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# Phylogenetic Community and Nearest Neighbor Structure of Disturbed Tropical Rain Forests Encroached by *Streblus macrophyllus*

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**Abstract:** Although woody plant encroachment of tropical forest ecosystems has been related to altered disturbance regimes, its impacts on the nearest neighborhood structures and community phylogenetics are still poorly understood. *Streblus macrophyllus* is a light-demanding species during its early life stages and is shade-tolerant as a mature tree. *S. macrophyllus* can be found in tropical karst evergreen forests in northern Vietnam. It often regenerates at high densities in anthropogenic disturbed forest stands. To understand the structural patterns of disturbed forests encroached by *S. macrophyllus* at different abundance levels, three fully mapped 1-ha plots were established in Cuc Phuong National Park. Methods considering the phylogenetic community and nearest neighbor statistics were applied to identify how community structure changes during *S. macrophyllus* encroachment. Results showed that phylogenetic distance, phylogenetic diversity, and mean phylogenetic distance increased when species diversity increased and the abundance of *S. macrophyllus* decreased in forest communities. Net related index values were positive, which indicates a clustered phylogenetic structure among all sampled forest communities. *S. macrophyllus* trees were mixed well with heterospecifics and had regular to aggregated distributions, whereas the species showed evidence of being a strong competitor with its neighbors. Competition could be a major ecological process regulating forest communities encroached by *S. macrophyllus*. According to the forest disturbance effects, phylogenetic community properties showed the loss of phylogenetic relatedness when *S. macrophyllus* increased in abundance. To our knowledge, *S. macrophyllus* encroaches tropical rain forest communities as a disturbance-adapted species.

**Keywords:** dominance; mingling; nearest neighborhood; phylogenetic structure; self-thinning; uniform angle index

## 1. Introduction

A fundamental aim in ecological studies is to understand processes and mechanisms that control the distribution and abundance of species [1]. It is critical to understand various ecological mechanisms and processes that influence species assemblage in order to gain deeper insights into species associations and community structure. Ecological theories such as competition, facilitation, dispersal limitation, habitat preference, neutral theory, or the Janzen–Connell hypothesis (proposed for explaining community structure and species coexistence in species-rich forests) are mainly developed based on species spatial characteristics [2].

For example, intraspecific aggregation can be described by dispersal limitation or ecological niches that may reduce the importance of interspecific competition [3]. Moreover, spatial segregation of tree species involves competitive interactions between superior species, which prevents the elimination of inferior species and promotes species diversity [4,5]. The Janzen–Connell hypothesis assumes that, in species-rich forest communities, tree individuals tend to be regularly distributed according to their conspecific interactions [6]. Species coexistence in diverse communities (i.e., tropical forests) can also be described by neutral theory, which assumes that since species are functionally equivalent, the process rate is the same for each species on a per capita basis, and variation in abundance between species is a result of “accidental” dispersal and ecological drift [7].

Forest structure is a set of attributes that results from forest dynamics and biophysical processes [8,9]. However, it is increasingly important to establish a number of methods that describe forest structural attributes with exact descriptions of small-scale structural attributes. In recent decades, multiple individual tree indices have been proposed, such as the uniform angle index, species mingling index, and dominance index [8,10,11], and these have been widely adopted [12,13]. The basic idea of these indices is to characterize the neighborhood interactions of a reference tree by using its *n*-nearest neighbors. The technique of nearest neighbor statistics allows us to determine the relationship between neighborhood tree groups like species mixture, tree size dominance, and spatial distribution at small spatial scales.

Nearest neighbor analysis in forest communities has been previously used to evaluate spatial structure [13]. A community’s phylogenetic structure should provide insight into the ecological processes that organize a community [14]. The nearest neighbor relationship between tree individuals is highly applicable for describing competitive interactions for limited environmental resources, mutual dependence of interactions, and species coexistence [13]. Phylogenetic information can be used to distinguish the mechanisms regulating community structure, such as phylogenetic density dependence and competition, since these mechanisms may have a different imprint on phylogenetic diversity than on species diversity [15]. Deforestation and forest fragmentation can drive species to local extinction, potentially changing the phylogenetic community structure and diversity of remaining assemblages [16]. For example, if the taxa that are favored by disturbances are more phylogenetically related than those that are disadvantaged, we may expect a loss of phylogenetic alpha diversity with increasing forest loss and local disturbances [16].

*Streblus macrophyllus* Blume (Moraceae) can be found in mixed forests of Guangxi, Yunnan (China), Indonesia, Malaysia, the Philippines, and Vietnam [17]. In the mixed tropical rain forests of the Karst mountains in northern Vietnam, *S. macrophyllus* appears in areas of high soil moisture and beneath canopy gaps in valleys below an elevation of 700 m a.s.l. [17–19]. *S. macrophyllus* is shade-intolerant during its early life stages, but becomes shade-tolerant when matured, occupying the mid-canopy with species in the Clusiaceae, Ulmaceae, and Annonaceae families [18]. Under gap-phase regeneration [19], it encroaches quickly into mixed forests. Following large disturbances, it may form pure and dense stands that reduce the regeneration chances of other species and forest community diversity. However, spatial structural characteristics of encroached forest stands and *S. macrophyllus* ecology are poorly studied.

Our objective is to study the spatial structure of tropical forest communities encroached by *S. macrophyllus* in Cuc Phuong National Park after long-term disturbances by illegal logging of local people. We performed two different types of analyses that use the current technique to attain nearest neighbor statistics and the phylogenetic community structure in three forest stands with different *S.*

*macrophyllus* abundance levels. For a better understanding of the nearest neighbor structure, we used bivariate distributions by combining pairs of two structural indices for each species, including the mingling, dominance, and uniform angle indices. This approach quantified the spatial structure of a forest stand from two different aspects and provided detailed information. Therefore, it has advantages over univariate distributions of structural parameters. Based on the analyses, we addressed the following research questions: (1) How did forest community structures change in response to *S. macrophyllus* encroachment? (2) Do nearest neighbor relationships vary depending on the density of *S. macrophyllus* populations?

## 2. Materials and Methods

### 2.1. Study Sites and Data Collection

The study was conducted at Cuc Phuong National Park in northern Vietnam (Figure 1). The area is surrounded by limestone mountains with a maximum elevation of 300–400 m a.s.l. and is covered by tropical evergreen rain forest. The limestone mountains strongly affect the local climate. The mean annual temperature is 20.6 °C, but the mean temperature in winter (from December to February) is only 9 °C. The annual mean humidity is 85%, and the average annual rainfall is about 2138 mm.

We installed three 1-ha plots from 2011 to 2016 in tropical secondary forests (Figure 2). The study region was occupied by local communities before 1988 and the forest was illegally logged for their livelihoods until they were removed from the core zone. Three study forest stands were selected as an indication of different levels of encroachment of *S. macrophyllus*: P1-high density (20°17' N; 105°39' E), P2-medium density (20°14' N; 105°43' E), and P3-low density (20°15' N; 105°42' E). Unfortunately, we did not perform a real estimation of disturbance intensity within each plot, mainly due to the impossibility of reliably recognizing the signs of human interventions after a long time. All live trees with a diameter at breast height (DBH)  $\geq 2.5$  cm were mapped and tree positions and their characteristics (species and DBH) were recorded. In each study plot, the relative coordinates (x, y) of each tree were recorded via a grid system of subplots (10 m  $\times$  10 m) by using a laser distance measurer (Leica Disto D5) and compass (Figure 2).

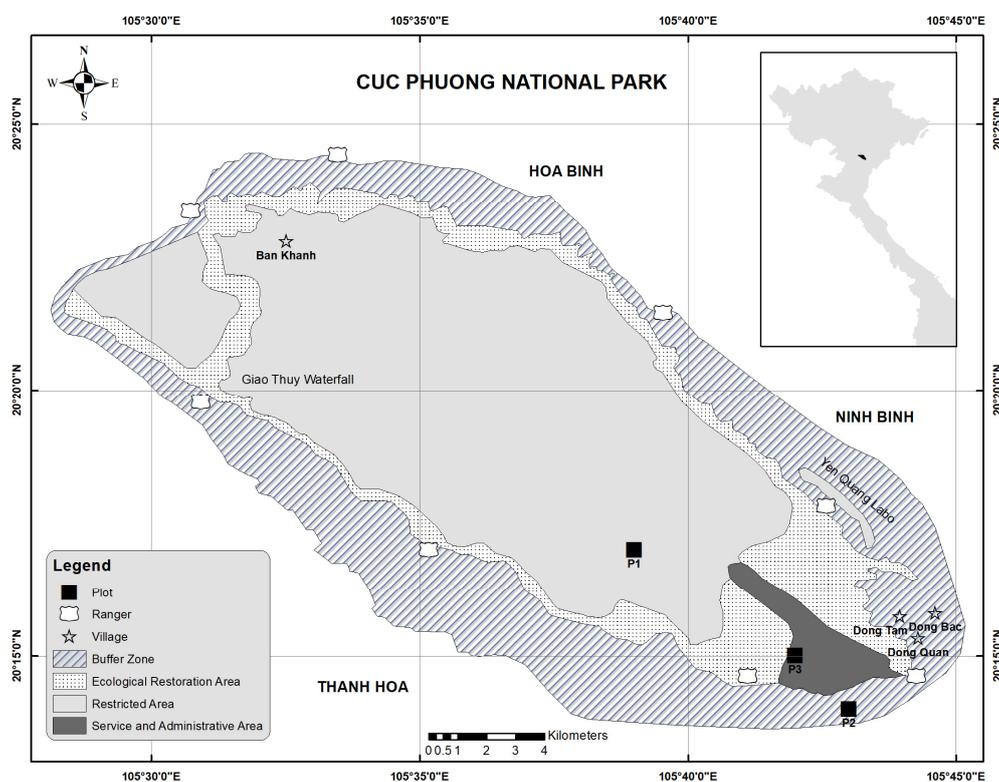
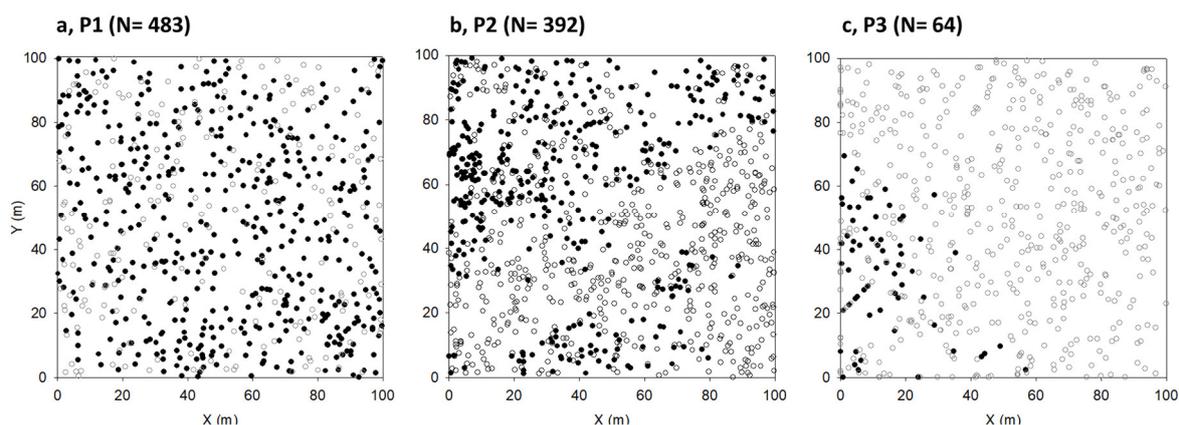


Figure 1. Map of Cuc Phuong National Park and three study plots P1–P3.



**Figure 2.** Maps of tree individuals in three study plots P1 (a), P2 (b) and P3 (c). Black circles are *S. macrophyllus* and white circles are other species. N: number of *Streblus macrophyllus* individuals.

## 2.2. Data Analysis

### 2.2.1. Community Phylogenetic Structure

We used a phylogenetic mega-tree approach to construct separate family level phylogenetic trees to study forest communities. At first, a species list based on the Angiosperm Phylogeny Group (APG) III [20] was created for each plot. We assembled species lists into phylogenies using Phylomatic and the maximum resolved super-tree of angiosperms (R20120829.new) [21] **Error! Hyperlink reference not valid.** and the Taxonomic Name Resolution Service v4.0 [22] to check whether the species names match the APG III. To evaluate changes in the phylogenetic dimension of tree communities, we used two phylogenetic metrics, the mean phylogenetic distance (MPD) and net related index (NRI) [14], which were both calculated with Phylocom software version 4.2 [23]. The NRI analyzes the degree of phylogenetic relatedness by measuring the mean pair-wise phylogenetic distance among constituent species in a community relative to that found in the plot's species pool. Thus, the NRI analyzes the phylogenetic structure throughout the phylogeny. The branch lengths of the phylogenies were calibrated using the function Bladj [24], while the alpha MPD and NRI were calculated through the construct function in the software using the '-a' argument to weigh species by their abundance. To calculate NRI, we first compared the observed values of MPD with those obtained by chance after generating 999 communities from the null model 0, which randomized phylogenetic relationship among species [25]. The NRI is calculated as follows:

$$\text{NRI} = \frac{-(\text{MPD} - \text{MPD}_{\text{rnd}})}{\text{MPD}_{\text{sd}}} \quad (1)$$

where  $\text{MPD}_{\text{sd}}$  represents the standard deviation of the mean expected by chance,  $\text{MPD}_{\text{md}}$  is expected mean phylogenetic distance of randomized species assemblages.

A positive NRI value (>0) indicates phylogenetic clustering (i.e., species are more closely related than expected by chance) while a negative value (<0) indicates phylogenetic overdispersion (i.e., species are more distantly related than expected by chance) [25]. Using Phylocom 4.2, we measured Faith's phylogenetic distance (PD), which was the sum of branch lengths of the subtending tree of the species present in a community [26]. This does not account for species abundance and Rao's quadratic entropy index  $D_p$ , which is an extension of the Simpson diversity index that incorporates the phylogenetic distance between each pair of species [27].

### 2.2.2. Community Nearest Neighbor Structure

We applied the current techniques of nearest neighbor statistics that are based on the assumption that the spatial structure of a forest stand is determined by the distribution of specific structural relationships within neighborhood tree groups. A forest stand is composed of neighborhood structural units of N trees. We used three structural indices, mingling, dominance, and uniform angle

index [28], to describe tree homogeneity or heterogeneity through a variety of species, diameter classes, and spatial arrangements with equations from 2.1 to 2.3 [11,13].

The species mingling index ( $M$ ) describes the species diversity in the vicinity of a target tree and is defined as the proportion of the four nearest neighbors that belong to species different to the reference tree.

$$M_i = \frac{1}{4} \sum_{j=1}^4 v_j \quad (2.1)$$

where  $v_j = 1$  if neighbor  $j$  is not the same species as reference tree  $i$ . Otherwise,  $v_j = 0$ . Interpretations of  $M$  values have the following levels: no mixture ( $M = 0.00$ ), low mixture ( $M = 0.25$ ), medium mixture ( $M = 0.50$ ), high mixture ( $M = 0.75$ ), and complete mixture ( $M = 1.00$ ).

The dominance ( $U$ ) describes the size differentiation between a reference tree and its four nearest neighbors. It is defined as the proportion of the four nearest neighbors that are smaller than the reference tree.

$$U_i = \frac{1}{4} \sum_{j=1}^4 v_j \quad (2.2)$$

where  $v_j = 0$  if neighbor  $j$  is smaller than reference tree  $i$ . Otherwise,  $v_j = 1$ . A tree could be classified as predominant ( $U = 0.00$ ), subdominant ( $U = 0.25$ ), medium ( $U = 0.50$ ), disadvantaged ( $U = 0.75$ ), and absolutely disadvantaged ( $U=1.00$ ).

The uniform angle index ( $W$ ) describes the degree of regularity of the spatial distribution of the four nearest neighbors to the reference tree. It is defined as the proportion of angle ( $\alpha$ ) smaller than the standard angle ( $\alpha_0$ ). In the case of the 4 nearest neighbors ( $n = 4$ ), the standard angle value is  $72^\circ$  ( $\alpha_0 = 360^\circ/(n+1)$ ).

$$W_i = \frac{1}{4} \sum_{j=1}^4 w_j \quad (2.3)$$

where  $W_i = 1$  if  $\alpha_j < \alpha_0$ . Otherwise,  $W_i = 0$ . The spatial distribution pattern tends to be very regular ( $W = 0.00$ ), regular ( $W = 0.25$ ), random ( $W = 0.50$ ), clumped ( $W = 0.75$ ), or very clumped ( $W = 1.00$ ). Ecologically, this index describes the degree of clustering in the spatial distribution of individuals.

To evaluate dominance, we measured the diameter at breast height (DBH) for each individual tree. The methods described above were implemented with Crancord software, which is a program that analyzes and reconstructs spatial forest structure [29]. To eliminate the edge effect of the estimates in  $M_i$ ,  $W_i$ , and  $U_i$  calculations, we applied the nearest neighbor edge correction method [8].

Differences between the three plots in mingling index ( $M$ ), uniform angle index ( $W$ ), DBH-dominance index ( $U$ ) and mean phylogenetic distance (MPD) were tested using the non-parametric Mann–Whitney U test. We performed a non-parametric test due to the lack of accomplishment of ANOVA assumptions for data of all plots (normality of residuals was assessed with the Kolmogorov–Smirnov test and homoscedasticity of variances with the Levene test). All data analyses were performed using Statistica 9.1 (StatSoft, Inc., Tulsa, OK, USA).

In addition, to test the environmental heterogeneity in the three plots, we compared the spatial distributions of all mature trees with  $DBH \geq 10$  cm to the null model of the complete spatial randomness by using a univariate pair-correlation  $g$ -function and  $L$ -function. The grid-based software Programita [30] was used with 199 Monte Carlo simulations, a spatial resolution of 1 m, and a bandwidth of  $R = 50$  m to construct approximately 95% confidence envelopes using the fifth lowest and fifth highest values. If environmental conditions are heterogeneous, the spatial patterns of mature trees are significant at large spatial scales, as proposed by Nguyen et al. in 2014 [19] and Nguyen et al. in 2016 [31].

### 3. Results

#### 3.1. Forest Community Structure

The severe disturbance effect in plot P1 was shown to be associated with the highest level of *S. macrophyllus* abundance, with 483 (68.5%) individuals. It also had the lowest species richness (34 species) and total basal area (36.39 m<sup>2</sup> ha<sup>-1</sup>) (Table 1), especially when compared to other study plots (Table A1). Plot P2 was less disturbed and showed the highest abundance and species richness with 1006 (38.9%) individuals from 77 species, as well as a total basal area of 36.60 m<sup>2</sup> ha<sup>-1</sup>. Plot P3 was also strongly disturbed, leading to the lowest total basal area of 19.79 m<sup>2</sup> ha<sup>-1</sup>, as well as the lowest number of individual trees (601 trees, 10.9% of *S. macrophyllus*) and the highest species number with one individual (38 species in Plot 3 have one individual). Moreover, it also showed high species richness (66 species). The mean nearest distance among all trees and, in particular, *S. macrophyllus* individuals, were larger in P1 and P3 compared to P2 (Table 1). The spatial patterns of mature trees showed a large-scale environmental homogeneity in all three study plots (Appendix A, Figure A1).

**Table 1.** The characteristics of the three sample plots.

Characteristics	Plot P1	Plot P2	Plot P3
Number of individuals	705	1006	601
Number of species	34	77	66
Number of genus	30	62	60
Number of families	21	39	31
Number of <i>S. macrophyllus</i> individuals	483	392	64
Number of species with one individual	17	26	38
Number of species with $\geq 30$ individuals	3	5	7
Mean nearest distance of all trees (m)	2.06	1.56	2.07
Mean nearest distance of <i>S. macrophyllus</i> (m)	2.15	1.55	1.83
Total basal area (m <sup>2</sup> /ha)	36.39	36.60	19.79

Species presented by species richness and the Simpson's diversity index increased from P1 to P3 (Table 2). When increasing species diversity, phylogenetic distance (PD), and phylogenetic diversity (Pd) also increased from P1 to P3. The mean phylogenetic distance (MPD) differed significantly among study plots with the lowest value at P1 and the highest value at P3. NRI values were positive, indicating a clustered phylogenetic structure in all study forest communities.

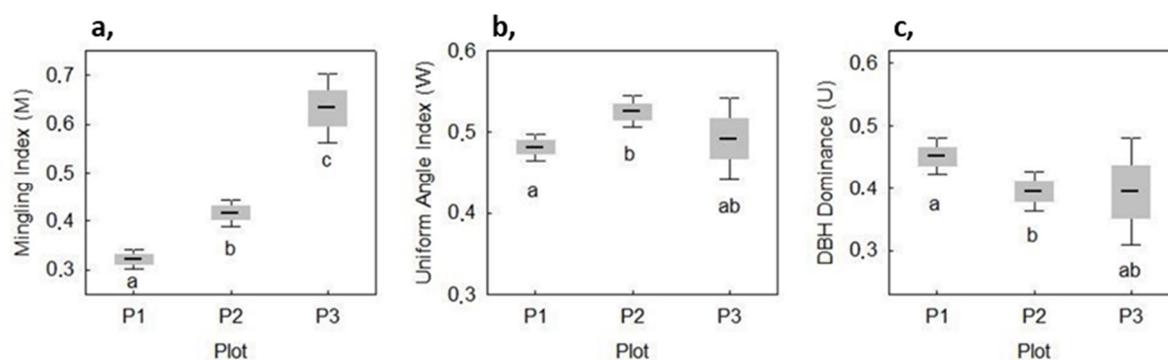
**Table 2.** Phylogenetic diversity of three sampled plots.

Phylogenetic Metrics	Plot P1	Plot P2	Plot P3
Species number	34	77	66
Simpson's diversity	0.49	0.81	0.93
Phylogenetic distance (PD)	208	344	355
Phylogenetic diversity (Pd)	5.79	9.05	11.88
Mean phylogenetic distance (MPD $\pm$ Standard deviation)	11.58 $\pm$ 2.07	18.11 $\pm$ 2.22	23.77 $\pm$ 2.46
Net related index (NRI)	0.74	1.47	0.73

#### 3.2. Community Nearest Neighbor Structure

The mingling index values increased significantly when the abundance of *S. macrophyllus* decreased. The highest value was recorded in P3 (M=0.63) when *S. macrophyllus* individuals were least frequent (Figure 3). In P1, the mixture of *S. macrophyllus* individuals with other species was the lowest (M = 0.32), whereas in P2 the mingling index showed an intermediate position (M = 0.41). Significant differences in the mingling index were tested between all pair-plot comparisons. The uniform angle index varied slightly among the studied plots (from 0.48 in P1, 0.49 in P3, to a

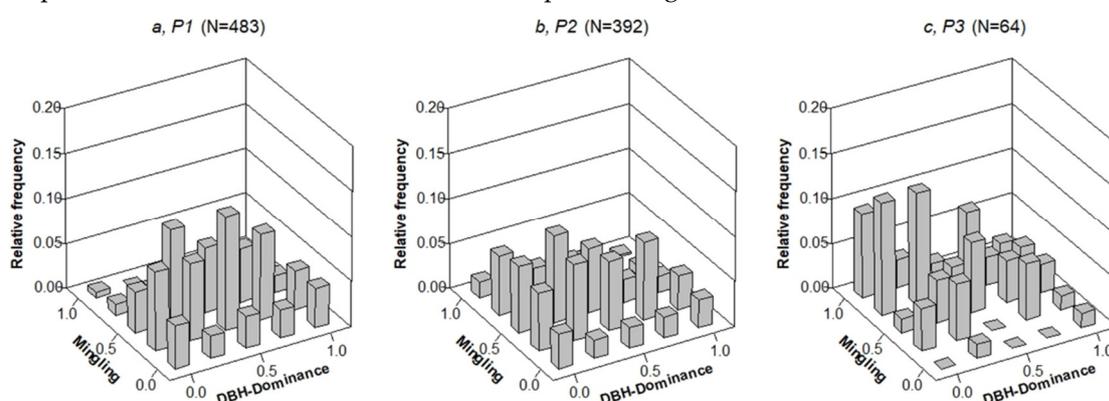
maximum of 0.53 in P2) (Figure 3). However, a significant difference was found between P1 and P2 (significant increase of the W index with a decrease in the number of individual *S. macrophyllus*). However, in the DBH dominance index, the general trend was a decrease when *S. macrophyllus* decreased in abundance (from 0.45 in P1 to 0.39 in P2 and P3). A significant difference was only detected between P1 and P2 (Figure 3).



**Figure 3.** The mingling index (a), uniform angle index (b), and DBH dominance index (c) variation in all three plots. The dashed box indicates mean  $\pm$  standard error of mean and the whiskers are 95% confidence intervals. Different letters indicate significant differences between plots ( $p < 0.05$ ; Mann–Whitney U test; non-parametric test.).

### 3.2.1. M-U Bivariate Distribution

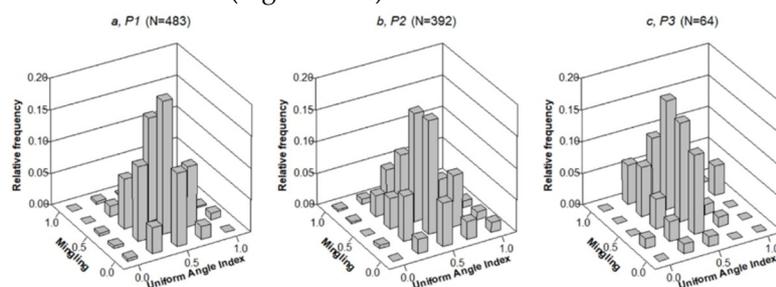
The species mixture for *S. macrophyllus* increased with its abundance (Figure 4a–c). At plot P1, the mingling values indicated low mixture levels ( $M = 0\text{--}0.5$ ), ranging from no mixture to medium mixture with mean frequency values ranging from 0.05 to 0.12 (Figure 4a). In P2, the mixture of *S. macrophyllus* with other species increased from no mixture to high mixture levels (frequency values ranged from 0.03 to 0.09, Figure 4b). At P3, the species mingling index was concentrated at high and complete mixture levels with heterospecific species (frequency values vary from 0.09 to 0.12, Figure 4c). Ranging from low to high mixtures, the DBH dominance of *S. macrophyllus* moved from predominant to absolute disadvantage with a mean frequency of 0.03 to 0.12 in P1 and 0.02 to 0.09 in P2 (Figure 4a,b). Concentrated at high and complete mixture levels, dominance of *S. macrophyllus* in DBH ranged from predominant to medium levels ( $U = 0\text{--}0.5$ ) with high frequency values of 0.06 to 0.15 in P3 (Figure 4c). The results indicated that the mixture of *S. macrophyllus* with other tree species increased in adjacent neighbors, while its abundance decreased from P1 to P3. The DBH dominance of *S. macrophyllus* became weaker when its abundance decreased. *S. macrophyllus* acted as a strong competitor, which led to an increase in its conspecific neighbors.



**Figure 4.** Bivariate distributions of mingling versus diameter at breast height (DBH) dominance on three sample plots P1 (a), P2 (b) and P3 (c). N: number of *S. macrophyllus* individuals.

### 3.2.2. M-W Bivariate Distribution

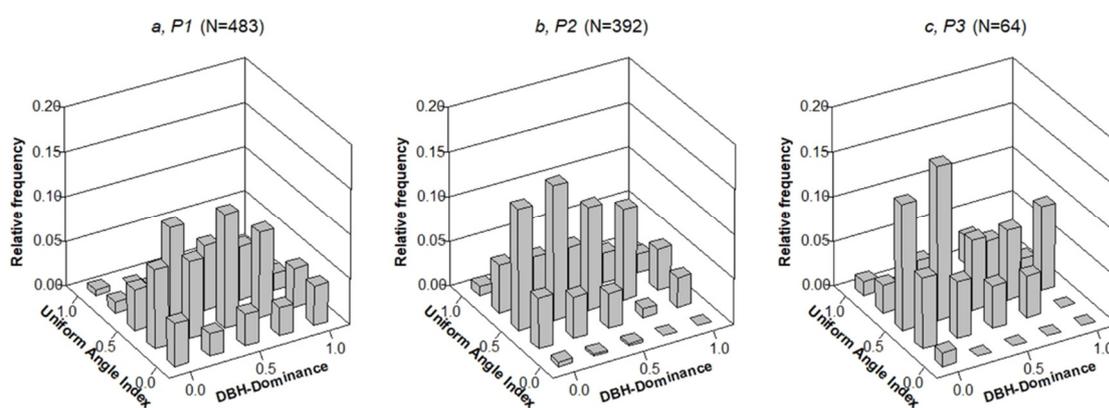
The M-W bivariate distribution clearly showed that heterospecific associations of *S. macrophyllus* increased when abundance decreased, whereas its distributions went from a regular to an aggregated pattern (Figure 5a–c). High frequencies were found in bivariate distributions, such as in the M index = 0.25 to 0.5 and the W index = 0.5. There was a variance between 0.16 to 0.18 in all three plots. There was a shift of the M-W bivariate pattern from low (P1) to high species mixture (P3) according to the decreasing *S. macrophyllus* abundance. The spatial distribution of *S. macrophyllus* in all three plots varied from regular to clumped (W = 0.25–0.5) with a mean frequency ranging from 0.04 to 0.2, which was mainly distributed at random (Figure 5a–c).



**Figure 5.** Bivariate distributions of mingling versus uniform angle index on three sample plots P1 (a), P2 (b) and P3 (c). N: number of *S. macrophyllus* individuals.

### 3.2.3. W-U Bivariate Distribution

The W-U bivariate distribution showed a similar pattern in all three plots (Figure 6a–c). Spatial distributions of *S. macrophyllus* moved from regular to aggregated patterns (W = 0.25–0.75). In all study plots, there were highly concentrated random patterns (W = 0.5). DBH dominance was approximately symmetrical at all levels and especially in P1 and P2, each with a mean frequency between 0.10 and 0.15. P3, however, was highly concentrated at DBH dominance levels (0 to 0.25) for frequency values of 0.14 to 0.17. The results show that *S. macrophyllus* competed strongly with its neighbors in tree size. This was revealed by the concentration of high frequency values in DBH dominance.



**Figure 6.** Bivariate distributions of the uniform angle index versus DBH dominance on three sample plots P1 (a), P2 (b) and P3 (c). N: number of *S. macrophyllus* individuals.

## 4. Discussion

A fragmented landscape may form a mosaic of patches impacted by different disturbance intensities with heterogeneity in the vegetation structure. This could lead to patchiness in tree species composition because of different environmental conditions within patches that encourage different species, either recruited or encroached by chance from the local species pool [32]. In this study, we found that the loss of phylogenetic diversity in disturbed forest communities is according to *S.*

*macrophyllus* encroachment. This species competes with other species and encroaches forest communities as a disturbance-adapted species.

#### 4.1. Forest Community Structure

Because of long-term illegal logging by local people, no disturbance intensity was recorded in this study. However, our results emphasized the impact of the disturbance on the forest community structure, such as species richness, basal area, phylogenetic diversity, and *S. macrophyllus* encroachment. This may correspond with the intermediate disturbance hypothesis [33], which predicts local species diversity to be maximal during an intermediate disturbance level due to the coexistence of late successional and pioneer species. For example, *Caryodaphnopsis tonkinensis* is a shade-intolerant and pioneer species found in P1 and P2; its basal area covered 41.7% (15.21 m<sup>2</sup> ha<sup>-1</sup>) in P1 and 33.6% (12.31 m<sup>2</sup> ha<sup>-1</sup>) in P2, respectively.

It is not a novelty that tropical forest communities are naturally highly variable in terms of their taxonomic composition and community structure, including patterns of phylogenetic diversity [16]. Our results showed a little evidence of change in the phylogenetic community structure, such as a decrease in *S. macrophyllus* abundance (Table A1), phylogenetic diversity, and distance, as well as increasing the net related index, which showed a close phylogenetic relatedness from sample plots P1–P3. In our study, the total basal area and phylogenetic diversity showed a similar trend to species richness and *S. macrophyllus* abundance. The results are in accordance with Steudel et al. [34] and Lasky et al. [35], who concluded that the relationship between biomass productivity (i.e., basal area) and phylogenetic diversity is strongly driven by species. Moreover, our results regarding MPD and the total basal area in the three study plots were in line with the findings of Cadotte [36] and Satdichanh et al. [37], each of whom showed that communities containing more distantly related species tend to have higher biomass production, suggesting a consequence of species that are ecologically different.

Ding et al. [38] used data from 18 1-ha plots in tropical old-growth and secondary forests with different disturbance histories, finding that phylogenetic clustering predominated across all size classes and spatial scales in highly disturbed lowland forest types. They assumed that severe disturbances can lead to abiotic filtering, which generates a community dominated by closely related species with disturbance-adapted traits and where biotic interactions play a relatively minor role. This finding is supported by our results, where *S. macrophyllus* is characterized by a gap-phase regeneration mode [19] and encroaches forest communities with its disturbance-adapted traits. In general, phylogenetic diversity provided better information for management and restoration interventions than species richness, particularly in Cuc Phuong National Park, because phylogenetic diversity reflects the species response to environmental gradients through time [39].

#### 4.2. Community Nearest Neighbor Structure

The bivariate distributions in the three forest stands revealed that *S. macrophyllus* trees were well mixed with other species and had regular to aggregated distributions, and strong intraspecific competition. Aggregation is a common distribution pattern of tree species that is mainly caused by dispersal limitation [31,40] and habitat preference [41] mechanisms, especially in species-rich communities such as tropical forests [42]. In this study, random and regular distributions were major patterns of *S. macrophyllus* with high frequency values, and DBH dominance occurred in high levels of species mixture (Figure 4c). These findings could be evidence of competitive interactions. When the canopy closed, the competition among conspecific plants for the same resources gradually intensified because of their similar requirements, leading weaker trees to die. Therefore, this resulted in self-thinning. Intra-specific competitive effects were also presented by increasing the nearest distance between individuals, leading to random or regular *S. macrophyllus* species distributions. Nguyen et al. [19] analyzed spatial point patterns of *S. macrophyllus* in a 1-ha plot and found that *S. macrophyllus* was a predominant competitor with other species when following a gap-phase regeneration mode. Moreover, evidence of self-thinning was suggested by *S. macrophyllus* individual recruitment into larger tree sizes [19], which lead to a more regular distribution in larger sized

individuals. In a previous study, Zhang et al. [43] stated that during the successional process to a climax state, the forest community gradually shifts from clumped to regular distribution patterns. Furthermore, the process is constantly accompanied by a random weakening of interspecific associations among the dominant species. The findings of our study support this scenario. Our study also showed that *S. macrophyllus* was highly mixed with other species. This can be explained by its ecological characteristics of subcanopy, shade tolerance, and gap-phase regeneration mode. Moreover, a high mixture with heterospecific neighbors promotes the maintenance of tree species co-occurrence by thwarting the transmission of biotic plant pests, as has been recently suggested [44]. This model is critical in species-rich tropical forests, where few near neighbors are likely to be conspecific even among the most common species [45]. The model was confirmed by our analyses in this case study of forest stands dominated by *S. macrophyllus*.

## 5. Conclusions

We used current techniques to understand phylogenetic diversity and nearest neighbor structure of disturbed forest stands in Cuc Phuong National Park. These approaches were useful for adjusting spatial structures and optimizing/restructuring forest management practices. In comparison with more traditional methods, the approaches were advantageous and provided more detailed information in order to aid the qualitative and quantitative selection of harvested trees. For example, in the case of promoting target species development towards higher quality or productivity, individual trees with low commercial values and high density would be thinned according to the frequency distribution. Regarding forest quality and productivity, low taxonomical and functional tree communities should be taken into account in National Park conservation activities.

According to forest disturbance effects, structural community properties were changed when *S. macrophyllus* abundance increased. This was due to *S. macrophyllus* encroaching on tropical rain forest communities as a disturbance-adapted species. Moreover, to diminish the disturbance of rain forest diversity structure, artificial gaps should be limited and proper forest management should limit *S. macrophyllus* colonization in these areas.

**Author Contributions:** N.H.H. and B.T.Q. conceived/designed the experiment and collected the data; N.H.H., E.Y., B.T.Q., and P.I.C. analyzed the data; N.H.H., E.Y., B.T.Q., A.M.P., T.H.M., and P.I.C. wrote the paper. All authors have read and agreed to the published version of the manuscript.

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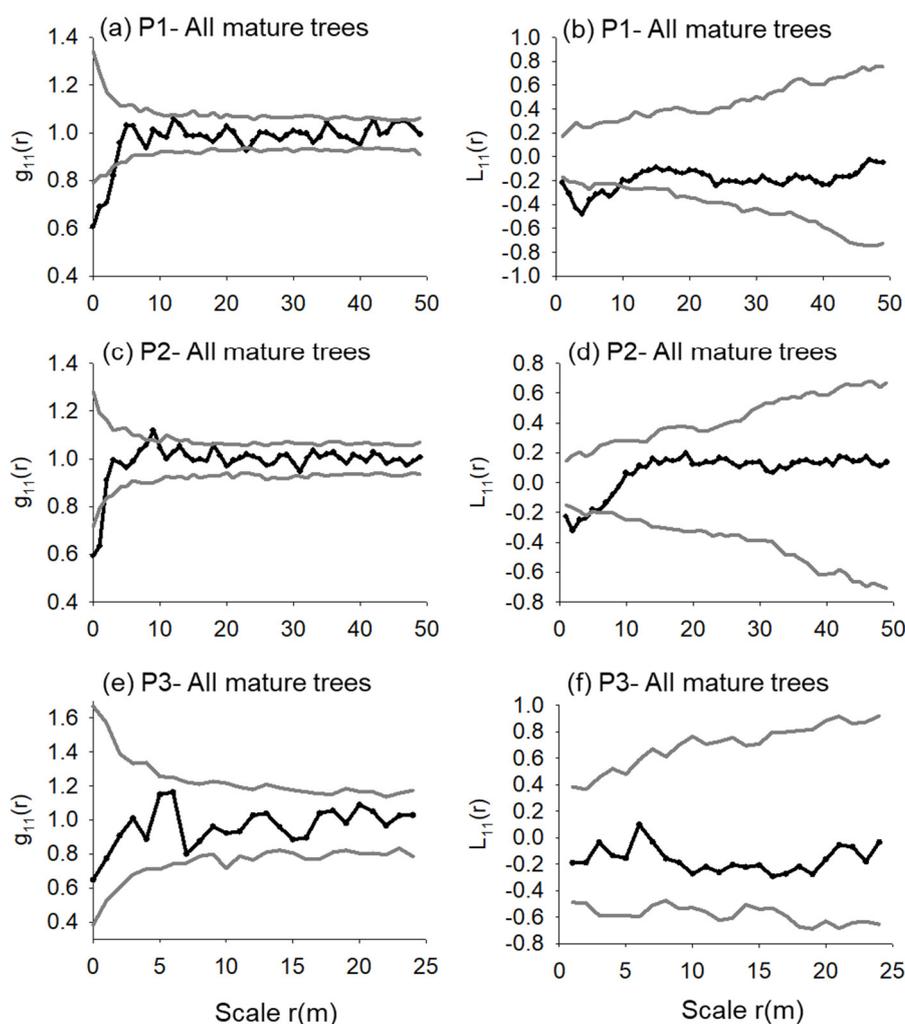
**Conflicts of Interest:** The authors declare no conflict of interest.

## Appendix A

**Table A1.** Species list in three sample plots.

No.	P1		P2		P3	
	Species	N	Species	N	Species	N
1	<i>Streblus macrophyllus</i>	483	<i>Streblus macrophyllus</i>	392	<i>Miliusa balansae</i>	68
2	<i>Hydnocarpus kurzii</i>	33	<i>Saraca dives</i>	117	<i>Bleekrodea tonkinensis</i>	66
3	<i>Caryodaphnopsis tonkinensis</i>	29	<i>Hydnocarpus kurzii</i>	94	<i>Streblus macrophyllus</i>	64
4	<i>Saraca dives</i>	22	<i>Ficus cyrtophylla</i>	32	<i>Saraca dives</i>	63
5	<i>Cleidion bracteosum</i>	21	<i>Caryodaphnopsis tonkinensis</i>	29	<i>Dimocarpus longan</i>	48
6	<i>Litsea balansae</i>	16	<i>Toxicodendron rhesoides</i>	27	<i>Mischocarpus pentapetalus</i>	36
7	<i>Miliusa balansae</i>	16	<i>Chisocheton ceramicus</i>	14	<i>Chionanthus macrocarpus</i>	33
8	<i>Pterospermum acerifolium</i>	8	<i>Sterculia lanceolata</i>	14	<i>Amesiodendron chinense</i>	22
9	<i>Amesiodendron chinense</i>	7	<i>Aglaia lawii</i>	13	<i>Streblus asper</i>	20
10	<i>Garcinia fagraeoides</i>	7	<i>Clerodendrum chinense</i>	12	<i>Albizia lucidior</i>	10
11	<i>Cryptocarya concinna</i>	6	<i>Amesiodendron chinense</i>	11	<i>Cryptocarya oblongifolia</i>	10
12	<i>Antidesma montanum</i>	5	<i>Antidesma ambiguum</i>	11	<i>Castanopsis lecomtei</i>	9

13	<i>Albizia lucidior</i>	3	<i>Carya sinensis</i>	10	<i>Goniothalamus macrocalyx</i>	9
14	<i>Alphonsea boniana</i>	3	<i>Chionanthus macrocarpus</i>	10	<i>Vitex stylosa</i>	8
15	<i>Aglaia spectabilis</i>	2	<i>Dysoxylum cauliflorum</i>	10	<i>Pilea plataniflora</i>	7
16	<i>Carya sinensis</i>	2	<i>Cryptocarya oblongifolia</i>	9	<i>Senna hirsuta</i>	7
17	<i>Castanopsis kawakamii</i>	2	<i>Diospyros bonii</i>	9	<i>Canarium album</i>	6
18	<i>Ilex chinensis</i>	2	<i>Teucrium viscidum</i>	9	<i>Callicarpa longifolia</i>	5
19	<i>Syzygium lanceolatum</i>	2	<i>Albizia lucidior</i>	8	<i>Coffea canephora</i>	5
20	<i>Toxicodendron rhesoides</i>	2	<i>Cleidion bracteosum</i>	8	<i>Ficus nervosa</i>	5
21	<i>Vitex quinata</i>	2	<i>Glycosmis cyanocarpa</i>	8	<i>Syzygium lanceolatum</i>	5
22	<i>Aglaia lauii</i>	1	<i>Goniothalamus macrocalyx</i>	8	<i>Antidesma ambiguum</i>	4
23	<i>Bridelia balansae</i>	1	<i>Holarrhena pubescens</i>	8	<i>Elaeocarpus sylvestris</i>	4
24	<i>Callicarpa longifolia</i>	1	<i>Castanopsis lecomtei</i>	7	<i>Radermachera boniana</i>	4
25	<i>Camellia flava</i>	1	<i>Adina pilulifera</i>	6	<i>Scleropyrum pentandrum</i>	4
26	<i>Canarium bengalense</i>	1	<i>Callicarpa longifolia</i>	6	<i>Aglaia spectabilis</i>	3
27	<i>Castanopsis lecomtei</i>	1	<i>Garcinia fagraeoides</i>	6	<i>Bridelia balansae</i>	3
28	<i>Drypetes perreticulata</i>	1	<i>Knema globularia</i>	6	<i>Camellia flava</i>	3
29	<i>Ficus nervosa</i>	1	<i>Beilschmiedia laevis</i>	5	<i>Cleistanthus monoicus</i>	3
30	<i>Ficus tinctoria</i>	1	<i>Drypetes perreticulata</i>	5	<i>Clerodendrum glandulosum</i>	3
31	<i>Ficus vasculosa</i>	1	<i>Gironniera subaequalis</i>	5	<i>Kydia glabrescens</i>	3
32	<i>Polyalthia lauii</i>	1	<i>Turpinia montana</i>	5	<i>Sapindus saponaria</i>	3
33	<i>Sterculia lanceolata</i>	1	<i>Canarium album</i>	4	<i>Toxicodendron rhesoides</i>	3
34	<i>Teucrium viscidum</i>	1	<i>Meliosma pinnata</i>	4	<i>Adina pilulifera</i>	2
35	Unidentified	18	<i>Baccaurea ramiflora</i>	3	<i>Chisocheton ceramicus</i>	2
36			<i>Cinnanomum bejolghota</i>	3	<i>Dracontomelon duperreanum</i>	2
37			<i>Elaeocarpus griffithii</i>	3	<i>Ficus trivialis</i>	2
38			<i>Firmiana colorata</i>	3	<i>Garcinia fagraeoides</i>	2
39			<i>Ilex chinensis</i>	3	<i>Knema globularia</i>	2
40			<i>Illigera celebica</i>	3	<i>Lithocarpus bacgiangensis</i>	2
41			<i>Lithocarpus bacgiangensis</i>	3	<i>Micromelum integerrimum</i>	2
42			<i>Litsea balansae</i>	3	<i>Trevesia sphaerocarpa</i>	2
43			<i>Litsea glutinosa</i>	3	<i>Vatica odorata</i>	2
44			<i>Polyalthia lauii</i>	3	<i>Wrightia arborea</i>	2
45			<i>Prunus zippeliana</i>	3	<i>Ageratum conyzoides</i>	1
46			<i>Aglaia spectabilis</i>	2	<i>Albizia lebbeck</i>	1
47			<i>Albizia lebbeck</i>	2	<i>Alphonsea boniana</i>	1
48			<i>Dimocarpus longan</i>	2	<i>Alphonsea tonquinensis</i>	1
49			<i>Dysoxylum gotadhora</i>	2	<i>Anogeissus acuminata</i>	1
50			<i>Ficus nervosa</i>	2	<i>Archidendron clypearia</i>	1
51			<i>Ficus trivialis</i>	2	<i>Artocarpus lacucha</i>	1
52			<i>Garcinia oblongifolia</i>	2	<i>Baccaurea ramiflora</i>	1
53			<i>Heteropanax fragrans</i>	2	<i>Brownlowia tabularis</i>	1
54			<i>Oreocnide integrifolia</i>	2	<i>Castanopsis chinensis</i>	1
55			<i>Ormosia balansae</i>	2	<i>Cleidion bracteosum</i>	1
56			<i>Pilea plataniflora</i>	2	<i>Ficus altissima</i>	1
57			<i>Pterospermum acerifolium</i>	2	<i>Firmiana colorata</i>	1
58			<i>Scleropyrum pentandrum</i>	2	<i>Garuga pinnata</i>	1
59			<i>Syzygium lanceolatum</i>	2	<i>Macaranga denticulata</i>	1
60			<i>Vitex quinata</i>	2	<i>Magnolia henryi</i>	1
61			<i>Ardisia crenata</i>	1	<i>Mallotus microcarpus</i>	1
62			<i>Bridelia balansae</i>	1	<i>Ocotea lancifolia</i>	1
63			<i>Camellia flava</i>	1	<i>Polyalthia lauii</i>	1
64			<i>Castanopsis kawakamii</i>	1	<i>Prunus zippeliana</i>	1
65			<i>Celtis timorensis</i>	1	<i>Pterospermum heterophyllum</i>	1
66			<i>Chionanthus ramiflorus</i>	1	<i>Teucrium viscidum</i>	1
67			<i>Clerodendrum glandulosum</i>	1		
68			<i>Ficus hispida</i>	1		
69			<i>Flacourtia indica</i>	1		
70			<i>Helicia cochinchinensis</i>	1		
71			<i>Ilex cinerea</i>	1		
72			<i>Litsea verticillata</i>	1		
73			<i>Microdesmis caseariiifolia</i>	1		
74			<i>Mischocarpus pentapetalus</i>	1		
75			<i>Polyalthia cerasoides</i>	1		
76			<i>Senna hirsuta</i>	1		
77			<i>Syzygium bullockii</i>	1		



**Figure A1.** Spatial patterns of all mature trees with DBH  $\geq 10$  cm in three plots (P1, P2, and P3) using univariate pair-correlation  $g$ -function (a,c,e) and  $L$ -function (b,d,f). Null models used complete spatial randomness (CSR). In all three plots, the  $g$ -function and  $L$ -function showed no large-scale departure from the null model of CSR, which indicated environmental homogeneity. Particularly in P1 and P2, the  $g$ -function ( $< 1$ ) and  $L$ -function ( $< 0$ ) were significant for scales smaller than 10 m, as they did not approach value 0 under the null model of CSR. Moreover, the spatial arrangement of mature trees in P3 fit very well under the null model of CSR when analyzed by the  $g$ - and  $L$ -functions. These evidences significantly exhibited a large scale of environmental homogeneity at P1, P2, and P3. Note:  $L$ -function is a transformation of Ripley's  $K$ -function ( $L(r) = (K(r)/\pi)^{0.5} - r$ ). The  $g$  pair-correlation function is the derivative of the  $K$  function  $g(r) = K'(r)/(2\pi r)$  and  $r$  is the circle's radius from a randomly chosen tree. Black lines are observed patterns; grey lines are approximately 95% confidence envelopes.

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