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Spatial Distribution of Critically Endangered *Hopea chinensis* Plant Seedlings and Relationships with Environmental Factors

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Abstract: *Hopea chinensis* is a representative tree species in evergreen monsoon forests in the northern tropics, but it is currently in a critically endangered state due to destruction by human activities and habitat loss. In this study, we measured and analyzed the number of regenerating seedlings and habitat factors in wild populations of *H. chinensis* by combining field surveys with laboratory analysis. The aim of this study was to clarify the spatial distribution of *H. chinensis* seedlings and related factors to provide a scientific basis for conserving its germplasm resources and population restoration. In six populations, most size-class seedlings had aggregated distributions at three scales, and the intensity of aggregation decreased as the sample plot scale increased for most size-class seedlings. In the northern foothills of the Shiwandashan Mountains, size class I seedlings tended to be distributed in habitats with a higher rock bareness rate, whereas size class II and III seedlings tended to be distributed in habitats with a higher canopy density, thicker humus layers, and higher soil moisture content. In the southern foothills of the Shiwandashan Mountains, size class I and II seedlings tended to be distributed in habitats with higher available nitrogen contents, and size class III seedlings tended to be distributed in habitats with higher available nitrogen and soil moisture contents. Therefore, in the southern foothills of the Shiwandashan Mountains, the survival rate of *H. chinensis* seedlings can be improved by artificially adding soil to increase the thickness of the soil layer in stone crevices and grooves, regularly watering the seedlings during the dry season, and appropriately reducing the coverage of the shrub layer. In the northern foothills, the survival rate of *H. chinensis* seedlings can be enhanced by regularly applying nitrogen fertilizer and watering to increase the available nitrogen and soil moisture contents.

Keywords: aggregation intensity; environmental factor; seedling; spatial distribution pattern

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1. Introduction

Due to overexploitation and climate change, more and more plants are becoming endangered, especially for species with narrow distributions [1]. In 2021, the Botanic Gardens Conservation International reported that tree species throughout the world are facing a major crisis due to a combination of factors, such as deforestation, pests and diseases, and climate change, and 30% (17,500 species) of tree species are on the brink of extinction [2]. Studying the mechanisms that threaten endangered plants and developing scientific and effective measures for protecting and restoring their germplasm resources and ecological environments is a critical issue in global biodiversity conservation research [3,4]. For most threatened species, the difficulty or slow population renewal leads to their difficulty in maintaining population size and structural stability, which is a key reason for their endangerment or extinction [5,6]. Therefore, we need to closely monitor the early life history stages of species to inform conservation and restoration efforts for endangered plants. The seedling stage is the most vulnerable plant growth period and is highly sensitive to environmental changes. Under the combined effects of biotic and abiotic factors, the individual characteristics and spatial distribution of seedlings become heterogeneous. The growth and distribution of seedlings have important effects on the future composition, structure, and function of the population [7]. Biological factors such as bacteria, herbivores, herbivorous insects can cause tissue necrosis, metabolic disorders, and loss of function by infection and gnawing on seedlings, consequently preventing the growth of the seedlings and even death [8]. Abiotic factors such as light, temperature, and soil can affect the growth and development of seedlings by affecting photosynthesis, metabolic rate, and nutrient supply [9]. These factors work together on the temporal and spatial scales to determine the growth and distribution of seedlings by influencing their growth and development and ecological environment [10]. By studying the spatial distribution of population seedlings, we can understand the biological characteristics of plant populations, interactions between populations, and the relationship between populations and the environment. Then, we can infer the regeneration strategies and dynamics of plant populations based on changes in their spatial distribution. This information is highly significant for exploring the formation of plant community biodiversity and maintenance mechanisms. Additionally, it will provide an effective scientific basis for understanding the status of endangered populations, analyzing mechanisms that lead to endangerment, and developing conservation strategies [11,12].

Currently, the most widely used method for studying spatial population patterns is large sample plot monitoring combined with point pattern analysis techniques. This method overcomes the limitations of traditional methods, which can only be analyzed at a single scale. It is based on continuous spatial survey data within large sample plots and analyzes population patterns at various scales according to the spatial coordinates of individual plants [13–15]. However, rare and endangered plants often have low-density or very low-density populations with sparse numbers and scattered distributions. Thus, traditional sample plot survey methods are more applicable [16,17].

Hopea chinensis, in the family Dipterocarpaceae and genus *Hopea,* is an evergreen tree and representative species found in the tropical evergreen monsoon forests in the northern and southern regions of Guangxi, China. *H. chinensis* has significant value for studies of the composition, geographical distribution, and ecological habits of tropical rainforest flora [18]. *H. chinensis* is a relict species from the Tertiary period distributed in "refugia" formed by the local topography. *H. chinensis* was originally distributed in the foothills, valleys, and slope forests below an altitude of 600 m in the Shiwandashan and Daqing Mountains of the Guangxi Zhuang Autonomous Region. However, the wild population in the Daqing Mountains has become extinct due to the destruction caused by human activities and the impacts of climate change. Currently, it is only sporadically distributed in valleys and along stream banks in the southern and northern foothills of the Shiwandashan Mountains. *H. chinensis* has been listed as a national Class II key protected plant and a species with an extremely small population in China, and is classified as critically endangered (CR) by the International Union for Conservation of Nature (IUCN) [19].

Huang et al. [18] indicated that the main reasons for the endangerment of *H. chinensis* are destruction and a decrease in population numbers caused by human activities and habitat loss, and slow regeneration under natural conditions is the main factor restricting population recovery. Jia et al. [20] identified further limitations in the conversion process from seedlings to saplings and from saplings to small trees within the wild population of *H. chinensis*, which constrain population development. Clearly, difficult or slow population regeneration is an important cause of the endangerment of *H. chinensis*. However, the causes and factors that influence slow population regeneration in *H. chinensis* require elucidation. Consequently, in the present study, we investigated wild populations of *H. chinensis* in the southern and northern foothills of the Shiwandashan Mountains and set up survey sample plots based on the characteristic strip-like distribution of the population along areas such as streams, sparse forests, and scattered growth. On-site investigations, observations, and analyses of the characteristics and distribution of population seedlings, as well as environmental factors, were conducted. The aim of which was to explore the spatial distribution and characteristic patterns of regenerating *H. chinensis* seedlings, and to analyze the relationships between the spatial distribution of seedlings and environmental factors. The findings obtained in this study are expected to facilitate the development of strategies and a scientific basis for conserving *H. chinensis* germplasm resources and population recovery.

2. Materials and Methods

2.1. Overview of the Study Area

The Shiwandashan Mountains are located in the southern part of Guangxi Zhuang Autonomous Region, China (21°40′03″–22°04′18″ N, 107°29′59″–108°13′11″ E), where they stretch in a northeast–southwest direction, with a length of about 100 km, a width of 30–40 km, and an elevation of 700–1000 m [21]. The Shiwandashan Mountains are an important climatic divide in southern Guangxi. The southern foothills have a northern tropical marine humid climate with higher rainfall and temperatures. The vegetation is primarily tropical monsoon forest, and the soil is lateritic red, with a pH of 4.5–5.5 [22]. The northern foothills have a southern subtropical monsoon humid climate, and they are relatively dry with lower rainfall and temperatures. The vegetation is primarily subtropical, and the soil is latosolic red with a pH of 4.5–5.5 [22]. *H. chinensis* is distributed patchily or sporadically in the evergreen broad-leaved forests along streams in both the southern and northern foothills, including areas such as Fulong Town, Nasuo Town, Naqin Town, Banba Township in Fangcheng District, Fangchenggang City, Malu Town in Dongxing City, and Jiao'an Town and Gongzheng Township in Shangsi County.

2.2. Sample Plots and Investigation

Based on preliminary survey results, in July and August 2023, three sites with patchy distributions of wild *H. chinensis* populations were selected in both the southern and northern foothills of the Shiwandashan Mountains to set up survey sampling plots. The three sites in the northern foothills were Hongqi Forest Farm in Jiao'an Town, Shangsi County (HQ), Huangpao Mountain in the Shiwandashan National Nature Reserve in Jiao'an Town, Shangsi County (HP), and Wanghao Village in Gongzheng Township, Shangsi County (WH) (Figure 1). The three sites in the southern foothills were Shimengu Valley in Pingfeng Forest Park in Malu Town, Dongxing City (SMG), Yanglan Village in Nasuo Town, Fangcheng District, Fangchenggang City (YL), and Nanshan Station at Golden Camellia National Nature Reserve in Nasuo Town, Fangcheng District, Fangchenggang City (NS) (Figure 1). The sampling plot settings were restricted due to the uneven and patchy distribution of *H. chinensis* along the stream banks. Three quadrats measuring 10 m × 10 m were established in the concentrated and larger area of each population. Basic information for these populations is shown in Table 1.

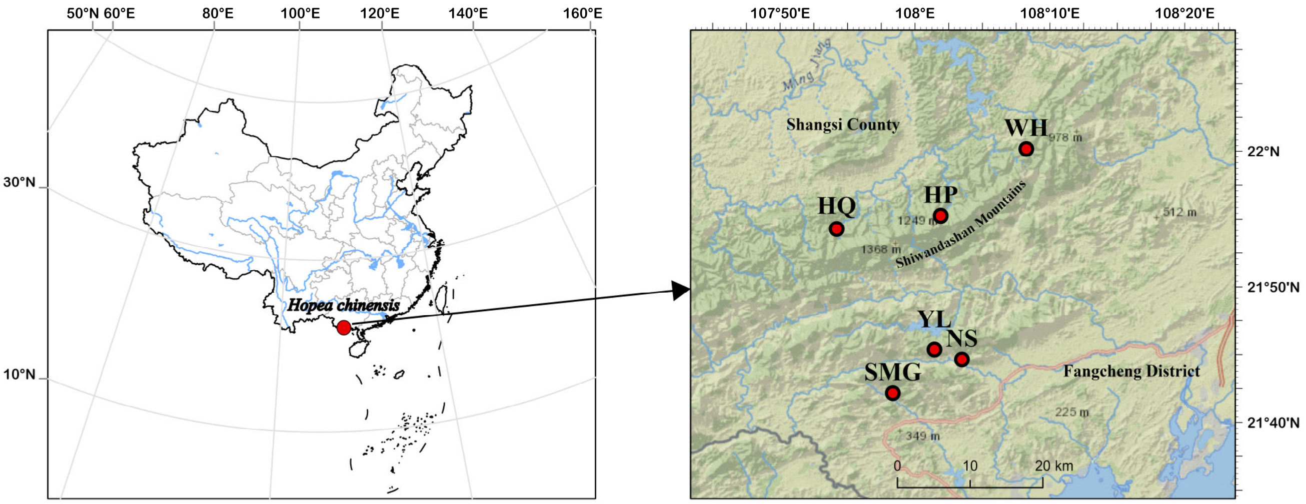

Figure 1. Geographical distribution of *H. chinensis* populations. HP: Huangpao Mountain in the Shiwandashan National Nature Reserve in Jiao'an Town, Shangsi County; HQ: Hongqi Forest Farm in Jiao'an Town, Shangsi County; WH: Wanghao Village in Gongzheng Township, Shangsi County; NS: Nanshan Station at Golden Camellia National Nature Reserve in Nasuo Town, Fangcheng District, Fangchenggang City; YL: Yanglan Village in Nasuo Town, Fangcheng District, Fang-chenggang City; SMG: Shimengu Valley in Pingfeng Forest Park in Malu Town, Dongxing City.

Table 1. Geographic and climate information for *H. chinensis* populations.

Population Information	Northern Foothills			Southern Foothills		
	HQ	**HP**	**WH**	**SMG**	**YL**	**NS**
GPS	E: 107.9031 N: 21.9047	E: 108.0403 N: 21.9544	E: 108.1375 N: 22.0028	E: 107.9726 N: 21.7026	E: 108.0406 N: 21.7558	E: 108.0580 N: 21.7439
Al (m)	274	263	276	200	253	31
MAT (°C)	20.9	20.6	20.6	21.8	22.1	22.3
MAP (mm)	1979.6	2050.1	1893.4	3214.6	3305.3	3373.1
MARH (%)	85.3	84.9	84.7	86.4	86.3	86.1
SA	Southeast	East	East	East	South	Southeast
SD (°)	15	20	23	18	21	18
HDS (m)	1.2–1.8	1.3–1.6	1.5–1.8	0.3–0.6	0.3–0.5	0.2–0.5
VDS (m)	1.2–1.6	1.3–1.8	1.6–2.2	0.2–0.4	0.1–0.3	0.0–0.4
Dominant plant species	*Pinus massoniana*, *Hopea chinensis*, *Altingia chinensis*, *Quercus griffithii*, *Symplocos adenopus*	*Hopea chinensis*, *Altingia chinensis*, *Bennettiodendron lanceolatum*, *Craibiodendron stellatum*, *Quercus griffithii*	*Hopea chinensis*, *Castanopsis hystrix*, *Bennettiodendron leprosipes*, *Aidiacochinchinensis*, *Acronychia pedunculata*	*Hopea chinensis*, *Macaranga tanarius*, *Lithocarpus hancei*, *Castanopsis faberi*, *Mallotus hookerianus*	*Hopea chinensis*, *Pleioblastus amarus*, *Cyclobalanopsis glauca*, *Aporusa dioica*, *Aidia canthioides*	*Sterculia lanceolata*, *Ficus benjamina*, *Hopea chinensis*, *Podocarpus nagi*, *Pithecellobium clypearia*

Notes: Al: altitude; MAT: mean annual temperature; MAP: mean annual precipitation; MARH: mean annual relative humidity; SA: slope aspect; SD: slope degree; CD: canopy density; HDS: horizontal distance from stream; VDS: vertical distance from stream. Climate information was based on observations from 2020 to 2023 by small meteorological instruments, which were placed 20 to 30 m away from *H. chinensis* populations.

Each quadrat measuring 10 m × 10 m was subdivided into four small quadrats of 5 m × 5 m using the adjacent grid method, and the diameter at breast height (DBH) (the ground diameter was measured for seedlings) and tree height were determined for all *H. chinensis* individuals within each small quadrat. According to the method described by Jia et al. [20], *H. chinensis* plants with a DBH less than 2.5 cm were classified as regeneration layer individuals and divided into three size classes: seedlings with a height of 0–50 cm in size class I; seedlings with a height of 50–100 cm in size class II; and seedlings with a height greater than 100 cm and DBH less than 2.5 cm in size class III.

2.3. Analysis of Environmental Factors

A handheld GPS was used to record the latitude, longitude, and elevation of each 10 m × 10 m sample plot. A rangefinder was used to measure the horizontal and vertical distances from the sample plot to a stream. A compass was used to measure the slope and aspect of the sample plot. The canopy density (CD) was determined for the sample plot by visual estimation. At the same time, each 10 m × 10 m plot was divided into four 5 m × 5 m subplots. The height and coverage of all shrubs in each and every subplot should be determined—the height determined by an altimeter, and the coverage determined via the grid ratio method. Then, five points were randomly selected in each and every subplot to determine the thickness of the litter layer and humus layer by ruler. The distance between two adjacent points was more than 1 m [23].

After removing the surface litter and humus layer at four corners and central locations of each 10 m × 10 m sample site, a ring knife with a volume of 100 cm^3 was used to collect soil samples of 0–20 cm for the determination of soil water content and bulk density. Then, about 1 kg of soil sample in 0–20 cm sections was drilled with a soil drill. The mixture was evenly mixed by the quarter method and then put into a sealed bag and brought back to the laboratory for soil chemical property determination. The soil pH was determined at a soil to deionized water ratio of 1:2.5. SOC was measured using the potassium dichromate volumetric method, AN with the alkali-hydrolysis diffusion method, AP using the sodium bicarbonate method, and AK by ammonium acetate extraction-flame atomic absorption spectrophotometry [24].

2.4. Data Analysis

2.4.1. Analysis of Population Distributions

The distributions of the *H. chinensis* populations were analyzed at different quadrat scales (5 m × 5 m, 5 m × 10 m, and 10 m × 10 m). The distribution pattern and clumping intensity of each population were comprehensively determined using the diffusion coefficient (C), clumping index (I), negative binomial parameter (K), mean crowding (m^*), patchiness index (PAI), Cassie index (Ca), and Morisita index (I_δ). If four or more of the seven indices yielded consistent results, the pattern was considered determined; otherwise, the field survey of the population distribution was used for further assessment [17,25].

(1) Diffusion coefficient (C)

$$C = \frac{S^2}{\bar{X}}$$

where $\overline{X}$ indicates the average population abundance and S^2 is the variance of the population abundance. A population is randomly distributed when $C = 1$, aggregated when $C > 1$, and uniformly distributed when $C < 1$.

The degree of deviation between the measured and theoretical values was determined using the t-test:

$$t = (C-1)/\left[\frac{2}{n-1}\right]^{1/2}$$

where n is the number of quadrats. The difference is not significant when $|t| = t_{n-1,\,0.05}$, the population is aggregated when $|t| > t_{n-1,\,0.05}$, and the population is randomly distributed when $|t| < t_{n-1,\,0.05}$.

(2) Clumping index (I)

$$I = \frac{S^2}{\overline{X}} - 1$$

where a larger I value indicates a greater clumping intensity. A population is randomly distributed when $I = 0$, uniformly distributed when $I < 0$, and aggregated when $I > 0$.

(3) Mean crowding (m^*)

$$m^* = \overline{X} + \frac{S^2}{\overline{X} - 1}$$

A population is aggregated when $m^* > \overline{X}$, randomly distributed when $m^* = \overline{X}$, and uniformly distributed when $m^* < \overline{X}$.

(4) Patchiness indicator (PAI)

$$PAI = \frac{m^*}{\overline{X}}$$

A population is aggregated when $PAI > 1$, randomly distributed when $PAI = 1$, and uniformly distributed when $PAI < 1$.

(5) Cassie index (Ca)

$$Ca = \frac{S^2 - \overline{X}}{\overline{X}}$$

A population is aggregated when $C\alpha > 0$, randomly distributed when $C\alpha = 0$, and uniformly distributed when $C\alpha < 0$.

(6) Negative binomial parameter (K)

$$K = \frac{\overline{X}^2}{S^2 - \overline{X}}$$

A population is aggregated when $K > 0$, where a smaller K value indicates a greater clumping intensity. A population can be considered randomly distributed when the K value tends toward infinity (generally > 8). A population is uniformly distributed when $K < 0$. The K value can be used to determine the distribution pattern for the population and to distinguish the clumping intensity.

(7) Morisita index (I_δ)

$$I_\delta = n \times \frac{\sum \overline{X}^2 - \sum \overline{X}}{\left(\sum \overline{X}\right)^2 - \sum \overline{X}}$$

A larger I_δ value indicates a greater clumping intensity. A population is randomly distributed when $I_\delta = 1$, aggregated when $I_\delta > 1$, and uniformly distributed when $I_\delta < 1$.

All of the indices above were calculated using Excel 2016 software.

2.4.2. Analysis of Causes of Aggregated Distributions of *H. chinensis* Populations

The aggregation average value (λ) proposed by Blackkish was used to analyze the causes of the aggregated spatial distributions of *H. chinensis* seedlings [26] according to the following equation:

$$\lambda = \overline{X} \times \frac{\gamma}{2K}$$

where γ is the chi-square distribution value with $2K$ degrees of freedom at a probability of 0.05, and K is the negative binomial distribution parameter. When $\lambda < 2$, the aggregated distribution of the biological population is caused by environmental factors. When $\lambda > 2$, aggregation is associated with the biological characteristics of the organism itself or the biological characteristics combined with environmental factors. Biological factors primarily include biological characteristics, intraspecific and interspecific competition, and external disturbances. Environmental factors primarily include nutrient distribution and spatial non-uniformity. Excel 2016 software was used to calculate λ.

2.4.3. Analysis of Relationships Between Seedling Distributions and Environmental Factors

SPSS 19.0 software was used to conduct an analysis of variance and multiple comparisons of different population environmental factors (with Duncan's new multiple-range method). Origin 2022 software was used to analyze correlations and to map seedling distributions and environmental factors. The significance level for these statistical analyses was set at $\alpha = 0.05$.

The selection of the sorting model in detrended correspondence analysis (DCA) was discriminated with the "lengths of gradient". In this study, the maximum "lengths of gradient" for the *H. chinensis* populations in the southern and northern foothills were 0.9 and 1.2, respectively, and a linear sorting model was selected. To further understand the relationships between seedling distributions and environments, the forward selection method was employed to explore the relationships between microhabitats and seedling distributions, and the significance of the results was tested using the Monte Carlo method. Sorting analysis was performed using redundancy analysis (RDA) with Canoco 5.0 software.

3. Results

3.1. Spatial Distributions of Seedlings in H. chinensis Populations

The six populations of *H. chinensis* were distributed on the east slope, south slope or southeast slope with a slope of 18–23° and 0.2 m–1.8 m from the stream. Among the communities of six *H. chinensis* communities, the dominant tree species in YL, SMG, HP, and WH communities were *H. chinensis*. The dominant tree species in NS and HQ communities were *Sterculia lanceolata* and *Pinus massoniana*, respectively (Table 1).

Among the six populations of *H. chinensis*, the SMG population had the highest number of seedlings in size class I, with 243 plants, and the WH population had the highest numbers of seedlings in size classes II and III, with 94 and 151 plants, respectively (Figure 2A). The number of seedlings in size class I was higher in the *H. chinensis* populations in the southern foothills of the Shiwandashan Mountains (502 plants) than in the northern foothills (335 plants). The numbers of seedlings in size class II and size class III were lower in the southern foothills, with 122 and 91 plants, respectively, than those in the northern foothills, with 155 plants and 197 plants. Among the six populations of *H. chinensis*, the HP, HQ, SMG, and NS populations had the largest proportions of seedlings in size class I, with 68.0%, 67.4%, 68.5%, and 85.4%, respectively (Figure 2B). The WH and YL populations had the largest proportions of seedlings in size class III, with 42.5% and 37.0%, respectively.

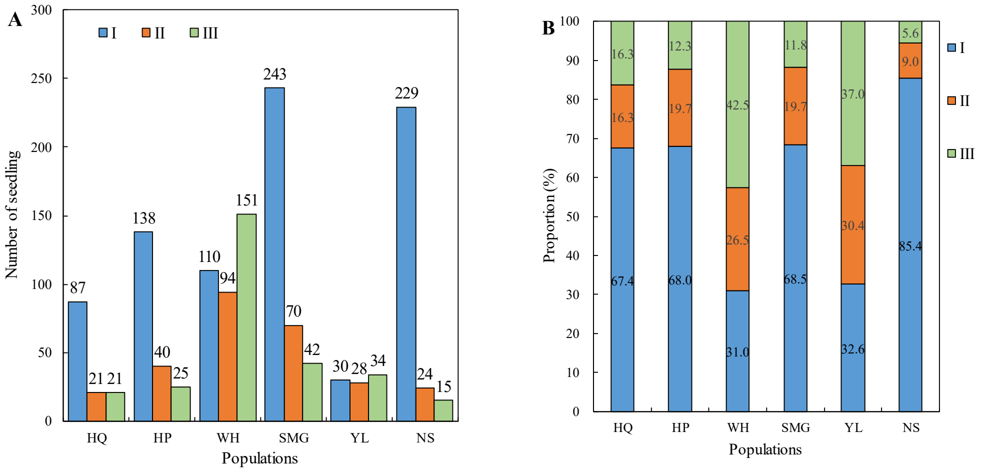

Figure 2. Numbers and proportions of seedlings in different size classes in *H. chinensis* populations. (**A**): Numbers of seedlings in populations of *H. chinensis*; (**B**): proportions of seedlings in populations of *H. chinensis*; I: seedlings with a height of 0–50 cm; II: seedlings with a height of 50–100 cm; III: seedlings with a height greater than 100 cm and DBH less than 2.5 cm.

Based on the statistical results in terms of various indices, the seedlings in three size classes (size classes I, II, and III) in the HQ, SMG, and YL populations all exhibited aggregated distributions across the three scales (5 m × 5 m, 5 m × 10 m, and 10 m × 10 m). The seedlings in size classes II and III in the HP population exhibited aggregated distributions at all three scales, whereas the seedlings in size class I had aggregated distributions at the 5 m × 5 m and 5 m × 10 m scales, and an even distribution at the 10 m × 10 m scale (Table 2). The seedlings in size classes I and III in the WH population exhibited aggregated distributions at all three scales, whereas the seedlings in size class II were clumped at the 5 m × 5 m and 5 m × 10 m scales, and they had an even distribution at the 10 m × 10 m scale. The seedlings in size classes I and II in the NS population exhibited aggregated distributions across all three scales, whereas the seedlings in size class III had even distributions at all scales (Table 2).

The negative binomial parameter (K) and Morisita's index (I_δ) can be used to measure the degree of clustering, and they objectively reflect the intensity of the pattern. A smaller K value indicates a greater degree of aggregation, whereas a larger I_δ, denotes a greater degree of aggregation. The aggregation intensities of seedlings in the three size classes in the HQ, SMG, and YL populations all decreased as the sample plot scale increased. The aggregation intensities of seedlings in size classes II and III in the HP population, size classes I and III in the WH population, and size class I in the NS population also decreased as the sample plot scale increased (Table 2). Among the six populations, the aggregation intensity was highest for seedlings in size class I in the HQ population, and the aggregation intensity was highest for seedlings in size classes II and III in the SMG population.

Across the three scales, the aggregation intensity of seedlings in the SMG population increased with the size class, whereas the aggregation intensity of seedlings in the NS population decreased with the size class, and the aggregation intensity of seedlings in the YL population tended to increase initially and then decrease with the size class. At the 5 m × 5 m scale, the aggregation intensities of seedlings in the HQ and WH populations decreased with the size class, whereas the aggregation intensity of seedlings in the HP population increased with the size class. At the 5 m × 10 m scale, the aggregation intensities of seedlings in the HQ and HP populations tended to increase initially and then decrease with the size class, whereas the aggregation intensity of seedlings in the WH population tended to decrease initially and then increase with the size class. At the 10 m × 10 m scale, the aggregation intensity of seedlings in the HP population tended to increase initially and then decrease with the size class, whereas the aggregation intensities of seedlings in the WH and HQ populations tended to decrease initially and then increase with the size class.

Table 2. Spatial distributions of *H. chinensis* seedlings with different regeneration grades.

Population	Size Class	Sampling Scale (m)	*t*-Test	*C*	*I*	*K*	*m**	*PAI*	*Ca*	I_δ	Distribution Type	λ
HQ	I	5 × 5	32.48 **	14.8	13.8	0.5	21.1	2.9	1.9	2.8	C	27.3
		5 × 10	18.34 **	12.6	11.6	1.3	26.1	1.8	0.8	1.7	C	40.0
		10 × 10	3.28	4.3	3.3	8.9	32.3	1.1	0.1	1.1	C	46.7
	II	5 × 5	6.94 **	4.0	3.0	0.6	4.7	2.7	1.7	2.6	C	6.2
		5 × 10	3.43 *	3.2	2.2	1.6	5.7	1.6	0.6	1.5	C	8.9
		10 × 10	0.29	1.3	0.3	24.5	7.3	1.0	0.0	1.0	C	9.5
	III	5 × 5	6.46 **	3.8	2.8	0.6	4.5	2.6	1.6	2.5	C	6.2
		5 × 10	3.98 *	3.5	2.5	1.4	6.0	1.7	0.7	1.6	C	9.3
		10 × 10	0.86	1.9	0.9	8.2	7.9	1.1	0.1	1.1	C	11.4
HP	I	5 × 5	17.47 **	8.5	7.5	1.5	19.0	1.6	0.6	1.6	C	29.7
		5 × 10	8.02 **	6.1	5.1	4.5	28.1	1.2	0.2	1.2	C	43.1
		10 × 10	−0.80	0.2	−0.8	−57.2	45.2	1.0	0.0	1.0	U	—
	II	5 × 5	6.14 **	3.6	2.6	1.3	6.0	1.8	0.8	1.7	C	9.1
		5 × 10	2.56	2.6	1.6	4.1	8.3	1.2	0.2	1.2	C	12.8
		10 × 10	2.93	3.9	2.9	4.6	16.3	1.2	0.2	1.2	C	24.9
	III	5 × 5	4.09 **	2.7	1.7	1.2	3.8	1.8	0.8	1.8	C	5.8
		5 × 10	1.21	1.8	0.8	5.4	4.9	1.2	0.2	1.2	C	7.5
		10 × 10	0.24	1.2	0.2	34.7	8.6	1.0	0.0	1.0	C	10.8
WH	I	5 × 5	20.63 **	9.8	8.8	1.0	18.0	2.0	1.0	1.9	C	27.0
		5 × 10	14.90 **	10.4	9.4	1.9	27.8	1.5	0.5	1.4	C	43.8
		10 × 10	10.49 **	11.5	10.5	3.5	47.2	1.3	0.3	1.2	C	73.7
	II	5 × 5	12.40 **	6.3	5.3	1.5	13.1	1.7	0.7	1.6	C	20.5
		5 × 10	7.81 **	5.9	4.9	3.2	20.6	1.3	0.3	1.3	C	32.4
		10 × 10	−0.93	0.1	−0.9	−33.9	30.4	1.0	0.0	1.0	U	—
	III	5 × 5	20.75 **	9.8	8.8	1.4	21.4	1.7	0.7	1.6	C	33.3
		5 × 10	24.97 **	16.8	15.8	1.6	41.0	1.6	0.6	1.5	C	64.2
		10 × 10	16.29 **	17.3	16.3	3.1	66.6	1.3	0.3	1.2	C	104.7
SMG	I	5 × 5	39.43 **	17.8	16.8	1.2	37.1	1.8	0.8	1.8	C	56.6
		5 × 10	40.44 **	26.6	25.6	1.6	66.1	1.6	0.6	1.5	C	103.5
		10 × 10	1.38	2.4	1.4	58.6	82.4	1.0	0.0	1.0	C	99.2
	II	5 × 5	41.21 **	18.6	17.6	0.3	23.4	4.0	3.0	3.8	C	22.4
		5 × 10	36.62 **	24.2	23.2	0.5	34.8	3.0	2.0	2.7	C	44.7
		10 × 10	13.24 **	14.2	13.2	1.8	36.6	1.6	0.6	1.4	C	57.6
	III	5 × 5	33.29 **	15.2	14.2	0.2	17.7	5.1	4.1	4.8	C	13.4
		5 × 10	27.24 **	18.2	17.2	0.4	24.2	3.5	2.5	3.1	C	26.9
		10 × 10	13.36 **	14.4	13.4	1.0	27.4	2.0	1.0	1.7	C	41.2
YL	I	5 × 5	1.15	1.5	0.5	5.1	3.0	1.2	0.2	1.2	C	4.6
		5 × 10	0.82	1.5	0.5	9.6	5.5	1.1	0.1	1.1	C	7.9
		10 × 10	0.30	1.3	0.3	33.3	10.3	1.0	0.0	1.0	C	13.0
	II	5 × 5	9.87 **	5.2	4.2	0.4	6.0	3.4	2.4	3.3	C	6.7
		5 × 10	5.09 **	4.2	3.2	1.1	6.9	1.9	0.9	1.8	C	10.5
		10 × 10	2.05	3.0	2.0	3.6	9.4	1.3	0.3	1.2	C	14.6
	III	5 × 5	1.69	1.7	0.7	3.9	3.6	1.3	0.3	1.2	C	5.5
		5 × 10	2.18	2.4	1.4	4.1	7.0	1.2	0.2	1.2	C	10.9
		10 × 10	1.24	2.2	1.2	9.2	12.6	1.1	0.1	1.1	C	18.1
NS	I	5 × 5	78.35 **	34.4	33.4	0.6	52.5	2.8	1.8	2.6	C	69.3
		5 × 10	51.07 **	33.3	32.3	1.2	70.5	1.8	0.8	1.7	C	107.5
		10 × 10	37.55 **	38.5	37.5	2.0	113.9	1.5	0.5	1.3	C	180.1
	II	5 × 5	1.28	1.5	0.5	3.7	2.5	1.3	0.3	1.3	C	5.1
		5 × 10	0.13	1.4	0.4	10.0	4.4	1.1	0.1	1.0	C	6.3
		10 × 10	1.71	1.1	0.1	64.0	8.1	1.0	0.0	1.6	C	9.7
	III	5 × 5	−0.85	0.6	−0.4	−1.1	0.1	0.1	−0.9	0.0	U	-
		5 × 10	−1.26	0.2	−0.8	−1.0	0.0	0.0	−1.0	0.0	U	-
		10 × 10	−0.80	0.2	−0.8	−2.1	0.9	0.5	−0.5	0.6	U	-

Note: I: seedlings with a height of 0–50 cm; II: seedlings with a height of 50–100 cm; III: seedlings with a height greater than 100 cm and DBH less than 2.5 cm; C: diffusion index (variance/mean); *I*: clumping index; *K*: negative binomial distribution; *m**: mean crowding; *PAI*: patchiness index, *Ca*: Cassie index; I_δ: Morisita index; C: aggregated distribution; U: uniform distribution; λ: mean aggregation; * indicates $p < 0.05$, ** indicates $p < 0.01$; - indicates no data.

The mean aggregation (λ) was used to reflect the causes of differences in the spatial distributions of aggregation by *H. chinensis* seedlings. The λ values for the three size classes of seedlings in the six *H. chinensis* populations across the three scales were all greater than 2 (excluding seedlings with a uniform distribution), thereby indicating that the distributions of *H. chinensis* seedlings were influenced by the environment but also by their reproductive capacity, dispersal characteristics, and interspecific competition.

3.2. Differences in Environmental Factors Among H. chinensis Populations

Significant differences (p < 0.05) were found in the soil BD, SM, SOC, AN, AP, and AK among the six *H. chinensis* populations, but the differences in the soil pH were not significant (p > 0.05). In particular, the soil BD was lowest for the WH population at 0.9 g/cm^3, the soil SM contents were highest for the WH and YL populations, the SOC contents were highest for the HP and WH populations at 38.2 g/kg and 35.5 g/kg, respectively, the soil AN and AP contents were highest for the SMG population at 214.9 mg/kg and 26.4 μg/g, respectively, and the AK contents were highest for the HQ, WH, NS, and YL populations (Table 3).

Table 3. Differences in soil physical and chemical properties in *H. chinensis* populations.

Population	BD (g/cm^3)	SM (%)	pH	SOC (g/kg)	AN (mg/kg)	AP (μg/g)	AK (mg/kg)
HQ	1.3 ± 0.02 a	30.7 ± 1.53 ab	4.9 ± 0.78 a	21.3 ± 3.16 bc	190.7 ± 9.75 b	20.8 ± 1.24 b	155.8 ± 4.77 a
HP	1.1 ± 0.02 b	28.0 ± 1.73 b	4.4 ± 0.29 a	38.2 ± 4.64 a	122.2 ± 5.21 e	20.7 ± 0.49 b	142.9 ± 9.40 b
WH	0.9 ± 0.02 d	34.0 ± 2.00 a	4.2 ± 0.09 a	35.5 ± 6.77 a	143.3 ± 6.92 d	19.9 ± 1.19 b	160.2 ± 5.79 a
SMG	1.2 ± 0.03 a	28.7 ± 3.06 b	4.8 ± 0.08 a	14.6 ± 0.82 bc	214.9 ± 7.34 a	26.4 ± 1.30 a	132.6 ± 3.08 b
YL	1.0 ± 0.06 c	33.3 ± 2.08 a	4.2 ± 0.37 a	13.0 ± 5.79 c	162.3 ± 7.24 c	21.6 ± 1.52 b	161.9 ± 5.11 a
NS	1.3 ± 0.01 a	31.3 ± 2.08 ab	4.6 ± 0.31 a	22.7 ± 5.45 b	184.1 ± 6.19 b	22.2 ± 1.31 b	160.4 ± 5.74 a

Note: BD: bulk density; SM: soil moisture content; SOC: soil organic carbon. AN: available nitrogen; AP: available phosphorus; AK: available potassium. Different lowercase letters in the same column indicate significant differences at p < 0.05.

Significant differences (p < 0.05) were also found in the six forest stand factors among the six populations. In particular, CD was largest for the WH population at 80.0%, the RD values were highest for the NS and YL populations at 75.7% and 76.0%, respectively, the litter thickness (LT) values were larger for the WH and SMG populations at 2.8 cm and 3.0 cm, respectively, the humus thickness (HT) was highest for the WH population at 2.8 cm, the shrub cover (SC) values were largest for the HQ and NS populations at 41.6% and 53.7%, respectively, and the shrub height (SH) was highest for the SMG population at 87.7 cm (Table 4).

Table 4. Differences in forest stand factors for *H. chinensis* populations.

Population	CD (%)	RD (%)	LT (cm)	HT (cm)	SC (%)	SH (cm)
HQ	60 ± 0.00 c	62.7 ± 7.02 b	1.5 ± 0.87 b	0.7 ± 0.29 c	41.6 ± 5.95 a	64.7 ± 2.52 b
HP	70 ± 5.00 b	66.3 ± 1.53 b	2.0 ± 0.70 ab	0.8 ± 0.29 bc	17.7 ± 8.02 b	49.7 ± 8.50 c
WH	80 ± 0.00 a	60.3 ± 6.43 b	2.8 ± 0.70 a	2.8 ± 0.76 a	11.6 ± 9.30 b	68.7 ± 3.21 b
SMG	77 ± 5.77 ab	68 ± 3.46 ab	3.0 ± 0.50 a	1.5 ± 0.50 b	18.5 ± 1.20 b	87.7 ± 3.79 a
YL	77 ± 5.77 ab	76.0 ± 2.00 a	1.3 ± 0.25 b	0.5 ± 0.00 c	19.0 ± 3.90 b	72.0 ± 3.00 b
NS	68 ± 7.64 bc	75.7 ± 4.04 a	1.7 ± 0.29 b	0.7 ± 0.29 c	53.7 ± 22.70 a	60.0 ± 13.89 bc

Notes: CD: canopy density; RD: rock bareness rate; LT: litter thickness; HT: humus thickness; SC: shrub cover; SH: shrub height. Different lowercase letters in the same column indicate significant differences at p < 0.05.

3.3. Relationships Between Spatial Distributions of Seedlings and Environmental Factors

For the *H. chinensis* population in the northern foothills of the Shiwandashan Mountains, NS-I had a highly significant positive correlation with RD. NS-II had highly significant positive correlations with CD and HT, a significant positive correlation with SM, highly significant negative correlations with BD and SC, and significant negative correlations with the slope aspect (SA) and mean annual precipitation (MAP). Additionally, NS-III had highly significant positive correlations with SM and HT, significant positive correlations with CD and LT, and significant negative correlations with BD and MAP. Significant correlations were also found among environmental factors, e.g., BD had a highly significant positive correlation with SA, a significant positive correlation with SC, highly significant negative correlations with CD and HT, and a significant negative correlation with LT (Figure 3).

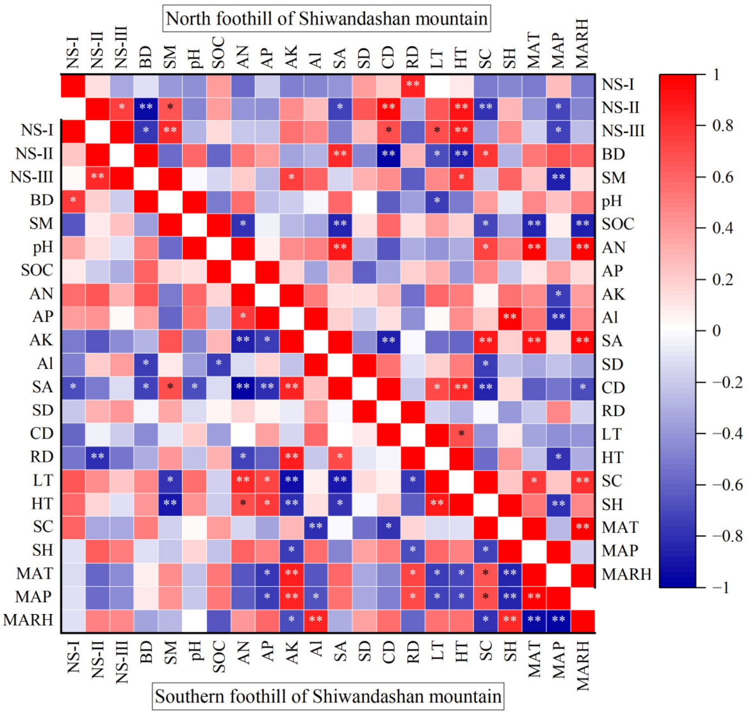

Figure 3. Correlations between numbers of seedlings in *H. chinensis* populations and environmental factors. NS-I: number of size class I seedlings; NS-II: number of size class II seedlings; NS-III: number of size class III seedlings; BD: bulk density; SM: soil moisture content; SOC: soil organic carbon. AN: available nitrogen; AP: available phosphorus; AK: available potassium; Al: altitude; SA: slope aspect; SD: slope degree; CD: canopy density; RD: rock bareness rate; LT: litter thickness. HT: humus thickness; SC: shrub cover; SH: shrub height; MAT: mean annual temperature; MAP: mean annual precipitation; MARH: mean annual relative humidity. * and ** indicate significance at the 0.05 and 0.01 probability levels, respectively.

For the *H. chinensis* population in the southern foothills of the Shiwandashan Mountains, NS-I had a significant positive correlation with BD and a significant negative correlation with SA; NS-II had a highly significant negative correlation with RD. NS-III had no significant correlations with any of the 19 environmental factors. Significant correlations were also found among environmental factors, e.g., AK had highly significant positive correlations with SA, RD, mean annual temperature (MAT), and MAP, highly significant negative correlations with LT and HT, and significant negative correlations with SH and mean annual relative humidity (Figure 3).

By combining forward selection and Monte Carlo testing, environmental factors closely associated with the spatial distributions of *H. chinensis* seedlings were screened further. The main environmental factors that affected the spatial distributions of *H. chinensis* seedlings on the northern and southern foothills of the Shiwandashan Mountains were significantly different. In the northern foothills, environmental factors such as HT, RD, SC, MAT, CD, and SM had significant effects on the spatial distribution of *H. chinensis* seedlings, where HT and RD had the strongest associations, with contribution rates of 53.2% and 32.2%, respectively. In the southern foothills, environmental factors such as RD, SM, CD, AK, and AN had significant effects on the spatial distribution of *H. chinensis* seedlings, where RD, SM, and CD had the strongest associations, with contribution rates of 39.8%, 23.5%, and 15.0%, respectively (Table 5).

Table 5. Forward selection of environmental factors associated with spatial distribution of populations of *H. chinensis* in northern and southern foothills of the Shiwandashan Mountains.

	Northern Foothills						**Southern Foothills**				
	HT	**RD**	**SC**	**MAT**	**CD**	**SM**	**RD**	**SM**	**CD**	**AK**	**AN**
F	7.9	13.2	8.7	4.1	7.3	8.3	4.6	3.8	3.5	5.9	5.8
p	0.004	0.002	0.002	0.044	0.036	0.028	0.014	0.038	0.046	0.036	0.020
R (%)	53.2	32.2	9.3	2.7	1.9	0.6	39.8	23.5	15.0	13.0	5.7

The selected factors were subjected to sorting by RDA relative to the distribution of the number of seedlings. As shown by the RDA sorting diagram, the distributions of the *H. chinensis* seedlings were highly distinct along the environmental gradient. In the northern foothills of the Shiwandashan Mountains, the *H. chinensis* seedlings in size class I tended to be distributed in habitats with higher RD values, and the seedlings in size classes II and III tended to be distributed in habitats with higher CD, HT, and SM values (Figure 4A). In the southern foothills of the Shiwandashan Mountains, the *H. chinensis* seedlings in size classes I and II tended to be distributed in habitats with higher AN contents, and the seedlings in size class III tended to be distributed in habitats with higher AN and SM contents (Figure 4B).

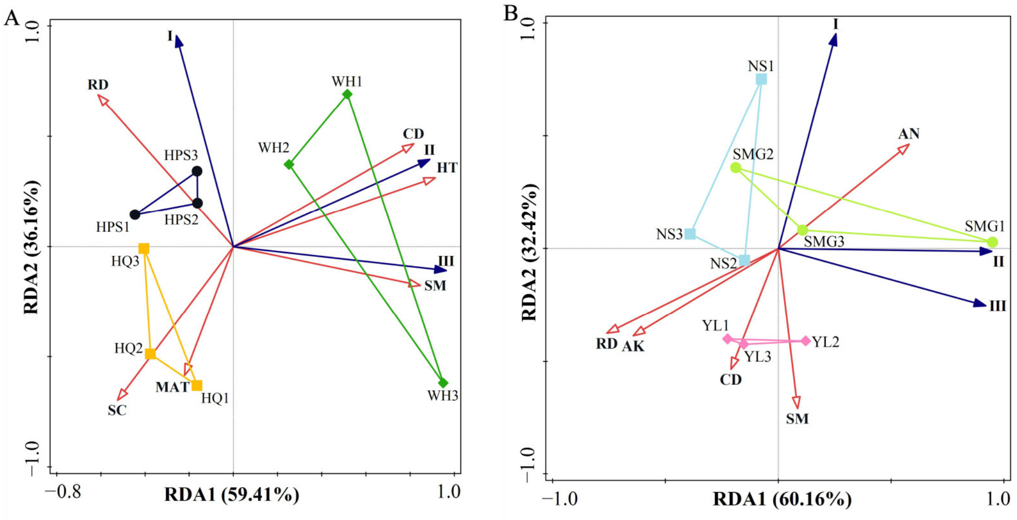

Figure 4. RDA ordination of key environmental factors that affected the spatial distributions of seedlings in *H. chinensis* populations. (**A**): *H. chinensis* population in the northern foothills of the Shiwandashan Mountains; (**B**): *H. chinensis* population in the southern foothills of the Shiwandashan Mountains.

4. Discussion

4.1. Quantitative Characteristics of Regenerated Seedlings in H. chinensis Populations

In this study, according to the seedling quantity characteristics of six populations, the regeneration types were divided into two types: (1) The number of class I seedlings was higher in HP, HQ, SMG, and NS populations, while the number of class II and III seedlings decreased sharply. It indicated the regeneration rate of seedlings within the population was higher, but the survival rate was lower, which was consistent with the results of Jia et al. [20]. (2) Although the number of seedlings in each size class of WH and YL populations was similar, the regeneration rate of the YL population was low, and the survival rate was high, while the regeneration rate of the WH population was relatively high and the survival rate was also high. Four stages, including provenance generation, seed germination, seedling colonization, and sapling growth, need to be completed before successful natural regeneration. Problems at any stage will hinder the success of the population's natural regeneration [27]. In normal years, *H. chinensis* has a large number of seeds, which are mainly felled near the mother plant; the seeds germinate quickly and have a high germination rate [20]. Consequently, a large number of seedlings appear near the mother plant, and the regeneration rate of seedlings is high. Relevant studies have reported that when the density of the same species is high, it is easier to attract specific natural enemies, at the same time, the intraspecific competition and allelopathy are intensified, resulting in higher mortality risk of species in the same high-density area. These factors may lead to the negative density constraint [28,29]. This may be the reason for the high regeneration rate and low survival rate of HP, HQ, SMG, and NS populations. The YL population had a low seedling regeneration rate and high survival rate, which may be due to the limited seed germination caused by their seed quality or habitat conditions. As a result, there were fewer seedlings near the mother tree and no negative density restriction effect was formed, and the survival rate of seedlings was correspondingly high. The high seedling regeneration rate and survival rate of the WH population may be due to the special microhabitat characteristics of the WH population that were more suitable for seedling growth. *H. chinensis* seedlings prefer a cool and moist environment [18]. The WH population had a large canopy density and a thick humus layer, which provided a suitable environment for seedling growth. The specific reasons need to be further studied.

In general, the dominant species will compete for more resources to occupy a dominant position in a community [30]. It is worth noting that in the HP, HQ, SMG, and NS communities, *H. chinensis* was the dominant species in the HP and SMG communities, but not in the HQ and NS communities. However, the types of seedling regeneration in the four communities are consistent. The possible reason is that the ecological niche of the dominant species is different from that of *H. chinensis*. They have differences in resource utilization, living space, and other aspects, which reduce the direct competition between species to a certain extent [31]. Huang et al. [18] have studied the ecological characteristics of *H. chinensis* in the Shiwan Dashan region. They suggested that the competition index between *H. chinensis* and other species was 39.935, while the competition index within species was 64.569, and the competition between seedlings and young trees was higher than that between adult trees. These also indicated that the intraspecific competition was the main type among the individuals of *H. chinensis*.

4.2. Spatial Distributions of H. chinensis Populations

The formation of spatial population distribution patterns is influenced by numerous factors. Under natural conditions, the long-term interactions among various biotic factors (seed dispersal mechanisms, reproductive characteristics, intraspecific and interspecific competition, etc.) and abiotic factors (topography, soil, temperature, moisture, light, etc.) at different scales are considered to be the main causes [32,33]. In the present study, the *H. chinensis* populations had aggregated distributions in most sample plots at the 0–10 m scale and uniform distributions in only some sample plots. Similar spatial distributions have been reported for other rare and endangered plant populations, such as *Scrophularia takesimensis* [34], *Abies georgei* var. *smithii* [35], and *Tamarix chinensis* [17]. The aggregated distributions of *H. chinensis* populations are associated with its biological characteristics and the heterogeneity of its habitats. The seeds of *H. chinensis* have wings that facilitate seed dispersal to some extent, where the seeds can be dispersed over greater distances under the action of wind. However, due to the weight of the seeds, their dispersal is influenced greatly by gravity, and the effect of wind dispersal is much weaker than the gravitational pull on the seeds themselves. Consequently, most seeds fall near the parent plant, especially under the tree canopy, which reduces the likelihood of seeds falling into direct sunlight or dry habitats and losing viability, but it also narrows the range of seed distribution and limits the outward spread of the *H. chinensis* population [36,37]. In addition, the steep terrain and high rock exposure rate in the habitat of *H. chinensis* mean that after seeds mature and fall, they tend to disperse downhill due to gravity and accumulate in depressions in the soil, which leads to a band-like distribution along valleys without external assistance, preventing the population from expanding its range and yielding an aggregated distribution. The seedlings in size class I in the HP population and in size class II in the WH population both had uniform distributions at the 10 m × 10 m scale, possibly due to self-thinning and other-thinning effects in intraspecific and interspecific competition leading to the death of some seedlings and producing a uniform distribution [38], although the actual reasons require further study. The seedlings in size class III in the NS population had a uniform distribution at all three scales, which may have been due to the small number of individuals counted. The variable distribution patterns of *H. chinensis* seedlings validate the view that population distribution patterns are consequences of long-term mutual adaptation and interactions between species and their environment. These patterns are associated with the biological and ecological characteristics of the species and intraspecific and interspecific competition, as well as being closely associated with the habitats of species.

The spatial distributions of populations also vary in different developmental stages. Populations have different ecological niches, physiological needs, and competitive pressures in different life history stages. Individuals form different distribution patterns in different developmental stages to make the best use of limited resources, such as light, heat, moisture, and soil [39,40]. Many studies have shown that as plant populations age, their spatial distributions shift from aggregated to random or uniform patterns, or the degree of clumping gradually decreases [38,41]. However, the results obtained in the present study did not conform to this pattern. In the present study, the spatial distribution of seedlings in the SMG population shifted from an aggregated to uniform distribution as the size class increased, and the intensity of the aggregation of seedlings in the HQ and WH populations decreased as the size class increased at the 5 m × 5 m scale. The distributions of the remaining seedlings in the populations varied at the three scales as the size class increased. These results suggested that there were significant differences in the distributions of seedlings in various size classes among the *H. chinensis* populations, which may have been associated with the sampling area and the environmental conditions where they were located. First, the spatial patterns of species are strongly scale-dependent, and they change with the scale. *H. chinensis* has a narrow distribution range, where trees are scattered or occur in small patches along stream banks in the Shiwandashan Mountains region. The harsh habitat conditions also limited the size of the sample plots. We only selected three 10 m × 10 m sample plots for each population, which are relatively small areas, and they may have affected the spatial patterns of the populations as they aged. Second, the spatial distributions of the populations were influenced by habitat heterogeneity. The geographical and climatic factors were similar for the three populations in the southern foothills and the three populations in the northern foothills, but significant differences were found in some environmental factors (such as the soil properties, light intensity within the forest stand, and vegetation conditions) among populations. These spatially heterogeneous environmental factors led to differences in the growth, recruitment, and mortality of individual plants, thereby resulting in different seedling distribution patterns in various size classes among the *H. chinensis* populations.

4.3. Key Environmental Factors That Affected the Distributions of H. chinensis Populations

The mean aggregation (λ) indicated that the aggregated distributions of *H. chinensis* populations were primarily caused by biotic factors and environmental factors. Biotic factors include biological characteristics, intraspecific and interspecific competition, and external disturbances. Environmental factors include nutrient distributions and spatial heterogeneity. Jia et al. [20] analyzed the structural characteristics of the *H. chinensis* population in the Shiwandashan region. They found that the *H. chinensis* population had a higher mortality rate during the juvenile stage, where the population dynamic index, sensitivity to random disturbance index, and risk probability of random disturbance were 52.61%, 4.38%, and 8.33%, respectively. The population was sensitive to external disturbances, and the environment had a strong selection effect on individuals. In the present study, we demonstrated that HT, RD, SC, MAT, CD, and SM were the dominant factors that affected the distribution of *H. chinensis* seedlings in the northern foothills of the Shiwandashan Mountains, and RD, SM, CD, AK, and AN were the dominant factors in the southern foothills. These suggested that RD, SM, and CD had widespread impacts on the distribution of *H. chinensis* seedlings, and other factors may have been associated with habitat heterogeneity.

Correlation analysis and RDA indicated that in the northern foothills of the Shiwandashan Mountains, the distribution of *H. chinensis* seedlings in size class I was highly positively correlated with RD. The seedlings in size class I tended to be distributed in habitats with higher rock exposure rates. The seedlings in size classes II and III had negative correlations with RD. While in the southern foothills of the Shiwandashan Mountains, the distribution of *H. chinensis* seedlings in size class III was negatively correlated with RD. The reason for this was that the *H. chinensis* seedlings in the population in the northern foothills were distributed on slopes 1.0 m to 1.5 m above the banks of streams where exposed rocks in the forest formed large natural outcrops. When the seeds of *H. chinensis* mature and fall, the exposed rocks hinder seed dispersal, and thus seeds tend to accumulate on rock surfaces or in the crevices and grooves created by rocks. Seeds that fall on the rocks may die due to water loss (the seeds of *H. chinensis* are recalcitrant and readily die from desiccation) [37]. By contrast, seeds that fall into crevices and grooves and nearby areas are protected from direct sunlight by the rocks and benefit from the accumulation of precipitation, litter, and nutrients in these areas among the exposed rocks [42,43], providing a favorable environment for seed germination and the growth of early seedlings. However, as the seedlings grow and develop, the growth environment within the crevices and grooves could not meet the soil requirements for root growth. In the present study, this lack of soil led to seedling death and reduced the probability of seedlings developing into size classes II and III, which is why negative correlations were found the distributions of seedlings in size classes II and III and the rock exposure rates. In the southern foothills of the Shiwandashan Mountains, the reason why rock exposure restricted the distribution of seedlings in size class I was that the *H. chinensis* population was distributed directly along the banks of streams, where the crevices and grooves formed by rocks in the forest were often filled with small pebbles due to stream erosion. Seeds that fell on these rocks were likely to die from desiccation, and it was difficult for seedlings to germinate. Even when seeds successfully germinated into seedlings, they were unlikely to develop into size classes II or III due to soil limitations. Seeds that fell outside the exposed rock areas in soil containing higher levels of AN could directly absorb and utilize this nutrient after seedling germination. Thus, the chlorophyll content and superoxide dismutase activity could be improved, as well as enhance the effect of photosynthesis and the ability to resist external disturbances to increase the probability of seedlings being categorized as size classes II and III [44,45]. Therefore, in the southern foothills of the Shiwandashan Mountains, the *H. chinensis* seedlings in size class I tended to be distributed in habitats with higher AN content.

Analysis of the dominant factors that affected the distributions of *H. chinensis* seedlings in size classes II and III showed that in the northern foothills, the distributions of these seedlings were positively correlated with CD, HT, and SM and negatively correlated with

SC and MAT. By contrast, in the southern foothills, the distributions of these seedlings were positively correlated with AN and SM and negatively correlated with AK and CD. Thus, the distributions of seedlings in size classes II and III in the northern foothills were primarily influenced by temperature, light, and moisture, whereas the distributions in the southern foothills were mainly influenced by light, moisture, and soil nutrients. Claussen et al. [46] also demonstrated that light, temperature, and moisture significantly affected seed germination and seedling growth in their study of the regeneration patterns of tropical rainforest tree species. *H. chinensis* seeds and seedlings are sensitive to drought. The seasonal drought in the Shiwandashan region leads to decreased stream water levels and significantly affects the survival of *H. chinensis* seedlings, in particular, in the northern foothills, where members of the *H. chinensis* population were farther from the banks of streams (horizontal distance: 1.2 m–1.8 m; vertical distance: 1.2 m–2.2 m). Only in the areas with higher CD, lower temperatures, and thicker humus layers could provide sufficient moisture for seedling growth. Although the growth of *H. chinensis* seedlings requires a shaded environment, it also requires a certain amount of sunlight [18]. In forest stands with high canopy density, if the shrub layer coverage is too high, it may excessively block sunlight, affecting the photosynthesis and growth and development of seedlings [47]. Therefore, the seedlings in size classes II and III in the northern foothills tend to be distributed in habitats with high canopy density, thick humus layer, high soil moisture content, and low shrub cover. By contrast, the population of *H. chinensis* in the southern foothills has abundant annual rainfall. Under the condition of sufficient water, the seedlings in size classes II and III were distributed in the areas with higher content of alkali-hydrolytic nitrogen, less canopy and sufficient sunlight to obtain resources to improve the photosynthesis and biomass. This will help improve the competitiveness and survival rate of seedlings. The distribution of the seedlings in size classes II and III in the southern foothills had a negative correlation with AK, which indicated that the growth of size classes II and III seedlings was inhibited by AK in the soil. The reason may be that AK in soil affected the absorption of nitrogen, calcium, magnesium, zinc, and other elements by seedlings and destroyed the acid–base balance and ion balance of soil, leading to the poor growth of seedlings [48,49]. The regeneration niche hypothesis suggests that species form differentiation niches in different life history stages by balancing vegetative competition and reproductive regeneration strategies. Environmental factor preferences change to different degrees to avoid competitive exclusion [50]. The different preferences for environmental factors among the *H. chinensis* seedlings in three size classes in various populations are consistent with the regeneration niche hypothesis.

5. Conclusions

Among the six *H. chinensis* populations, the largest proportions of seedlings in size class I were found in the HP, HQ, SMG, and NS populations, whereas the largest proportions of seedlings in size class III were in the WH and YL populations. In most of the populations, the seedlings in various size classes exhibited aggregated distributions at the three scales, and the intensity of aggregation for seedlings in most size classes decreased as the sample plot scale increased. At the same scale, the trend in the intensity of seedling aggregation as the size class increased varied among different populations. The mean aggregations for seedlings in the three size classes in the six *H. chinensis* populations were all greater than two at the three scales (except for uniformly distributed seedlings). It indicated that the spatial distributions of seedlings were influenced by environmental factors, reproductive capacity, dispersal characteristics, and interspecific competition. Environmental factors such as HT, RD, SC, MAT, CD, and SM were the dominant factors that affected the spatial distribution of *H. chinensis* seedlings in the northern foothills of the Shiwandashan Mountains, and RD, SM, CD, AK, and AN were the dominant factors in the southern foothills. In the northern foothills, seedlings in size class I tended to be distributed in habitats with a higher rock exposure rate, and the seedlings in size classes II and III tended to be distributed in habitats with higher CD, HT, and SM values. In the southern foothills, seedlings in size classes I and II tended to be distributed in habitats with higher soil AN contents, and seedlings in size class III tended to be distributed in habitats with higher AN and SM contents.

In summary, we make the following recommendations to improve the management, protection, and restoration of wild *H. chinensis* resources. For the *H. chinensis* populations in the southern foothills of the Shiwandashan Mountains, it is important to focus on the management and protection of seedlings in size class I, especially those growing in stone crevices and grooves, which can be supplemented with artificial soil to increase the soil thickness and improve the survival rate of seedlings. During the dry season, regular watering should be applied to increase the SM content, and the coverage of the shrub layer should be reduced in an appropriate manner. In the northern foothills of the Shiwandashan Mountains, the *H. chinensis* populations should be managed by regular fertilization with nitrogen and watering to increase the AN and SM contents.

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Abbreviations

The following abbreviations are used in this manuscript:

HQ	Hongqi Forest Farm in Jiao'an Town, Shangsi County
HP	Huangpao Mountain in the Shiwandashan National Nature Reserve in Jiao'an Town, Shangsi County
WH	Wanghao Village in Gongzheng Township, Shangsi County
SMG	Shimengu Valley in Pingfeng Forest Park in Malu Town, Dongxing City
YL	Yanglan Village in Nasuo Town, Fangcheng District, Fangchenggang City s
NS	Nanshan Station at Golden Camellia National Nature Reserve in Nasuo Town, Fangcheng District, Fangchenggang City
Al	Altitude
MAT	Mean annual temperature
MAP	Mean annual precipitation
MARH	Mean annual relative humidity
SA	Slope aspect
SD	Slope degree
CD	Canopy density
RD	Rock bareness rate
HDS	Horizontal distance from stream
VDS	Vertical distance from stream
I	Seedling with height of 0–50 cm

DS	Distance from stream
II	Seedling with height of 50–100 cm
III	Seedling with height greater than 100 cm and DBH less than 2.5 cm
C	Diffusion index
I	Clumping index
K	Negative binomial distribution
m^*	Mean crowding
PAI	Patchiness index
Ca	Cassie index
I_δ	Morisita index
C	Aggregated distribution
U	Uniform distribution
λ	Mean aggregation
BD	Bulk density
SM	Soil moisture content
SOC	Soil organic carbon
AN	Available nitrogen
AP	Available phosphorus
AK	Available potassium
NS-I	Number of grade I seedling
NS-II	Number of grade II seedlings
NS-III	Number of grade III seedlings
LT	Litter thickness
HT	Humus thickness
SC	Shrub cover
SH	Shrub height

References

1. Cai, C.; Zhang, X.; Zha, J.; Li, J.; Li, J. Predicting climate change impacts on the rare and endangered *Horsfieldia tetratepala* in China. *Forests* **2022**, *13*, 1051. [CrossRef]
2. Harvey-Brown, Y.; Shaw, K.; Davies, K.; Rivers, M. Using the global tree assessment at multiple scales of planning and action. *Diversity* **2022**, *14*, 891. [CrossRef]
3. Xu, J.; Xiao, P.; Li, T.T.; Wang, Z. Research Progress on endangered plants: A bibliometric analysis. *Biodivers. Conserv.* **2022**, *31*, 1125–1147. [CrossRef]
4. Xu, Y.; Zang, R. Conservation of rare and endangered plant species in China. *iScience* **2023**, *26*, 106008. [CrossRef]
5. Xiao, Z.; Zou, T.; Lu, S.; Xu, Z. Soil microorganisms interacting with residue-derived allelochemicals effects on seed germination. *Saudi J. Biol. Sci.* **2020**, *27*, 1057–1065. [CrossRef] [PubMed]
6. Gao, R.; Hou, J.; Zhao, R.; Yang, X.; Hou, X.; Huo, L.; Hidayati, S.N.; Walck, J.L. Seed dormancy and germination of a critically endangered plant, *Elaeagnus mollis*, on the Loess Plateau of China. *Eur. J. Forest Res.* **2021**, *140*, 451–461. [CrossRef]
7. Yang, Y.C.; Huang, L.; Qian, S.H.; Fukuda, K. Completing the life history of *Castanopsis fargesii*: Changes in the seed dispersal, seedling and sapling recruitment patterns. *Eur. J. Forest Res.* **2015**, *134*, 1143–1154. [CrossRef]
8. Liu, H.; Chen, Q.; Chen, Y.; Xu, Z.; Dai, Y.; Liu, Y.; Jiang, Y.; Peng, X.; Li, H.; Wang, J.; et al. Effects of biotic/abiotic factors on the seedling regeneration of *Dacrydium pectinatum* formations in tropical montane forests on Hainan Island, China. *Glob. Ecol. Conserv.* **2020**, *24*, e01370. [CrossRef]
9. Atanasso, J.A.; Mensah, S.; Salako, K.V.; Tohoun, R.J.; Glèlè Kakaï, R.; Assogbadjo, A.E. Factors affecting survival of seedling of *Afzelia africana*, a threatened tropical timber species in West Africa. *Trop. Ecol.* **2021**, *62*, 443–452. [CrossRef]
10. Lusk, C.H.; Laughlin, D.C. Regeneration patterns, environmental filtering and tree species coexistence in a temperate forest. *New Phytol.* **2017**, *213*, 657–668. [CrossRef]
11. Li, W.; Zhang, G.F. Population structure and spatial pattern of the endemic and endangered subtropical tree *Parrotia subaequalis* (Hamamelidaceae). *Flora* **2015**, *212*, 10–18. [CrossRef]
12. Dong, H.; Zhang, N.; Shen, S.; Zhu, S.; Fan, S.; Lu, Y. Effects of climate change on the spatial distribution of the threatened species *Rhododendron purdomii* in Qinling-Daba mountains of Central China: Implications for conservation. *Sustainability* **2023**, *15*, 3181. [CrossRef]

13. Law, R.; Illian, J.; Burslem, D.F.; Gratzer, G.; Gunatilleke, C.V.S.; Gunatilleke, I.A.U.N. Ecological information from spatial patterns of plants: Insights from point process theory. *J. Ecol.* **2009**, *97*, 616–628. [CrossRef]
14. Yusup, A.; Halik, Ü.; Abliz, A.; Aishan, T.; Keyimu, M.; Wei, J. Population structure and spatial distribution pattern of *Populus euphratica* riparian forest under environmental heterogeneity along the Tarim River, Northwest China. *Front. Plant Sci.* **2022**, *13*, 844819. [CrossRef] [PubMed]
15. Zhao, C.; Zhao, W.; Jin, M.; Zhou, J.; Ta, F.; Wang, L. Spatial patterns of *Picea crassifolia* driven by environmental heterogeneity and intraspecific interactions. *J. For. Res.* **2023**, *34*, 949–962. [CrossRef]
16. Liu, H.D.; Chen, Q.; Xu, Z.Y.; Wu, C.Y.; Chen, Y.F. Natural population structure and spatial distribution pattern of rare and endangered species *Dacrydium pectinatum*. *Acta Ecol. Sinica.* **2020**, *40*, 2985–2995.
17. Chen, P.; Xia, J.; Ma, H.; Gao, F.; Dong, M.; Xing, X.; Li, C. Analysis of spatial distribution pattern and its influencing factors of the *Tamarix chinensis* population on the beach of the muddy coastal zone of Bohai Bay. *Ecol. Indic.* **2022**, *140*, 109016. [CrossRef]
18. Huang, S.; Chen, H.; Tang, W.; Luo, W.; Wang, Y. Biological and ecological characteristics of *Hopea chinensis*, a plant endemic to Guangxi. *Biodiv. Sci.* **2008**, *16*, 15–23.
19. Shi, Y.; Duan, N.; Liu, B. Complete chloroplast genome sequence of *Hopea chinensis* (Dipterocarpaceae), a rare and critically endangered species. *Mitochondrial DNA B* **2019**, *4*, 4079–4080. [CrossRef]
20. Jia, Q.Y.; Liu, X.S.; Liao, N.Y.; Huang, H.M.; Huang, R.L.; Xiao, Y.F. Population structure and dynamics characteristics of an extremely small population plant *Hopea chinensis* (Merr.) Hand. –Mazz. *Southwest China J. Agr. Sci.* **2024**, *37*, 1078–1086.
21. Jiang, D.; Luo, Y.; Lin, J.; He, Q.; Qin, L.; Ling, Y. Spatial distribution pattern and correlation of dominant species of evergreen broad-leaved forest in Shiwandashan mountain. *J. Cent. South Univ. Forest. Technol.* **2024**, *44*, 151–161.
22. Zhang, Z.; Hu, B.; Qiu, H. Comprehensive assessment of ecological risk in southwest Guangxi-Beibu bay based on DPSIR model and OWA-GIS. *Ecol. Indic.* **2021**, *132*, 108334. [CrossRef]
23. Tong, H.; Pan, C.; Zhao, S.; Hu, W.; Tian, C.; Song, M. Relationship between microhabitat factors and natural regeneration seedling traits of *Picea schrenkiana* var. *tianschanica*. *J. Forest Environ.* **2023**, *43*, 160–168.
24. Lu, R.K. *Analysis Methods of Soil Agricultural Chemistry*; China Agricultural Science and Technology Press: Beijing, China, 1999; pp. 474–490.
25. Diaz, S.; Mercado, C.; Alvarez-Cardenas, S. Structure and population dynamics of *Pinus lagunae* MF. Passini. *Forest Ecol. Manag.* **2000**, *134*, 249–256. [CrossRef]
26. Di, H.; Liu, J.Q.; Ding, G.M. Changes of the spatial distribution pattern of Qinghai spruce populations along the altitude gradient in the Dongdahe forest area. *Gansu Sci. Technol.* **2012**, *28*, 149–152.
27. Vieira, D.L.; Scariot, A. Principles of natural regeneration of tropical dry forests for restoration. *Restor. Ecol.* **2006**, *14*, 11–20. [CrossRef]
28. Janzen, D.H. Herbivores and the number of tree species in tropical forests. *Am. Nat.* **1970**, *104*, 501–528. [CrossRef]
29. Paine, C.T.; Norden, N.; Chave, J.; Forget, P.M.; Fortunel, C.; Dexter, K.G.; Baraloto, C. Phylogenetic density dependence and environmental filtering predict seedling mortality in a tropical forest. *Ecol. Lett.* **2012**, *15*, 34–41. [CrossRef]
30. Smith, M.D.; Knapp, A.K. Dominant species maintain ecosystem function with non-random species loss. *Ecol. Lett.* **2003**, *6*, 509–517. [CrossRef]
31. Ingram, T.; Costa-Pereira, R.; Araújo, M.S. The dimensionality of individual niche variation. *Ecology* **2018**, *99*, 536–549. [CrossRef]
32. Condit, R.; Ashton, P.S.; Baker, P.; Bunyavejchewin, S.; Gunatilleke, S.; Gunatilleke, N. Spatial patterns in the distribution of tropical tree species. *Science* **2000**, *288*, 1414–1418. [CrossRef] [PubMed]
33. Zhang, L.; Gao, Y.; Li, J.; Zhang, C.; Li, M.; Hu, Z.; Cui, X. Effects of grazing disturbance of spatial distribution pattern and interspecies relationship of two desert shrubs. *J. For. Res.* **2022**, *33*, 507–518. [CrossRef]
34. Lim, Y.; Na, S.T.; Lee, S.J.; Cho, K.H.; Shin, H. Spatial distribution patterns and implications for conservation of *Scrophularia takesimensis* (Scrophulariaceae), an endangered endemic species on Ulleung Island, Korea. *J. Plant Biol.* **2008**, *51*, 213–220. [CrossRef]
35. Shen, Z.; Lu, J.; Hua, M.; Fang, J. Spatial pattern analysis and associations of different growth stages of populations of *Abies georgei* var. *smithii in Southeast Tibet, China. J. Mt. Sci.* **2016**, *13*, 2170–2181.
36. Tang, W.X.; Mao, S.Z.; Pan, B.; Huang, S.X.; Mo, L.; Luo, W.H. Spatial distribution pattern of seed rain and seed germination characteristics of endangered plant *Hopea chinensis*. *J. Fujian Coll. For.* **2009**, *29*, 97–102.
37. Liu, X.; Xiao, Y.; Ling, Y.; Liao, N.; Wang, R.; Wang, Y.; Liang, H.; Li, J.; Chen, F. Effects of seed biological characteristics and environmental factors on seed germination of the critically endangered species *Hopea chinensis* (Merr.) Hand.-Mazz. in China. *Forests* **2023**, *14*, 1975. [CrossRef]
38. Jiang, J.; DeAngelis, D.L.; Zhang, B.; Cohen, J.E. Population age and initial density in a patchy environment affect the occurrence of abrupt transitions in a birth-and-death model of Taylor's law. *Ecol. Model.* **2014**, *289*, 59–65. [CrossRef]
39. Lai, J.; Mi, X.; Ren, H.; Ma, K. Species-habitat associations change in a subtropical forest of China. *J. Veg. Sci.* **2009**, *20*, 415–423. [CrossRef]

40. Velázquez, E.; Martínez, I.; Getzin, S.; Moloney, K.A.; Wiegand, T. An evaluation of the state of spatial point pattern analysis in ecology. *Ecography* **2016**, *39*, 1042–1055. [CrossRef]
41. Wilcox, C.; Elderd, B. The effect of density-dependent catastrophes on population persistence time. *J. Appl. Ecol.* **2003**, *40*, 859–871. [CrossRef]
42. Wang, D.; Shen, Y.; Li, Y.; Huang, J. Rock outcrops redistribute organic carbon and nutrients to nearby soil patches in three Karst ecosystems in SW China. *PLoS ONE* **2016**, *11*, e0160773. [CrossRef] [PubMed]
43. Shen, Y.X.; Wang, Q.H.; Zhao, Z.M.; Yuan, C. Fine-scale effect of karst rock outcrops on adjacent soil and plant communities in Southwest China. *Catena* **2022**, *219*, 106592. [CrossRef]
44. Mao, P.; Zhang, Y.; Cao, B.; Guo, L.; Shao, H.; Cao, Z.; Jiang, Q.; Wang, X. Effects of salt stress on eco-physiological characteristics in *Robinia pseudoacacia* based on salt-soil rhizosphere. *Sci Total Environ* **2016**, *568*, 118–123. [CrossRef] [PubMed]
45. Han, J.; Gu, L.; Wen, J.; Sun, Y. Inference of photosynthetic capacity parameters from chlorophyll a fluorescence is affected by redox state of PSII reaction centers. *Plant Cell Environ.* **2022**, *45*, 1298–1314. [CrossRef] [PubMed]
46. Claussen, J.W. Acclimation abilities of three tropical rainforest seedlings to an increase in light intensity. *Forest Ecol. Manag.* **1996**, *80*, 245–255. [CrossRef]
47. Fan, W.; Guo, H.; Wang, X.; Duan, R. The effects of microhabitat, plant litter, and seed burial on the regeneration of *Quercus wutaishanica* and *Pinus tabulaeformis*. *Scand. J. Forest Res.* **2014**, *29*, 183–192. [CrossRef]
48. Wright, S.J.; Yavitt, J.B.; Wurzburger, N.; Turner, B.L.; Tanner, E.V.J.; Sayer, E.J.; Santiago, L.S.; Kaspari, M.; Hedin, L.O.; Harms, K.E.; et al. Potassium, phosphorus, or nitrogen limit root allocation, tree growth, or litter production in a lowland tropical forest. *Ecology* **2011**, *92*, 1616–1625. [CrossRef]
49. Daoud, B.; Pawelzik, E.; Naumann, M. Different potassium fertilization levels influence water-use efficiency, yield, and fruit quality attributes of cocktail tomato—A comparative study of deficient-to-excessive supply. *Sci. Hortic-Amst.* **2020**, *272*, 109562. [CrossRef]
50. Araújo, M.S.; Bolnick, D.I.; Layman, C.A. The ecological causes of individual specialization. *Ecol. Lett.* **2011**, *14*, 948–958. [CrossRef]