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Spatial Distribution Pattern and Genetic Diversity of *Quercus wutaishanica* Mayr Population in Loess Plateau of China

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Abstract: The *Quercus wutaishanica* forest influences the ecological environment and climate characteristics and plays an important ecological role in the Loess Plateau region. However, we still know relatively little about the genetic diversity and spatial distribution of *Q. wutaishanica*. Here, we assessed the genetic diversity of *Q. wutaishanica* using simple sequence repeats and used the point pattern method to analyze the spatial distribution patterns as well as intraspecific relationships. Our results indicate that the diameter structure of the *Q. wutaishanica* population was inverted J-type, showing a growing population. In addition, the population maintained high genetic diversity on a small scale. Due to dispersal constraints, the spatial distribution pattern of *Q. wutaishanica* seedlings (DBH < 1 cm) tended to aggregate at small scales and the degree of aggregation decreased with increasing spatial scale. However, trees (DBH > 5 cm) and saplings (1 cm ≤ DBH < 5 cm) showed more random distribution at the scale, indicating that *Q. wutaishanica* individuals shift from aggregation to random distribution at the spatial scale. In addition, although individuals of different diameter classes showed facilitative (trees vs. saplings, 5–6.5 m) and competitive effects (trees vs. seedlings, 13.5–16 m) on some scales, they showed no correlation on other scales, especially for saplings and seedlings, where they were not correlated on any scale. The results contribute to revealing the status and dynamics of *Q. wutaishanica* in the Loess Plateau, thereby providing a theoretical basis for further study on the maintenance mechanism of the population.

Keywords: *Quercus wutaishanica*; simple sequence repeats (SSR); point pattern; diameter classes structure; intraspecific association

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Citation: Hu, D.; Xu, Y.; Chai, Y.; Tian, T.; Wang, K.; Liu, P.; Wang, M.; Zhu, J.; Hou, D.; Yue, M. Spatial Distribution Pattern and Genetic Diversity of *Quercus wutaishanica* Mayr Population in Loess Plateau of China. *Forests* **2022**, *13*, 1375. https://doi.org/10.3390/f13091375

Academic Editors: Xiao-Dong Yang, Nai-Cheng Wu and Xue-Wei Gong

Received: 27 July 2022
Accepted: 26 August 2022
Published: 28 August 2022

1. Introduction

The spatial distribution patterns of populations, which are the basic constituent units of plant communities, have been one of the trending topics of ecological research [1–3]. Different distribution patterns and spatial correlations can directly reflect the processes of individual biology, intra-species competition, and population–environment interactions [4], and the mechanism of population formation can be deduced from the distribution patterns and spatial correlations of populations [5]. Therefore, studying the spatial distribution patterns of populations and their correlations is of great importance to real successional trends, intra-species relationships, environmental adaptation mechanisms, and the formation of forest community structure [6–8].

One of the main drivers of species coexistence and community dynamics is species competition for scarce resources [9,10]. Competition can occur through density-dependent mortality events, which affect the survival and growth of species by robbing each other of

living space and resources [11,12]. When larger trees disproportionately affect the growth and survival of smaller trees, asymmetric competition between individuals occurs [13]. For example, adult trees may inhibit seedling formation through competition, allelopathy, or increased populations of herbivores and pathogens [14]. Thus, tree size is a key factor influencing the spatial pattern and structure of forest populations.

Biological polymorphism and species diversity are based on genetic variation. Ecological processes such as interspecific interactions and community structure are significantly influenced by genetic diversity [15]. In recent years, the development of polymorphic markers and statistical analysis tools has allowed us to understand population maintenance mechanisms from a molecular perspective. For example, researchers have used inter-simple sequence repeat analysis (ISSR) to determine that genetic variation can explain intraspecific variation in plant–soil biotic interactions [16]. In addition, genetic diversity can also be analyzed by other molecular makers, such as random amplified polymorphic DNA (RAPD), restriction fragment length polymorphisms (RFLPs), amplified fragment length polymorphisms (AFLPs), single nucleotide polymorphisms (SNPs) [17,18] and simple sequence repeats (SSRs) [19]. In the last two decades, SSR markers have become a powerful tool for such studies because they are highly informative, polymorphic, and co-dominant, and present transferability between closely related species [20,21]. Researchers have studied the genetic diversity of some *Quercus* spp. by using SSR markers [22–26], but there are fewer experiments on the study of *Quercus wutaishanica* as a target, especially in the Loess Plateau region, and there are almost no studies on the genetic diversity of *Q. wutaishanica* for this region. Therefore, the study of the genetic diversity of *Q. wutaishanica* is important for understanding the level of species diversity and population genetic structure as well as the development of species conservation strategies and measures.

Q. wutaishanica is a deciduous tree belonging to the *Quercus* subgenus *Quercus* in the Fagaceae family. It is closely related to *Quercus mongolica* and considered by some scholars to be a synonym of the *Q. mongolica*. However, some researchers used SSR and AFLP analysis methods to analyze 15 separately distributed and mixed populations of *Q. wutaishanica* and *Q. mogolica* in China and found that *Q. wutaishanica* and *Q. mogolica* have clearly identifiable independent gene pools not only in separately distributed populations, but also in mixed populations, so they should remain as independent taxonomic units [27]. The Loess Plateau region, with its severe erosion and intense soil erosion, is a key area for ecological restoration in China, and the dynamics of its ecological environment have traditionally received widespread attention. The *Q. wutaishanica* forest is a relatively stable terminal forest community in the Loess Plateau region, which has an important influence on the ecological environment and climate characteristics of the region and plays an important ecological role [28]. At present, research on *Q. wutaishanica* in the Loess Plateau region has focused on taxonomy, morphological, and physiological characteristics [29,30], seed dispersal, and population renewal [31], but less on genetic diversity and spatial distribution patterns. Therefore, in this paper, we investigated populations' genetic diversity and spatial distribution patterns and their associations using SSR analysis and scale-based point pattern analysis, respectively, with populations of *Q. wutaishanica* in the Loess Plateau region as the research object. Specifically, our primary aims were to: (1) assess the population structure and genetic diversity of *Q. wutaishanica*; and (2) determine the distribution pattern and compare differences in the spatial association between trees of different diameter classes. The findings are discussed in the context of conservation and restoration strategies of *Q. wutaishanica* in the Loess Plateau region.

2. Materials and Methods

2.1. Study Area

The research was conducted in the Shuanglong Forest Farm (35°32′06″–35°45′55″ N, 108°33′40″–109°19′41″ E), Yan'an City, Shaanxi Province, China, which belongs to the Ziwuling Mountain region in the middle of the Loess Plateau. This area has a warm-

temperate continental monsoon climate with an average annual temperature of 9–11 °C [32]. The mean annual precipitation is 550–650 mm [33]. The elevation ranges from 800 to 1700 m.

Historically, the natural forests in the Ziwuling Mountain region of the Loess Plateau were widely distributed, but the forests were severely damaged due to the interference of historical human activities [34]. Since the vegetation began to recover naturally, it has been 150 years, and now the Ziwuling Mountain has formed a large and continuous secondary forest landscape [34–36], with a denseness of 0.7–0.9. Typical secondary forest species in the forest area include *Q. wutaishanica*, *Betula platyphylla* Sulk., *Populus davidiana* Dode, etc. Among them, the *Q. wutaishanica* forest was the most widely distributed as the natural climax vegetation [37], and its mixed plants mainly include *Quercus acutissim* var. *acutissima*, *Quercus aliena* Blume, *B. platyphylla*, *Carpinus turczaninowii* Hance, etc. The forest area is currently growing well and playing an important role in the regional ecosystem.

2.2. Data Collection

In July 2018, a 50 m × 50 m plot was set up at the Qiaoshan forest ecosystem positioning and research station in Shaanxi Province, and this plot was divided into 25 quadrats of 10 m × 10 m (Figure 1). We recorded the coordinate position of all *Q. wutaishanica* individuals in the plot, measured diameter at breast height (DBH, defined as 1.3 m above the ground) or basal diameter (for seedlings), and numbered each individual. Then, we divided stems into separate sizes classed based on DBH. We defined seedlings as individuals <1 cm DBH, saplings as ≥1 cm and <5 cm DBH, and trees as ≥5 cm DBH [38,39]. For all saplings and trees, about three fresh and healthy leaves were collected from each plant, placed in a self-sealing bag, and dried with silica gel for genetic analysis.

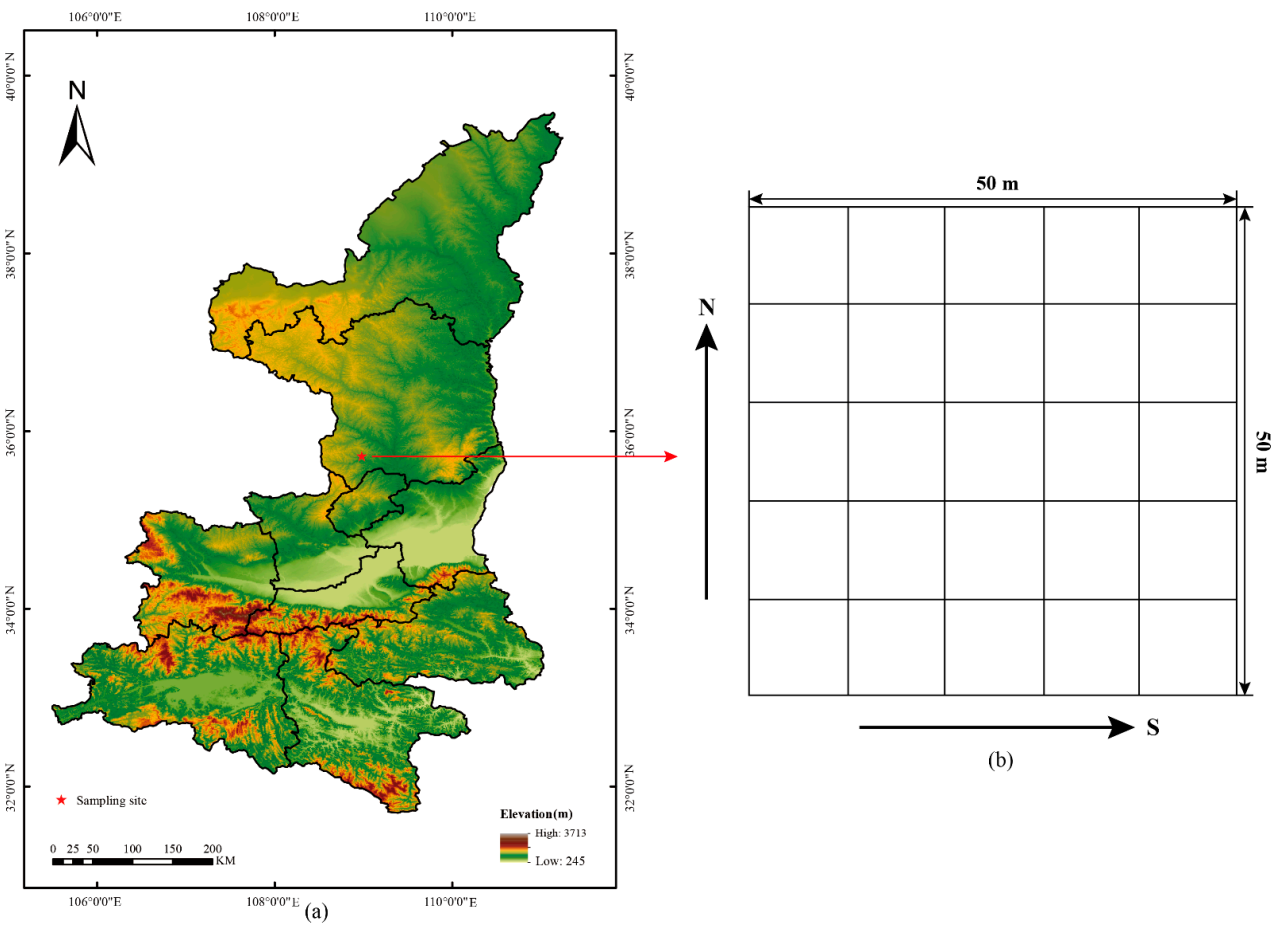

Figure 1. Map of the study area showing (**a**) the sampling site in an elevation map of the administrative regions of the Shaanxi Province, and (**b**) the layout of the plot and quadrats.

2.3. DNA Extraction and SSR Analysis

The dried leaves were ground on a TissueLysser (Scientz-48) before the DNA extraction. Genomic DNA was extracted following the method of Hormaza [40] and using the Speedtools Plant DNA Extraction Kit (Bioteke, Beijing, China) according to the manufacturer's instructions [41–43]. The extracted DNA was measured by a nucleic acid analyzer and quality was checked by 0.8% agarose gel electrophoresis.

A preliminary screening of primers for *Q. wutaishanica* was carried out by reviewing the literature [25,26,44–46], and a total of 20 pairs of primers were finally selected. Forty samples were randomly selected from the extracted DNA samples and subsequent experiments were carried out with the initially screened pairs of primers. The PCR reaction system was 25 μL: 1 μL template DNA, 1 μL each upstream and downstream primers, 12.5 μL PCR Premix (*Taq* DNA polymerase, dNTPs, $MgCl_2$, KCl reaction buffer, other stabilizers and enhancers), 9.5 μL ddH_2O. The PCR reaction procedure was: pre-denaturation at 94 °C for 5 min, denaturation at 94 °C for 45 s, denaturation at 46–59 °C for 40 s, extension at 72 °C for 45 s, and final extension at 72 °C for 7 min. The PCR products were detected by 1% agarose gel electrophoresis, and the primers with bright and clear bands were selected.

Of the 20 primer pairs selected, 12 were amplified successfully and the amplified products were obtained. Five pairs of primers with clear bands, good polymorphism, and high stability were selected for SSR analysis, and the primer sequences are shown in Table 1. The DNA samples were sent to the Tsingke Biotechnology Co., Ltd. (Bejing, China) to complete SSR analysis.

Table 1. Sequences and proper annealing temperature of 12 primer pairs.

Locus	Primer Sequence (5′–3′)	Annealing Temperature (°C)
PL123-124	(F) GCTTGAGAGTTGAGATTTGT (R) GCAACACCCTTTAACTACCA	55
PL127-128	(F) GCAATTACAGGCTAGGCTGG (R) GTCTGGACCTAGCCCTCATG	55
PL125-126	(F) CTTCACTGGCTTTTCCTCCT (R) TGAAGCCCTTGTCAACATGC	58
E79	**(F) CCATTAAAAGAAGCAGTATTTTGT (R) GCAACACTCAGCCTATATCTAGAA**	**52**
E71	**(F) CGTCTATAAGTTCTTGGGTGA (R) GTAACTATGATGTGATTCTTACTTCA**	**46**
Qden 05011	(F) CCCACTCCCTGTCCATTGT (R) CACTGTGTGCTGCGACTTG	59
ssrQrZAG 96	(F) CCCAGTCACATCCACTACTGTCC (R) GGTTGGGAAAAGGAGATCAGA	59
ssrQrZAG 7	(F) CAACTTGGTGTTCGGATCAA (R) GTGCATTTCTTTTATAGCATTCAC	55
01b	(F) GTTCAACAATTTTATTAGGGTGC (R) GCCTATTACACACAACAAGCC	56
02b	**(F) ATGTCAATATGGTCACCTACCG (R) TTTTTGTAGATTTTTAAGCACGC**	**53**
04b	**(F) TTCCTTTTCCTCAGTTTGGG (R) CCCGCATCAAAGAACTATTG**	**52**
10b	**(F) GAATGGATCTTCATTTATCGTTG (R) TCTGCATATTTTCAACATACATTTAG**	**55**

Note: Bold are 5 pairs of primers with clear bands, good polymorphism, and high stability selected in this study.

Popgene32 software was used to calculate the genetic diversity of trees and saplings, including the effective number of alleles (Ne), Shannon's information index (I), observed number of alleles (Na), observed heterozygosity (Ho), expected heterozygosity (He), and fixation index (Fis). In addition, we tested for differences in the number of alleles, genetic diversity, and fixation index between trees and saplings using the Wilcoxon Matched Pairs Test.

It is worth noting that due to data deficiencies (only two size groups' data), we did not calculate genetic differentiation indices (allele frequency differentiation, AFD) [47] for the three stages, as in previous studies [48,49].

2.4. Point Pattern Analysis and Null Model

The pairwise correlation function *g(r)* was used to study the distribution patterns of populations at different scales. The pairwise correlation function *g(r)* is derived from the K function, which is a non-accumulative distribution function compared with the K function, and can more sensitively discern the extent to which the actual distribution of points at a given scale deviates from the expected value, and is not affected by the cumulative effects at small scales when analyzing patterns at large scales [50]. We analyzed the spatial distribution patterns within tree species using the univariate *g(r)* function and the spatial association of size classes within species using the bivariate *g(r)* function.

The choice of a null model that has a clear ecological meaning and accurately describes the extent to which the data deviate from the theory is important for the analysis of spatial point patterns [38,51]. In our study, there were two different patterns (univariate pairwise correlation and bivariate pairwise correlation) using two different null model groups, and both of these two null model groups were based on heterogeneous Poisson. The heterogeneous Poisson model defines the distribution of individuals based on the density function $\lambda(x, y)$, which can exclude the effect of environmental heterogeneity at large scales. We used sigma = 30 m for this analysis [50].

The univariate pairwise correlation function was used to analyze the spatial distribution patterns of tree species as a whole and populations of different diameter classes and the bivariate pairwise correlation function was used to analyze the spatial relationships among individuals at different diameter classes. We performed 99 Monte-Carlo simulations, and the maximum and minimum values of the results were used to generate 99% confidence intervals formed by the upper and lower Poisson distribution envelopes. When the observed values were above the upper limits of the envelope line, within the intervals and below the lower limits, they corresponded to the aggregated or positive correlation, random or uncorrelated and uniform distribution or negative correlation, respectively [51]. All analyses were conducted using the 'statstat' package in R 4.1.2 (R Core Team, 2021).

3. Results

3.1. Individual Distribution and Population Structure

In this study, a total of 2964 individuals of *Q. wutaishanica* were counted (Figure 2a), of which 53 trees with DBH more than 5 cm, 53 saplings with DBH between 1 cm and 5 cm, and 2858 seedlings (DBH <1 cm). The large trees in the community were mainly distributed evenly in the plot, with only a few individual clusters. In addition, there were almost no saplings around the trees, but a large number of seedlings were distributed. However, the aggregation of seedlings around the saplings was not apparent.

The DBH size structure of the *Q. wutaishanica* showed an obvious inverted *J*-type distribution, in other words, the number of individuals decreased with increasing DBH size classes (Figure 2b). Moreover, the age structure population was dominated by small-sized individuals, and the age structure of the population was pyramidal-type and showed a growing population.

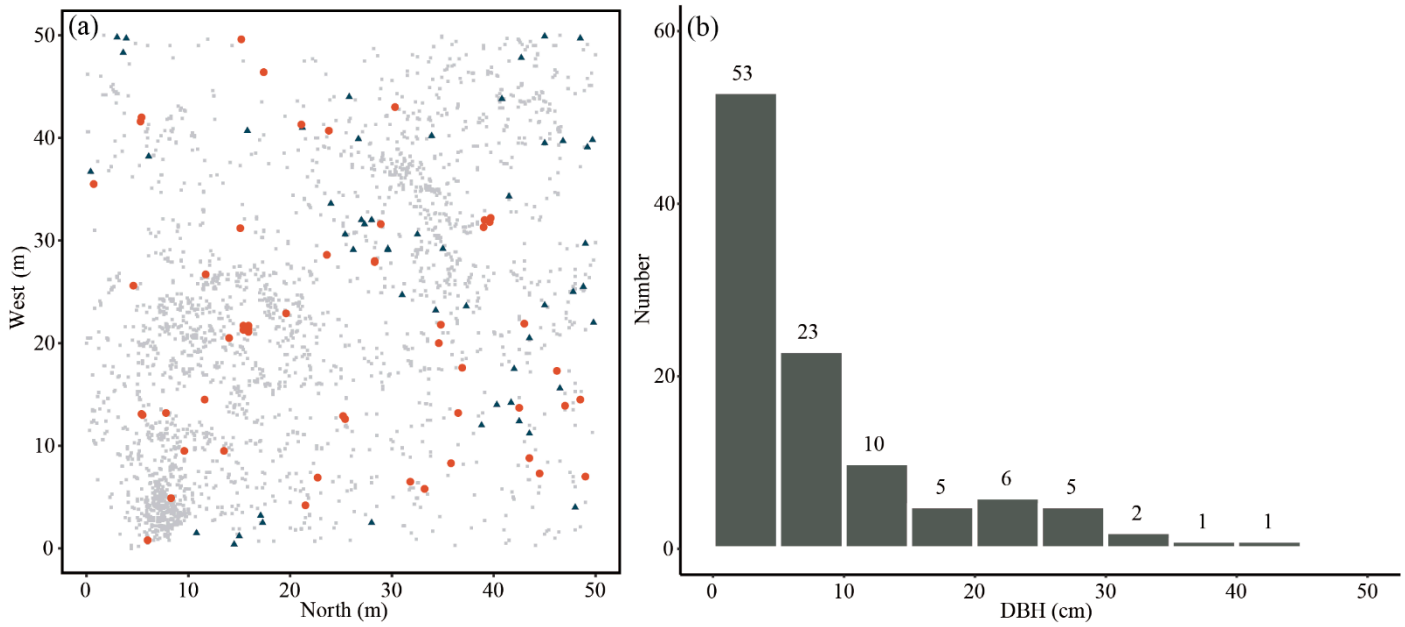

Figure 2. Spatial distribution of the sample plot (**a**), and diameter at breast height (DBH) structure of the *Quercus wutaishanica* (**b**). Trees, red circles; saplings, blue triangle; seedlings, gray rectangle.

3.2. Genetic Diversity

A total of 66 alleles were amplified using 5 SSR primers across 106 *Q. wutaishanica* (53 trees and 53 saplings). The number of alleles per locus (Na) ranged from 7 to 22, with an average value of 13.2 (Table 2). The lowest observed heterozygosity (Ho) ranged from 0.7980 (10b) to 0.8371 (E79), and the mean value was 0.8371 for all accessions. The expected heterozygosity (He) values ranged between 0.7419 for E79 and 0.8973 for 04b, with an average of 0.8159 per locus. In addition, the lowest Shannon's information index (I) was 1.5015 and the highest was 2.5257, with an average of 1.9410. The F-statistics showed moderate population differentiations for each locus and fixation index (Fis) varied from −0.2125 to 0.0810.

Although trees and saplings had high genetic diversity, the populations showed significant inbreeding in both life stages and total population (Table 2). The Wilcoxon paired test showed that trees and saplings were not significantly different in number of alleles (Na, $P = 0.68$), genetic diversity (He, $P = 0.58$), and fixation index (Fis, $P = 0.22$) ($P > 0.05$ for all comparisons).

Table 2. Genetic diversity in the different life stages in a population of *Quercus wutaishanica*.

Life Stage	Locus	N	Na	Ne	PIC	I	He	Ho	Fis
Trees and saplings	02b	105	7	3.8677	0.5525	1.5015	0.7450	0.8000	−0.0790
	04b	106	22	9.3555	0.4253	2.5257	0.8973	0.8208	0.0810
	10b	99	13	7.3060	0.5260	2.1323	0.8675	0.7980	0.0755
	E71	101	11	5.6719	0.5156	1.9138	0.8278	0.8713	−0.0578
	E79	105	13	3.8215	0.2940	1.6315	0.7419	0.8952	−0.2125
	Mean	—	13.2	6.0045	0.4627	1.9410	0.8159	0.8371	—
Trees	02b	53	7	3.6985	0.5284	1.4758	0.7736	0.7366	0.0370
	04b	53	18	9.3478	0.5193	2.4809	0.8302	0.9015	−0.0713
	10b	49	10	6.7067	0.6707	2.0250	0.7143	0.8597	−0.1454
	E71	50	10	5.7670	0.5767	1.9331	0.8800	0.8349	0.0451
	E79	53	11	4.3652	0.3968	1.7378	0.8302	0.7783	0.0519
	Mean	—	11.2	5.9770	0.5384	1.9305	0.8057	0.8222	—

Table 2. *Cont.*

Life Stage	Locus	N	Na	Ne	PIC	I	He	Ho	Fis
Saplings	02b	52	6	3.9132	0.6522	1.4981	0.7517	0.8269	−0.0752
	04b	53	16	7.9575	0.4973	2.2968	0.8827	0.8113	−0.0714
	10b	50	13	7.8125	0.6010	2.1930	0.8808	0.8800	0.0008
	E71	51	9	5.2229	0.5803	1.8111	0.8165	0.8627	−0.0462
	E79	52	8	3.1333	0.3917	1.3315	0.6875	0.9615	−0.2740
	Mean	—	10.4	5.6079	0.5445	1.8261	0.8038	0.8685	—

Note: N, number of sampled individuals; Na, observed number of alleles; Ne, effective number of alleles; PIC, Polymorphism Information Content; I, Shannon's information index; He, expected heterozygosity; Ho, observed heterozygosity; Fis, fixation index.

3.3. Spatial Distributions Patterns and Intraspecific Association

We found differences in the spatial distribution of three life stages of *Q. wutaishanica* in this study (Figure 3a–c). The trees were almost randomly distributed at the whole scale. For saplings of *Q. wutaishanica*, the spatial distribution was aggregated at some medium and small scales (0–1.5 m, 2.5–4.5 m and 10–11 m). In other scales, the saplings' distribution was random. However, *Q. wutaishanica* seedlings showed a regular distribution at large scale (>21 m) and aggregated distribution between 0 and 20 m. The degree of aggregation then decreased with increasing scale.

There was a positive correlation between individuals of different diameter classes of *Q. wutaishanica* at a small interval (Figure 3d–f). Trees and seedlings showed a positive association at 5–6.5 m, but there was no association at other scales. For trees and saplings, they showed a negative association at some medium scale (13.5–16 m). At small and large scales, they were not spatially correlated. Meanwhile, no obvious associations were observed between saplings and seedlings of *Q. wutaishanica.*

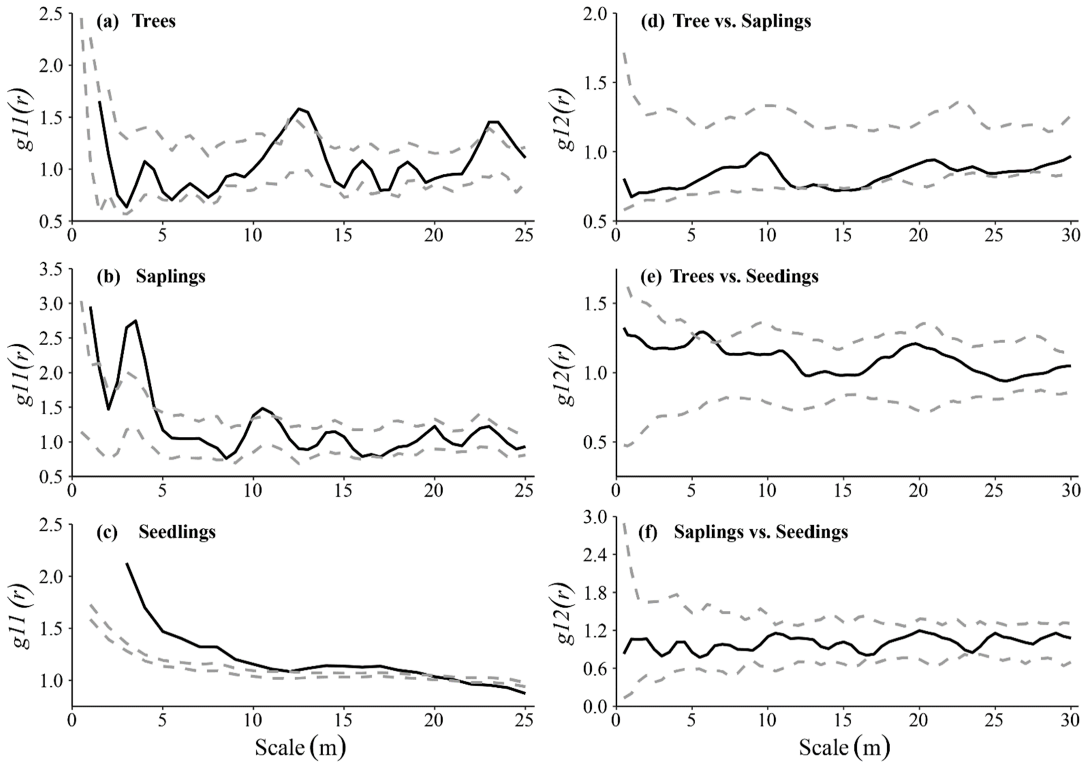

Figure 3. Univariate point pattern analyses show the spatial pattern using the pair-correlation function (**a**–**c**), and bivariate point pattern analyses show intra-species spatial associations among three size classes (**d**–**f**) of *Q. wutaishanica.* Black lines indicated the g11(r)/g12(r) function, dotted lines indicated the upper and lower limits of the 99% confidence interval.

4. Discussion

4.1. Diameter Classes Structure of Q. wutaishanica

The diameter class structure of plant populations is the result of the interaction between population viability and the external environment, and to a certain extent, it can reflect the current structure and renewal strategy of the population [52,53]. In the present study, the diameter class structure of the *Q. wutaishanica* population showed a typical inverted *J*-type distribution, with an abundance of individuals in seedlings and a gradual decrease in the number of individuals as the diameter class increased, and no individuals missing at any diameter class. In addition, a large number of renewed seedings were present and growing well in this area. The possible reason is that *Q. wutaishanica* will produce a large number of seeds, but its tannin content is high, bitter, and toxic, resulting in *Q. wutaishanica* seeds becoming an alternative food for animals [54], which in turn leads to a high number of saved seeds and the formation of a large number of seedlings. However, with the growth of individual plants, the demand for resources in the environment will become greater [55], the degree of nutrient specialization will increase [56], and strong competition will be formed within and between populations. Therefore, only a small number of seedlings will grow into saplings, and this will be more likely to occur in an area far from the adult trees, as predicted by the Janzen–Connell hypothesis. This also explains why only a small number of large-diameter individuals are in the plot. It can be seen that seed number and environmental adaptability are important reasons for the good regeneration of *Q. wutaishanica*.

4.2. Gene Diversity of Q. wutaishanica

Genetic diversity is a condition for the long-term survival and evolutionary basis of species [57], and the higher the genetic diversity, the better the species' ability to adapt to its environment [58]. During the survey and collection in the field, we speculated that the *Q. wutaishanica* population might have been propagated from the largest individual at DBH in the sample plot, and that the *Q. wutaishanica* individuals in the sample might be extremely close in kinship, or even have the possibility of identical SSR analysis results. However, the SSR analysis results do not correspond to our speculation. A total of 66 alleles were amplified by the set of SSR markers, emphasizing their high degree of polymorphism. In addition, the genetic diversity of *Q. wutaishanica* in this study was at a high level, with an average expected heterozygosity of 0.816, compared to 0.678 for *Castanea mollissima*, which is also a member of the Fagaceae family [59]. Furthermore, the expected heterozygosity of other families such as *Abies ziyuanensis* is 0.337 [60] and poplar is 0.552 [61]. This suggests that *Q. wutaishanica* at small scales can still maintain rich genetic diversity, which is very beneficial for the conservation of populations. Some researchers suggested that mating patterns have an important influence on the genetic diversity of plants [62]. In general, an increase in the proportion of self or inbred in plants leads to a decrease in genetic diversity, while plant outbreeding can increase the genetic diversity [63]. In addition, hybridization between closely related species of the same genus can also increase genetic diversity, and natural hybridization is very common in *Quercus* spp. Moreover, *Q. wutaishanica* is a anemophilous plant, and can be outbred [64]. Therefore, we guess that natural hybridization between *Q. wutaishanica* and *Q. aliena* leads to a high genetic diversity of *Q. wutaishanica.*

The level of genetic diversity of a species is the result of a combination of factors, including the biology of the species itself, its biological characteristics (life type, breeding system), external natural environmental changes, interactions with other species, and anthropogenic disturbances, all of which have an impact on the level of genetic diversity of the species [65]. In this study, the correlation between genetic distance and geographical distance among individuals of *Q. wutaishanica* was weak (Mantel test, r = 0.09, P = 0.044), indicating that at a small scale, spatial distribution pattern was not the main reason for influencing genetic diversity. In addition, because the *Q. wutaishanica* community is the climax community in the Loess Plateau region, its community species richness is higher

and the intensity of interactions between species is stronger, which also promotes the higher genetic diversity of *Q. wutaishanica* individuals to some extent.

4.3. Spatial Distribution Pattern of *Q. wutaishanica* at Different Life Stages

Spatial distribution patterns of plant populations reflect the survival strategies and adaptive mechanisms by which populations adapt to their environment [66]. Under natural conditions, biotic and abiotic factors and processes such as habitat heterogeneity, dispersal limitation, interactions between organisms, and disturbance are considered potential ecological mechanisms that influence the formation and variation of species patterns at different spatial scales [53,67–69]. In general, at smaller scales, the distribution patterns of populations are mainly determined by biological characteristics such as seed dispersal mechanisms, individual reproductive characteristics, and intraspecific competition; while at larger scales, they may be influenced by environmental factors such as topography, soil, moisture, and light [70,71]. In this study, seedlings showed clustered, random, and regular distributions in order of increasing spatial scale, i.e., the degree of aggregation decreased as the spatial scale increased. This generally differs from the results observed in the tropics but is consistently observed in the temperate zones. While both tropical and temperate studies showed species aggregation at certain scales, tropical studies did not find a significant decrease in species aggregation with increasing scale, and temperate forests showed a significant decrease in species aggregation [1,72,73]. The possible reasons are that the intensity and scale of spatial aggregation of populations are related to the way seeds disperse [74]. Seed dispersal is an extremely important ecological process in population dynamics and an important mechanism for explaining changes in the spatial pattern of populations [75,76]. In addition to environmental factors such as wind, water, animals, and topography, the factors affecting seed dispersal are also closely related to the reproductive and biological characteristics of plants [77,78]. The initial distribution pattern of the *Q. wutaishanica* population in this study may be related to seed dispersal and environmental factors [79]. Because the main way of seed dispersal is gravity and animal dispersal [80], and the seed can easily fall off after maturity, thus forming a cluster distribution pattern centered on the mother tree, while cluster distribution is conducive to mutual shelter between individuals of small diameter wood and improving interspecific competition [81]. In addition, as the spatial scale increases, it is also influenced by environmental heterogeneity, thus showing a random or regular distribution at large scales.

At smaller scales, the spatial distribution of adult trees is more dispersed than that of juveniles and saplings, mainly due to extreme competition among individuals [38]. In our study, sapling shows a random distribution at intermediate and large scales and trees at 0–25 m scales, a distribution pattern that is also found in other regional forest ecosystems [7,53,82,83]. As predicted by the classical Janzen–Connell hypothesis, large individuals tend to over-disperse in small areas because of intense competition among individuals of the same species. These results indicated that individuals of *Q. wutaishanica* changed from aggregated distribution (seedlings) to random distribution (trees) at a certain spatial scale. This finding confirms previous studies that density-dependent mortality leads to the observed increase in overdispersion from small to large sized trees [12,71]. This is because *Q. wutaishanica* seedlings have good shade tolerance and the shade of the forests provides good environmental conditions for the seedings to survive. However, as the plant grows, individuals of *Q. wutaishanica* need more light to promote their growth. This leads to rapid growth of plants at the edge of the forests or forest gaps, while plants in shaded conditions do not receive enough light and die [84]. In other words, when the population enters the middle and late life history, the plants' demand for light, water, nutrients, space, and other resources increases, intra- and interspecific competition intensifies, and the self-thinning and alien-thinning effects are enhanced, leading to a large number of plant deaths and eventually tending to a random distribution [85]. In summary, *Q. wutaishanica* communities showed different spatial patterns at different life stages, which is not only beneficial for individual plants to obtain sufficient water, growing space, light, soil, and

other environmental resources under different spatial distribution patterns, but also a survival strategy and adaptation mechanism for the population [86].

4.4. Spatial Correlation of Q. wutaishanica at Different Life Stages

Spatial correlations between different developmental stages of the same population can reveal the interactions between individuals within a population over some time and help to describe the status and dynamics of the population [6]. In addition, spatial relatedness can reflect the results of plants' mutual facilitation under unfavorable conditions or competing for limited resources [87]. Spatial associations between plants depend to some extent on the spatial and temporal distribution patterns of habitat resources, and habitat heterogeneity spatially constrains the distribution of individuals at different diameter classes, leading to different spatial associations between individuals at different diameter classes within a population. Many previous studies have proposed the existence of competition and facilitation in temperate forests [88–91]. Competition regulates the abundance and distribution of tree populations through intra- or interspecific density-dependent effects [11,92]. Facilitation may occur mainly among trees of different sizes or life history characteristics, such as sheltering of small trees by large trees and sheltering of newly established seedlings by shrubs [93,94]. In this study, *Q. wutaishanica* populations showed both facilitative and competitive effects between individuals of different diameter classes. Specifically, competitive effects occurred mainly between trees and saplings and only at intermediate scales, while trees and seedlings showed facilitative effects at small scales. The positive association indicates that individuals of different diameter classes of plants have similar needs for environmental resources. trees with larger canopy width can create a suitable renewal and growth microenvironment for seedlings, including protection from strong light, reduction of ground evaporation, and maintenance of soil moisture, providing shelter for the growth of small diameter classes, resulting in the higher survival rate of small diameter classes and thus dominance in the plots [95], thus creating a facilitating effect between trees and seedlings. In turn, when seedlings develop into young trees, there is competition for resources with adults [85], resulting in a negative correlation between adult and young trees at some scales. In addition, saplings and seedlings showed no correlation at all scales, due to the relatively low competition for resources such as nutrients and water between individuals at small diameter levels, and similar resource preferences that allow them to harmonize their relationships with each other and to jointly resist disturbance by herbivores [39].

4.5. Suggestions for Conservation and Management

The findings on the population structure and genetic diversity of *Q. wutaishanica* forests can be used as one of the bases for the management, can provide theoretical references for the conservation and management of populations, and have certain guiding significance for the sustainable management of Quercus forests in the Loess Plateau region. Given the population structure of this *Q. wutaishanica* forest, it is suggested that more efforts should be made to nurture *Q. wutaishanica* forests in this area, selectively adopt disturbance and carry out artificial thinning, which is not only conducive to the renewal and development of populations, but also of great significance to the conservation of forest ecosystems and biodiversity in the Loess Plateau region.

In addition, this study has some limitations. The scale of this study was small, and only a 50 m $\times$ 50 m sample plot was investigated. Subsequent studies can expand the scale and the research object and continue the survey sampling analysis to make the results more credible and scientific, and provide a theoretical basis for the conservation of this natural secondary forest.

Author Contributions: Conceptualization, D.H. (Dong Hu), M.Y. and Y.C.; investigation, Y.X., T.T., K.W., P.L., M.W., J.Z. and D.H. (Dafu Hou); formal analysis, D.H. (Dong Hu), Y.X., K.W. and P.L.; writing—original draft, D.H. (Dong Hu); writing—review and editing, M.Y., Y.C. and D.H. (Dafu Hou); data curation, M.W. and J.Z.; supervision, M.Y. All authors have read and agreed to the published version of the manuscript.

Funding: This research was financially supported by the National Natural Science Foundation of China (41571500, 41871036).

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Not available.

Conflicts of Interest: The authors declare that they have no conflict of interest.

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