DISTANCE CORRELATIONS DO NOT SCALE WITH SIZE CORRELATIONS OF TREE SPECIES IN A TROPICAL RAIN FOREST STAND

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SUMMARY

Spatial patterns of forest trees have been long recognized as evidences of underlying biological processes within forests. We used point pattern analysis methods and process-based models to detect the demography and dynamics of trees in a primary rainforest stand. A fully mapped 1-ha plot was investigated in the tropical rain forest of Cuc Phuong National Park. Trees were stem-mapped, diameter-measured at breast height and classified into species. Spatial patterns and tree size correlations of life-history stages, intra-species and inter-species were analyzed using the pair-correlation and *r*-mark-correlation functions to reveal scale dependent patterns. At the community level, sapling and juvenile stages were clustered up to large scales, while pre-mature and mature trees were regular and had random distributions, respectively. The strong evidence of competitive interaction was shown by distance correlations. However, tree sizes did not correlate significantly to the same tendency with tree-tree distances. In intra-specific interactions, three of four abundant species were significantly clustered while negative correlations in tree size were clearly shown within *Hydnocarpus kurzii* and *Saraca dives*. In addition, marginal repulsions were found in distance correlations approved by size correlations when considering the inter-specific interactions with dominant species. We suggest that self-thinning was an important driver of the forest community dynamics. Clustered distributions were predominant among conspecific trees. Weak inter-specific interactions between light demanding species (*S. dives*) and other species can be explained by competition for light. High diversity of species could cause the equilibrated competition for limited resources as an overall competitive effect. Here, tree size (diameter at breast height) correlations and inter-tree distance correlations did not scale well, however they also indicated competitive interactions between tree individuals.

Keywords: Tropical rain forest, Vietnam, *r*-mark-correlation function, pair-correlation function, spatial point pattern analysis.

I. INTRODUCTION

The spatial patterns of forest trees have long been recognized as evidence of underlying processes that drive population dynamics (Wiegand *et al.* 2007). Based on individual tree locations (point patterns), the spatial distribution of a given species may be clustered, random or regular while the spatial association between two species can be classified as repulsion, randomness or attraction. Moreover, taking tree diameters into account (marked point pattern), diameter-location interaction may give better insight into the neighborhood relationship because the relative locations of trees in dense natural forest are often related to their size.

In some forest communities, for example temperate or boreal forests, the spatial pattern of trees may be driven by a single dominant regime or a relatively predictable mechanism. However, in more complex communities, such as tropical rainforest, trees are regulated by multiple controlling mechanisms, for example intra- and inter-specific interaction, habitat association and disturbance. In general, competition is one of the most studied issues in plant ecology since it is fundamental in structuring natural communities.

Among the mechanisms that have been proposed, there are two prominent theories that attempt to explain the density dependence of trees. The hypothesis of Janzen-Connell states that sapling survival decreases with decreasing distance to the closest parent tree due to increasing pressure from species-specific pathogens and herbivores. According to the theory of self-thinning, competition for limited resources should prune down individuals that are nearby neighbors, preventing recruitment into larger size classes and thus maintaining species coexistence as well. Consequently, after the natural regulation process (es), the distribution of mature trees should be less aggregated than those in smaller size classes.

Recent studies of tropical rain forests have shown the effects of high species diversity on spatial distribution. It may promote inter-specific individuals into functional similarity and adaptation to average environmental conditions. Moreover, functional equivalence or phenotypic plasticity may also explain the difficulty in detecting hetero-specific interactions, particularly between large trees. Considering only large trees (dbh > 10 cm) (Lawes *et al.* 2008; Getzin *et al.* 2011) in snap-shot investigations may be insufficient for detecting subtle effects of tree interactions. In our case, we studied a fully mapped 1-ha plot at a species-rich forest stand in Cuc Phuong National Park, Vietnam, to detect spatial neighborhood effects of individual trees.

To understand the spatial structure and tree interactions in our study stand, we showed (1) the stand structural characteristics, (2) uni- and bivariate pattern analyses of all species together based on life-history stages, and (3) intra- and inter-specific interactions of abundant species. Instead of analyzing only inter-tree distances, we used tree diameters at breast height (dbh) as additional data. In each spatial pattern analysis, we compared results from point pattern and size correlation to find out the potential interactions of trees. If self-thinning process occurs at community level, we expect the spatial pattern of trees within each life stage to become more regular with increasing tree size. Aggregated or over-dispersed distribution of intra-specific individuals may also coincide with positive or negative correlation in tree size. Similarly, attraction or repulsion effects between two species may be captured by positive or negative size correlation.

II. MATERIAL AND METHODS

2.1. Study area

Cuc Phuong National park was established in 1962 and is the oldest National park in Vietnam. It is located on the karst mountain region about 120 km southwest of Hanoi and covers an area of 22,200 ha (figure 1) wrapped by tropical rain forest. The park is surrounded by limestone mountain ranges that elevates to 648 m (Maybac peak). Because the geographical and topographical conditions are complex, the flora is highly diverse with 1924 species in 990 genera and 229 families. The climate is strongly affected by the karst mountains. The mean annual temperature is 20.6°C, but the mean winter temperature only 9°C. The annual mean humidity is 85%, annual rainfall is 2138 mm, concentrated mainly from May to October.

The site was selected in the primary forest located in the center of the national park (NP), at 20°20.98’ North and 105°35.78’ East, at an elevation of 386 m. The plot was chosen in the core zone of the Cuc Phuong NP in order to avoid the influence of human activities on its flora. There has been very little human disturbance in this core zone.

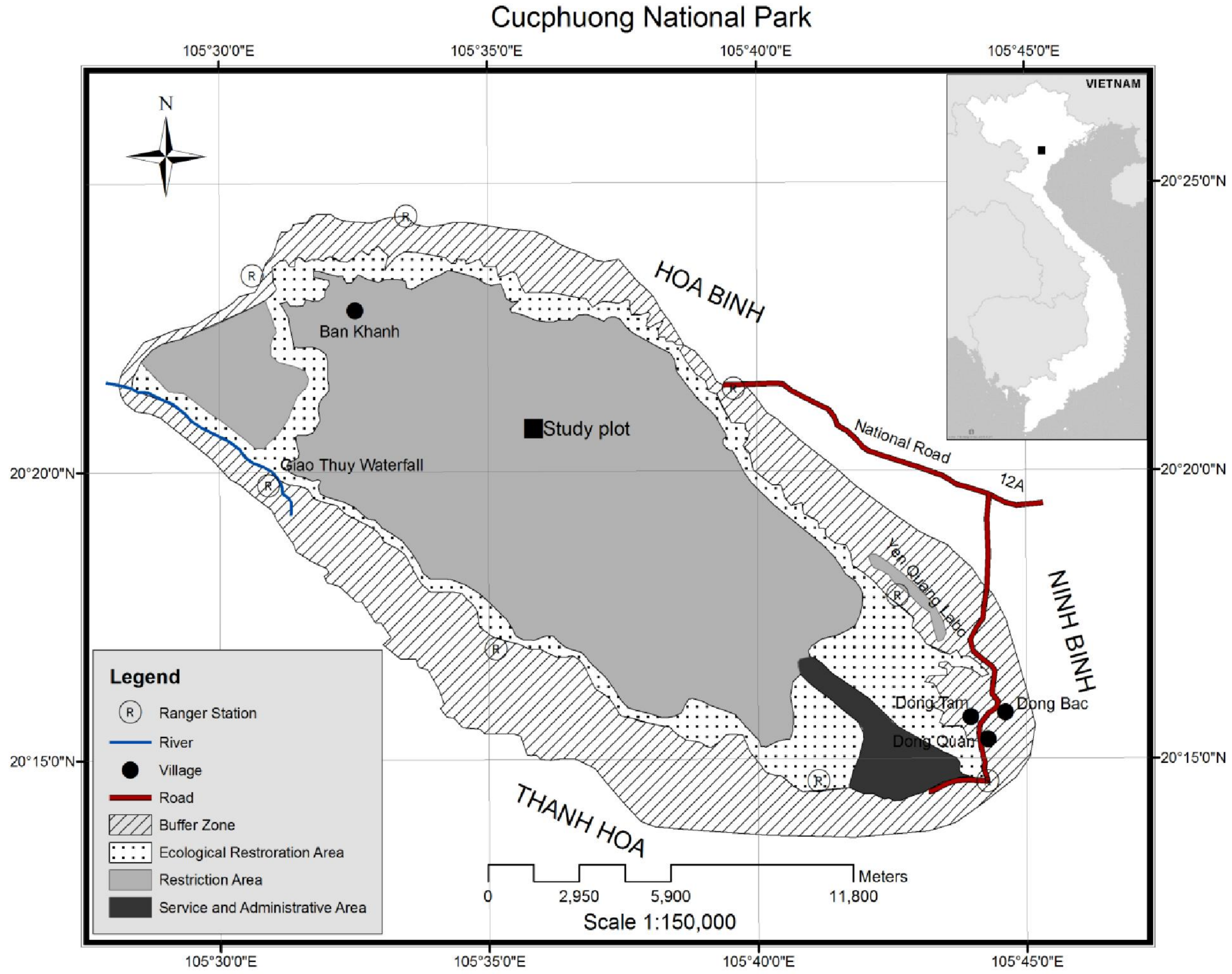

Figure 1. Map of Cuc Phuong National Park

2.2. Data collection

A 1-ha plot was established and subdivided into one hundred 10 m × 10 m subplots. The diameter at breast height (dbh; at 1.3 m above ground), tree coordinates (*x*,*y*) and tree species were recorded for all woody plants with dbh ≥ 2.5 cm. Stem-mapping of individuals was done using a laser distance measurement (Leica Disto D5) and compass. Trees were classified to species in the field or, in uncertain cases, samples were taken to identify them in the herbarium of the NP. Furthermore, we classified all individuals into four life-history stages: sapling (dbh < 5 cm), juvenile (5 ≤ dbh < 10 cm), pre-mature (10 ≤ dbh < 30 cm) and mature (dbh ≥ 30 cm).

2.3. Statistical analysis

The pair-correlation function

The pair-correlation function $g(r)$ is a spatial correlation function describing the spatial arrangement of points at a range of spatial scales. Based on distances of point-point pairs, the *g*-function describes a standardized density at a given scale r and can be interpreted as the expected density of points at a given distance r of an arbitrary point, divided by the intensity λ of the pattern (Stoyan and Stoyan 1994). The univariate *g*-function is related to the derivative of the *K*-function:

$$K(r) = 2\pi \int_0^r g(r')r'dr' \text{ or } g(r) = \frac{K'(r)}{(2\pi r)} \text{ for } r \geq 0$$

Thus, with the univariate pair-correlation function $g_{11}(r) = 1$ is under complete spatial randomness (CSR), values of $g_{11}(r) > 1$ indicate aggregation. Values of $g_{11}(r) < 1$ indicate regularity at distance r. Regularity means that there are less points at distance r from an arbitrary point of the pattern than expected under CSR.

Transformed from the univariate version, the bivariate pair-correlation function can be used to analyze the spatial relation between two groups of points. It is the expected density of points of pattern 2 at distance r from an arbitrary point of pattern 1, divided by the intensity λ_2 of pattern 2. $g_{12}(r) = 1$ shows independence (no interaction), $g_{12}(r) > 1$ indicates that there are on average more points of pattern 2 at distance r from points of pattern 1 than expected under independence, hence indicating attraction between two point patterns at distance r. Conversely, $g_{12}(r) < 1$ indicates repulsion between the two patterns at distance r.

r-mark-correlation function

The r-mark-correlation function (r-MCF) (Illian *et al.* 2008) describes dependence between marks (such as dbh and tree height) of trees that are distance r apart. Given two trees i and j distance r apart and with marks m_i and m_j, their mark relationship is quantified by a test function $t(m_i,m_j)$. Based on all pairs of trees distance r apart, an estimator of r-MCF is given by:

$$\widehat{k}_t(r) = \frac{1}{c_t}\frac{\sum_{i=1}^{n}\sum_{j=1}^{n}[t(m_i, m_j)]k(\|x_i - x_j\| - r)}{\sum_{i=1}^{n}\sum_{j\neq i}^{n}k(\|x_i - x_j\| - r)}$$

where c_t is the non-spatial expectation of the test function and $k(\|x_i - x_j\| - r)$ is a kernel function. If the distance $\|x_i - x_j\|$ is close to r, the kernel function yields a value of 1, and 0 otherwise.

For the univariate r-MCF, $k_{m\cdot}(r)$, we used the test function $t_2(m_i,m_j) = m_i$ normalized by the mean mark μ. In case of bivariate r-MCF ($k_{\cdot m}(r)$), we applied the test function $t_3(m_i,m_j) = m_j$, where only mark values of pattern 2 were considered. In the following, we will denote the univariate and bivariate r-MCF as described above with $k_{m1\cdot}(r)$ and $k_{\cdot m2\cdot}(r)$, respectively.

In case of independent marks r-MCF = 1, if r-MCF < 1 then marks are negatively correlated, and if r-MCF > 1, marks are positively correlated at distance r. For example, inhibition (negative correlation) is expected if trees distance r apart compete and therefore have marks smaller than the average mark (Illian *et al.* 2008).

Null models

The basic hypothesis of our analyses was that the environmental conditions at our plot are homogeneous, because environmental heterogeneity would strongly influence the spatial distribution of trees and would require the use of null models appropriate to heterogeneity. We based our homogeneity test on the spatial pattern of all mature trees (dbh ≥ 10 cm) because mature trees are expected to have experienced all available sites and to have undergone excessive thinning. Consequently, heterogeneous habitat quality would be reflected in a heterogeneous distribution of mature trees. Here, we applied complete spatial randomness (CSR) as the null model and the g-function to describe the pattern. Our plot is indeed homogeneous (see Results).

Analysis 1 – Overall univariate correlations: To detect possible non-randomness in the spatial pattern of all trees in specific life history stages, we used CSR as the null model for univariate distance correlation with the g-function. We tested for possible size correlations between the tree individuals using the null model of independent marks and the univariate r-mark-correlation function (test function t_2). The independent-marks null model is realized by shuffling the dbh values between pairs of trees (Illian *et al.* 2008).

Analysis 2 - Overall bivariate correlations: To investigate relationships between matures and early life-history stages, we used the antecedent condition null model for bivariate distance correlations $g_{12}(r)$. In these cases, we assumed that the two types of points were created at different times and mature trees (pattern 1) may influence the development of younger life-history stages (pattern 2), but this assumption should not happen in the reverse direction (Wiegand and Moloney 2004).

Analysis 3 – Intra-specific interactions: At species level, for detecting the spatial pattern of trees of a given species, the methods of analysis 1 were applied to the four most abundant species (table 1).

Analysis 4 - Inter-specific interactions: To investigate interaction between two tree species, we applied the toroidal shift as the null model for bivariate distance correlations $g_{12}(r)$. The hypothesis behind this null model is that the patterns of the two tree species were generated by two independent processes; i.e. the absence of interaction between the two patterns. For analyses of bivariate size correlations, we used the bivariate *r*-mark-correlation with test function t_3 and a variant of the independent marks null model: marks of pattern 1 were left unchanged and the mark values of pairs of trees of pattern 2 were reshuffled (Illian *et al.* 2008).

For all analyses, we performed 199 Monte Carlo simulations of the null model and used the 5th lowest and 5th highest values to approximate 95% confidence envelopes. Significant departure from the null hypothesis was obtained if the empirical pattern was outside the simulation envelopes. All point pattern and *r*-mark-correlation analyses were performed by using the grid-based software Programita (Wiegand and Moloney 2004).

III. RESULTS

3.1. Stand structure and composition

We found that the total density of trees ≥ 2.5 cm was 825 individuals/ha belonging to 106 species in 80 genera of 38 families. The four most abundant species *Archidendron chevalieri* (Mimosaceae), *Hydnocarpus kurzii* (Flacourtiaceae), *Saraca dives* (Fabaceae-Caesalpiniaceae), *Wrightia macrocarpa* (Apocynaceae) comprised 304 individuals (ca. 36%). *A. chevalieri* occurred in high density, but its basal area was much lower than those of other species. *S. dives* and *W. macrocarpa* were equivalent in tree size shown by their average dbh and the ratio between density and basal area (Table 1). Across all species, there were 252 saplings, 247 juveniles, 326 pre-matures and 103 matures (figure 2).

Table 1. Species composition and stand structure of live trees ≥ 2.5 cm dbh in a 1-ha plot of tropical rain forest in Cuc Phuong National Park, Vietnam (NN- Nearest neighbour)

Species	Density (N/ha)	Basal area (m^2/ha)	Mean dbh (cm)	Maximum dbh (cm)	Median NN distance (m)
Archidendron chevalieri	101	0.53	7.28	19.4	3.73
Hydnocarpus kurzii	94	1.29	10.17	43.6	4.53
Saraca dives	67	3.79	22.99	52.5	5.61
Wrightia macrocarpa	42	1.81	17.96	50.9	8.63
Others (102 species)	521	28.63	15.96	152.8	1.64
Total	825	36.06	14.92	152.8	1.46

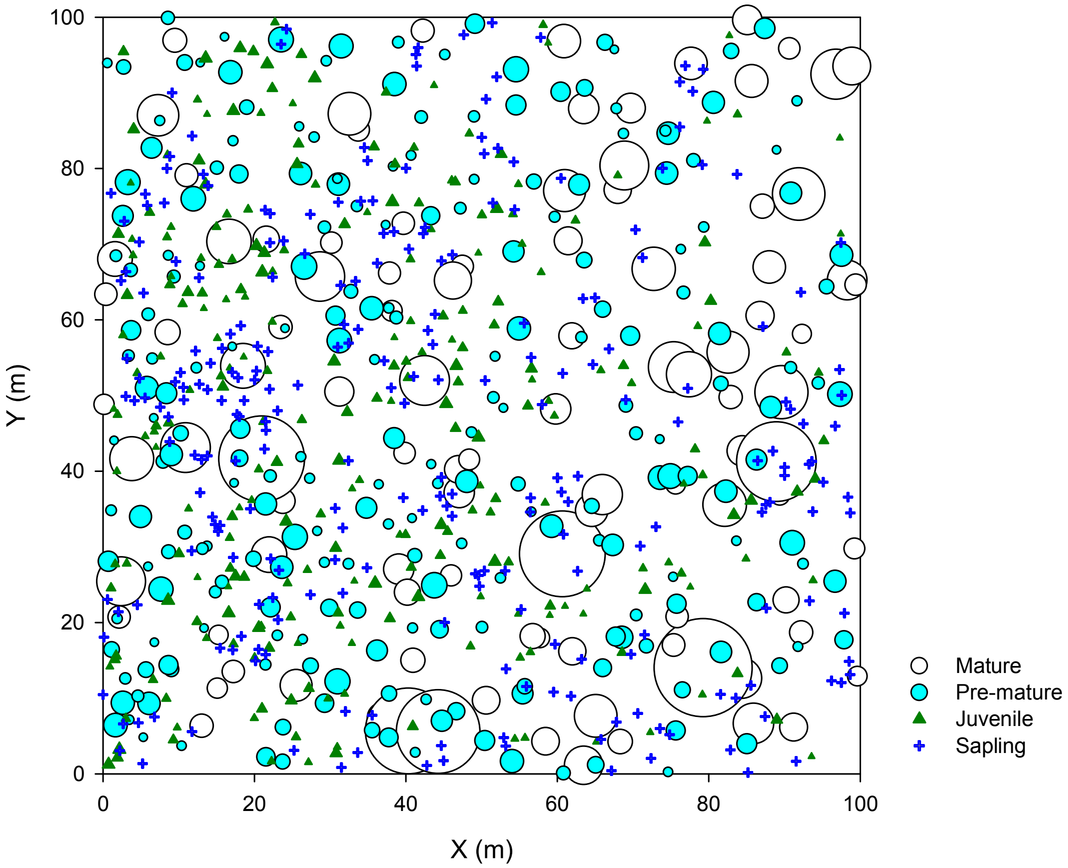

Figure 2. Distribution map of all tree individuals in four size classes
The unit of (x, y) axes is meters

The overall size frequency distribution of all individuals of all species had a reverse J-shaped population structure as expected for a self-replacing population (figure 3a). This is a typical characteristic for uneven-aged and multi-species stands with a high concentration of individuals in small size classes (Richards 1996). *A. chevalieri* also showed a reverse J-shape, but with a "short foot" (figure 3b), since there were no mature individuals. *H. kurzii* had the tendency of a reverse J-shaped distribution of dbh, which was not clear in case of *W. macrocarpa* (figure 3c, e). *S. dives* had a bimodal size distribution with its major peak at dbh of 20 – 30 cm (figure 3d), and a minor peak for the 0-5 cm class.

3.2. Spatial pattern analysis

Given that the large-scale pattern of mature trees follows CSR, we assume that the study plot has homogeneous site conditions. In each figure, the observed patterns (dark line) lying beyond the confidence envelopes (grey lines) indicate significant departures from the null models.

Analysis 1: Overall univariate correlations

At the community level, spatial patterns of tree distribution shifted from a strong clumping in saplings to regularity in pre-matures and randomness in matures (figure 4a-d). That means the distribution of trees was less aggregated with increasing size. These results could be explained by inter-tree competition and density dependent mortality. More explicitly, saplings were clumped from 1-9 m and at some larger scales (figure 4a). Juvenile individuals were clumped at all scales ≥ 1 m and up to 50 m (figure 4b). Pre-mature trees showed repulsion up to scales of 2 m (figure

4c); a pattern typical for situations with locally strong competition for living space. For mature trees, $g_{11}(r) < 1$ for $r < 5$ m, however this was not significant and thus matures showed a completely random distribution (figure 4d).

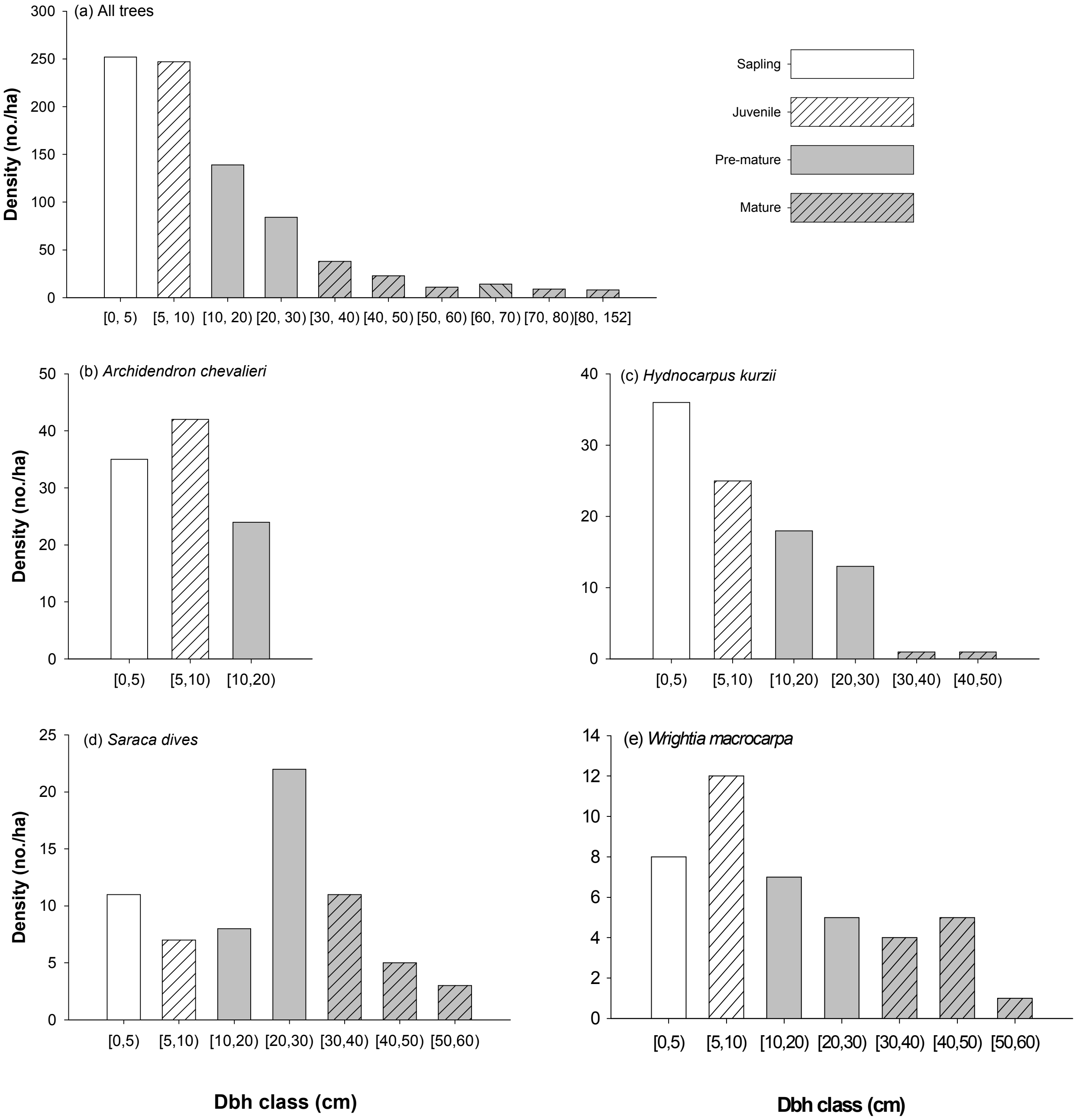

Figure 3. Dbh class distribution of all species (a) and of the four most abundant species (b-e) with dbh ≥ 2.5 cm in the 1-ha plot

When considering tree dbh as a mark, weak negative correlations were observed at scales 7-9 m for saplings and at 12-15 m in pre-mature trees (figure 4e, g). Juveniles and mature trees showed no correlation in tree size (figure 4f, h). However, tree size correlations were surprisingly weak and tree distance and tree size correlations did not scale together. This indicates that inter-tree competition is not important for the overall pattern.

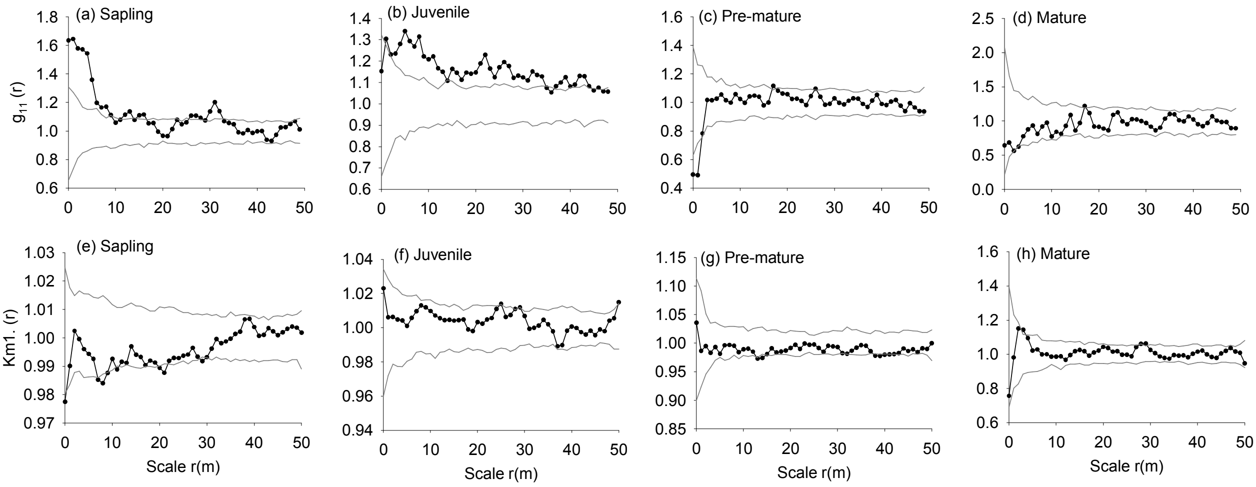

Figure 4. Spatial correlation within different life-history stages of all species are shown by the univariate pair-correlation (a-d) and r-mark-correlation functions (e-h)

Analysis 2: Overall bivariate correlations

Saplings occurred independently from their potential parents at all scales (figure 5a). We found slight but significant repulsion between matures and juveniles at distances up to 2 m (figure 5b); thus, we have to reject the hypothesis of independence between matures and juveniles. Also, marginal repulsion was observed at some scales for mature versus pre-mature trees (figure 5c).

In dbh correlation, we found marginally negative effects between mature versus sapling and juvenile stages (figure 5d, e). These confirmed the marginal negative interaction in distance correlations of the respective life history stages. No significant correlation was found between mature and pre-mature trees (figure 5f).

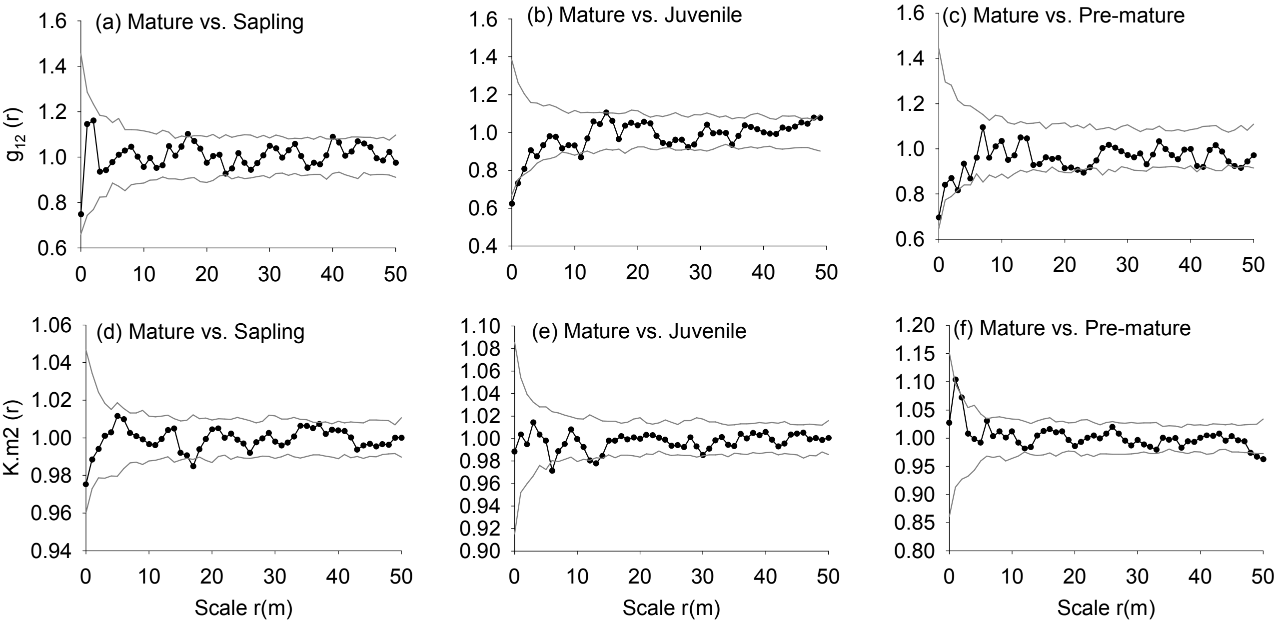

Figure 5. Spatial correlation between mature trees and trees of younger life-history stages are shown by the bivariate pair-correlation (a-c) and r-mark-correlation functions (d-f)

Analysis 3: Intra -specific interactions

The spatial pattern of *A. chevalieri* was aggregated at scales of 3-8 m, while *r*-MCF indicated a positive correlation from 7-8 m (figure 6a, e). This means that *A. chevalieri* individuals can be distributed close together without competitive effects, evident from the tree sizes at short scales. This pattern would even be in agreement with facilitation. Both *H. kurzii* and *S. dives* showed clearly clustered patterns at different scales (figure 6b, c). *r*-MCF showed significantly negative dbh correlations at scales up to 4 m in *H. kurzii* and *S. dives* (figure 6f, g). This is an inverse effect to the distance correlation and indicates strong competition that reduces tree size. The observed patterns of *W. macrocarpa* completely fell inside the confidence intervals suggesting that the species was spatially randomly distributed and independent in tree size (figure 6d, h).

Analysis 4: Inter-specific interactions

We performed a total of 12 (4 x 3) bivariate point pattern analyses for pairs of the 4 most abundant species (figure 7). Two general trends of association occurred: either (1) there was independence between species pairs (*A. chevalieri* - *H. kurzii*, *A. chevalieri* - *W. macrocarpa* and *H. kurzii* - *W macrocarpa*) (figure 7a, c, e), or (2) there was marginally significant repulsion between species pairs (*A. chevalieri* - *S. dives*, *H. kurzii* - *S. dives* and *W. macrocarpa* - *S. dives*) (figure 7b, d, f). Interestingly, *S. dives* showed negative association (repulsion or segregation) with all other abundant species. In correlations of tree dbh, there were also two trends of interaction. Independent correlations were observed in almost all pairs: *A. chevalieri* - *H. kurzii*, *A. chevalieri* - *W. macrocarpa, H. kurzii* - *S. dives* and *W. macrocarpa* - *S. dives* (figure 8a, c, d, f). Negative correlations were found in the pairs of *A. chevalieri* - *S. dives* and *H. kurzii* - *W macrocarpa* (figure 8b, e).

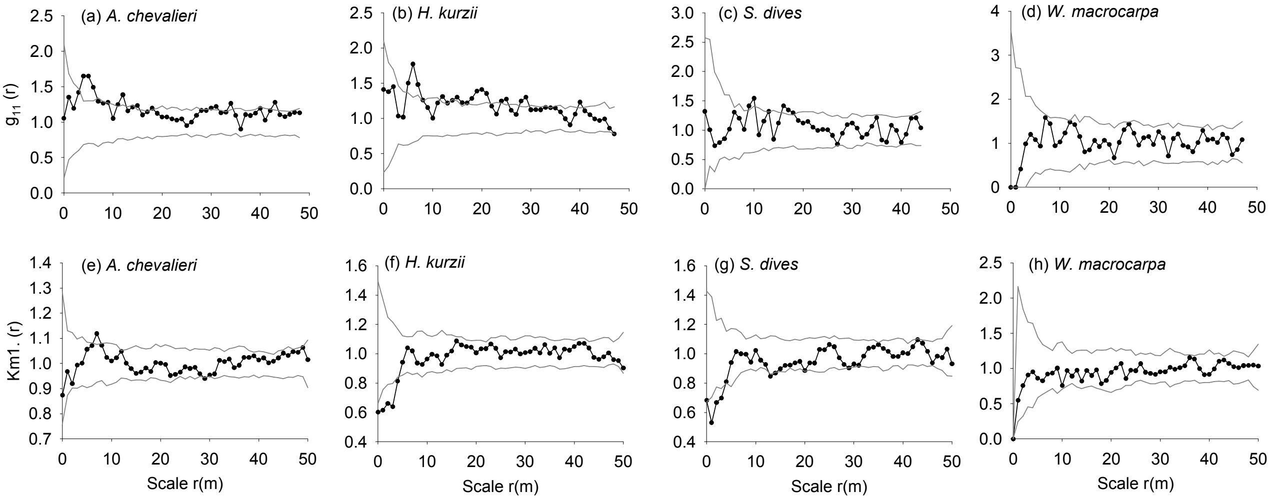

Figure 6. Spatial correlation within the most abundant tree species are shown by the univariate pair-correlation function (a-d) and r-mark-correlation functions (e-h)

IV. DISCUSSION

Stand characteristics

We found that population structure was dominated by small size classes, resulting in a reverse J-shaped distribution of all individuals. This is typical for a population that recruits with sufficient numbers to maintain itself (Richards 1996). At species level, *A. chevalieri* and *H. kurzii* followed the overall tree size distribution suggesting continuous regenerations and favorable conditions for the development of juveniles. Decreasing recruitment with increasing tree size is a common property of shade-tolerant species, specifically in case of *A. chevalieri* ; or *H. kurzii*. In contrast to this, the bell-shape dbh distribution in *S. dives* indicated poor recruitment, as often observed in shade-intolerant species, even *S. dives* is classified as neutral tree growing in the second storey of the forest; and as a fast growing species like *W. macrocarpa* as synonym of *W. laevis*.

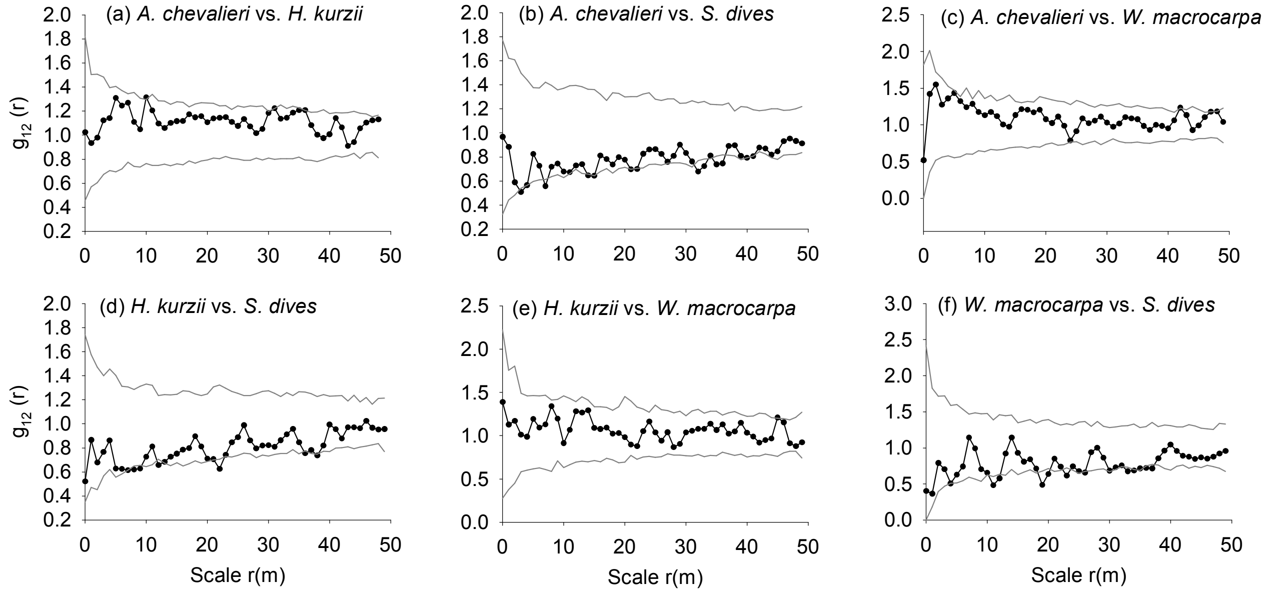

Figure 7. Spatial correlations between the most abundant tree species are shown by the bivariate pair-correlation function. The observed patterns (dark line) that lie out of the confidence envelopes (grey lines) indicate significant departures from the null model of toroidal shift (spatial independence)

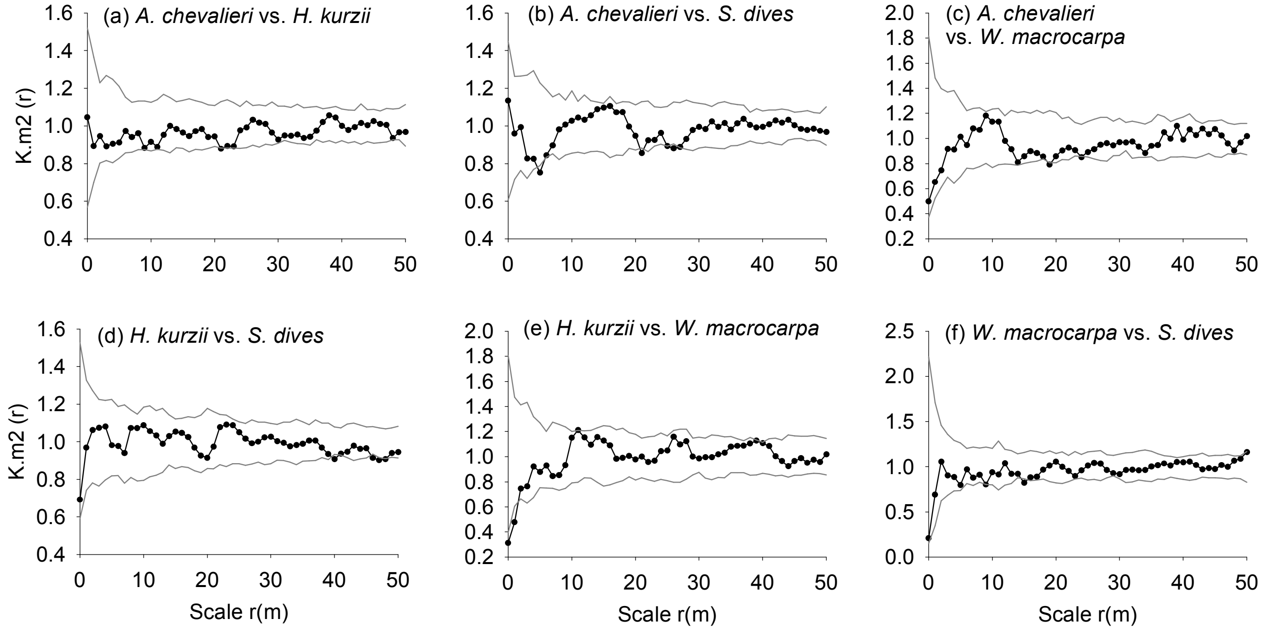

Figure 8. Spatial correlation between the most abundant tree species are shown by the bivariate r-mark-correlation function. The observed patterns (dark line) that lie beyond the confidence envelopes (grey lines) indicate significant departures from the null model of independent marks

Overall patterns

Previous studies on competition and dynamics have used static data to compare spatial patterns of trees within a stand in the pre-mortality and post-mortality stage, or small versus large trees. If tree-tree competition occurs within a population, spatial patterns shifting from clumping in small individuals toward regularity in larger trees or the post-mortality stage are expected. In this study, we took the approach of comparing trees in different life-history stages (based on tree dbh) to detect the importance of competition in a stand of tropical rain forest. To contrast the results from pair-correlation and *r*-mark-correlation functions has advantages because they represent two patterns of tree locations and tree-size attributes. Therefore, they combine properties of distance-dependent and size-dependent interaction measures. At the community level, evidence for negative density dependence was explicitly shown by patterns changing from clustered to regular with increasing tree size classes. We found at sapling and juvenile stages (dbh < 10 cm) that individuals were strongly clustered at a large range of scales. Aggregation caused by environmental heterogeneity was eliminated in the initial test indicating that the study stand is homogeneous in term of environmental conditions. Clustered patterns in young trees are often described as dispersal limitation, or as the remnant of past windfalls that would create large canopy gaps with favorable conditions for regeneration. We found significant evidence of negative interaction between pre-matures which was confirmed by small MCF values in tree size correlation up to scales of 2 m. Therefore, aggregated patterns observed in saplings and juveniles (analysis 1) may be caused by regeneration processes in canopy gaps. Regular patterns are common for mature or pre-mature trees, especially at small scales, resulting from competition for resources, for example light, moisture, soil and nutrients. We did not find evidence for mutual repulsion in the mature class (dbh> 30 cm) except for very weak effects of competition at small scales of 2-3 m, as well as no significant correlation in dbh of mature trees. Our findings were supported by two other studies in tropical rain forests Lawes *et al.*(2008) and Getzin *et al.*(2011). There are several possible explanations for this pattern, for example exogenous disturbance events (e.g. tree fall by wind, illegal logging), other density dependent mortality, or inherent tree-tree competition facilitating population dynamics. Moreover, a random pattern of matures could be explained by the functional equivalence of species that is difficult to detect via one snapshot investigation (Wiegand *et al.* 2007). Following this light, high-species diversity may lead to the niche differentiation and phenotypic plasticity of each species and this could blur the competitive effect of trees (Getzin *et al.* 2011). Weak repulsions in distance correlations between matures versus juveniles and mature versus pre-matures were approved by dbh correlation as well. Obviously, there are often less small trees near big trees as than expected from the density of the small trees. This suggests that asymmetric competition for limited resources between large and small trees leads to both less numbers and sizes of small trees near large trees. Mortality can cause the loss of a pattern (clumping or regularity) from one life history stage to the next. Furthermore, regular distance within large trees was outcome of a long-term competition between them.

Intra- and inter-specific patterns

At the species level, aggregation is a widely seen pattern in nature, particularly in species-rich tropical rain forests. Aggregated patterns at scales < 20 m suggest dispersal limitation of these tropical tree species. Differences between species were revealed, but three of the four most abundant species showed aggregated distributions. Aggregation intensities clearly decreased with increasing spatial scale and with the abundance of species. In *A. chevalieri*, the most abundant species, spatial patterns were compatible between size and distance correlations. Its ecological characteristics are shade tolerance and heavy seeds (ca. 3 cm high and 2.5 cm in diameter), suggesting dispersal limitation. But in *H. kurzii* and *S. dives*, clustered distributions at scales larger than 5 m contrasted to the strongly negative correlations at smaller scales in tree size. With *H. kurzii*, annual fruiting is not prolific, therefore young trees are rarely met. So, these aggregated patterns at large scales (figure 6b) may have been caused by individuals which concentrate outside the immediate crown of large trees. Moreover, with negative size correlations (figure 6f), these patterns suggested that large trees tend to have smaller neighbors and trees with similar sizes tend to repulse each other. Similar explanation for *S. dives* - a neutral tree species. The fourth most abundant species *W. macrocarpa* showed random spatial distribution and independence in tree size correlation. Considering inter-specific interactions, only *S. dives* was repulsed by other species in space while other inter-specific pairs were independent. *S.dives* is considered a neutral species inclining toward shade intolerant and dominant species, therefore it competes strongly with other species for living space. In addition, inferences from distance correlation were approved by negative correlations when considering stem diameter. *H. kurzii* and *W. macrocarpa* showed negative in size correlation but were independent in distance correlation suggesting that tree sizes of *W. macrocarpa* tend to be smaller at small scales when comparing pairs of these two species.

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TƯƠNG QUAN VỀ KHOẢNG CÁCH VÀ KÍCH THƯỚC KHÔNG CÙNG PHẠM VI KHÔNG GIAN CỦA CÂY RỪNG TỰ NHIÊN

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[2]Trường Cao đẳng Nông nghiệp và Phát triển Nông thôn Bắc Bộ

TÓM TẮT

Mô hình không gian của cây rừng được coi là bằng chứng của các quá trình sinh học đã và đang diễn ra trong lâm phần đó. Các phương pháp phân tích mô hình điểm và quá trình dựa vào mô hình để nhận dạng phân bố và biến động của cây rừng ở một lâm phần rừng nguyên sinh ở Vườn Quốc gia Cúc Phương. 01 ô tiêu chuẩn 1 ha được điều tra và xác định tên cây, vị trí, đường kính ngang ngực. Mô hình không gian và tương quan kích thước của cây theo giai đoạn sống, cùng loài, khác loài được phân tích bằng hàm tương quan theo cặp và hàm tương quan thuộc tính. Ở cấp quần thể, cây non và cây sào có phân bố cụm đến khoảng cách lớn trong khi cây tiền thành thục và thành thục có phân bố đều và ngẫu nhiên. Bằng chứng của quan hệ cạnh tranh được thể hiện trong quan hệ về khoảng cách. Tuy nhiên, kích thước cây và khoảng cách cây-cây không tương quan theo phạm vi không gian. 03 trong 04 loài cây chiếm đa số có phân bố cụm nhưng tương quan nghịch về đường kính được thể hiện ở 02 loài cây *Hydnocarpus kurzii* và *Saraca dives*. Quan hệ cạnh tranh yếu về cả khoảng cách và kích thước cây được tìm thấy ở những loài ưu thế. Kết quả cho thấy, tỉa thưa tự nhiên là cơ chế quan trọng của động thái rừng. Phân bố kiểu cụm là phân bố của các loài cây ưu thế. Quan hệ cạnh tranh yếu giữa loài ưa sáng *S. dives* và các loài khác là do nhu cầu ánh sáng. Tính đa dạng loài cao của quần thể có thể làm cân bằng quan hệ cạnh tranh giữa các loài. Tương quan về khoảng cách và kích thước cây không cùng phạm vi không gian, tuy nhiên cũng thể hiện tính cạnh tranh giữa các cá thể cây.

Từ khóa: Rừng tự nhiên nhiệt đới, Việt Nam, hàm tương quan thuộc tính, hàm tương quan theo cặp, phân tích mô hình điểm không gian.

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