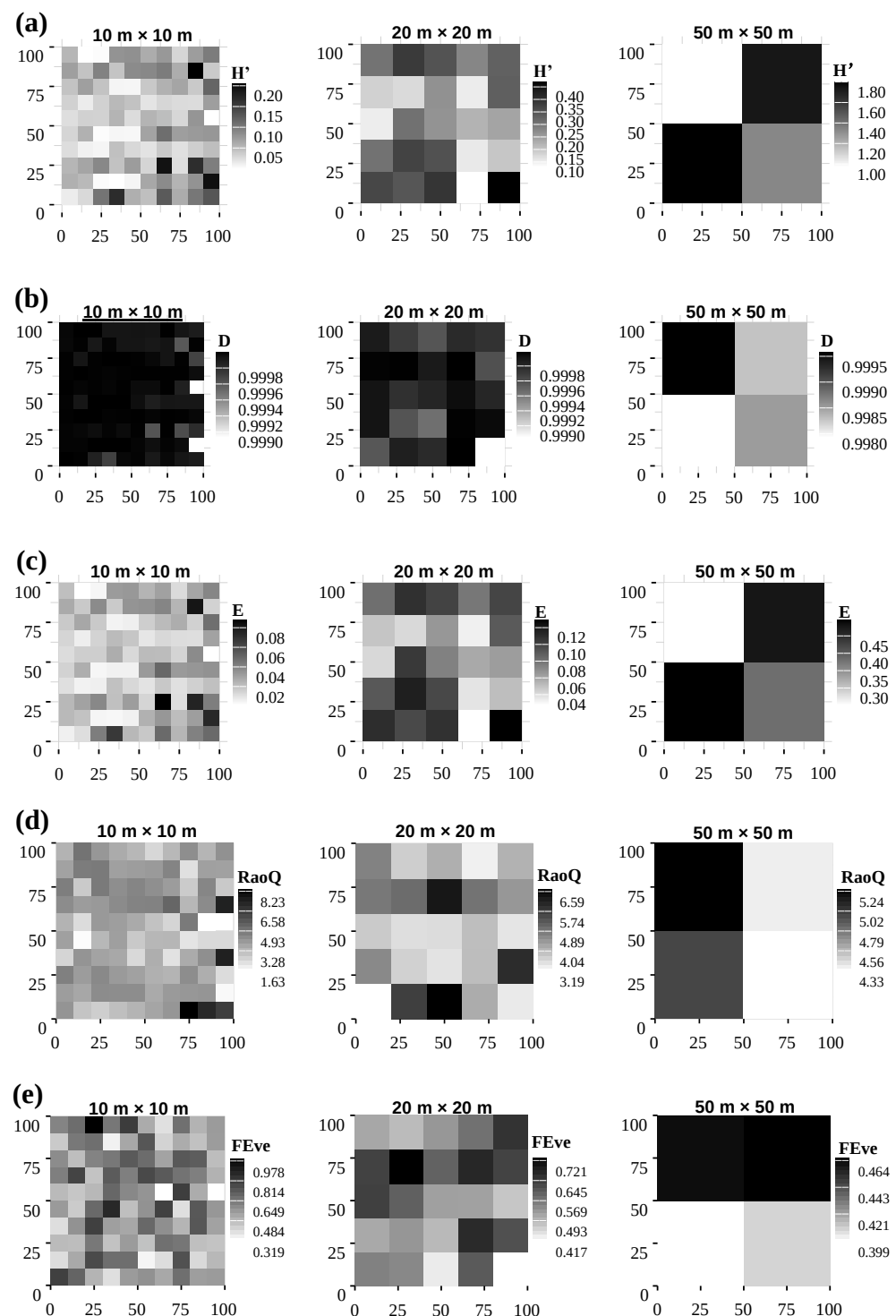


Figure 3. Spatial distributions of (a) Shannon–Wiener index (H'), (b) Simpson's diversity index (D), (c) Pielou's evenness index (E), (d) Rao's quadratic entropy ($RaoQ$), and (e) functional evenness index ($FEve$) within semifixed dunes at the three sampling scales (10 m × 10 m, 20 m × 20 m, and 50 m × 50 m). The color gradient from white to black represents increasing index values.

In shifting sand dunes, biodiversity patterns exhibited unstable and discontinuous characteristics across the different scales (Figure 4). With respect to species diversity, the Shannon–Wiener and Pielou index values were higher in the east and lower in the west at

the small scale. At the medium scale, high values occurred only in the southwest, while at the large scale, values in the southwest were consistently the highest, followed by those in the northeast. The Simpson index values did not significantly vary at the small and medium scales, whereas at the large scale, the values were highest in the northwest. The functional diversity index values exhibited no obvious regional differentiation at the small and medium scales. However, at the large scale, the Rao index values were highest in the southeast and lowest in the northwest, whereas the functional evenness index values were highest in the northeast and southwest and lowest in the southeast.

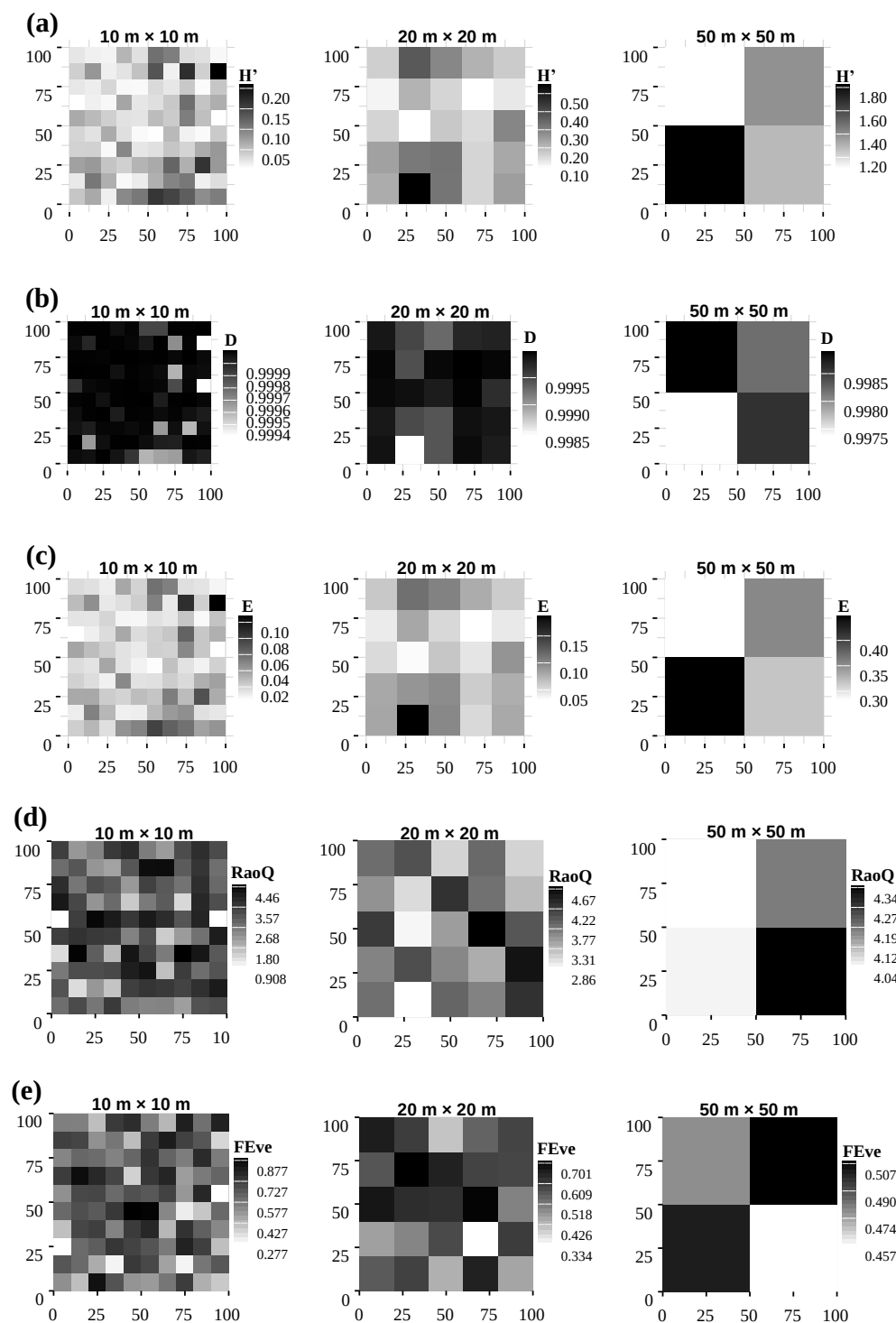


Figure 4. Spatial distributions of (a) Shannon–Wiener index (H'), (b) Simpson's diversity index (D), (c) Pielou's evenness index (E), (d) Rao's quadratic entropy ($RaoQ$), and (e) functional evenness index

(FEve) within mobile dunes at the three sampling scales (10 m × 10 m, 20 m × 20 m, and 50 m × 50 m). The color gradient from white to black represents increasing index values.

3.3. Patterns of the Spatial Variations in Species Diversity and Functional Diversity Indices Across Different Scales

Across all the dune types, the spatial variability (variance and coefficient of variation) in all the diversity indices monotonically decreased with increasing scale. However, the specific change patterns varied depending on the diversity index and dune type (Figures 5–7). Adopting fixed dunes as an example (Figure 5), the Shannon–Wiener and Pielou index values first gradually decreased but then rapidly decreased from the 10 m × 10 m scale to the 20 m × 20 m scale. In contrast, the Simpson index and functional evenness index values decreased at nearly constant rates, whereas the values of Rao’s quadratic entropy index decreased rapidly at the small and medium scales before they stabilized. Overall, the species diversity indices can be ranked as follows: Shannon–Wiener > Pielou > Simpson. With respect to the functional diversity indices, the variance indicated the order of functional evenness > Rao’s quadratic entropy. Notably, the coefficient of variation of Rao’s quadratic entropy index was higher at the small scale, while at larger scales, the coefficient of variation of the functional evenness index was higher.

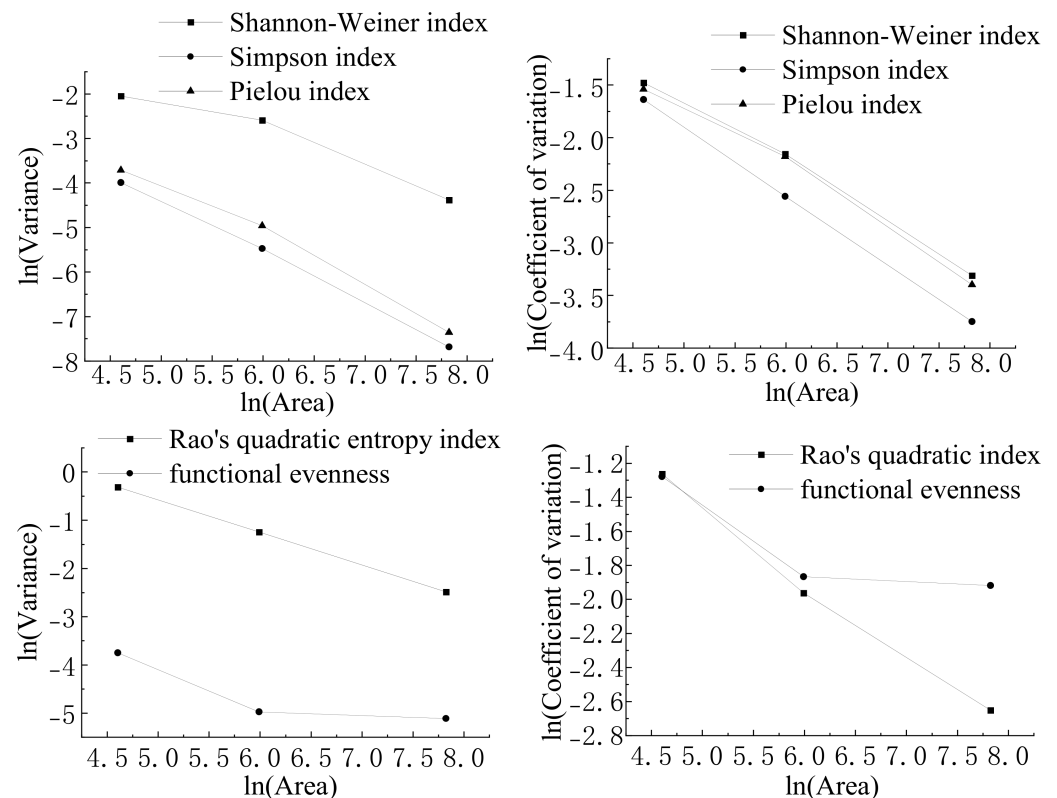


Figure 5. Spatial variation in diversity indices within fixed dunes.

In semifixed dunes (Figure 6), the variance and coefficient of variation of each index decreased with increasing scale, but the patterns differed. The variance in the Shannon–Wiener index values decreased gradually before the decrease rate accelerated slightly, while the coefficient of variation decreased rapidly at the small and medium scales before it stabilized. In contrast, the Simpson and Pielou index values decreased at nearly constant rates. The trends in the two functional diversity indices were similar: the values of Rao’s quadratic entropy index decreased slowly at the small and medium scales before the decrease rate increased, whereas the functional evenness index values gradually decreased

overall. Moreover, the decrease rate of the variance in Rao's quadratic entropy index was generally lower than that of its coefficient of variation. The order of the species diversity indices was Shannon–Wiener > Pielou > Simpson, while that of the functional diversity indices was Rao's quadratic entropy > functional evenness.

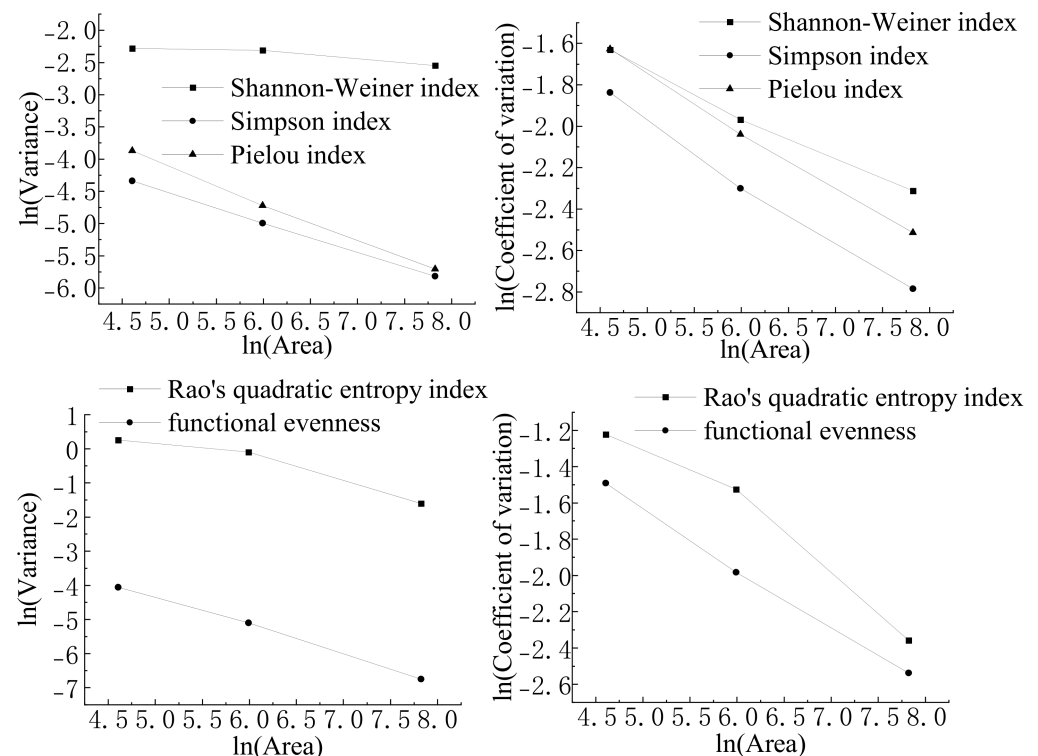


Figure 6. Spatial variation in diversity indices within semifixed dunes.

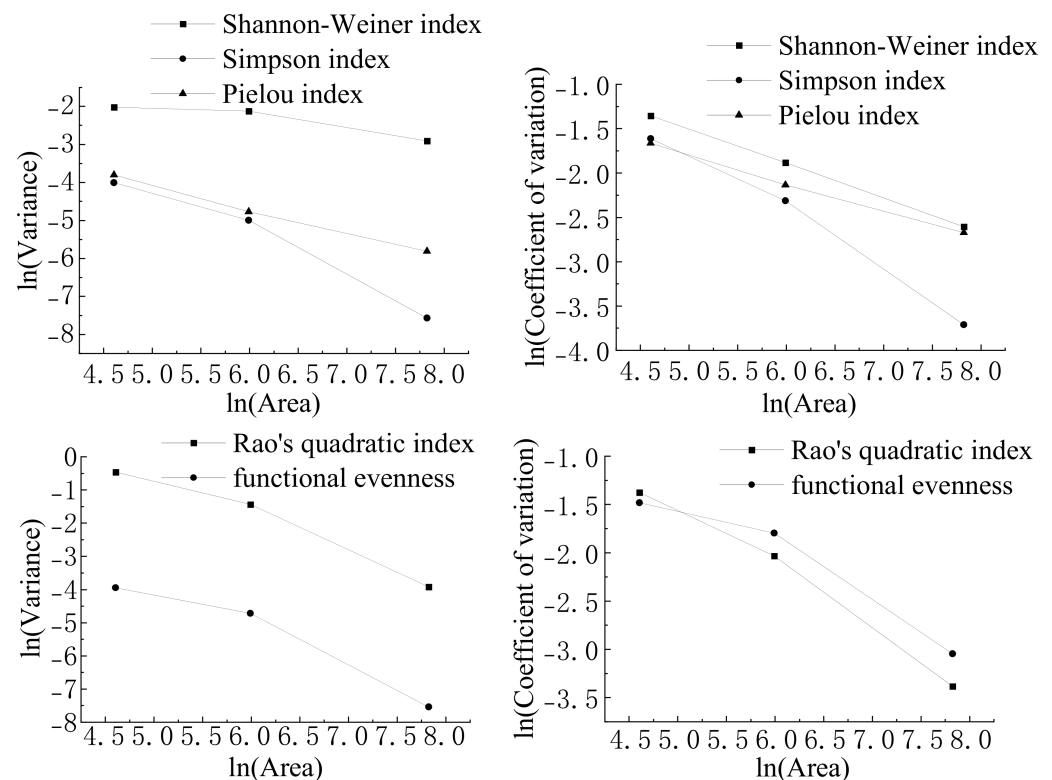


Figure 7. Spatial variation in diversity indices within mobile dunes.

In shifting dunes (Figure 7), the variance and coefficient of variation of each index also decreased with increasing scale. The Simpson index values decreased gradually at the small and medium scales before decreasing sharply, whereas the Pielou index values decreased at a nearly constant rate. The variance in the Shannon–Wiener index values decreased slowly at the small and medium scales before rapidly decreasing, whereas the coefficient of variation decreased at a constant rate. The values of both functional diversity indices first gradually decreased and then rapidly decreased. The variance in species diversity indices can be ranked as follows: Shannon–Wiener > Pielou > Simpson. At the small scale, the coefficients of variation indicated the order of Shannon–Wiener > Simpson > Pielou, while at larger scales, the order was Shannon–Wiener > Pielou > Simpson. With respect to functional diversity, the variance indicated the order of Rao’s quadratic entropy > functional evenness. Notably, the coefficient of variation was greater for Rao’s quadratic entropy index at the small scale, whereas that of the functional evenness index was greater at the other scales.

3.4. Influences of Species Richness on Species Diversity and Functional Diversity

The relationships between species richness and diversity indices clearly depended on the scale (Figures 8 and 9). At the small and medium scales (10×10 m and 20×20 m, respectively), the Shannon–Wiener and Rao’s quadratic entropy indices were strongly positively correlated with species richness ($p < 0.01$), whereas the functional evenness index was strongly negatively correlated with species richness at the 10×10 m scale ($p < 0.01$) and significantly negatively correlated at the 20×20 m scale ($p < 0.05$). The Simpson index was highly significantly positively correlated with species richness only at the 10×10 m scale ($p < 0.01$), while the Pielou index was highly significantly negatively correlated with species richness at the same scale ($p < 0.01$). None of the indices revealed significant correlations at the 50×50 m scale.

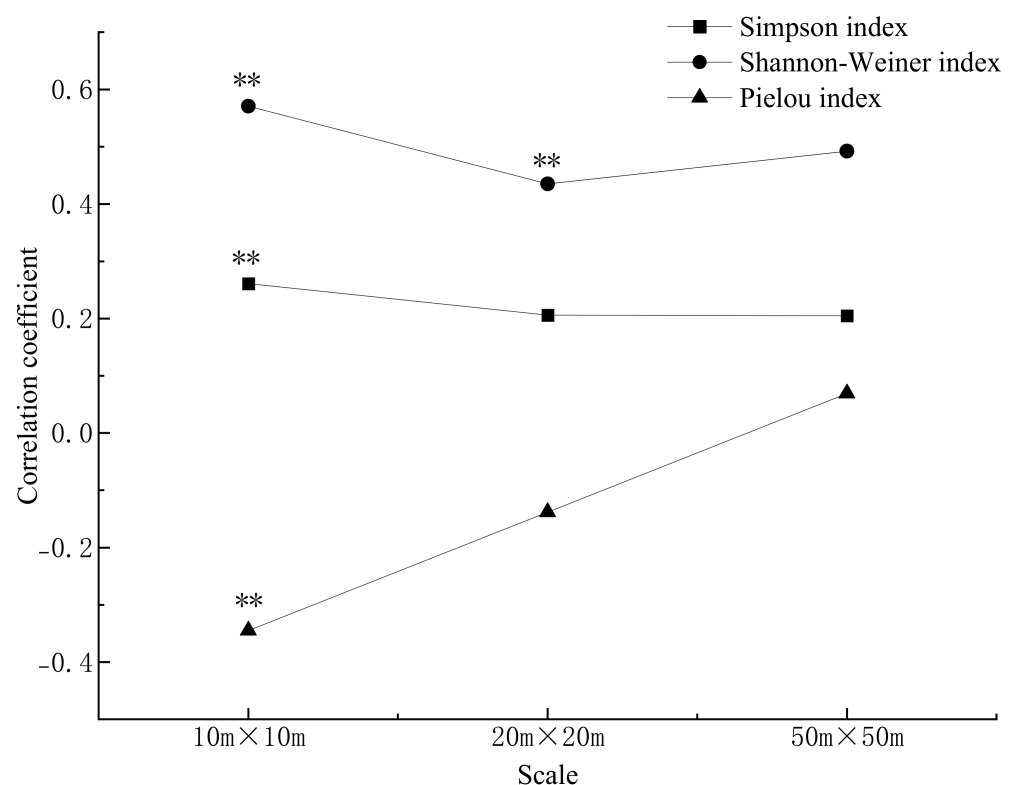


Figure 8. Correlation analysis between species richness and species diversity indices. ** indicates significant correlation at the 0.01 level.

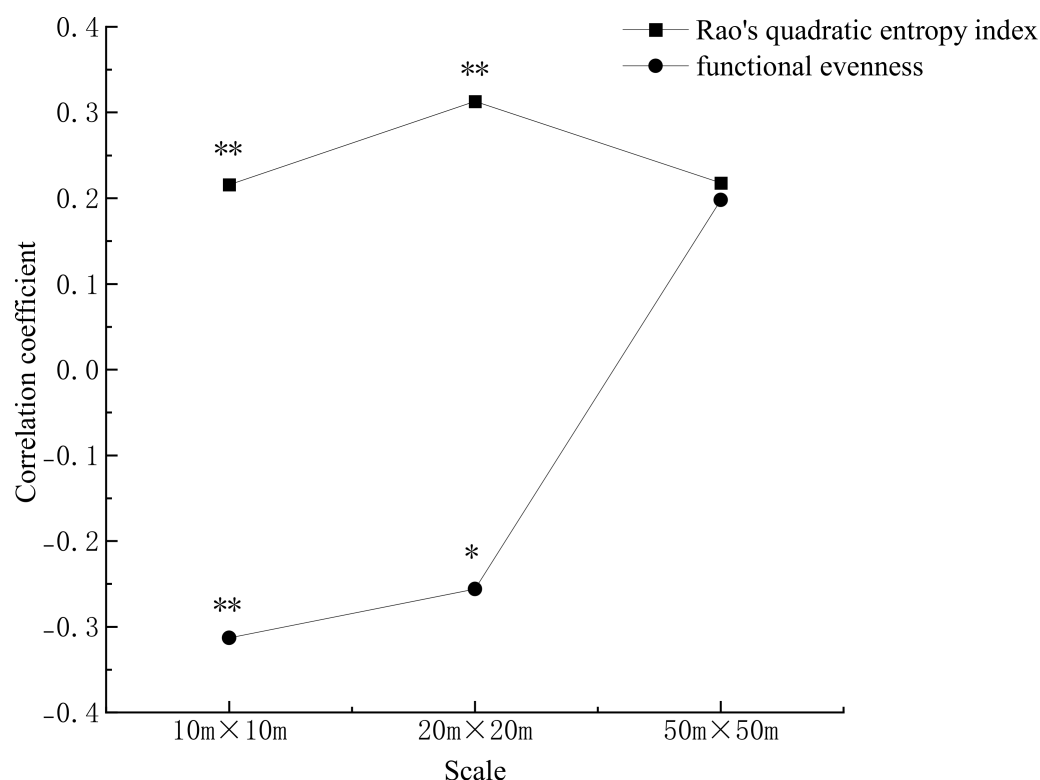


Figure 9. Correlation analysis between species richness and functional diversity indices. ** indicates significant correlation at the 0.01 level; * indicates significant correlation at the 0.05 level.

3.5. Pearson's Correlation Analysis of Species Diversity and Functional Diversity

The results of Pearson's correlation analysis indicated that the correlations between species and functional diversity indices varied significantly across scales (Table 3). At the small and medium scales (10 m × 10 m and 20 m × 20 m, respectively), all three species diversity indices were strongly positively correlated with Rao's quadratic entropy index ($p < 0.01$), whereas at the large scale (50 m × 50 m), none were significantly correlated. The correlations with the functional evenness index were generally weak: only the Simpson and Pielou indices were significantly positively correlated with the functional evenness index at the 10 m × 10 m scale ($p < 0.01$), whereas the Shannon–Wiener index was not significantly correlated with the functional evenness index at any scale.

Table 3. Results of Pearson correlation analysis between species diversity indices and functional diversity indices.

Scale		10 m × 10 m	20 m × 20 m	50 m × 50 m
Shannon–Wiener index and Rao's quadratic entropy index	Correlation coefficient	0.603 **	0.588 **	0.065
	<i>p</i>	<0.01	<0.01	0.84
Shannon–Wiener index and functional evenness index	Correlation coefficient	0.096	0.013	0.282
	<i>p</i>	0.096	0.91	0.375
Simpson index and Rao's quadratic entropy index	Correlation coefficient	0.658 **	0.560 **	0.114
	<i>p</i>	<0.01	<0.01	0.724
Simpson index and functional evenness index	Correlation coefficient	0.173 **	−0.056	0.106
	<i>p</i>	0.003	0.636	0.744

Table 3. Cont.

Scale		10 m × 10 m	20 m × 20 m	50 m × 50 m
Pielou evenness index and Rao's quadratic entropy index	Correlation coefficient	0.485 **	0.464 **	−0.048
	<i>p</i>	<0.01	<0.01	0.881
Pielou evenness index and functional evenness index	Correlation coefficient	0.426 **	0.154	0.198
	<i>p</i>	<0.01	0.188	0.537

** indicates significant correlation at the 0.01 level.

4. Discussion

This study revealed that the pattern of plant diversity in the Gurbantunggut Desert significantly depends on scale. Within fixed dunes, areas of high Simpson's index values exhibited a spatially complementary distribution with those of high Shannon–Wiener and Pielou index values. These findings are consistent with results from the Aibi Lake Basin [13] and the southeastern margin of the Tengger Desert [38], suggesting that this pattern is likely the result of the combined effect of dispersal limitation and competitive exclusion. At small scales, the “fertilizer island effect” formed by shrubs leads to significant nutrient-enriched patches [39,40]; the number and spatial arrangement of these habitat patches have an important impact on diversity per unit area [41]. Differences in patch characteristics among dominant species (e.g., *Corispermum lehmannianum*, *Tamarix chinensis*, and *Haloxylon ammodendron* in Table 2) [42,43] may be one of the important reasons why the scale effects of diversity patterns vary among different dune types.

All metrics of the spatial variations in the diversity indices (variance and coefficient of variation) monotonically decreased with increasing scale. At small scales, the fertile island effect and microtopographic variations create significant resource heterogeneity [39,40], resulting in the greatest variation in diversity; with increasing scale, local variations are averaged, and the influence of regional environmental factors (such as the soil pH, total nitrogen, and organic matter) becomes dominant [44]. This finding indicates that the dominant ecological processes shift from local stochastic processes to regional environmental filtering processes. It should be noted that the present study used 10 m × 10 m as the smallest sampling unit. This choice is based on the sparse vegetation of the Gurbantunggut Desert and existing research consensus [28,35,45]: this scale can effectively capture representative species composition and lies within the strongest scale-dependent range (<100 m²) for desert plant diversity [41]. Furthermore, when assigning species occurring on plot boundaries, we adopted the “centroid principle” (determining the grid membership of each plant based on the position of its main stem or the geometric centre of its dominant ramet) to minimize the influence of edge effects on diversity index calculations [46].

At the small and medium scales, species richness was negatively correlated with the functional evenness index but positively correlated with Rao's quadratic entropy index, indicating that an increase in species does not yield a more even distribution of functional traits but rather exacerbates aggregation while simultaneously increasing functional differences among species. This mechanism reflects how, at small scales, environmental filtering and competitive exclusion jointly yield species assemblages that are functionally similar yet distinctly differentiated. Studies of the aridity gradient in northern China have indicated that intense competitive exclusion constitutes a key mechanism driving community functional homogenization [47], while local research has confirmed that soil moisture is a critical limiting factor [19]. Consequently, at small scales, a pattern of clustered differentiation emerges, which is jointly shaped by competition and dispersal limitation, whereas at large

scales, regional environmental filtering becomes the dominant factor, which is manifested as functional spatial convergence and species convergence.

In summary, the spatial patterns of plant diversity in the Gurbantunggut Desert stem from systematic shifts in ecological processes across different scales: at the local scale, biological interactions and stochastic processes dominate, yielding tightly coupled diversity and high variability; at the regional scale, abiotic environmental filtering predominates, causing diversity relationships to become decoupled and variability to decrease monotonically. This multiscale process transition mechanism is consistent with scenario niche theory, in which the constraints of biological interactions are considered local-scale processes and regional environmental filtering is identified as the key factor shaping functional ranges [48]. The innovation of this study lies in being the first to reveal the scale-effect patterns of species and functional diversity and the underlying process-shift mechanism in this desert system. However, several limitations should be acknowledged: heterogeneity indicators such as the number of habitat patches were not quantitatively included [41]; the treatment of edge effects was simplified (e.g., no buffer-zone correction was applied [46]); and the environmental drivers of diversity change were only preliminarily explored. These limitations do not affect the main conclusions of this study. Future research should further integrate heterogeneity indicators and adopt more refined spatial analysis methods. Clarifying this scale dependency provides important guidance for monitoring desert biodiversity and formulating multiscale conservation strategies.

The results of this study can also be interpreted from the perspective of biodiversity loss. Based on the power-law species–area relationship $S = cA^z$, when habitat area is reduced, the proportion of species loss can be estimated as $(1 - A_{\text{remaining}}^z)$. He et al. [41] found that in the desert region of northwest China, the z -value is as high as 0.37 at small scales ($<100 \text{ m}^2$), but decreases to 0.0396 at scales larger than 100 m^2 . Applying this parameter to the three scales in this study: if one $10 \text{ m} \times 10 \text{ m}$ (100 m^2) quadrat is lost, the expected number of species lost is relatively high because this scale falls within the highest z -value range; if a $50 \text{ m} \times 50 \text{ m}$ (2500 m^2) quadrat of the same total area is lost, the number of species lost per unit area is much lower because the z -value has already decreased substantially. In other words, the loss of small-scale patches has a much greater impact on species diversity than the loss of the same total area of large-scale patches.

This scale effect has important conservation implications. The probability of losing multiple species simultaneously from a single $50 \text{ m} \times 50 \text{ m}$ large plot is actually lower than the risk of losing some species from multiple scattered $10 \text{ m} \times 10 \text{ m}$ small plots. In a highly heterogeneous desert landscape, species spatial distributions tend to be aggregated and patchy [27]; small-scale patches harbour more edge habitats and rare species, making them more sensitive to disturbance [45]. From a biodiversity conservation perspective, the smallest-scale ($10 \text{ m} \times 10 \text{ m}$) diversity indicators are the most sensitive and best reflect the immediate impact of habitat loss on species composition. This also implies that in desert ecosystem conservation practice, priority should be given to maintaining the integrity of small-scale habitat patches, rather than focusing only on large-scale landscape connectivity.

5. Conclusions

The multiscale patterns of plant diversity in the Gurbantunggut Desert reflect the variation in the relationship between species diversity and functional diversity with observation scale. This study revealed that the relationships between species richness and diversity indices and functional diversity indices exhibit a distinct scale effect: they were significantly correlated at the small and medium scales but were decoupled at the large scale. Concurrently, the spatial variation in diversity monotonically decreased with increasing scale, indicating that cross-scale environmental filtering serves as the core driver

shaping desert diversity patterns. These results collectively confirm that the assembly of desert communities is driven by the synergy among multiple processes: at small scales, the community assembly is influenced primarily by the combined effect of dispersal limitation and competitive exclusion, whereas at large scales, environmental filtering becomes the dominant factor, thus reflecting the cross-scale interaction between deterministic and stochastic processes. In summary, an integrated multiscale research framework encompassing both species and functional dimensions holds significant value for elucidating the maintenance mechanisms of desert ecosystems and provides a theoretical basis for scale-based management of biodiversity conservation and restoration in arid regions.

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Appendix A

Mathematical Details of Indicator Calculations

This appendix provides the mathematical formulas for the species diversity indices [49], functional diversity indices [50,51], and spatial variation metrics used in the main text.

Appendix A.1. Species Diversity Indices

The Shannon–Wiener index is calculated as:

$$H = -\sum_{i=1}^S (P_i \ln P_i) \quad (A1)$$

where S is the number of species in a plot, and P_i is the proportion of the abundance of the i -th species relative to the total abundance.

The Simpson index is calculated as:

$$D = 1 - \sum_{i=1}^S P_i^2 \quad (A2)$$

where S and P_i are as defined above.

The Pielou evenness index is calculated as:

$$E = H / \ln(S) \quad (A3)$$

where H is the Shannon–Wiener index, and S is the number of species.

Appendix A.2. Functional Diversity Indices

Rao's quadratic entropy index is calculated as:

$$\text{Rao, } Q = \sum_{i=1}^s \sum_{j=1}^s d_{ij} P_i P_j \quad (\text{A4})$$

where d_{ij} is the functional trait dissimilarity between species i and j , and P_i and P_j are the relative abundances of species i and j , respectively.

Functional evenness (FEve) is calculated as:

$$\text{FEve} = \frac{\sum_{i=1}^{s-1} \min\left(\text{PEW}_i \times \frac{1}{s-1}\right) - \frac{1}{s-1}}{1 - \frac{1}{s-1}} \quad (\text{A5})$$

where PEW_i is the weighted evenness of species i , and S is the number of species.

Appendix A.3. Spatial Variation Metrics

Variance is calculated as:

$$\delta^2 = \left(\sum_{j=1}^n (x_j - \mu)^2 \right) / (n - 1) \quad (\text{A6})$$

where n is the total number of plots, x_j is the value of the diversity index for the j -th plot, and μ is the mean value across all plots.

Coefficient of variation is calculated as:

$$\text{CV} = (\text{sd} / \mu) \times 100\% \quad (\text{A7})$$

where sd is the standard deviation, and μ is the mean value across all plots.

Appendix A.4. Variables

S : Number of species in a plot.

P_i : Relative abundance of the i -th species (abundance of species i divided by total abundance across all species in the plot).

d_{ij} : Functional trait dissimilarity between species i and j .

PEW_i : Weighted evenness of species i .

n : Total number of plots.

x_j : Value of the diversity index for the j -th plot.

μ : Mean value across all plots.

sd : Standard deviation across all plots.

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