STRUCTURE, COMPOSITION AND SPATIAL PATTERN SOF DEGRADED LIMESTONE FORESTS

Nguyen Hong Hai
Vietnam National University of Forestry

SUMMARY

Structural and spatial patterns of tree species in forests are important indicators to explain which underlying mechanisms or processes regulating forest structure. In this article, techniques of spatial point pattern analysis were used to characterize structural and spatial patterns of two secondary rain forest stands in Cuc phuong National park, Vietnam. The findings shown that: (1) The forest structures were significantly affected by disturbance in tree species diversity and size distribution. (2) Intra-specific competition of *Streblus macrophyllus* was found in low – species and blur in high-species richness communities. (3) Most of inter-specific associations were independent except repulsions of *S. macrophyllus* in the high-species community. (4) Self thinning and gap phase regeneration were major processes controlling mutual life stage associations of *S. macrophyllus* while dispersal limitation acted on other species. In conclusion, *S. macrophyllus* is a gap opportunist and strong competitor. Disturbed forest and canopy openness facilitate it competing to occupy all available space.

Keywords: Cuc phuong National park, point pattern analysis, spatial pattern, tropical evergreen forest.

I. INTRODUCTION

Structural and spatial patterns of forest trees are important indicators to explain which processes govern the composition and association in species communities (Wiegand et al. 2007). Based on spatial arrangement of individuals, ecological hypotheses can be generated assuming to possible underlying processes controlling the observed structure (Wiegand & Moloney 2004). Several ecological processes or mechanisms have been proposed explaining species coexistence and community structure, such as neutral theory, competition or facilitation, dispersal limitation, habitat preference and the Janzen - Connell hypothesis.

The Janzen - Connell hypothesizes that spatial pattern of individual species should be less aggregated with increasing tree sizes because high density clumping of a given species leads to concentrate of predation or host specific pests. Similarly, self-thinning mechanism or intra-specific competition is also expected to leave a same pattern. Neutral theory assumes that all individual species are demographically equivalent in terms of their rates of birth, reproduction and death, regardless of species identity. Beside of successes, this hypothesis have caused a heated debate because it suggests that other proposed mechanisms are unimportant for certain community attributes. In spatial pattern analysis, studying of species interaction is more complicated in cases of habitat heterogeneity because it may mask effects of species habitat preference (e.g., shading, soil nutrients, moisture) and direct tree-tree interaction (e.g., facilitation or competition) (Wright 2002).

Undisturbed tropical forests have become extremely rare, therefore secondary forests are mostly remain. In this study, we evaluated effect of forest disturbance on tree species diversity and community structure of secondary tropical forests. In addition, we used current techniques of spatial point pattern analysis to study how dominant tree species partition space and mutually interact in disturbed forests. To solve these issues, we first tested the hypothesis of environmental homogeneity, then we used univariate and bivariate pair correlation functions to explore intra- and interspecific interactions under null models of complete spatial randomness and independence.

II. MATERIAL AND METHODS

2.1. Study area

Cuc phuong National park is surrounded by Karst mountains and covers an area of 22,200 ha with tropical evergreen rain forest distributed in the core zone. It is surrounded by limestone mountains with a mean maximum height of 300 - 400 m and is covered by tropical evergreen rain forest. Here, climate is strongly affected by the limestone mountains. The mean annual temperature is 20.6^{0}C, but the mean temperature in winter is only 9^{0}C. The annual mean humidity is 85% and the average annual rainfall is 2138 mm/ year. Our objectives focused on the secondary forest located at the center of the national park with different levels of forest disturbance.

2.2. Data collection

Two 1-ha plots was chosen in the core zone of the National park, P1 at (105°39,64'E, 20°17,88'N) and P2 at (105°42,12'E, 20°16,26'N) in 2015. All woody plants with diameter at breast height (dbh) ≥ 2.5 cm were identified to a species, stem-mapped to their relative geographical coordinates (*x*,*y*), and measured their dbh to the nearest 0.5 cm by using a laser distance measurement device (Leica Disto D2), compass and diameter tape in two grid systems of 100 subplots 10 m × 10 m. The tree species were directly classified according to their morphological characteristics on the field.

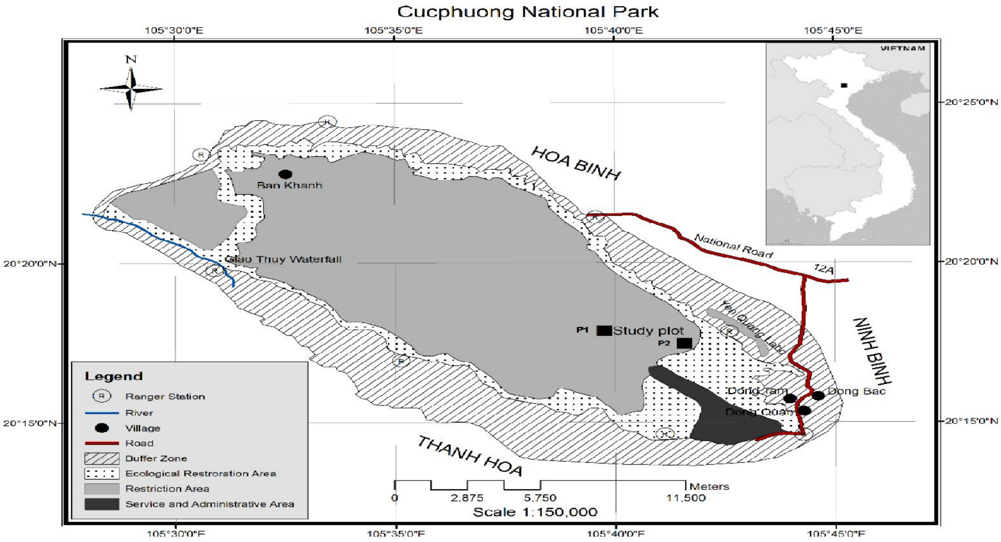

Fig. 1. Map of study site

2.3. Data analysis

Community structure and composition

We calculated summary statistics for each stand using Microsoft Excel. We examined species composition, stem density per hectare, diameter distribution and basal area. We calculated importance value index (IVI) for each species where IVI = relative dominance + relative density, relative frequency was not included because this is census data.

Tree species diversity

We calculated diversity and evenness for both stands using species richness, Shannon indexes, Simpson's indexes and Margalef diversity (Magurran 1988, Margalef 1978). Where p_i is the proportion of individuals of the *i*th species when calculated using stem density, S is the species richness, n_i is the number of individuals in the *i*th species and N is the total number of individuals.

1- Shannon diversity (H'): $H' = -\sum p_i \ln p_i$

2- Shannon evenness (J'): $J' = H'/\ln S$

3- Simpson's index (D): $D = \sum \frac{n_i[n_i-1]}{N[N-1]}$

4- Simpson's evenness (E): $E = \frac{1/D}{S}$

5- Margalef diversity (R): $R = \frac{(S-1)}{\ln N}$

Spatial pattern analysis

The pair correlation function and Ripley's *K* function base on the distribution of distances of pairs of points (e.g. (*x*,*y*) coordinates of trees) to analyze tree density for various scales (Stoyan & Stoyan 1994). The functions are now standard methods for analyzing mapped point patterns in forestecology and particularly used to quantify the spatial patterns of tree species. Ripley's *K*-function is defined as the expected number of points within distance *r* of an arbitrary point divided by the intensity λ, where λ is the intensity of the pattern in the study area(Ripley 1976). We used the *L*-function, a transformation of Ripley's *K*-function, $L(r)=(K(r)/\pi)^{0.5} - r$.

The pair-correlation function is the derivative of the *K* function(Stoyan & Stoyan 1994; Illian et al. 2008), $g(r) = K'(r)/(2\pi r)$. Specifically, it is non-cumulative and is defined as the expected density of trees at a distance radius *r* from a randomly chosen tree. The univariate pair-correlation function (*g*-function) describes the spatial distribution of trees at a given radius *r* using a standardized density. Consequently, $g_{11}(r) = 1$ under complete spatial randomness (CSR), $g_{11}(r) > 1$ indicates aggregation and $g_{11}(r) < 1$ indicates regularity at distance *r* within trees of the pattern. Similarly, the bivariate pair-correlation function $g_{12}(r)$ is extended to describe tree patterns with two types of trees, for example two tree species. $g_{12}(r)$ is defined as the expected density of trees of species 2 at distance *r* from an arbitrary tree of species 1. Consequently, $g_{12}(r) = 1$ indicates independence, $g_{12}(r) < 1$ indicates repulsion and $g_{12}(r) > 1$ indicates attraction between two tree species at distance *r*, respectively.

Null models

Complete Spatial Randomness (CSR): we tested the null hypothesis of a random spatial distribution of specific species and each *S. macophyllus*'s life-history stages. If a random distribution over the entire plot is confirmed meaning that no strong interaction occurred within this species or life stages. Comparisons of the spatial distributions of thedominant species between two study plots allow us to interpret the abundance effect of the species.

Spatial independence: To describe the association in spatial patterning between two tree species, we used the null hypothesis of spatial independence assuming that the spatial interaction is independent. By using the bivariate pair correlation, we kept the first pattern unchanged and then randomly shifted the second pattern relative to the pattern 1 (Wiegand & Moloney 2014).

Significant departure from the null models was evaluated by using 199 Monte Carlo simulations; approximately 95% confidence envelopes were built by 5th lowest and 5th highest values of these simulations. All point pattern analyses were performed by using the grid-based software Programita http://programita.org/

III. RESULTS

Community structure and composition

In the plot P1, a density of 704 individualtrees/ha was composed by 41 tree species. With a total 61.2% of IVI values, three tree species formed a group of dominant species, containing *Streblus macrophyllus, Caryodaphnopsis tonkinensis* and *Hydnocarpus kurzii* (Table 1). In which, *S. macrophyllus* had the highest density and contributed 9.38 m^2/ ha of basal area even though it had the smallest mean dbh. *C. tonkinensis* was the lowest density species but it had the greatest basal area of 15.21 m^2/ ha caused by the largest mean dbh.

Table 1. Basic characteristics of dominant tree species

Plot/ Species	Density (N/ha)	dbh (cm)	Max dbh (cm)	Basal area (m^2/ha)	IVI (%)
P1					
S. macrophyllus	483	13.4 ± 8.3	50.63	9.38	42.8
C. tonkinensis	29	77.4 ± 26.7	133.75	15.21	18.4
H. kurzii	33	18.7 ± 10.8	42.99	1.20	5.7
37 other species	159	20.17 ± 20.96	155.09	10.58	27.1
P2					
S. macrophyllus	392	9.7 ± 7.3	39.71	4.53	20.8
C. tonkinensis	29	67.1 ± 30.5	124.20	12.32	13.8
S. dives	117	18.8 ± 12.7	54.42	4.7	11.1
H. kurzii	94	12.7 ± 8.8	36.85	1.76	7.4
F. cyrtophylla	32	4.9 ± 2.1	12.80	0.07	2.1
86 other species	342	15.42 ± 15.97	85.99	12.97	44.9

N- number of trees, dbh- diameter at breast height, max dbh- maximum dbh, IVI- Important Value Index

In the plot P2, 91 species/ ha of the species richness, 1006 individuals/ ha of tree density and 53.1% of IVI values constituted a dominant species group including *Streblus macropyllus, Caryodaphnopsis tonkinensis, Saraca dives, Hydnocarpus kurzii* and *Ficus cyrtophylla.* Comparing to P1, *S. macrophyllus* also had the highest tree density but it was smaller in the mean dbh. Similarly to P1, *C. tonkinensis* was the lowest species abundance, the largest mean dbh and the greatest basal areal. The two study plots shown the effects of forest disturbance in *S. macrophyllus* dominance, species richness and the total basal area of forest communities.

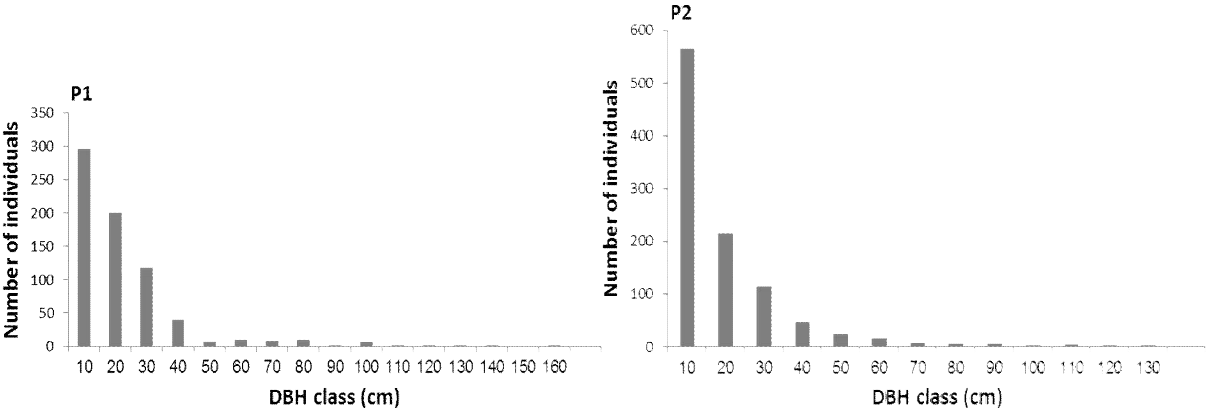

Fig.2. Diameter distributions of individual trees

Diameter distribution in both plots showed a reversed J-shape distribution (Fig. 2) but the overall shape of the curve and individual distribution were different in two stands. P1 had lower number of individuals in small size classes up to 60 cm than P2, both P1 and P2 stands were similar in a low number of individuals at larger size classes.

Tree species diversity

Table 2. Summary of diversity measures for the study plots (P1 and P2)

Index	P1	P2
Species richness (S)	40	91
Simpson diversity (D)	0.52	0.82
Simpson evenness (E)	0.05	0.01
Shannon diversity (H’)	1.54	2.79
Shannon evenness (J’)	0.42	0.62
Margalef diversity	5.95	12.73

All metrics pointed to lower diversities in the P1 except Simpson evenness because of species richness. Tree species richness was much higher in P2 than P1 (91 versus 40). Evenness is important because it is influenced by different processes than species richness and often associated with different suite of environmental factors.

Spatial pattern analysis

Environmental homogeneity

The spatial patterns of all adult trees (dbh ≥ 15 cm) in study plots were contrasted to the CSR null model to find significant departure at large scales. We used both cumulative and non-cumulative advantages of both *L*-function and *g* - functions in this analysis, respectively. Fig.3 shows the patterns of adults in P1 (Fig.3a-b) and in P2 (Fig.3c-d). The *g*-function showed that adults in both plots were regular at scales up to 5 m and that could be evidences of strong tree-tree competition (Fig.3a,c). Moreover, *L*-function also showed regular patterns at scales up to 10 m and no deviation from confidence envelopes at larger scales (Fig.3b,d). Therefore, no large scale departure from the CSR null model was observed and the hypothesis of environmental homogeneity was accepted in the study plots. Based on this finding, we applied the homogeneous *g*-function for the further spatial pattern analyses in this study.

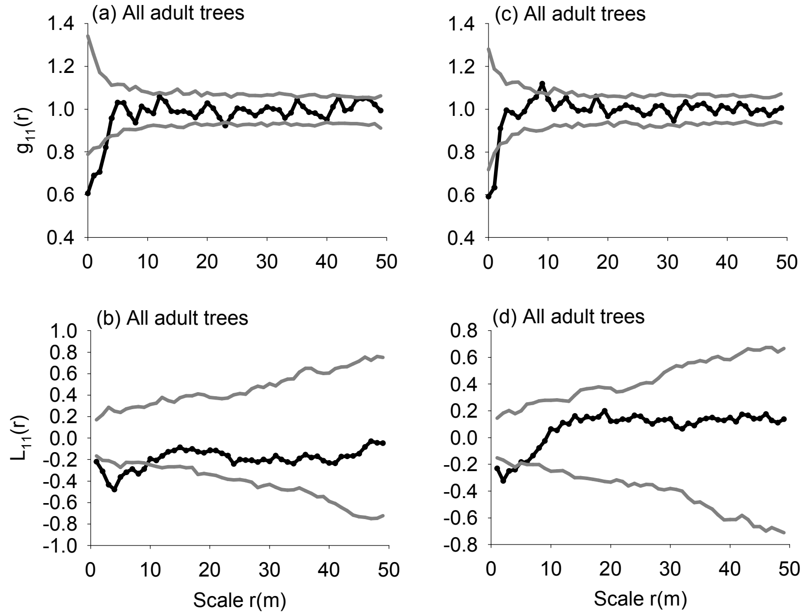

Fig.3. Spatial distributions of all adult trees (dbh ≥ 15 cm) shown by the univariate *L*-function and *g*-function. The observed patterns (dark line) lying beyond the 95% confidence envelopes (grey lines) indicate significant departure from the null models of CSR

Spatial patterns of dominant species

Among three dominant species in P1, *S. macrophyllus* was regular at scales from 0-2 m, being an evidence for intra-specific competition while *H. kurzii* and *C. tonkinensis* had a random pattern for all scales (Table3). Moreover, a marginal aggregated pattern of *S. macrophyllus* was found at scales from 4-6 m.

In the P2, four of five studied species were aggregated at different scales within the entire stand, including *S. macrophyllus*, *S. dives*, *H. kurzii* and *F. cyrtophylla* (Table3). Only *C. tonkinensis* was random at all scales. Particularly, *S. macrophyllus* was aggregated up to large scale of 35 m and its density clearly decreased with increasing spatial scales.

Overall, *S. macrophyllus* had both regular and aggregated distributions in two study plots emphasizing its dissimilar intra-specific interactions there.

Table 3. Intra- and inter-specific interactions in the P1 and P2 analyzed by *g*-function

P1	*S. macrophyllus*	*C. tonkinensis*	*H. kurzii*
S. macrophyllus	- (0÷2 m)	0	0
C. tonkinensis	0	0	0
H. kurzii	0	0	0

P2	*S. macrophyllus*	*C. tonkinensis*	*H. kurzii*	*F. cyrtophylla*	*S. dives*
S. macrophyllus	+ (0÷35 m)	- (2÷15 m)	- (25÷30 m)	- (0÷22 m)	0
S. dives	0	0	0	0	+ (2÷12 m)
C. tonkinensis	- (2÷15 m)	0	0	0	0
F. cyrtophylla	- (0÷22 m)	0	+ (10÷12 m)	+ (3÷7 m)	0
H. kurzii	- (25÷0 m)	0	+ (4÷8 m)	+ (10÷12 m)	0

+: *positive interaction*, -: *negative interaction, 0*: *independence, (i.e., 0÷8 m)*: *significant scales*

In the P1, no significant association was found meaning that three dominant species interacted independently from each other. At the P2, *S. macrophyllus* had negative interactions up to large scales with *C. tonkinensis* (to 15 m) and *F. Cyrtophylla* (to 22 m) while from large scales with *H. Kurzii* (from 25 m). Positive interaction was found between *H. kurzii* and *F. cyrtophylla* at scales larger than 10 m. In addition, no significant deviation from null model was found in interaction of the remaining species pairs.

The compared results showed that *S. Macrophyllus* differs in interspecific interactions between two study plots containing similar dominant tree species. *S. Macrophyllus* was independent in the P1 while it competed significantly with other species in the P2.

III. DISCUSSION

Stand structure and diversity

The size structure of a species reflected regeneration processes and it can provide insight into the forest dynamics when compared to the spatial structure of forest. A reversed J-shape of diameter distribution suggests the continuous population regeneration and favorable conditions for establishment and survival of seedling, especially in karst forests.

The tree densities of P1 and P2, from 704 to 1006 individuals/ha, were low in comparison to tropical rain forests. The target species,*S. macrophyllus*, had small mean dbh but the highest percentage of IVI values compared to overall two plots. Moreover, the dominance of *S. macrophyllus* in P1 significantly differs from P2 not only in tree density but also in basal area. The target species is a shade tolerant growing understorey but it uses gap phase generation contributing to its invasion (detail analyses below). The difference of two disturbed forests shown in species richness of communities, abundance of *S. macrophyllus* and tree size of *C. tonkinensis*- a shade intolerant species. Consequently, seedlings are hardly to recruit, therefore this could be explained for low numbers of tree individuals and species in P1 compared to P2.

The species richness differences may be explained by stochastic events driving biotic events (i.e., dispersal, interaction) and abiotic events (ex. light, moisture and canopy gap). Our results suggest that diversity is significant different between P1 and P2 because of forest disturbance. Our study shown that species evenness is more sensitive than species richness to human activities and environmental change, this is also confirmed by previous studies.

Environmental homogeneity

At scales smaller than 30 m, aggregation pattern of trees can be explained as tree-tree interaction, while at larger scales, it is attributed to environmental heterogeneity caused by rock outcrops, stream, slope, or soil nutrients. To test hypothesis of environmental homogeneity, we based on cumulative and non-cumulative advantages of L-function and g-function to contrast results on adult tree pattern because adult trees can be distributed at all available places. Here, no large scale aggregation was captured in both study plots and the hypothesis of environmental homogeneity was accepted with approximate 95% confidence intervals. Based on this initial inference, it allows us to choose appropriate null models to generate relevant hypotheses for further tests of tree interactions in the study.

Spatial patterns of dominant species

Aggregated pattern of tree species is common in tropical forests and often explained by results of dispersal limitations, or patchy distribution of suitable micro-habitat, environmental heterogeneity, canopy gap or disturbance, however effect of environmental heterogeneity was excluded in this study. Among studied dominant species, only *S. macrophyllus* in the P1 had regular pattern, as discussed, this could be result of intra-specific competition. The remaining species were mainly aggregated at various scales while some have random distributions. That could be results of dispersal limitation process and different depending on tree species. These findings are compatible with previous studies that aggregated or random patterns are common in most of tropical tree species.

Independence or no interaction is major in inter-specific associations of both study plots. Lacking of significant species interactions in tropical forests is also confirmed in previous studies of forest ecology both in theory and field studies (Hubbell 2006). Surprisingly, at the P2, *S. macrophyllus* was negative interaction with three dominant neighbors. *S. macrophyllus* could be a gap opportunist with gap phase regeneration, therefore it would occupy all available gaps and become more abundant in its community.

We recommend focusing on the population dynamics and spatial pattern of tree species and on specific guilds and functional traits. However, such studies will require larger study plots and data were observed regularly in periods of time.

Management implications

The two study plots are significantly different in tree species structure, species diversity, and spatial patterns. The effects of forest disturbance by human activities were emphasized significantly through forest community structure. *S. macrophyllus* was considered as an intra-specific competitor and uses gap phase regeneration for its invasion that is facilitated by disturbed forest and canopy openness. The findings can be used as suggestions for silvicultural treatments and biodiversity conservation of tropical rain forests in Cuc phuong National park.

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CẤU TRÚC, THÀNH PHẦN VÀ MÔ HÌNH KHÔNG GIAN CỦA RỪNG THỨ SINH TRÊN NÚI ĐÁ VÔI

Nguyễn Hồng Hải

Trường Đại học Lâm nghiệp

TÓM TẮT

Cấu trúc và mô hình không gian của các loài cây rừng là những chỉ tiêu giải thích cho những cơ chế hay quá trình đã tạo nên cấu trúc rừng. Trong bài báo này, kỹ thuật phân tích mô hình điểm không gian được sử dụng để mô tả cấu trúc và phân bố không gian của hai trạng thái rừng tự nhiên thứ sinh ở Vườn quốc gia Cúc Phương. Các kết quả cho thấy rằng: (1) Cấu trúc rừng bị ảnh hưởng rõ rệt bởi các tác động thông qua thành phần loài cây và phân bố của chúng. (2) Cạnh tranh cùng loài của Nhò vàng thể hiện rõ ở lâm phần có đa dạng loài thấp và không rõ ở lâm phần có đa dạng loài cao. (3) Hầu hết các quan hệ giữa các loài cây là độc lập, ngoại trừ quan hệ cạnh tranh khác loài của Nhò vàng ở lâm phần có đa dạng loài cao. (4) Tỉa thưa tự nhiên và tái sinh lỗ trống là hai quá trình cơ bản chi phối quan hệ giữa các giai đoạn sống của Nhò vàng trong khi phát tán hạn chế được thể hiện ở các loài khác. Vì thế, Nhò vàng là loài cây tái sinh dưới lỗ trống và cạnh tranh mạnh. Rừng bị tác động và độ mở của tán rừng là nguyên nhân thúc đẩy Nhò vàng cạnh tranh để xâm chiếm không gian dinh dưỡng.

Từ khóa: Mô hình không gian, phân tích mô hình điểm, rừng nhiệt đới thường xanh, Vườn quốc gia Cúc Phương.

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