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The Influence of Intraspecific Trait Variation on Plant Functional Diversity and Community Assembly Processes in an Arid Desert Region of Northwest China

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Abstract: Exploring how functional traits vary along environmental gradients has long been one of the central questions of trait-based community ecology. Variation in functional traits includes both intraspecific trait variation (ITV) and interspecific trait variation (V_{inter}); however, the effects of ITV on functional diversity and community assembly remain to be explored. In this study, we compared functional diversity among three communities (i.e., riverbank, transition zone, and desert margin communities) at three spatial scales (i.e., 10 m × 10 m, 20 m × 20 m, and 50 m × 50 m) in the desert ecosystem of the Ebinur Lake basin in Xinjiang. We also analyzed the effects of ITV and environmental and spatial factors on functional diversity. Our results showed that incorporating ITV increased measurements of functional richness at the 10 m × 10 m scale in all three communities ($p < 0.01$). Rao's quadratic entropy (RaoQ) represents the differences in functional traits between different species. ITV significantly increased RaoQ at the 50 m × 50 m scale in the riverbank and desert margin community, whereas it significantly decreased RaoQ in the transitional zone community. Similarly, ITV significantly increased functional β -diversity at the 10 m × 10 m and 20 m × 20 m scales in the transitional zone community. Spatial factors mainly influenced functional diversity at smaller scales, whereas environmental factors were influential mainly at larger scales. After considering ITV, spatial factors had less of an effect on functional β -diversity, except for the 50 m × 50 m scale in the transitional zone and desert margin community, indicating that ITV can reduce the measured effect of dispersal on functional β -diversity. Considering ITV did not change the interpretation of the main ecological processes affecting functional diversity. However, it did change the extent to which environmental filtering and dispersal effects explained functional diversity.

Keywords: functional trait; intraspecific trait variation; functional diversity; community assembly; arid desert region



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1. Introduction

Plant functional traits are a set of core plant attributes closely related to plant colonization, growth, survival, and mortality. They reflect the plant's response and adaptation to the growing environment, effectively linking individual plant characteristics to environmental conditions and influencing ecosystem function [1]. Plant functional traits can vary due to differences in the external environment. By exploring how functional plant traits vary in heterogeneous habitats, we can identify the main ecological processes of different environments [2]. The leaves are the main organ of photosynthesis and plant material production. They are closely related to the plant's resource acquisition capacity and utilization efficiency [3,4]. Leaves are sensitive to environmental changes during plant evolution,

and their traits result from plants' adaptation to habitat heterogeneity and environmental changes [5]. Functional traits in leaves are easier to measure than other plant traits and are one of the main targets of current plant functional trait research.

Variations in plant functional traits within communities include interspecific (V_{inter}) and intraspecific trait variation (ITV). V_{inter} refers to the difference in functional traits between different species. ITV refers to the difference in traits between different individuals within the same species. However, most studies examining community assembly processes and the mechanisms of plant diversity have used the mean values of plant traits to calculate functional diversity. This approach has successfully determined factors leading to variation in community structure and ecosystem function [6–9]. Previous studies have shown that the magnitudes of ITV and V_{inter} in communities are comparable [6]. Furthermore, ITV has been found to account for 25% of the total trait variation within communities and 32% of the total trait variation between communities [10]. However, ecologists have recently become increasingly concerned about considering ITV when measuring functional diversity [11]. Ignoring intraspecific variation may obscure ecological patterns or lead to inaccurate interpretations [12]. Some studies have reported that intraspecific variation accounts for about 10% or even more than 50% of the total variation in some important functional traits [10,13]. Hulshof et al. (2013) found that ITV was greater than V_{inter} in specific leaf areas at low latitudes [14]. Considering ITV during secondary succession in semi-arid forest ecosystems may lead to higher values of functional α -diversity, while not significantly affecting the main process of forest succession. However, its consideration in top communities led to a divergence in the structure of the community's functional traits [15]. By contrast, Niu et al. showed that the importance of ITV in plant communities increased with environmental harshness in alpine meadows in Tibet [16]. One study using a large dataset of 10 leaf and petiole traits in temperate forest seedlings found that about 40% of trait variation was explained by intraspecific variation [17]. In conclusion, these findings suggest that using mean values for functional traits ignores actual trait variation and that the effect of intraspecific variation on functional diversity varies among ecosystems.

Previous studies have shown that salinity stress in arid desert areas causes leaf area and nitrogen traits to converge [18]. Soil organic carbon significantly affects functional α -diversity, whereas soil water content and salinity mainly drive changes in functional β -diversity [19]. Photosynthetic and carbohydrate-related traits adapted to drought stress in the same way in both small trees and shrubs, whereas leaf hydraulic traits adapted to environmental stress differently. This finding suggests that small trees and shrubs have different trait variations to adapt to drought due to genetic constraints and long-term ecological niche differentiation [20]. However, there are few studies on the effects of ITV on functional diversity in arid desert regions and the patterns of functional trait variation at different scales. Including ITV in an analysis can more accurately determine the causes of functional trait variation and functional diversity of desert plants in response to environmental changes. Based on this, we selected three communities at three different scales in the arid desert region to study ITV's effects on functional diversity and its magnitude in response to environmental and spatial factors. We also analyzed the phylogenetic signals of plant traits in the three communities to investigate the effects of genetic, environmental, and spatial factors on functional traits and diversity. To verify this hypothesis, this study aims to: (1) What are the characteristics of variations in plant functional traits among different plant communities? The worse the environment, the lower the plasticity of traits. (2) What is the relative contribution of variation sources of plant functional traits at different scales? (3) What is the impact of intraspecific variation on plant functional diversity and community-building mechanisms?

2. Materials and Methods

2.1. Study Area

The Ebinur Lake Wetland National Nature Reserve is located at the southwest edge of the Junggar Basin in the arid region of Northwest China. It is a good site for studying biodiversity in the arid desert regions of Xinjiang [18]. The region has a dry typical continental climate. The annual evaporation exceeds 1600 mm, the annual precipitation is about 100 mm, the extreme maximum temperature is 44 °C, and the extreme minimum temperature is −33 °C. The soil types are sandy soil, grey-brown desert soil, and grey desert soil, which are severely affected by desertification [19]. The vegetation structure is composed of annual herbs, perennial herbs, and shrubs.

2.2. Sample Layout

We set up one large sample plot of 1 hectare (100 m × 100 m) each on the riverbank, transition zone, and desert margin north of the Aqikesu River near the East Bridge Management Station in the Ebinur Lake Wetland National Nature Reserve. Each sample plot was divided into 400 sample squares of 5 m × 5 m each (Figure 1). The riverbank community mainly consisted of *Populus euphratica*, *Nitraria roborowskii*, *Lycium ruthenicum*, *Apocynum venetum*, *Halimodendron halodendron*, *Alhagi sparsifolia*, *Phragmites australis*, *Suaeda microphylla*, and other plants. The transition zone community mainly contained *A. venetum*, *P. euphratica*, *L. ruthenicum*, *Tamarix chinensis*, *Karelinia caspia*, *Suaeda glauca*, *A. sparsifolia*, *P. australis*, *Reaumuria soongarica*, *Halocnemum strobilaceum*, and other plants. The desert margin community mainly contained *Haloxylon ammodendron*, *S. glauca*, *Calligonum mongolicum*, *R. soongarica*, *N. roborowskii*, *A. sparsifolia*, *Seriphidium terrae-albae*, *Kali collinum*, and other plants.

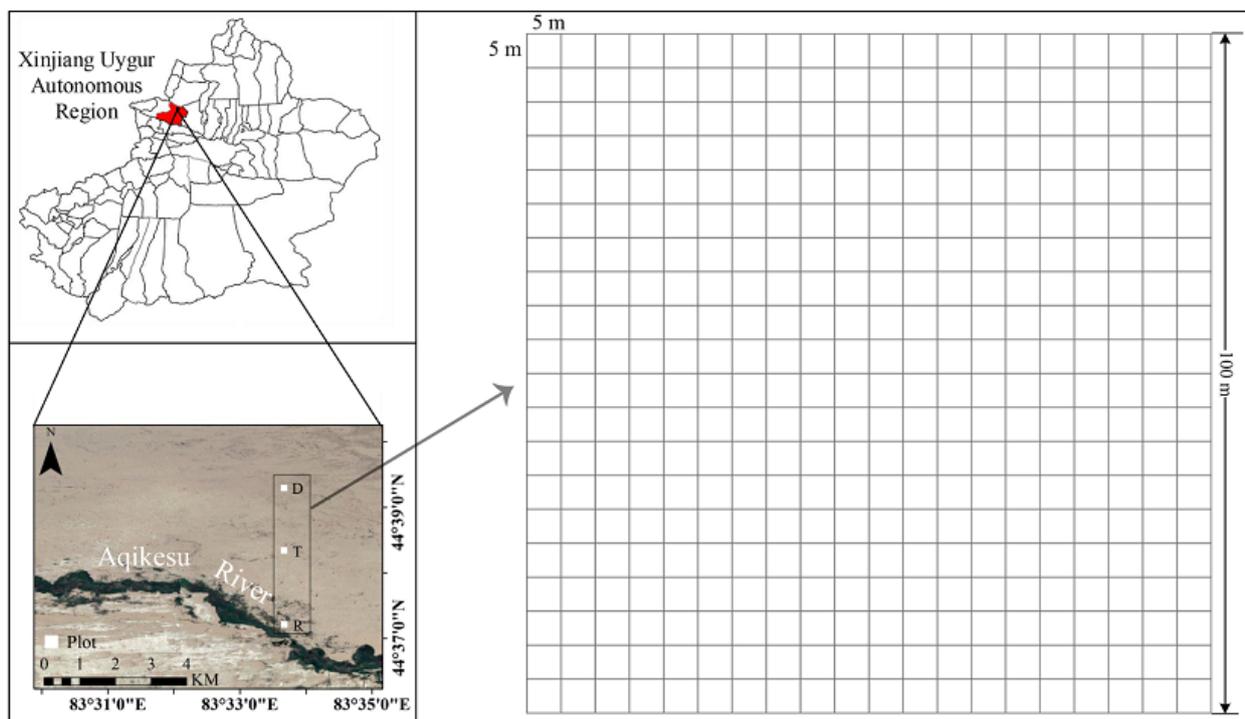


Figure 1. Schematic diagram of plot. Note: R, T, and D in the figure represent the riverbank community, transitional zone community, and desert margin community, respectively.

2.3. Collection and Measurement of Vegetation and Soil Samples

We investigated the plant community characteristics in each of the sample plots, including species composition, abundance, crown width, and maximum height of plants (H_{max}). The height of trees is measured using a laser altimeter, and the height of herbs and

shrubs, as well as the crown width of all plants, were measured using a steel tape measure. We collected about 20 mature leaves from each plant in a 5 m sample square and measured the leaves' length (LL), leaves' width (LW), and thickness (LT) with vernier calipers. The leaf area was calculated using the photographed method (we laid the leaves flat on 1 mm² grid paper, photographed them, and uploaded the images to Photoshop 7.0 software). We weighed the fresh weight on a one-in-ten-thousand balance, placed it in an envelope, brought it back to the laboratory, dried it in an oven at 80 °C for 48 h, and immediately weighed it with an electronic balance with an accuracy of 0.001 g. Then, we calculated the dry weight. The leaves' dry weight was measured and used to calculate the specific leaf area (SLA) and dry matter content (LDMC). About 20 g of plant leaves were placed into paper envelopes, air-dried, and brought back indoors to determine the leaf carbon (LC), nitrogen (LN), and phosphorus (LP) contents. The LC, LN, and LP contents were determined using the potassium dichromate dilution heat method, the H₂SO₄-H₂O₂-Kjeldahl method, and the molybdenum antimony resistance colorimetric method [21].

In each 5 m × 5 m sample square, we used the diagonal method to select the center point. We took two samples from 0–20 cm of topsoil. One sample was collected in pre-weighed aluminum boxes, which were then numbered and weighed immediately after collection. It was then returned to the laboratory, dried in an oven, and weighed dry to calculate the soil water content. We returned the second sample to the laboratory and dried it naturally for later soil index determination.

We determined the soil salinity content (SA) and soil pH using the weighing method and a pH meter, respectively. The soil organic carbon (SOC), total nitrogen (TN), ammonium nitrogen (AN), and nitrate nitrogen (NN) were determined using the potassium dichromate dilution heat method, Kjeldahl digestion method, indophenol blue colorimetric method, and dual wavelength UV spectrophotometric method, respectively. The total phosphorus (TP) and available phosphorus (AP) were determined using the Mo–Sb colorimetric method. We determined the above physicochemical properties using soil agrochemical analysis [21]. The soil particle size was determined using a laser particle size meter.

2.4. Statistical Analysis

2.4.1. Functional Trait Variation and Relative Contribution

Interspecific (V_{inter}) and intraspecific trait variation (ITV) constitute the main body of functional trait variation. In this study, the degree of interspecific (V_{inter}) and intraspecific trait variation (ITV) was quantified by the coefficient of variation: (CV) = standard deviation (σ)/mean (μ). The interspecific trait variation (V_{inter}) was calculated from the mean trait values of all species in the study area using the standard deviation and mean [22].

The total functional trait variation (V_{total}) is a measure of functional diversity calculated with the trait values of each individual of a species and includes both ITV and interspecific variation (V_{inter}) [23]. The calculation formulas are as follows. To measure the relative contribution of V_{inter} and ITV to community trait variation, we conducted variance decomposition analysis using the vegan package [24].

$$V_{\text{total}} = \sum_{i=1}^n A_{ij} T_{ij}$$

$$V_{\text{inter}} = \sum_{i=1}^n A_{ij} T_i$$

$$\text{ITV} = V_{\text{total}} - V_{\text{inter}}$$

Among them, n is the number of species, A_{ij} is the richness of the i -th species in plot j , T_{ij} is the trait value of species i in quadrat j , and T_i is the average of the trait values of species i in all plots.

2.4.2. Phylogenetic Signal of Functional Traits

Stochastic models of character evolution make a tree with any amount of hierarchical structure. Under such models as Brownian motion (stochastic models), evolutionary changes were simply added to values present in the previous generation or at the previous node on a phylogenetic tree. K is a descriptive statistic, to gauge the amount of phylogenetic signal. We used the K values of the Brownian motion evolutionary model to test whether functional traits were phylogenetically conserved [25]. K values and their significance were obtained using picante analysis in the statistical software R4.1.2 (R Core Team; Vienna, Austria).

2.4.3. Calculation of Functional α - and β -Diversity

We calculated functional α -diversity indices using the *FD* package [26]. functional α -diversity indices included functional richness (FRic), functional evenness (FEve), functional dispersion (FDis), functional divergence (FDiv), and RaoQ. The calculation formula is as follows:

- (1) FRic: Functional richness measures how many Ecological niche spaces are occupied by existing species in the community.

$$R_{ts} = \max_{i \in S} [x_{its}] - \min_{i \in S} [x_{its}] = \int I_{st(x)} dx$$

$$FRic = \frac{U_{S \in S_c} R_{ts}}{U_{S \cup S_c} R_{ts}} = \frac{\int \max_{s \in S_c} [I_{st(s)}] dx}{\int \max_{s \cup S_c} [I_{st(s)}] dx}$$

In the above equation: S is the number of species, i is the individual of species S , t is the trait, x is the trait value, $I_{st}(x)$ is the indicator function of trait t of species s ; S_c represents the community c to which species S belongs, and R_{ts} represents the range of traits t of species S .

- (2) FEve: The functional evenness index measures the distribution pattern of species traits in the occupied trait space.

$$EW_I = \frac{\text{dist}(i, j)}{W_i + W_j}$$

$$PEW_I = \frac{EW_I}{\sum_{i=1}^{s-1} EW_I}$$

$$FEve = \frac{\sum_{i=1}^{s-1} \min(PEW_I \frac{1}{S-1})}{1 - \frac{1}{S-1}}$$

In the above equation, S is the number of species, EW is the weight of evenness, $\text{dist}(i, j)$ is the Euclidean distance between species i and j , W_i is the relative richness of species i , I is the branch length, and PEW_I is the weight of branch length.

- (3) FDiv: Functional divergence is the degree of aggregation of species along the trait axis.

$$g_k = \frac{1}{s} \sum_{i=1}^s x_{ik}$$

$$d_G = \sqrt{\sum_{k=1}^T (x_{ik} - g_k)^2}$$

$$\overline{dG} = \frac{1}{S} \sum_{I=1}^S dG_i$$

$$\Delta d = \sum_{i=1}^s w_i \times (dG_i - \overline{dG})$$

$$\Delta|d| = \sum_{i=1}^s w_i \times |dG_i - \overline{dG}|$$

$$FD_{iv} = \frac{\Delta d + \overline{dG}}{\Delta|d| + \overline{dG}}$$

In the above equation, w_i is the abundance of species i , x_{ik} is the k trait value of species i , g_k is the center of gravity of trait k , S is the number of species, T is the number of traits, dG_i is the Euclidean distance between x_{ik} and the center of gravity, \overline{dG} is the average distance between species i and the center of gravity, and d is the diversity weight dispersion.

- (4) FDis: Functional dispersion index measures the maximum statistical dispersion of the multi-degree distribution of community functional traits in the trait space.

$$c = [c_i] = \frac{\sum w_j x_{ij}}{\sum w_j}$$

$$FDis = \frac{\sum w_j z_j}{\sum w_j}$$

In the above equation, w_j is the relative abundance of species j , z_j is the weighted distance from species j to the center of gravity c , and x_{ij} is the value of the i -th trait of species j .

- (5) RaoQ: Rao uses the quadratic entropy equation to measure the differences in functional traits among different species.

$$RaoQ = \sum_{i=1}^s \sum_{j>1}^s d_{ij} w_i w_j$$

In the above equation, S represents the number of species, d_{ij} represents the Euclidean distance between species i and j in traits, and w_i and w_j represent the relative abundance of species i and j , respectively.

We calculated functional β -diversity as the dissimilarity among plots in community-weighted mean (CWM) trait values [25]. The calculation method of CWM is based on the formula in Section 2.4.1. We used Euclidean distances based on CWM trait values for all nine traits to represent functional β -diversity, both considering ITV and without considering ITV. We calculated β -diversity as the average distance-to-centroid, measured as the average distance. The β -diversity index calculation was carried out in the vegan package.

2.4.4. Impact of Trait Variation on Community Assembly Processes

- (1) Obtaining spatial factors

Calculate the spatial distance between different plots based on relative coordinates to quantify spatial factors. To obtain spatial factors (related to dispersal limitation), we used the R language `adespatial` package for MEM (Moran's Eigenvector Maps) analysis [27].

- (2) Distance-Based Redundancy Analysis (dbRDA) and Variance Decomposition

We used distance-based redundancy analysis and variance decomposition to explore the impact of different environmental and spatial factors on functional beta diversity. The variance decomposition analysis was conducted using the "varpart" function. The adjusted R^2 used in this study is more accurate [28].

3. Results and Analysis

3.1. Sources of Variation in Functional Traits

In this study, we found that leaf dry matter content variation in arid desert areas mainly stemmed from interspecific variation. The intraspecific variation in chemical element content in plant leaves was greater than the interspecific variation. There was also greater intraspecific variation in leaf area than in leaf dry matter content (Table S1).

Trait variation in the riverbank community was mainly influenced by ITV, with variation contribution rates of 70.04, 78.01, and 45.38% at the three scales, respectively. However, at the 10 m × 10 m and 20 m × 20 m scales in the transitional zone and desert margin communities, the impact of interspecific variation on community trait variation was greater than that of ITV (Figure 2).

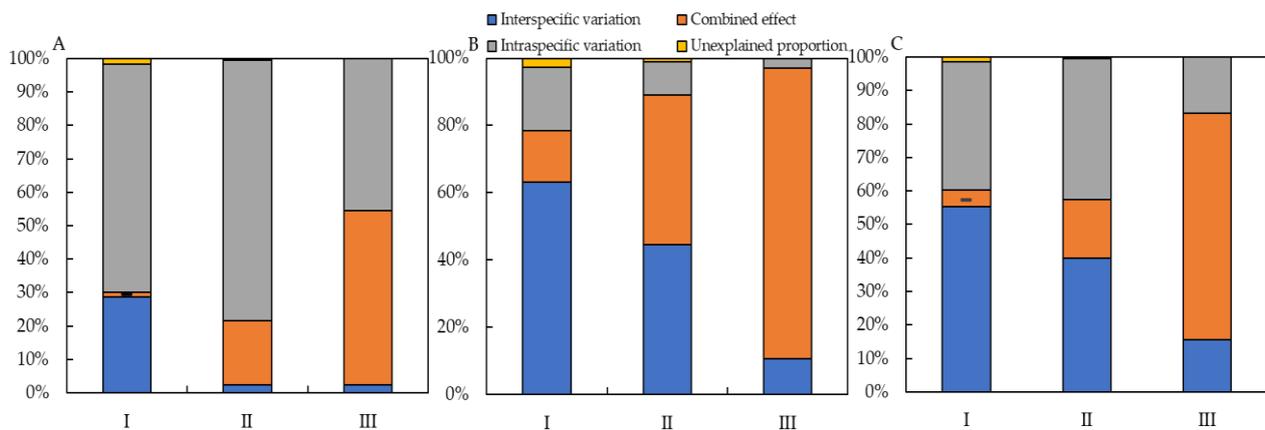


Figure 2. Impact of intraspecific and interspecific variation on functional trait variation in plant communities in the Ebinur Lake basin ((A) riverbank, (B) transitional zone, and (C) desert margin, —represents negative value. I, II and III represent the scale of 10 m × 10 m, 20 m × 20 m and 50 m × 50 m.).

The K values of leaf thickness and width in the three communities were all >1, indicating significant phylogenetic signals ($p < 0.05$). The leaf carbon content in the riverbank and transitional zone communities also showed strong phylogenetic signals ($p < 0.05$). However, traits such as the maximum plant height, specific leaf area and dry matter, nitrogen, and phosphorus contents did not show significant phylogenetic signals ($p > 0.05$). The plant functional traits in this area show a certain degree of phylogenetic conservation, and the influence of historical evolutionary factors varies for different functional traits. The overall influence is weak, except for the greater influence of leaf width, thickness, and carbon content (Table 1).

Table 1. The phylogenetic signals of plant functional traits.

Functional Trait	Riverbank		Transitional Zone		Desert Margin	
	K value	<i>p</i>	K value	<i>p</i>	K value	<i>p</i>
H _{max}	0.36	NS	0.56	NS	0.23	NS
LL	0.84	NS	0.82	*	0.53	NS
LW	1.23	**	1.08	**	1.44	*
LT	1.29	*	1.47	**	1.50	**
LDMC	0.71	*	0.85	NS	0.46	NS
SLA	0.34	NS	0.51	NS	0.31	NS
LC	1.37	**	1.15	0.001	0.79	NS
LN	0.67	NS	0.27	NS	0.45	NS
LP	0.60	NS	0.54	NS	0.36	NS

Note: * $p < 0.05$, ** $p < 0.01$, NS represents no significance.

3.2. Effect of Trait Variation on Functional Diversity

3.2.1. Effect of Intraspecific Variation on Functional α -Diversity

In the riverbank community, considering ITV greatly and significantly increased the values of functional richness (FRic) at the $10\text{ m} \times 10\text{ m}$ and $20\text{ m} \times 20\text{ m}$ scales ($p < 0.01$), and significantly decreased the functional evenness (FEve) at the $20\text{ m} \times 20\text{ m}$ and $50\text{ m} \times 50\text{ m}$ scales ($p < 0.01$). The RaoQ values at the $20\text{ m} \times 20\text{ m}$ and $50\text{ m} \times 50\text{ m}$ scales were significantly greater ($p < 0.01$) than those without ITV (Figure 3A–E).

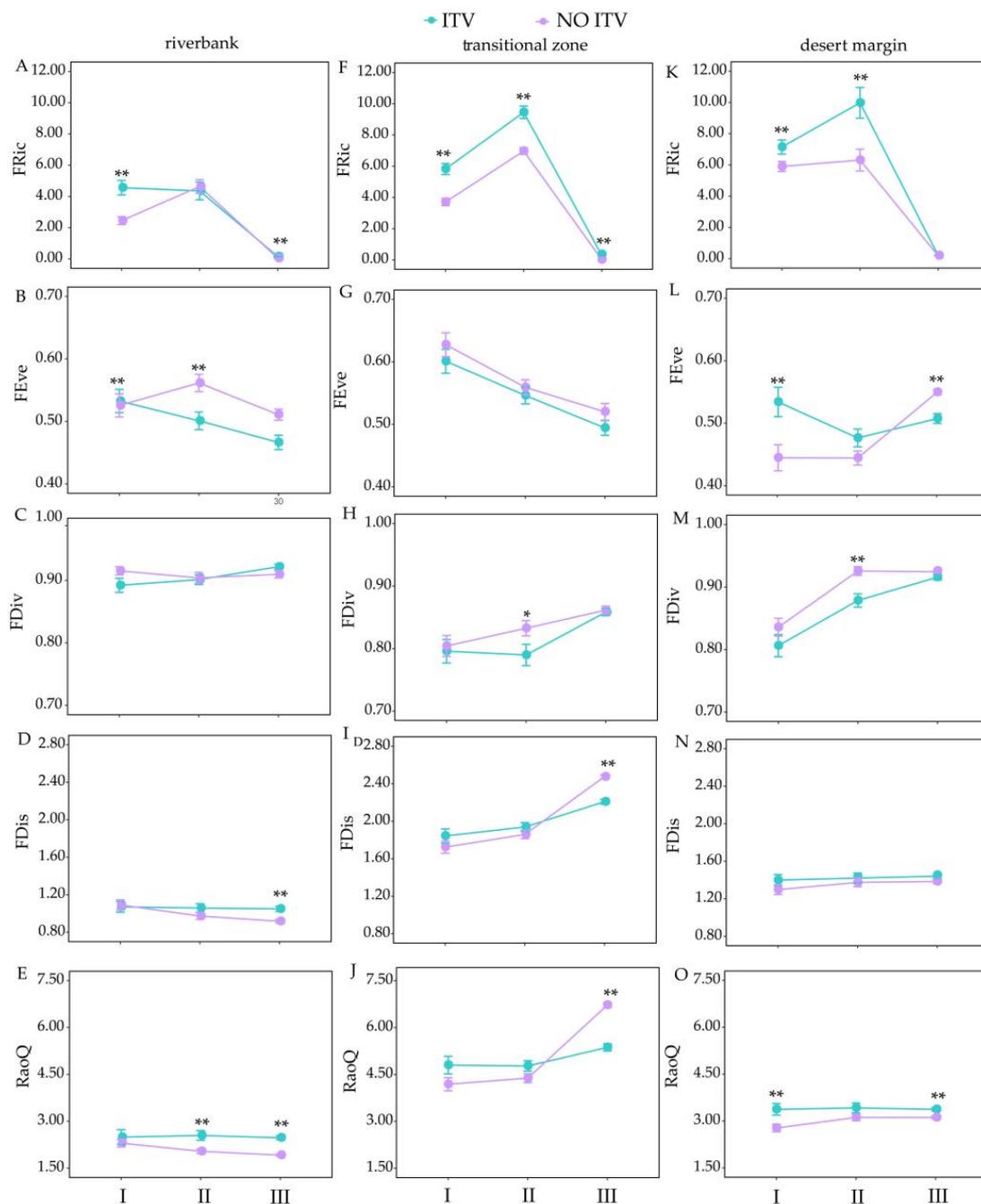


Figure 3. Effect of intraspecific variation on functional α -diversity in desert plant communities (* $p < 0.05$, ** $p < 0.01$, (A–E) represent the changes in FRic, FEve, FDis, FDiv and RaoQ index in river bank, (F–J) represent the changes in FRic, FEve, FDis, FDiv and RaoQ index in transitional zone, (K–O) represent the changes in FRic, FEve, FDis, FDiv and RaoQ index in desert margin. I, II, and III represent the scale of $10\text{ m} \times 10\text{ m}$, $20\text{ m} \times 20\text{ m}$, and $50\text{ m} \times 50\text{ m}$).

Considering ITV increased the values of functional richness ($p < 0.01$) and decreased the FEve at all scales in the transition community. It significantly decreased the functional dispersion (FDis) and RaoQ at the $50\text{ m} \times 50\text{ m}$ scale. The functional divergence (FDiv) decreased at all scales when ITV was considered, but the difference was significant only at the $20\text{ m} \times 20\text{ m}$ scale (Figure 3F–J).

Considering ITV in the desert margin community increased FRic significantly at the $10\text{ m} \times 10\text{ m}$ and $20\text{ m} \times 20\text{ m}$ scales ($p < 0.01$). FEve significantly decreased at $50\text{ m} \times 50\text{ m}$. Considering ITV decreased FDiv, the difference was highly significant at the $20\text{ m} \times 20\text{ m}$ scale ($p < 0.01$). Considering intraspecific variation increased the functional dispersion at all scales, while RaoQ decreased. The RaoQ values obtained when considering ITV at the $10\text{ m} \times 10\text{ m}$ and $50\text{ m} \times 50\text{ m}$ scales were significantly greater than those obtained when ITV was not considered ($p < 0.01$) (Figure 3H–O).

3.2.2. Effect of Intraspecific Variation on Functional Beta Diversity

The incorporation of ITV significantly increased measures of functional β -diversity. The functional β -diversity increased significantly at all three scales in the riverbank and desert margin communities ($p < 0.01$) and the $10\text{ m} \times 10\text{ m}$ and $20\text{ m} \times 20\text{ m}$ scales in the transitional zone community. The functional β -diversity decreased with increasing scale, whereas it increased with increasing scale for riverbank communities when intraspecific variation was considered. It decreased with increasing scale without intraspecific variation. The functional β -diversity increased and then decreased with increasing scale both when considering and not considering intraspecific variability in desert margins, reaching a maximum at the 20 m scale. The functional β -diversity was significantly smaller when ITV was not considered (Figure 4).

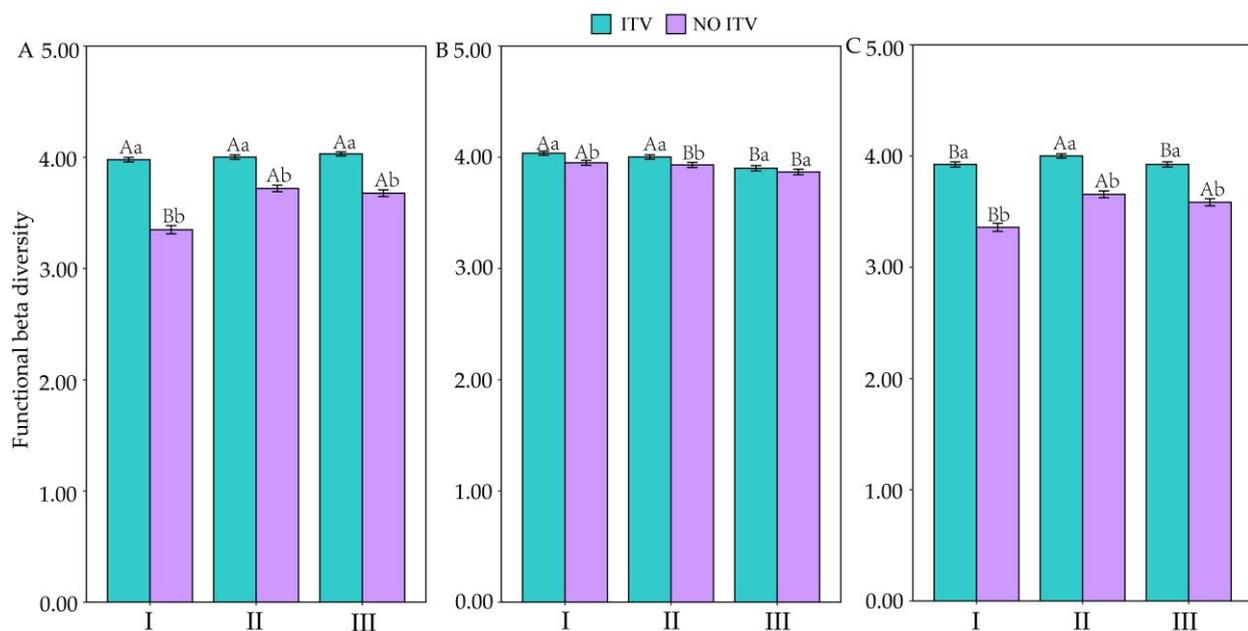


Figure 4. Effect of intraspecific variation on functional β -diversity in desert plant communities ((A) riverbank, (B) transitional zone and (C) desert margin, a and b means significant differences of plant function α diversity between ITV and NO-ITV at the same scale, A and B means significant differences of plant function α diversity between in different scales, the units of dissimilarity (functional beta diversity) is average difference in number of functional traits among plots. I, II, and III represent the scale of $10\text{ m} \times 10\text{ m}$, $20\text{ m} \times 20\text{ m}$, and $50\text{ m} \times 50\text{ m}$).

3.3. Effects of Intraspecific Variation on Community Assembly

3.3.1. Based on Functional α -Diversity

At the 10 m \times 10 m scale, the spatial and environmental factors explained the changes in functional α -diversity of 0.28 and 0.05, respectively, and explanation ratios were 0.45 and 0.07 without considering ITV the riverbank community. The changes in functional α -diversity of 0.41 and 0.04 were explained, explanation ratios were 0.54 and 0.11 without considering ITV in the transitional community; The changes in functional diversity of 0.36 and 0.08 were explained, explanation ratios were 0.46 and 0.16 without considering ITV in the desert margin. At all scales, the proportion of unexplained variation was greater in all three communities when ITV was considered than when it was not.

As the scale increased, the environmental and spatialized environmental roles gradually increased, the role of spatial factors gradually decreased, and the proportion of unexplained variation also gradually decreased (Table 2).

Table 2. Relative contributions of environmental and spatial factors to the functional α -diversity of desert plant communities at different scales.

Community	Types	Scale	Soil Factors	Space Factors	Soil and Space	Unexplained Proportion
riverbank	ITV	10 m \times 10 m	0.05	0.28	−0.01	0.69
		20 m \times 20 m	0.07	0.44	0.12	0.28
		50 m \times 50 m	0.49	0.23	0.12	0.16
	NO-ITV	10 m \times 10 m	0.07	0.45	−0.06	0.54
		20 m \times 20 m	0.03	0.50	0.18	0.20
		50 m \times 50 m	0.07	0.13	0.79	0.01
transitional zone	ITV	10 m \times 10 m	0.04	0.41	0.09	0.46
		20 m \times 20 m	0.09	0.33	0.41	0.16
		50 m \times 50 m	0.43	0.14	0.35	0.11
	NO-ITV	10 m \times 10 m	0.11	0.54	−0.04	0.40
		20 m \times 20 m	0.24	0.27	0.34	0.16
		50 m \times 50 m	0.41	0.16	0.40	0.03
desert margin	ITV	10 m \times 10 m	0.08	0.36	−0.06	0.62
		20 m \times 20 m	0.18	0.37	0.18	0.27
		50 m \times 50 m	0.03	0.21	0.68	0.08
	NO-ITV	10 m \times 10 m	0.16	0.46	−0.10	0.48
		20 m \times 20 m	0.11	0.61	0.12	0.16
		50 m \times 50 m	0.07	0.10	0.80	0.03

3.3.2. Based on Functional β -Diversity

At the 10 \times 10 m scale, the spatial and environmental factors explained the changes in functional β -diversity of 0.20 and 0.03, respectively, and explanation ratios were 0.37 and 0.05 without considering ITV the riverbank community. The changes in functional β -diversity of 0.09 and 0.02 were explained, explanation ratios were 0.48 and 0.07 without considering ITV in the transitional community; The changes in functional β -diversity of 0.29 and 0.10 were explained, explanation ratios were 0.45 and 0.08 without considering ITV in the desert margin. At the 10 m \times 10 m scale, the functional β -diversity was more sensitive to spatial factors when ITV was not considered. The proportion of functional α -diversity explained by spatial factors with ITV was greater than that explained by functional diversity without ITV. Except for the transitional zone community at the 50 m \times 50 m scale, the proportion of unexplained factors influencing functional diversity with ITV was greater than without ITV in all three communities (Table 3).

Table 3. Relative contributions of environmental and spatial factors to the functional β -diversity of desert plant communities at different scales.

Community	Types	Scale	Soil Factors	Space Factors	Soil and Space	Unexplained Proportion
riverbank	ITV	10 m × 10 m	0.03	0.20	−0.02	0.79
		20 m × 20 m	0.02	0.52	0.16	0.31
		50 m × 50 m	0.37	0.25	0.28	0.09
	NO-ITV	10 m × 10 m	0.05	0.37	−0.07	0.62
		20 m × 20 m	0.04	0.61	0.16	0.20
		50 m × 50 m	0.05	0.25	0.67	0.03
transitional zone	ITV	10 m × 10 m	0.02	0.09	0.10	0.80
		20 m × 20 m	0.12	0.36	0.30	0.22
		50 m × 50 m	0.24	0.18	0.47	0.11
	NO-ITV	10 m × 10 m	0.07	0.48	0.00	0.45
		20 m × 20 m	0.11	0.41	0.35	0.13
		50 m × 50 m	0.39	0.02	0.39	0.20
desert margin	ITV	10 m × 10 m	0.10	0.29	−0.03	0.64
		20 m × 20 m	0.05	0.49	0.08	0.39
		50 m × 50 m	0.11	0.18	0.62	0.08
	NO-ITV	10 m × 10 m	0.08	0.45	−0.16	0.53
		20 m × 20 m	0.10	0.66	0.10	0.14
		50 m × 50 m	0.06	0.10	0.81	0.04

4. Discussion

The importance of ITV when quantifying functional diversity has been emphasized [29], because ignoring it may strongly alter estimates of functional diversity and obscure ecological processes [11,12]. In particular, when assessing mechanisms of variation in functional diversity at local scales, ITV is expected to become increasingly important as the scale of study decreases [11]. On the other hand, increasing the scale tends to increase variability, so interspecific trait variation (V_{inter}) is expected to be relatively greater than ITV [11]. By contrast, there has been less focus on ITV during community assembly processes [30]. In this sense, ITV can potentially contribute to ecosystem functioning [31,32].

ITV has been reported for alpine grassland, scrubland, subtropical, and tropical rainforest communities [33,34]. However, relatively little research has been conducted on desert plant communities. The degree of trait variation represents the range of inherent characteristics and individual differences; the wider the range of resources available to plants, the greater the variability of plant functional traits [35]. Intraspecific variation in plant functional traits is influenced by a combination of genetic variation and environmental conditions [36]. Furthermore, its magnitude or degree can reflect plants' ability to adapt to environmental conditions [37]. Albert et al. conducted a study on 13 living species. They found that about 30% of trait variation came from within the species, with the highest intraspecific variability in leaf nitrogen content and carbon content [13]. ITV in specific stem densities of subtropical broadleaf evergreen forest plants in China explained up to 51.50% of total trait variation [38]. We found that the variation in leaf dry matter content in the arid desert region mainly originated from interspecific variation. This finding is consistent with Burton et al., who found greater interspecific variation in leaf dry matter content [39]. The intraspecific variation in the chemical element content of plant leaves was greater than the interspecific variation in this study, which is consistent with studies that found greater intra-species variation in plant leaf chemical element content [10,30,40]. The photosynthetic rate and nutrient cycling are correlated with the leaf element content. There may be a link between the large intraspecific variation in this study and intraspecific trait differentiation due to competition between species. In addition, ITV has been shown to have ecological effects similar to interspecific variation [41]. For example, controlled experiments in North Carolina scrub communities in the USA found that fire conditions significantly altered the community-weighted mean of specific leaf areas. Furthermore,

changes in the community-weighted mean were primarily driven by intraspecific variation, i.e., plants adapted to fire disturbance through intraspecific variation in functional traits [41]. The specific leaf area and leaf dry matter content, which are also leaf economic-type spectral traits, showed greater intraspecific variation, possibly due to the greater genetic variation in specific leaf areas [42]. The larger intraspecific variation in leaf area allows for greater variation among individuals of the same species, which promotes species coexistence [43]. The lowest overall trait variation in the desert margin community may be due to its harsher habitat conditions than the other two communities. It has been suggested that species with low variation are more commonly found in harsh habitats. The low plasticity of traits may be due to specialization toward unfavorable habitats [43].

Inferring species coexistence mechanisms based on phylogenetic structures requires conserving functional traits on phylogenetic trees [44]. The phylogenetic and functional trait structures of a community are consistent when the functional traits of the community have a phylogenetic signal [44]. Examining leaf functional traits and phylogenetic signals in different desert communities revealed that more than half of the nine functional traits did not exhibit phylogenetic signals (Table 1). Therefore, the functional traits in those sites were not all evolutionarily conserved, and inconsistencies in the community's phylogenetic and functional trait patterns were observed. The K values of leaf thickness and width in all three communities were >1, showing significant phylogenetic signals. No significant phylogenetic signals were detected for most functional traits, suggesting that evolutionary history has not influenced plant communities in the Ebinur Lake basin with much intensity. This observation is consistent with Che's findings in subalpine meadow communities [45]. Due to long-term environmental adaptation, these functional traits do not always exhibit significant phylogenetic signals, which can lead to the convergent evolution of more distantly related species [46].

In this study, we found that considering ITV increased the values of functional richness and RaoQ. Greater ITV implied a wider distribution of traits and a higher complementarity of ecological niches within the community, which contributes to its stability [47]. These observations are consistent with those made of grassland plants in the Mediterranean, where ITV significantly influenced the size of FRic and RaoQ [48]. Furthermore, considering ITV significantly increased indices of functional β -diversity in our study. The effects of environmental and spatial factors on β -diversity have been controversial. Some studies have suggested that environmental factors such as climate, soil, and topography or spatial factors are more important for β -diversity [49,50]. By contrast, others have suggested that both roles are equally important [51]. Our results indicated that the relative importance of environmental and spatial factors on functional β -diversity varies with scale. On a small scale, spatial factors play a major role in functional diversity, while on a large scale, environmental factors and spatialized environmental effects play a role. The main reason is that as the sampling scale increases, the differences in species habitats become greater, and the role of environmental factors also becomes greater [52]. Dispersal limitation generally occurs at smaller scales, so the effect of spatial factors is more pronounced at smaller scales [53]. The results of this study are consistent with those of previous studies [53]. Therefore, dispersal limitation significantly impacts functional diversity at smaller scales, while environmental filters have a significant impact at larger scales. In recent years, more studies have shown that ITV plays an important role in species coexistence, niche differentiation, community assembly, and maintenance of ecosystem function [54–56]. In addition to explaining community trait variation, intraspecific trait variation has important implications for community assembly and ecosystem function [57]. A global meta-analysis showed that ITV accounted for 25% of the total variation within communities and 32% between communities, particularly in grassland community assembly [10,58]. Regarding community assembly, Jung et al. found that intraspecific trait variation helps more species pass through biotic and abiotic screens and promotes species coexistence [22]. Siefert also concluded that using a null model with ITV enhances the effects of environmental filtering and provides more comprehensive information on community assembly [59]. Spasojevic

et al. found that variance decomposition analysis based on functional β -diversity without considering ITV may hinder the explanation of habitat filtering processes [60]. Spatial factors had less of an effect on functional β -diversity after considering ITV, except at the 50 m \times 50 m scale in the transitional zone and desert margin communities. This finding indicated that ITV could reduce the effect of dispersal on functional diversity. Although considering ITV did not change the main ecological processes affecting functional diversity, it changed the extent to which its environmental filtering and dispersal effects explained functional diversity. Moreover, the proportion of unexplained factors in the variance decomposition of functional diversity, in which environmental and variance factors increased after considering ITV, suggests that there are other factors affecting ITV, such as genetic factors, ecological drift, and species extinction [61,62] or unmeasured spatial and environmental factors [63].

5. Conclusions

Including measurements of ITV significantly increased functional richness at the 10 m \times 10 m scale in all three communities. It significantly increased RaoQ at the 50 m \times 50 m scale in the riverbank and desert margin communities, whereas it significantly decreased RaoQ in the transition zone community. ITV significantly increased functional β -diversity except at the transition zone community's 50 m \times 50 m scale. Considering ITV significantly increased functional β -diversity. The dispersal limitation significantly impacts functional diversity at small scales, while environmental filtering significantly impacts functional diversity at larger scales. Spatial factors had less of an effect on functional β -diversity after considering intraspecific variation at all scales, except at the 50 m \times 50 m scale in the transitional zone and desert margin communities. This finding indicates that ITV can reduce the effect of dispersal on functional diversity. Although considering ITV did not change the interpretation of the main ecological processes affecting functional diversity, it changed the extent to which environmental filtering and dispersal effects explained functional diversity.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/f14081536/s1>, Table S1: Coefficient of variation for interspecific and intraspecific functional traits in the Ebinur Lake basin.

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