Prevalence of Inter-Tree Competition and Its Role in Shaping the Community Structure of a Natural Mongolian Scots Pine (*Pinus sylvestris* var. *mongolica*) Forest

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Abstract: Inter-tree competition is considered one of the most important ecological processes of forest development. However, its importance in structuring the spatial patterns of plant communities remains controversial. We collected observational data from two plots in a natural Mongolian Scots pine forest to study the contribution of competition to tree growth, mortality, and size inequality. We used the nearest neighbour method to determine the presence of competition, and unmarked and marked spatial point pattern analyses to test the density-dependent mortality effects and the spatial autocorrelation of tree size. We identified significant positive correlations between tree canopy diameter and nearest neighbour distance in both plots, which were more evident in the denser plot. The pair correlation functions of both plots indicated regular distribution patterns of living trees, and trees living in more crowded environments were more likely to die. However, the mark differentiation characteristics showed weak evidence of a negative spatial autocorrelation in tree size, particularly in the high-density plot. The high mortality rate of suppressed trees and weak asymmetric competition may have accounted for the lack of dissimilarity in tree size. This study showed that inter-tree competition is an important determinant of the development of Mongolian Scots pine forests.

Keywords: inter-tree competition; nearest neighbour analysis; spatial point pattern analysis; regular spacing; sizes dissimilarity; Mongolian Scots pine

1. Introduction

Numerous attempts have been made to understand the processes and mechanisms that determine tree spatial patterns [1,2]. Inter-tree competition is considered one of the most important ecological processes driving plant community structure [3–8]. Although a number of studies have found evidence of competition among plants [9–13], its importance in structuring plant spatial patterns remains controversial [5,12,14–16]. Studies of spatial distribution patterns have detected the prevalence of competition among plants, and concluded that competition is a significant contributor to tree mortality [4,17,18]; however, inconsistent results have been observed in some tree species [5,15,19]. When using spatial pattern analysis methods, determining the prevalence of competition in the structuring of plant communities largely depends on the intensity of inter-tree interactions [9,20] and habitat heterogeneity [21]. For example, competition among shade-tolerant species may be
weaker compared to shade-intolerant species; therefore, spatial patterns of shade-intolerant species may be more readily structured by competition [22]. In addition, heterogeneous habitats can result in more complex plant spatial patterns that confound the effects of competition in structuring plant spatial distribution patterns [21]. Thus, the contribution of competition to plant community patterns may be more easily detected in shade-intolerant species growing in homogeneous habitats.

Mongolian Scots pine (Pinus sylvestris var. mongolica) is a geographical variety of Scots pine (P. sylvestris), and is widely distributed throughout Northern China [23,24]. It is considered a crucial ecological species in Northern China, particularly in sandy areas, because of its high adaptability to infertile soil, and cold and arid habitats [24,25]. Despite its strong ability to endure and adapt to unfavourable conditions, P. sylvestris var. mongolica is a highly shade-intolerant species, and intraspecific competition caused by crowding can influence its population dynamics (i.e., changes in growth, death, and regeneration over time). Therefore, spatial patterns caused by competition may be easy to detect in this shade-intolerant species in natural monospecific forests. Apart from spatial pattern analyses, studying the ecological processes that drive population dynamics is important for the conservation and sustainable management of Mongolian pine forests.

In addition to direct long-term tree dynamics monitoring experiments [26,27], approaches for identifying the prevalence of competition among trees include analysing a snapshot of the current state of the spatial arrangement of individuals within a community, where the current forest tree spatial pattern is the result of various natural ecological processes [28,29]. Nearest neighbour summary statistics and second-order analyses of spatial point patterns are widely used to detect the presence of competition in structuring plant communities [4–6,16]. Nearest neighbour methods assume that competition between individual trees and their nearest neighbours results in a reduction in the sizes of both the individuals and their neighbours [6,12]. If competition is prevalent, a significant positive correlation can be detected between the distances of individual trees to their neighbours and the sum of their sizes. In other words, tree size increases if there is more space between individual trees and their nearest neighbours.

Second-order characteristics of tree spatial distribution patterns can be used to identify density-dependent mortality effects [5,29,30], whereby strong competition occurs when trees of younger growth stages grow into late stages due to increasing demand on scarce resources. The death of a tree is often the result of many factors, including small-scale tree–tree interactions (e.g., pathogens and competition) and large-scale environmental hazards (e.g., extreme climatic events) [14]. If it is assumed that trees in more crowded environments are more likely to die, competition-induced mortality processes can be inferred [5,18,30], because strong competition may eliminate suppressed trees that are close to others. This would result in a more regular spacing of surviving trees after competition-induced mortality than expected from random-thinning [17,31].

Another expected effect of the presence of competition is an unequal tree size (i.e., size variation) pattern [15,32,33]. Competition among unequal-sized neighbouring trees often leads to asymmetric competition which was defined as larger individuals obtaining a disproportionate share of resources (for their relative size) and suppressing the growth of smaller trees [34]. Under asymmetric competition among high-density plants, smaller-sized individuals receive insufficient resources for growth and, as a result, larger individuals are surrounded by smaller neighbours [10]. This can be described as a negative autocorrelation in plant size, and has been observed in various forest types [35,36]. Weiner et al. [33] argued that intensive competition alone cannot determine the degree of size variation, and size asymmetry due to competition is important in structuring negative autocorrelations of plant size. Furthermore, Reed and Burkhart [37] proposed that, in density-dependent mortality (i.e., self-thinning), the mortality rate of suppressed small trees is higher than that of large trees, resulting in the development of a positive autocorrelation in tree size. Therefore, the contribution of competition to spatial autocorrelation of tree size remains unclear, and additional data are needed to test its role in the formation of plant size spatial patterns.

Investigating spatial autocorrelation in tree size is a case of a marked point pattern analysis, which measures spatial patterns of attributes, such as tree species and size, attached to tree locations [38]. Pommerening et al. [39] and Hui and Pommerening [38] used diameter differentiation as the
constructed marks, and developed the mark differentiation function as a measure of detecting whether similar tree sizes are spatially aggregated or regularly distributed in a forest. In this study, we used the mark differentiation function as a second-order approach to analyse the processes underlying the observed spatial patterns of tree size.

In this study, we used tree data from a natural monospecific *P. sylvestris* var. *mongolica* forest to detect the importance of competition in structuring plant spatial patterns. We expected that: (1) due to evident intraspecific competition in a shade-intolerant species community, a positive correlation between the distances from individual trees to neighbours and the sum of their crown diameters would be detected, which would be more significant in the higher-density community; (2) competition would contribute significantly to tree mortality and suppressed trees in more crowded environments would tend to die; and (3) competition between larger and smaller trees would result in a negative spatial autocorrelation in tree size.

2. Materials and Methods

2.1. Study Site and Tree Data

The study site was located in the southern area of Hulunbuir (47°36′–48°35′ N, 118°58′–112°32′ E), eastern Inner Mongolia, Northeast China (Figure 1). This region is located in the transition belt between the Daxinganling Mountain forests and the grasslands of the Inner Mongolia Plateau. Undulating sandy land is the common geomorphic type, and the altitude ranges from 700 to 1100 m. This region is characterised by a subhumid-semiarid continental climate affected by monsoons with an annual mean temperature of 1.5 °C and an annual mean precipitation of 344 mm, which is largely concentrated during the summer. The soil types are mainly loose sandy soil, chernozem, and grey forest soil. Most of the forests in this region are natural forests dominated by *P. sylvestris* var. *mongolica*, although some broadleaved species, such as *Populus davidiana* and *Betula platyphylla*, accompany this species on shady slopes or floodplains. The understory vegetation is constituted of drought tolerant shrubs (e.g., *Caragana microphylla* and *Thymus serpyllum*) and herbaceous plants (e.g., *Stipa baicalensis*, *Festuca ovina*, and *Sanguisorba officinalis*) [40,41].

![Figure 1. Map of study site. The map was produced using the Ggmap package in R software [42].](image-url)
Two observational plots were established in a typical natural *P. sylvestris* var. *mongolica* forest in 2015 (Figure 2). The two stands developed after a fire that occurred approximately 60 years ago. Each plot was 1 ha (100 m × 100 m) and had a flat topography. Both plots (plot 1 and plot 2) were located in natural monospecific *P. sylvestris* var. *mongolica* stands with homogenous structures. *P. sylvestris* var. *mongolica* regeneration was inadequate, and saplings with diameters at breast height (DBH) < 3 cm were almost completely absent in the plots. All of the live trees and standing dead trees with a DBH > 5 cm were tagged, and their positions were mapped with a Topcon GTS602 (Topcon Corporation, Tokyo, Japan) autofocus total station. Tree DBH, height, and crown diameter were measured. Table 1 provides general information on the plots.

![Figure 2. Observed tree point patterns of the two plots: (a) plot 1 and (b) plot 2. Circles denote live trees and triangles denote standing dead trees. Symbol sizes are proportional to diameter at breast height (DBH). X and Y are two perpendicular coordinate axes of the plots.](image)

<table>
<thead>
<tr>
<th>Plot Number</th>
<th>Slope (°)</th>
<th>Canopy Cover</th>
<th>Tree Density (trees/ha)</th>
<th>Mean Basal Area (m²/ha)</th>
<th>Mean DBH (cm)</th>
<th>Number of Dead Stems</th>
<th>Mortality Percentage (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plot 1</td>
<td>&lt;3</td>
<td>0.7</td>
<td>940</td>
<td>33.6</td>
<td>21.3</td>
<td>67</td>
<td>7</td>
</tr>
<tr>
<td>Plot 2</td>
<td>&lt;3</td>
<td>0.7</td>
<td>1149</td>
<td>39.8</td>
<td>21.0</td>
<td>200</td>
<td>17</td>
</tr>
</tbody>
</table>

2.2. Nearest Neighbour Analysis

We used the coefficient of determination for a linear regression analysis as a measure of competition among *P. sylvestris* var. *mongolica* individuals. The sum of the crown diameter of the nearest neighbours plus the crown diameter of a focal tree was regressed against the sum of the distances of a focal tree to its nearest neighbours. Individual crown diameter was calculated as the average of two crown spreads measured along two perpendicular directions (south to north axis and east to west axis). The coefficient of determination ($r^2$) for the regression indicated the contribution of inter-tree competition to tree growth [5,12]. We assumed that the count of the first nearest neighbour was insufficient to describe competition effects [12] and that a reference tree would have direct interactions with its several nearest neighbours. In this study, we expected that a given tree may compete with its neighbours within a radius of approximately 5 m, and we used the six nearest neighbouring trees [30] for the analysis according to the tree density of the plots.
2.3. Spatial Pattern Analysis

We used a spatial point pattern analysis to detect the contribution of competition to tree mortality and size variation in the forest community. We applied a pair correlation function to describe whether trees that survived competition were distributed more regularly because of density-dependent effects. In addition, we used a marked point pattern analysis to explore whether tree sizes (defined as quantitative marks) were randomly distributed throughout the community rather than in a dependent manner.

2.3.1. Pair Correlation Function

The estimator of the pair correlation function (g(r)) can be derived from the product density (Π(r)), which denotes the conditional probability that, for two infinitesimally small discs in a given point process, each disk contains a point [43]. The two infinitesimally small discs have the areas dx₁ and dx₂ and are separated by distance r. Thus, the product density can be expressed as Π(r) = ρ(x₁, x₂)dx₁dx₂.

Since Π(r) = g(r)I²dx₁dx₂, the pair correlation function g(r) is g(r) = Π(r)/I²; therefore, g(r) can be estimated to be:

\[ g(r) = \frac{1}{I²} \sum_{i=1}^{n} \sum_{j=1}^{n} k(\|x_i - x_j\| - r) \times \omega_{i,j} \frac{A}{2\pi I A} \]

where I is an estimator of the intensity of points within a subwindow W and A is the area of the observation window. xᵢ and xⱼ are two arbitrary points of the point pattern within the observation window. k is the kernel function, \( \|x_i - x_j\| \) is the distance between xᵢ and xⱼ, and r is the focusing scale. \( \omega_{i,j} \) accounts for edge correction and n is the number of points in a given pattern.

We calculated the pair correlation functions for all trees, including both live and dead trees (pre-mortality pattern) and live trees (post-mortality pattern). Because the two study plots were flat and tree intensity was approximately constant, the environmental habitats could be considered homogenous. Therefore, we used the homogeneity assumption and complete spatial randomness as the null model for univariate analysis of the tree spatial patterns.

To investigate whether tree mortality was a random process, we used the random labelling as the null model according to the method of Getzin et al. [5]. If inter-tree competition was strong enough to cause tree mortality, trees living closer to their neighbours were more likely to die and the post-mortality pattern (live trees) was expected to become more regular than the pre-mortality pattern (live and dead trees). The null model was used to test if the surviving trees were a random subset of the live and dead trees. The observed pair correlation function for the live trees was compared to the tree distribution pattern, in which the set of dead trees was randomly removed from both dead and live trees [5].

The hypotheses testing was based on the calculation of pair correlation functions and comparison with simulated Monte Carlo envelopes derived from a null model process to decide whether the observed tree spatial patterns significantly deviates from the corresponding null model.

2.3.2. Mark Differentiation Function

Similar to other mark second-order functions, such as the mark correlation function and mark variogram, the mark differentiation function is used to describe how quantitative marks (i.e., the size of trees) are spatially correlated. A core element of this approach is the test function. Pommerening et al. [39] and Hui and Pommerening [38] used diameter differentiation as the test function for this second-order characteristic, which is defined as:

\[ t(m_1, m_2) = 1 - \min\{m_1, m_2\} \frac{\max\{m_1, m_2\}}{\max\{m_1, m_2\}} \]

where \( m_1 \) and \( m_2 \) are two tree size marks of point pairs that are separated by distance r.
Based on the test function, the second-order product density for the size differentiation mark pattern can be derived as analogous to the product density for the univariate pattern as follows:

\[
\hat{f}(r) = \frac{1}{2\pi r A} \sum_{i=1}^{n} \sum_{j=1}^{n} \left(1 - \frac{\min\{m_1, m_2\}}{\max\{m_1, m_2\}}\right) k(\|x_i - x_j\| - r) \times \omega_{i,j}
\]

(3)

Since the mark product function \(\hat{f}(r)\) contains information on both the structure of the unmarked pattern and correlation structure of marks [43], the mark differentiation function \(\hat{t}_v(r)\) can be obtained by removing the conditional spatial structure of the points (i.e., product density of the univariate pattern) as \(\hat{t}_v(r) = \frac{1}{ET} \hat{f}(r)\), where ET is the expected mark differentiation as a normalisation term [39].

\[
\hat{t}_v(r) = \frac{\sum_{i=1}^{n} \sum_{j=1}^{n} \left(1 - \frac{\min\{m_1, m_2\}}{\max\{m_1, m_2\}}\right) k(\|x_i - x_j\| - r) \times \omega_{i,j}}{\sum_{i=1}^{n} \sum_{j=1}^{n} k(\|x_i - x_j\| - r) \times \omega_{i,j}}
\]

(4)

Thus, we can define a simple interpretation of the non-normalised mark differentiation function, \(\hat{t}_v(r)\), from its function form as the mean value of size differentiation for point pairs \(i\) and \(j\) located within a distance \(r\) of each other.

All analyses were performed using the R statistical software [44]. The calculations of nearest neighbour analysis and second-order characteristics were developed based on R scripts and C++ files from Pommerening’s Forest Biometrics Lab [45]. The Spatstat package [46] and Rcpp package [47] were used in our calculations.

3. Results

3.1. Non-Spatial Stand Structure Characteristics

Both plots were only composed of \(P. sylvestris\) var. Mongolica trees, but had different tree densities, DBH size structures, and numbers of dead trees. The live tree density (number of trees) was lower in plot 1 (\(n_1 = 940\)) than plot 2 (\(n_2 = 1149\)), and the number of dead trees was much higher in plot 2 (Figure 2).

Figure 3 shows the DBH size distribution of dead and live trees in the two plots. Dead trees were mainly suppressed small-sized trees. For surviving trees, both plots had multimodal size distributions and a significant peak at intermediate sizes, but different skewness. Plot 1 exhibited a slightly right-skewed distribution (skewness = -0.0985), whereas plot 2 was left-skewed (skewness = 0.1526). This suggested that plot 1 had a slightly greater proportion of large trees than plot 2 [48].

![Figure 3. Tree DBH size distributions for plots 1 (a) and 2 (b). Black areas represent dead trees and grey areas represent live trees.](image-url)
3.2. Reduction in Tree Size Caused by Competition

The crown diameter of a focal tree plus its neighbours and the distance of a focal tree to its nearest neighbours exhibited significant positive correlations in both plots \((p < 0.001)\) (Figure 4), suggesting that neighbourhood crowding among \(P.\ sylvestris\ var.\ mongolica\) trees can affect tree size.

The relationship between the combined canopy diameters and nearest neighbour distances was stronger in plot 2 \((r^2 = 0.38)\) than plot 1 \((r^2 = 0.34)\), in which trees were less crowded.

![Figure 4](image-url)  
**Figure 4.** Relationship between the sum of the crown length of the nearest neighbours plus the crown length of a focal tree and the sum of the distance of a focal tree to its nearest neighbours.

3.3. Competition-Induced Tree Mortality

In both plots, the spatial distribution patterns of all trees, including live and dead trees (pre-mortality pattern), exhibited a regular pattern at a close range (Figure 5a,b), but they were slightly aggregated at approximately 8 m. However, live trees (post-mortality pattern) were regularly distributed at a small scale (1–3 m), and were randomly distributed at larger scales (>3 m) (Figure 5c,d). The post-mortality patterns of both plots exhibited a greater degree of deviation from complete spatial randomness than the pre-mortality patterns at a small scale.

The random labelling null model clearly rejected the random mortality hypothesis in both plots (Figure 6). Surviving trees were more regularly distributed than dictated by processes of the random removal of dead trees. The post-mortality pattern of plot 2, which had a higher density and greater number of dead trees, exhibited more regular patterns and a greater range of interactions (0–9 m) compared to plot 1 (0–5 m).
Figure 5. (a,b) Pair-correlation function of pre-mortality patterns (live and dead trees) and (c,d) post-mortality patterns (live trees) for plots 1 and 2, respectively. Red lines denote the observed pair-correlation function. The envelopes (grey areas) denote the range of pair-correlation function of a random spatial distribution pattern, and were constructed from the 2.5% and 97.5% quantiles of 1000 Monte Carlo simulations based on the complete spatial randomness null model. It implies a cluster or regular distribution pattern of points if the observed curve lies above or below the simulation envelopes, respectively.

Figure 6. Comparisons between post-mortality patterns and pre-mortality patterns using random labelling as the null model in plots 1 (a) and 2 (b). Red curves denote the observed pair-correlation function of live trees. The envelopes (grey areas) denote the range of pair-correlation function of a random mortality process, and were constructed from the 2.5% and 97.5% quantiles of 1000 Monte Carlo simulations. It indicates a more regular post-mortality pattern of surviving trees if the observed curve lies below the simulation envelopes.
3.4. Competition-Induced Size Variation

The tree size differentiation pattern in plot 1 differed from that in plot 2. The mark differentiation functions of tree DBH (Figure 7) illustrated that tree size had a negative spatial autocorrelation at small scales of about 0–2.5 m in plot 1 (Figure 7a). In other words, large trees were regularly distributed and surrounded by smaller neighbours. This effect was not observed in plot 2, in which the size differentiation patterns showed a random assignment of tree size at a small scale (1–10 m) based on DBH (Figure 7b).

Figure 7. Mark differentiation function of live trees using (a,b) tree DBH and (c,d) crown size as marks for plots 1 and 2, respectively. Red curves denote the observed mark differentiation function. The envelopes (grey areas) denote the range of mark differentiation function of a random assignment of tree size marks, and were constructed from the 2.5% and 97.5% quantiles of 1000 Monte Carlo simulations based on the random labelling null model. Observed lines that fall above the simulation envelopes indicate an aggregation of different tree sizes. Observed lines that fall below the simulation envelopes indicate an aggregation of similar tree sizes.

However, the mark differentiation functions did not deviate from the random process in plot 1 based on tree crown diameter (Figure 7c). Meanwhile, the tree crown size differentiation exhibited a positive spatial autocorrelation at 0–2 m and 15 m in plot 2 (Figure 7d).

4. Discussion

P. sylvestris var. mongolica is an important ecological tree species in Northern China because of its strong ability to endure drought, infertility, and low temperature [23,24]. However, due to its shade-intolerance, inter-tree competition for light may be pervasive and an important factor in monospecific P. sylvestris var. mongolica communities. Identifying the role of competition in determining community spatial patterns is of particular interest in this community, where tree–tree competition is the only interspecies interaction and forest structure is relatively homogeneous. The two P. sylvestris var. mongolica stands analysed in this study developed after a fire that occurred
approximately 60 years ago, and the environmental habitats were homogeneous and constant in both plots. Thus, the observed spatial patterns of the two stands were mainly the result of natural processes and inter-tree interactions. Our analysis, based on nearest neighbour and spatial point patterns analyses, illustrates that competition between *P. sylvestris* var. *mongolica* trees is an important process structuring the community.

4.1. Competition and Tree Growth

The nearest neighbour analysis of the correlation between the combined distances of the nearest neighbours to a focal tree and the combined crown diameter suggests that competition was an important factor in reducing individual tree growth (Figure 4). Both plots exhibited a significant positive correlation between crown size and nearest neighbour distances (greater distances indicating less crowding), but the correlation was more significant in the higher-density plot, suggesting that inter-tree competition is more intensive in crowded plant communities. Similar significant positive correlations have been observed in other studies that found evidence of both intra- and inter-tree competition in different forests [5,6,12,15], particularly in woody plant communities in African savannas. Shackleton [12] argued that detecting the presence of competition with nearest neighbour analyses may be affected by environmental habitat factors, such as slope and the amount of rainfall. However, because the environmental conditions were fairly constant in this study, and *P. sylvestris* var. *mongolica* is a highly light-demanding species, the significant positive correlation between tree crown size and living space was easily detected.

4.2. Competition and Regular Spacing

As forest stands develop and the trees increase in size, inter-tree competition for light becomes more intensive and subsequently the trees living in more competitive environments may be more likely to die, resulting in greater distances between surviving trees (regular spacing) [8]. The presence of a regular dispersion of plant individuals has been regarded as criterion for the importance of competition in plant populations [49]. The spatial pattern analysis in this study clearly showed that competition was an important determinant of shaping *P. sylvestris* var. *mongolica* community structure. All of the living trees displayed a regular distribution pattern at a small scale, and even the pre-mortality patterns were slightly regular at a small scale, suggesting that the spatial patterns of *P. sylvestris* var. *mongolica* trees have become increasingly regular over time. Furthermore, the non-random mortality process examined in our analysis demonstrated that the post-mortality pattern increased in regularity, thereby indicating that inter-tree competition is an important factor of tree mortality processes [5]. Similarly, a number of other studies have demonstrated that competition has a significant role in tree mortality in different forests [4,17,18,30], especially in young and even-aged forests. However, other studies using similar analyses failed to detect significant evidence of competition contributing to tree mortality processes [5,15,19], and most suggested that the competitive interactions were not strong enough to result in mortality, but rather, resulted in a reduction in tree size [15]. The importance of competitive mortality processes may also vary with forest development. Aakala et al. [50] found less evidence for density-dependent mortality in an old-growth red pine forest in northern Minnesota. However, a recent study conducted by Larson et al. [51] argued that density-dependent mortality was evident in young forests and caused regular distribution patterns of surviving trees, while mortality in old-growth forest was density independent and was the net combined effect of diverse mortality agents (e.g., competitive suppression, insects, diseases, wind, or snow).

Getzin et al. [5] suggested three reasons for the lack of evidence of regular spatial patterns caused by competition in a Douglas fir forest: clustered offspring regeneration in gaps caused by mortality of large trees, spatial environmental heterogeneity, and weak competition. Interestingly, there was a lack of regeneration in our study plots and *P. sylvestris* var. *mongolica* saplings were almost absent, although many seedlings were observed. This makes the interpretation of the process from the pattern more straightforward, because of the lack of forest regeneration processes, which is considered an important factor contributing to forest spatial pattern formation. Therefore, we suggest
that a combination of strong competition between light-demanding species trees and a lack of regeneration in a homogenous environment resulted in clear evidence of a process driving a regular spatial pattern [30]. As density-dependent self-thinning was evident in this study, we suggest that the spatial patterns of surviving *P. sylvestris* var. *mongolica* trees become increasingly uniform.

4.3. Competition and Tree Size Inequality

We only detected a negative spatial autocorrelation in tree size in plot 1 using tree DBH as the marks, and no autocorrelation was found using crown diameters. Meanwhile, plot 2, which had a higher density, exhibited a positive spatial autocorrelation in tree crown diameter. This indicated that the competition process was not necessarily the only condition for generating size inequality, despite strong inter-tree competition. Weiner et al. [33] noted that the contribution of size-asymmetric competition to size inequality observed within crowded plant communities was greater than that of the variation in local density. We suggest that asymmetric competition was more intensive in plot 1, as it had a slightly greater proportion of large trees than plot 2, which was illustrated by the right skewness of the DBH distribution of plot 1 [48]. The less intensive asymmetric competition in plot 2 was attributed to its denser growth, which imposed restrictions on the growth of large trees that may have contributed to the similarity in tree size in the denser plot.

Another possible explanation for the lack of evidence of tree size inequality in the denser plot (plot 2) was its greater number of dead trees. Reed and Burkhart [37] proposed that development of a spatial autocorrelation in tree size in plantation forests might change from a negative autocorrelation caused by asymmetric competition between superior trees and suppressed trees, to a positive autocorrelation caused by a high mortality of small trees. As most of the dead trees were small trees, and forest regeneration was almost absent in both plots, the spatial autocorrelation in tree size became positive when a number of suppressed small trees died during the self-thinning process. We suggest that weak asymmetric competition and a high mortality (i.e., self-thinning) accounted for the lack evidence of a negative spatial autocorrelation in tree size in these plots, particularly for the denser community.

4.4. Implications for Management

Maintaining the stability of *P. sylvestris* var. *mongolica* forests is crucial to support their role in windbreak and sand fixation processes in ecologically vulnerable regions of Northern China. Based on our results, inter-tree competition is an important ecological process in structuring the community; therefore, applying proper silvicultural practices to regulate competition may be effective for enhancing the stability of these forests. Studies also showed that tree density reductions through silvicultural thinning could enhance drought resistance and resilience [52]. In this region, most of the natural *P. sylvestris* var. *mongolica* forests are young or middle-aged dense forests in which successful regeneration is insufficient and plant species diversity is low. Competition processes continuously drive self-thinning (i.e., density-dependent mortality), resulting in an increasingly regular distribution of trees until large gaps, caused by the death of large trees or large-scale disturbances such as forest fires, are created that support adequate regeneration or the growth of other species. Zheng et al. [53] proposed that several primary disturbance factors related to edaphic properties, pathology, and human-caused fires particularly influenced the stability of *P. sylvestris* var. *mongolica* forests. Nevertheless, the high density in these relatively homogenous forests led to a large number of less vigorous trees that were susceptible to pathology and forest fires. Therefore, the high density was negatively related to stability of these forests. Furthermore, Daiqing et al. [54] found that stand density was negatively correlated with understory species diversity in *P. sylvestris* var. *mongolica* plantations. Because the self-thinning process is continuous but slow in these natural forests, we suggest that regulating competition is necessary for enhancing the stability and species diversity in young or middle-aged natural *P. sylvestris* var. *mongolica* forests.
5. Conclusions

The nearest neighbour analysis of the correlation between the combined distances of the nearest neighbours to a focal tree and the combined crown length showed significant positive correlations in both plots ($r^2 = 0.34$ and 0.38), suggesting that competition was an important factor in reducing individual tree growth. The pair correlation functions of both plots exhibited regular distribution patterns of all trees including dead and living trees and of living trees at small scales. The random labelling null model clearly rejected the random mortality hypothesis in both plots, indicating trees living in more crowded environments were more likely to die. However, the mark differentiation characteristics showed weak evidence of a negative spatial autocorrelation in tree size, particularly in the high-density plot. We suggest that the high mortality rate of suppressed trees and weak asymmetric competition may have accounted for the lack of dissimilarity in tree size. This study showed that inter-tree competition is an important determinant of the development of Mongolian Scots pine forests. Regulating competition is necessary for enhancing the stability and species diversity in young or middle-aged natural $P. sylvestris$ var. mongolica forests.

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Conflicts of Interest: The authors have declared that no competing interests exist.

References


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