SPATIAL ASSOCIATIONS AND SPECIES DIVERSITY OF TROPICAL BROADLEAVED FOREST, GIALAI PROVINCE

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SUMMARY

Spatial association and species diversity of species-rich tropical forests can be characterized by their spatial patterns. We applied the quantitative analyses based on relationships of spatial distribution of tree species. In a 2-ha plot of a tropical broadleaved forest stand in Kon Ha Nung, Gia Lai province, all tree individuals with DBH ≥ 2.5 cm were mapped and their characteristics (i.e., DBH and species) were recorded. We applied two different types of analyses: (1) Overall inter-specific associations through a classification scheme based on bivariate nearest neighbor distribution function $D_{12}(r)$ and Ripley's K function $K_{12}(r)$, (2) Individual species Area Relationship. The findings showed that: (1) In total of 506 species pairs analyzed up to spatial scales of 50 m, the most frequent association type was mixing of all species pairs (38.9%). Segregation and no association types between species were observed with 27.1% and 25.9%, respectively. The least frequent type was partial overlap (8.1%). (2) Among 23 dominant species, 13 species (56%) were regarded to diversity accumulators, three species (13%) were diversity repellers and seven species (31%) were neutral at different scales up to 50 m. We found significant evidences of the main ecological theories such as dispersal limitation, Neutral theory and other effects including the stochastic dilution and species herd protection. We suggest using both the bivariate nearest neighbor distribution function and the individual species area relationship as advantageous approaches in forest ecology study.

Keywords: Individual species area relationship, spatial pattern, spatial species diversity, tropical evergreen broadleaved forest.

1. INTRODUCTION

A principal goal of ecology is to understand the processes and mechanisms that control the distribution, abundance and coexistence of species (Brown et al., 1995). In tropical forests, several hundreds of tree species can be found within small areas (Losos, 2008), for example, up to 300 tree species per hectare have been recorded in the Amazonia (Gentry, 1988). McGill (2010) synthesized ecological theories of biodiversity producing macroscopic community patterns such as species-area curves, species-abundance distributions and decay of similarity of distance. He showed that these theories use the same three rules or assertions to describe a stochastic geometry of biodiversity, namely: (i) intraspecific clustering, (ii) the species abundance distribution shows typically many rare and few common species, and (iii) interspecific individuals are placed without regard to individuals of other species and sufficient for explaining several macroscopic community patterns.

One way of assessing the evidence for species interactions in plants is to analyse their spatial patterns (Wiegand et al., 2007; Law et al., 2009). Because plants cannot move and mainly interact with their close neighbours, their spacing may conserve an imprint of neighbourhood interactions that could be detected using point pattern analysis (Wang et al., 2010). This approach is promising because the intraspecific spacing of plants is also closely related with potential coexistence mechanisms (Pacala & Levin, 1997). For example, intraspecific clustering and interspecific segregation may retard competitive exclusion because the relative importance of interspecific versus intraspecific competition is reduced (Stoll & Prati, 2001). Analysis of the bivariate spatial patterns of all pairs of species allows testing if the interspecific arrangement of species is indeed independent as assumed by assertion (Lieberman & Lieberman, 2007; Perry et al., 2009). However, such analyses are challenging because they require complete mapping of large plots of a species-rich community and difficulties in teasing apart two majors, contrasting factors that can cause non-independence such as competition or facilitation (Wang et al., 2010).

Understanding the spatial pattern of species diversity is a fundamental goal of community ecology beacause it may link to ecological processes regulating spatial structure of community. Previously, species diversity has characterized over space by using the species area relationship-SAR (Tsai et al., 2015). The SAR quantifies changing of species richness from a plot centered perspective with sampling area bounded in a given geometrical shape, however spatial heterogeneity of the SAR is largely overlooked (Connor & McCoy, 1979). One of the promising technique in spatial statistics is the individual species area relationship-ISAR (Nguyen et al., 2018) to study species specific effects on local diversity in species-rich communities. ISAR considers individuals of a target species within (circular) plot of a given size around them and estimates spatial heterogeneity to examine community level consequence, therefore providing a chance to generate hypotheses about community structure.

The ISAR function allows to detect spatial patterns in diversity from the perspective of individual plants and to relate them with respect to underlying mechanisms (Rayburn & Wiegand 2012). If positive interactions with other species occur, such as shared responses to abiotic conditions or dispersed by the same frugivores, the target species would be accumulating and maintaining an over-representative proportion of species diversity in its proximity (Nguyen et al., 2018). In this case, target species is termed as a diversity accumulator. In contrary, if negative interactions present, such as competition for space, it can result in a lower density of hetero-specific neighbors. In which the focal species tolerates an under-representative proportion of other species, therefore namely as a diversity repeller. Hence, the net balance of positive and negative interactions can induce in reduced or elevated species richness of the neighbors of a focal species, or the neighborhoods species richness may not significantly differ from that of random neighborhoods (Nguyen et al., 2018).

2. RESEARCH METHODOLOGY

2.1. Study site and data collection

A 2-ha study plot (100 x 200 m) were established in Kon Ha Nung, Gia Lai province, Central highland of Vietnam at geographic coordinates 14°11.492' N and 108°39.938' E. The evergreen broadleave forest stand has been highly protected and undisturbed by human activities for decades. The climate here is tropical monsoon climate with the average annual temperature of 23.6°C and the average annual precipitation of 2,042 mm. About 90% of the total precipitation fall from May to December. Elevation of the plot ranges from 685 to 690 m a.s.l, with an average slope of 5 degrees.

All live trees with diameter at breast height (dbh) $\geq$ 2.5 cm were mapped, tree positions and their characteristics (species and dbh) recorded. The relative coordinates (x, y) of each tree were recorded via a grid system of subplots (10 × 10 m) by using a laser distance measurer (Leica Disto D5) and compass.

2.2. Data analysis

Species-species associations

Interspecific associations were classified into four schemes based on the K-function $K_{12}(r)$ and the nearest neighbour distribution function $D_{12}(r)$. The K-function $K_{12}(r)$ is the bivariate Ripley's function. The quantity $\lambda_2 K_{12}(r)$ can be interpreted as the number of 2nd tree species individuals within distance r from 1st tree species individuals where λ_2 is the density of 2nd species trees in the study area (= the number of plants of pattern 2 divided by the area of the study plot). $D_{12}(r)$ is the cumulative nearest neighbour distribution function that gives the probability that the nearest species 2 neighbour of an individual of species 1 is located within distance r. The expectations of the summary statistics under the null model yield $K_{12}(r) = \pi r^2$ and $D_{12}(r) = (1-\exp(-\lambda^2\pi r^2))$. The two axes of the classification scheme were defined as:

$$\hat{P}(r) = \hat{D}_{12}(r) - (1 - \exp(-\lambda_2\pi r^2)) \text{ and } \hat{M}(r) = \ln\left(\hat{K}_{12}(r)\right) - \ln(\pi r^2)$$

The theoretical values were subtracted under the null model to move the null expectation onto the origin of the scheme and log-transformed the K-function to weight positive or negative departures from the null model in the same way. The hat symbol indicates the observed value. The two dimensional scheme allows for the identification of four fundamental types of bivariate association as following:

'Segregation': if $(\hat{M}(r) < 0 \text{ and } \hat{P}(r) < 0)$ where individuals of species 2 occur on average less frequently within species 1 neighbourhoods than expected by chance.

'Partial overlap': if $(\hat{M}(r) > 0 \text{ and } \hat{P}(r) < 0)$ where some neighbourhoods of species 1 contain more individuals of species 2 and others less.

'Mixing': if $(\hat{M}(r) > 0 \text{ and } \hat{P}(r) > 0)$ where individuals of species 2 occur on average more frequently within species 1 neighbourhoods.

'No association': if $(\hat{M}(r) > 0, \hat{P}(r) < 0)$ which can only arise if strong second-order effects occur. Species pairs that show for a given neighbourhood r non-significant effects in both summary statistics are classified as 'no association' type and will be located close to the origin of the scheme.

To stabilize the variance, a transformation of $K_{12}(r)$, $L_{12}(r) = (K_{12}(r)/\pi)^{0.5}$, was used instead of $K_{12}(r)$.

The software Programita 2019 (http://programita.org/) is implemented for two summary statistics by using 199 simulations of the null model of independence with spatial resolution of 1 m. To evaluate a significant departure from the null model, the goodness-of-fit test is conducted at 2.5 per cent error rate which yields for two summary statistics an error rate of ≈ 5%. Because of using two test statistics $L_{ij}(r)$ and $D_{ij}(r)$ at the same time, the rank larger than 195 is used to be significant.

Spatial species diversity

ISAR(r) function is the expected number of species within circular areas of radius r, with $a = \pi r^2$, around an arbitrary chosen individual of a target species t (Wiegand et al., 2007). ISAR is used to analyzed the spatial diversity structure in forest ecosystem and combined both species area relationship and individual perspective of point pattern analysis (Wiegand & Moloney 2014). For a species, the ISAR can be estimated as:

$$\text{ISAR}(r) = \sum_{j=1}^{N}[1 - P_{tj}(0, r)]$$

$P_{tj}(0, r)$ is the emptiness probability that species j was not present in the circle with radius r around individuals of the target species t. If $a = \pi r^2$, the ISAR function can be expressed in terms of circular area a to resemble the common species area relationship (Wiegand et al., 2007).

To assess departure from the null model of Complete Spatial Randomness at different scales r, the 5th lowest and 5th highest values of 199 Monte Carlo simulations are used to construct confidence envelopes, then the Goodness-of- Fit test is applied with < 5% error to reduce type I error inflation. The species is regarded as a diversity accumulator with an approximate α level of 0.05 if the empirical ISAR(r) is greater than the 5th highest value of the 199 null model simulations at scale r. All analyses are performed by using software Programita 2019 (http://programita.org/). That means the target species have a more diverse local neighborhoods at scale r than expected by the null model. Conversely, if the empirical ISAR(r) is smaller than the 5th lowest value of the 199 null model simulations at scale r, the species is regarded as a diversity repellant or repeller, thereby have a less diverse local neighborhood at scale r than expected by the null model. If the empirical ISAR(r) is within the range of the null model, the target species is considered as neutral at scale r.

3. RESULTS

3.1. Forest stand characteristics

In total, there were 3453 tree individuals with dbh ≥ 2.5 cm recorded, belonging to 100 species and 99 families. The most common species were *Syzygium zeylanicum* (Myrtaceae), *Shorea roxburghii* (Dipterocarpaceae), *Wendlandia paniculata* (Rubiaceae), *Gironniera subaequalis* (Ulmaceae), *Casearia balansae* (Salicaceae), *Machilus thunbergii* (Lauraceae).

In this study, 23 most abundant species with number of individuals ≥ 50 were analyzed (Table 1). These species contributed the total IVI > 70% of whole forest community. The highest IVI species ≥ 5% including *Syzygium zeylanicum*, *Dacryodes Dungii*, *Michelia braianensis*. Moreover, nearest distance between tree individuals of intra-species increased with decreasing its abundance (Table 1).

Table 1. The most abundant species

No	Scientific name	Family	N	IVI (%)	Nearest distance (m)
1	*Syzygium zeylanicum*	Myrtaceae	278	6.57	4.28 ± 2.68
2	*Shorea roxburghii*	Dipterocarpaceae	229	4.34	4.36 ± 2.85
3	*Wendlandia paniculata*	Rubiaceae	200	3.93	4.99 ± 3.42
4	*Gironniera subaequalis*	Ulmaceae	184	3.15	5.52 ± 3.11
5	*Casearia balansae*	Salicaceae	182	2.79	4.48 ± 2.83
6	*Machilus thunbergii*	Lauraceae	131	4.32	6.51 ± 3.82
7	*Syzygium wightianum*	Myrtaceae	120	2.54	6.35 ± 3.58
8	*Machilus odoratissima*	Lauraceae	118	1.87	6.64 ± 4.47
9	*Dacryodes Dungii*	Burseraceae	116	5.98	6.84 ± 3.36
10	*Dialium cochinchinense*	Caesalpinioideae	113	2.11	6.52 ± 3.76
11	*Baccaurea harmadii*	Euphorbiaceae	106	2.18	6.56 ± 4.09
12	*Polyalthia nemoralis*	Annonaceae	108	4.48	6.95 ± 3.58
13	*Amesiodendron chinense*	Sapindaceae	96	2.97	7.61 ± 4.04
14	*Dimocarpus fumatus*	Sapindaceae	93	1.43	5.77 ± 6.36
15	*Symplocos sumuntia*	Symplocaceae	88	1.53	7.03 ± 5.11
16	*Michelia braianensis*	Magnoliaceae	81	11.92	9.48 ± 5.11
17	*Machilus leptophylla*	Lauraceae	68	2.33	8.00 ± 4.62
18	*Diospyros apiculata*	Ebenaceae	68	1.06	8.57 ± 5.56
19	*Cinamomum parthenoxylon*	Lauraceae	65	1.05	8.47 ± 7.69
20	*Syzygium levinei*	Myrtaceae	60	1.49	7.73 ± 4.29
21	*Antidesma ghaesembilla*	Phyllanthaceae	54	1.94	10.61 ± 6.63
22	*Machilus grandifolia*	Lauraceae	54	1.11	7.68 ± 7.34
23	*Sinosideroxylon bonii*	Sapotaceae	52	0.83	10.59 ± 6.60
24	76 other species	38 families	789	28	

N-number of individuals, IVI-Important Value Index, (relative abundance + relative basal area)/2, expressed as percentage proportion. Nearest distance- nearest distance between tree individuals (mean ± Standard deviation).

3.2. Analysis of species associations

The overall interspecific association patterns of 23 species were assessed up to large scales of 50 m (Figure 1). In total of 506 species pairs analyzed, the most frequent association type was mixing of all species (38.9%). Segregation and no association types between species were observed with 27.1%

and 25.9%, respectively. The least frequent type was partial overlap (8.1%) up to spatial scales of 50 m.

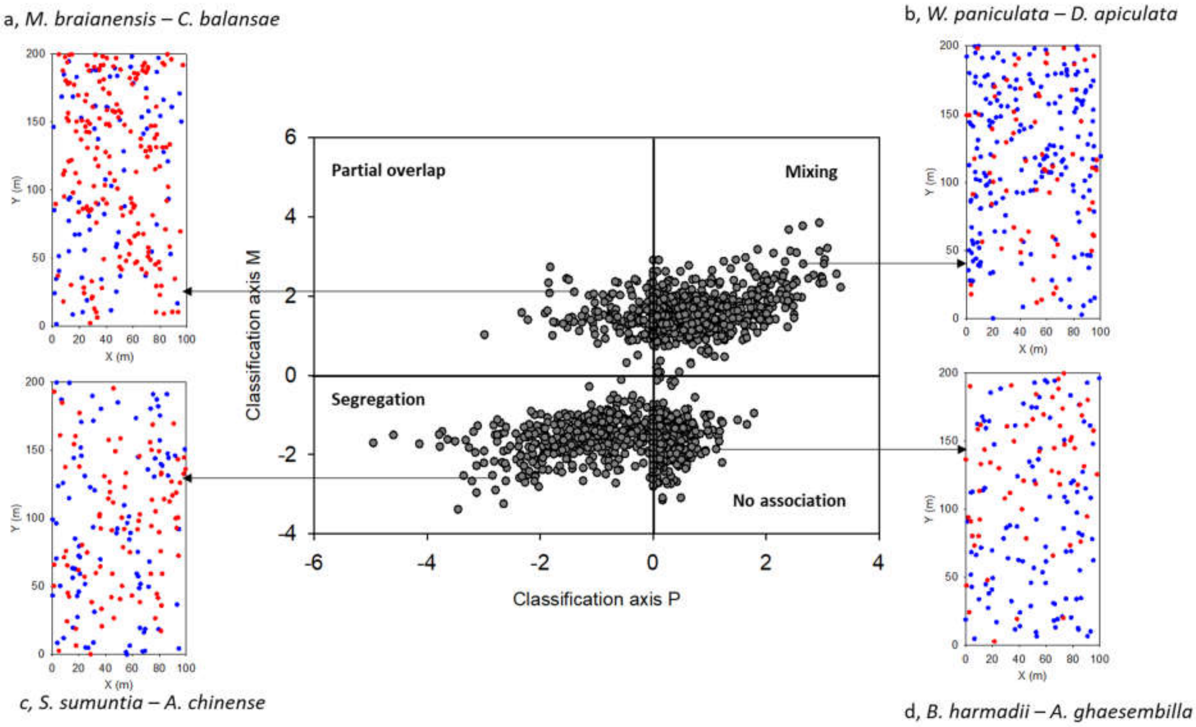


Figure 1. Classification of species associations at the study plot up to 50 m

(Figure 1a-d are examples of species associations under four schemes including Partial overlap (1a), Mixing (1b), Segregation (1c) and No association (1d). The red dots are the species 1 pattern and the blue dots are the species 2 pattern)

The results at large spatial scales up to 50 m showed four schemes of interspecific associations (Figure 2). At scales smaller than 20 m, mixing and segregation type were dominated interspecific associations while at larger scales, no association and partial overlap types were more frequent. Mixing and segregation types of 23 species decreased with increase of spatial scales. Conversly, no association and partial overlap types increased with increasing spatial scales. Mixing was the most frequent association type of all species pairs with its peak at scale of 4 m. Segregation dominated between species pairs up to 20 m. Partial overlap was the least frequent type of species association and reached to 10 species pairs at scale of 17 m. No association type increased with increasing spatial scales up to 40 m.

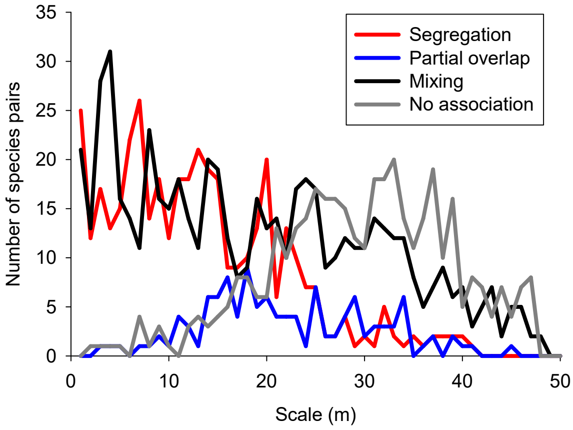
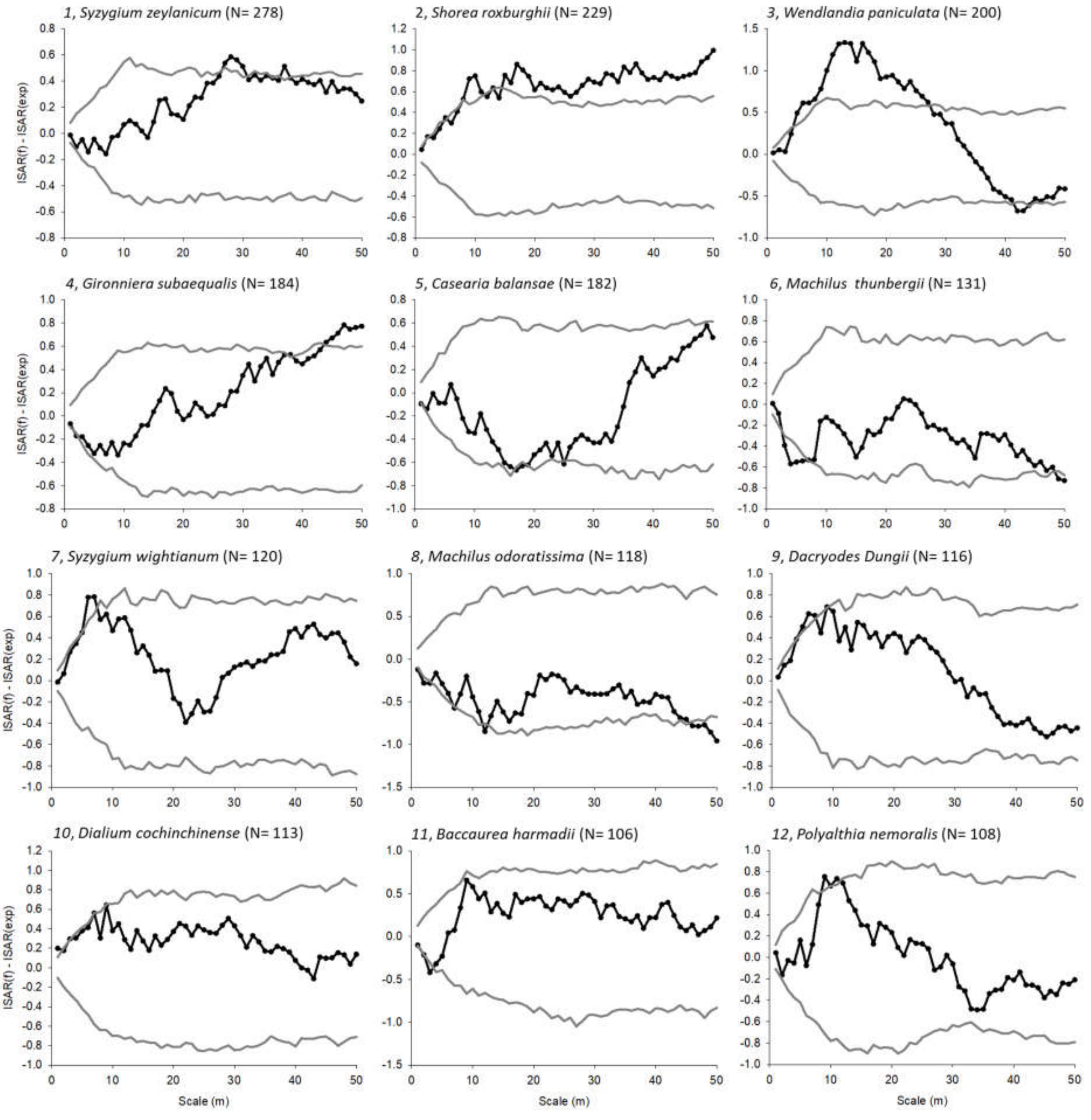


Figure 2. The overall interspecific associations at large scales

3.3. Analysis of individual species area relationship

The null model of Complete Spatial Randomness was used to test spatial diversity of tree species neibourhoods surrounding target species. Twenty three target species was selected based on their abundances with at least 50 individuals/species as suggested by Wiegand & Moloney (2014). After 199 Monte Carlo simulations, species is regarded as diversity accumulator if its pattern is above or as diversity repeller if its pattern is below or as neutral if its pattern is in between approximate 95% confidence envelopes. Those species regard as diversity accumulators that have more number of interspecific species in their neighborhoods while species regarded as diversity repeller mean that they have less number of inter-species in their neighborhoods than expected at their significant scales under the null model of CSR.

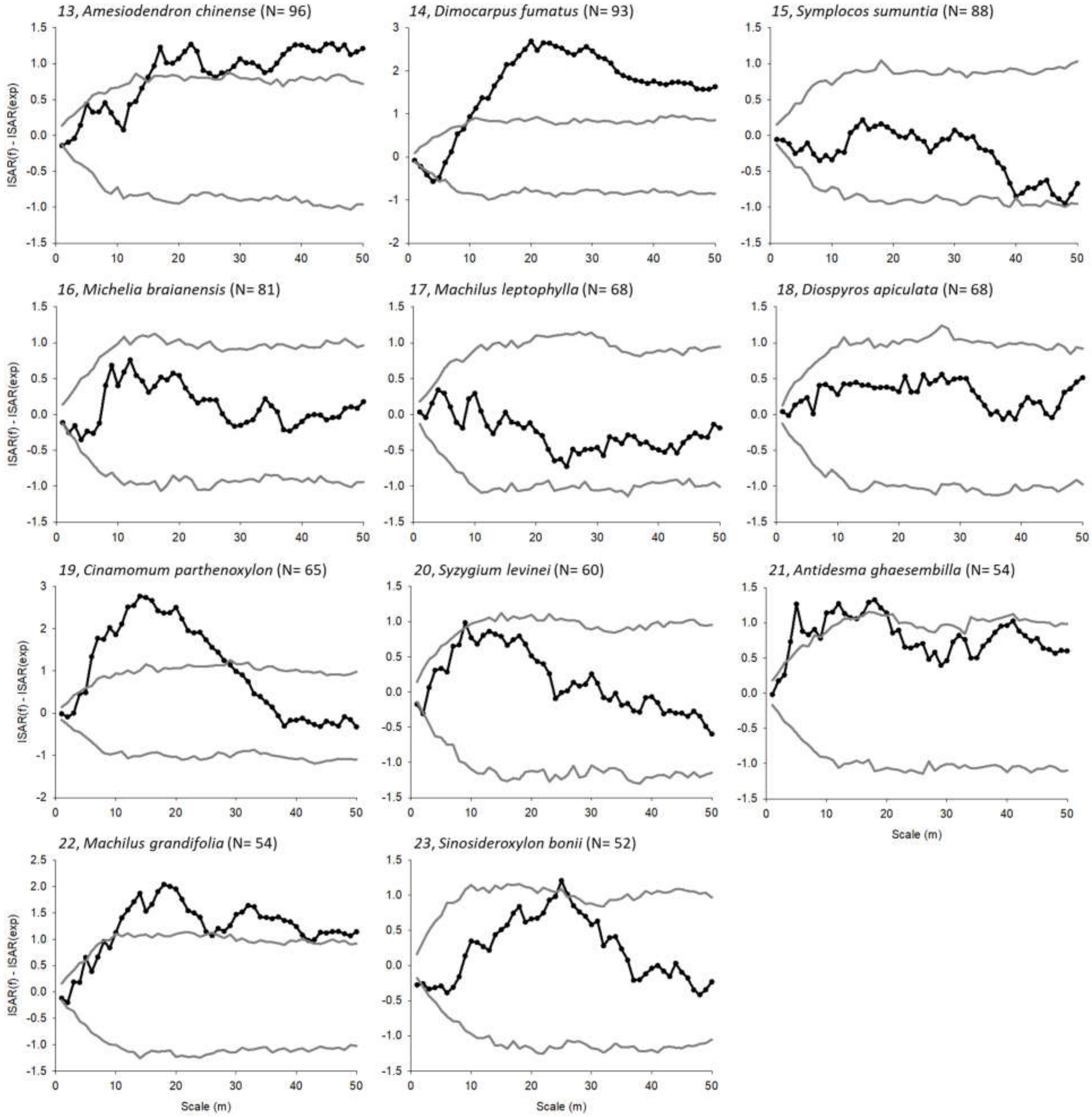
The results of ISAR analysis showed that, among 23 dominant species, 13 species (56%) were regarded to diversity accumulators, three species (13%) were diversity repellers and seven species (31%) were neutral at different scales up to 50 m.



1, *Syzygium zeylanicum* (N= 278)
2, *Shorea roxburghii* (N= 229)
3, *Wendlandia paniculata* (N= 200)
4, *Gironniera subaequalis* (N= 184)
5, *Casearia balansae* (N= 182)
6, *Machilus thunbergii* (N= 131)
7, *Syzygium wightianum* (N= 120)
8, *Machilus odoratissima* (N= 118)
9, *Dacryodes Dungii* (N= 116)
10, *Dialium cochinchinense* (N= 113)
11, *Baccaurea harmadii* (N= 106)
12, *Polyalthia nemoralis* (N= 108)

Figure 3. Results of ISAR analyses for twelve dominant species

(Black lines show ISARf(r)-ISARexp(r), the observed ISAR function minus the expectation of the CSR null model. Grey lines show the simulation envelopes minus the expectation of the null model. N- number of tree individuals)



13, *Amesiodendron chinense* (N= 96)

14, *Dimocarpus fumatus* (N= 93)

15, *Symplocos sumuntia* (N= 88)

16, *Michelia braianensis* (N= 81)

17, *Machilus leptophylla* (N= 68)

18, *Diospyros apiculata* (N= 68)

19, *Cinamomum parthenoxylon* (N= 65)

20, *Syzygium levinei* (N= 60)

21, *Antidesma ghaesembilla* (N= 54)

22, *Machilus grandifolia* (N= 54)

23, *Sinosideroxylon bonii* (N= 52)

Figure 3 (continue). Results of ISAR analyses for other eleven dominant species

(Black lines show ISARf(r)-ISARexp(r), the observed ISAR function minus the expectation of the CSR null model. Grey lines show the simulation envelopes minus the expectation of the null model. N- number of tree individuals)

Abundance of diversity accumulators ranged from high to low with N from 139 to 26 tree individuals/ha such as *S. zeylanicum* (Figure 3.1), *S. roxburghii* (Figure 3.2), *A. ghaesembilla* (Figure 3.21) and *S. bonii* (Figure 3.23). Most of diversity repellers were significant at small scales smaller than 10 m such as *M. thunbergii* (Figure 3.6), *M. odoratissima* (Figure 3.8), *B. harmadii* (Figure 3.11). *D. fumatus* (Figure 3.14) was diversity repeller at small scale below 10 m, then became diversity accumulator at larger scales. Seven neutral species varied in species abundance from high to low, for example *C. balansae* (Figure 3.5, N = 182) and *S. levinei* (Figure 3.20, N = 60). Consequently, species abundance showed no clear effect on species richness of neighborhoods.

4. DISCUSSION

Our analysis explored that a majority of species association exhibited mixing from their heterospecific neighbors and the number of species pairs showing mixing decreased with scale increase. These findings were in accordance with the results obtained by Wiegand et al. (2012) in a species-rich tropical forest at Barro Colorado Island (Panama), a tropical forest in Sinharaja (Sri Lanka). The proportion of no association type decreased with spatial scale and would be governed by stochastic dilution effect, especially in species rich communities, as explained by Wang et al. (2010). Our results partly supported the stochastic dilution hypothesis.

Segregation type among species had 27.1% of overall species associations and decreased with increasing spatial scales. Wiegand et al. (2012) found that segregation increased with spatial scale, while it decreased with species richness and explained that heterogeneity of physical environment may increase negative interspecific interactions between species with dissimilar habitat associations. In our study plot, environmental conditions were homogenous, therefore, segregation may be caused by dispersal limitation of tree species.

These findings were supported by the ISAR analyses which showed that 13 species (56%) were regarded to diversity accumulators, three species (13%) were diversity repellers and seven species (31%) were neutral at different scales up to 50 m. In which, the high number of species diversity accumulators was relevant to the high proportion of mixing type meaning that those species having more interspecific neighbours surrounding. Diversity repellers related to proportion of segregation of species associations by showing less interspecific neighbours arround them which would be caused by dispersal limitation where tree species are separated each other in space. Moreover, no association between species means those species interact independently as neutral species which supports for neutral theory assuming demographical equivalence of tree individuals in terms of their birth, reproduction and death regardless of species identity. Recent studies predict that stochastic dilution effects may result in species rich communities with independence of species spatial distribution (Nguyen et al., 2018), even underlying ecological processes structuring the community are driven by deterministic niche differences.

Diversity accumulators are compatible to positive association of species which would exhibited potential effects of species herd protection (Hai et al., 2016) which states that increased heterospecific crownding results in fewer encounters between a host and its species specific pests and pathogens (Lan et al., 2012). Therefore, survivals should be increased with density of heterospecifics (Peters, 2003, Comita et al., 2007).

5. CONCLUSION

In conclusion, our study support for the main ecological theories such as dispersal limitation and Neutral theory. We also found evidence of other effects on spatial association of tree individuals including the stochastic dilution and species herd protection. For further study, we suggest using both the bivariate nearest neighbor distribution function and the individual species area relationship as advantageous approaches, especially in studying spatial structure of forest community.

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QUAN HỆ KHÔNG GIAN VÀ ĐA DẠNG LOÀI CÂY RỪNG LÁ RỘNG THƯỜNG XANH, TỈNH GIA LAI

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[1]Trường Đại học Lâm nghiệp

TÓM TẮT

Quan hệ không gian và đa dạng loài của rừng nhiệt đới có thể được mô tả bởi phân bố không gian của chúng. Chúng tôi áp dụng các phân tích định lượng dựa vào quan hệ trong phân bố không gian của các loài cây. Trong một ô tiêu chuẩn 2 ha của rừng lá rộng thường xanh ở Kon Hà Nừng, tỉnh Gia Lai, tất cả cây có đường kính ngang ngực dbh ≥ 2,5 cm được định vị, đo đếm dbh và xác định tên loài. Chúng tôi áp dụng hai kỹ thuật phân tích: (1) Phân loại tương tác khác loài dựa vào hàm phân bố $D_{12}(r)$ và hàm Ripley's K $K_{12}(r)$, (2) Quan hệ loài cây theo diện tích. Kết quả cho thấy: (1) Trong tổng số 506 cặp loài được phân tích cho đến phạm vi không gian là 50 m, kiểu quan hệ trộn lẫn có tần xuất cao nhất (38,9%). Các quan hệ cạnh tranh và không tương tác giữa các loài cây chiếm 27,1% và 25,9%. Kiểu chồng lặp một phần có tần xuất thấp nhất (8,1%). (2) Trong số 23 loài chiếm đa số, 13 loài (56%) được phân loại là tích lũy đa dạng, ba loài (13%) là giảm trừ đa dạng và bảy loài (31%) là trung lập ở các phạm vi không gian khác nhau đến 50 m. Chúng tôi tìm thấy các bằng chứng có ý nghĩa của các lý thuyết sinh thái chính như phát tán hạn chế, lý thuyết trung lập và các hiệu ứng khác như phân tán ngẫu nhiên và bảo vệ nhóm loài. Chúng tôi đề xuất sử dụng hàm phân bố tần xuất hai biến số và quan hệ loài cây theo diện tích như là các cách tiếp cận có nhiều ưu điểm trong nghiên cứu sinh thái rừng.

Từ khóa: Đa dạng loài trong không gian, phân bố không gian, quan hệ loài cây theo diện tích, rừng lá rộng thường xanh.

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