INDIVIDUAL SPECIES AREA RELATIONSHIP OF TROPICAL TREE SPECIES AFTER SELECTIVE LOGGING REGIMES IN TRUONG SON FOREST ENTERPRISE, QUANG BINH PROVINCE

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SUMMARY

Explaining the high diversity of tropical rain forest has been a challenge for ecologists for decades. We applied a recent technique of spatial statistics that is Individual species area relationship (ISAR) to study diversity structure of a tropical broadleaved forest based on individual species. The ISAR is combined by species area relationship and Ripley's K to measure the expected α diversity of individual specific species in circular neighborhoods with variable radius of moving window circles around an arbitrary individual of a focal species. Data was collected from two fully mapped 2-ha plots of tropical broadleaved forest in Quang Binh province, Vietnam. Tree species with at least 30 individuals/species were analyzed. It was found that 21 of 53 species were diversity significant at probability of 0.05 in both study plots. In which, five diversity accumulators and five diversity repellers were identified in P1; 11 species were regarded to diversity accumulators in P2 at various spatial scales. Most of signatures on spatial diversity were mainly found at scales smaller than 30 m, while some were found at larger scales. Species diversity was assumed to be unaffected by tree size or species abundance. Effect of logging regimes on species diversity showed by lower number of accumulators and higher number of repellers with conventional logging (P1) than reduced impact logging (P2). Beside effect of logging regimes, the ecological processes such as dispersal limitation, species herd protection and scale separation were inferred as the main drivers regulating spatial diversity patterns of the studied forest stands.

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

1. INTRODUCTION

Understanding the spatial pattern of species diversity is a fundamental goal of community ecology. 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 and McCoy, 1979). One of the promising technique in spatial statistics is the individual species area relationship (ISAR, Wiegand et al. (2007a; 2014)) 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 and 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 (Punchi-Manage et al., 2015). 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 (Punchi-Manage et al., 2015).

In nature, plant species interactions can be observed differently from location to location due to plant-environmental interactions such as plant-plant interactions and habitat association (Wiegand et al., 2007b). In simulation process, if the homogeneous Poisson null model applied, it may be confounded by the first-order effects (i.e., effect of habitat association). Moreover, it factors out the first-order effects and allows a proper examination of the second-order effects (i.e., direct plant-plant interactions) within a given bandwidth of moving window circle (Wiegand et al., 2007a). Therefore, using of appropriate heterogeneous null models can account for the effects of habitat association and plant interactions (Rayburn and Wiegand, 2012). To account those effects, we used Monte Carlo simulations under the heterogeneous null model to assess if a species is significant diversity accumulator, repeller or neutral and at which spatial scales.

In this study, we used the ISAR framework to analyze spatial patterns of species diversity in tropical broadleaved forests in Truongson forest enterprise, Quang Binh province, North-Central Vietnam after applied selective logging regimes. Assessment of tree species diversity including proportion of accumulator, repeller and neutral species at different spatial scales allows us to understand the spatial structure of species-rich communities, critical scales and tree species behavior. Previous studies on spatial patterns of trees have shown that neighborhood effects on forest tree structure are within 30 m and fade away at larger scales (Hubbell, 2001; Peters, 2003; Uriarte et al., 2004; Stoll and Newbery, 2005).

2. RESEARCH METHODOLOGY

2.1. Study site and data collection

Two 2-ha study plots (100 x 200 m) were established in Truongson Forest enterprise, Quangbinh province, North-Central Vietnam. In this region, forests were cut under different regimes such as conventional and reduced impact logging before 2010. Here, reduced impact logging was applied to meet requirements of Sustainable Forest management certification. The climate here is tropical monsoon climate with the average annual temperature of 23.5°C and the average annual precipitation of 3,000 mm. About 60-70% of the total precipitation fall from October to December in the rainy season and the dry season lasts from March to August. Elevation of the plots ranges from 134 to 160 m a.s.l, with an average slope of 25 degrees.

All live trees with diameter at breast height (DBH) ≥ 2.5 cm were mapped, tree positions and their characteristics (species and dbh) recorded. If trees were multi-stemmed, each stem was considered a separate tree if the branching occur below breast height (1.3 m). The relative coordinates (x, y) of each tree were recorded via a grid system of subplots (10 m × 10 m) by using a laser distance measurer (Leica Disto D5) and compass.

2.2. Methods

ISAR function

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., 2007a). 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 and 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., 2007a).

Null models

The null model of Complete Spatial Randomness (CSR) randomizes the locations of individuals of the target species and thereby removing the potential effects of interactions with other species individuals while the heterogeneous Poisson null model assumes that density of individuals of target species is not constant. To estimate the intensity function of a heterogeneous Poisson null model, a non-parametric kernel estimation of the intensity function based on the Epanechnikov kernel with a bandwidth R = 50 m was used. In the estimation, all potential spatial structures in the pattern of the target species at scales up to 50 m are removed but maintained the spatial structure at scales > 50 m.

We estimated the ISAR only for tree species having ≥ 30 individuals. To cover scales of tree-tree interactions, we used a maximal scale of $r_{\max}$= 50 m and a spatial resolution of 1 m. To test for a given species if it is a significant diversity accumulator or repeller or it behaves neutrally, we performed 199 Monte Carlo simulations of the null models by using ISAR as test statistic.

Goodness-of-Fit tests for null models

We conducted Goodness-of-Fit (GoF) tests to reduce type I error inflation due to multiple simulations (Loosmore and Ford, 2006). We evaluated the accumulated deviations u_i with i = 0 for the observed ISAR function and i = 1…199 for null model simulations. The index u_i shows the accumulated deviation of the observed ensemble statistics from the expected ensemble statistics under the null model which is summed over an appropriate distance interval ($r_{\min}$, $r_{\max}$) as following:

$$u_i = \sum_{r=r_{min}}^{r_{max}} (\widehat{H}_i(r) - \overline{H}(r))^2$$

where $\widehat{H}_i(r)$ is an observed (i = 0) or simulated (i = 1 - 199) $\mathrm{ISAR}_f(r)$ function. $\overline{H}(r)$ is the averaged ensemble statistics, excluding the i^{th} function. The rank of the statistic u_0 of the observed ISAR among all u_i is used for GoF test. We used an approximate α level of 0.05, $r_{\min}$= 1 m, $r_{\max}$= 50 m, therefore the ranks of all $u_i \geq 190$ are assessed.

To assess departure from the null model at different scales r, the 5th lowest and 5th highest values of 199 Monte Carlo simulations were used to construct confidence envelopes, then the Goodness-of- Fit test was 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. 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. Diversity indices of tree species in both study plots were calculated following Maguran (2004).

3. RESULTS

3.1. Structural characteristics of tree species

The two study plots were designed in conventional logged forest stand (P1) and reduced impact logging stand (P2). Two study plots shared 47 similar species while they differed in total basal area (48.4 m^2 versus 64.6 m^2) and average dbh (8.6 cm versus 10.3 cm) (Table 1). Diversity indices showed that tree species diversity in P1 was lower than P2 (Table 1). Totally, 3,936 tree individuals were recorded belonging to 61 species in the study plot P1. The most dominant species were *Garuga pierrei*, *Tarrietia javanica*, *Ormosia balansae*, *Bursera tonkinensis* and *Paviesia annamensis* (Table 2). The study plot P2 contained 3,731 individual species belonging 52 species and shared most dominant species such as *Garuga pierrei*, *Tarrietia javanica* and *Ormosia balansae*.

Table 1. Basic description of two sampled plots

Characteristic	P1	P2
Number of individuals	3936	3731
Total basal area (m^2)	48.4	64.6
DBH (cm)	8.6	10.3
Number of species	61	52
Number of species with one individual	13	7
Number of species with ≥ 30 individuals	25	28
Number of shared species	47	47
Number of individuals from shared species	3732	3698
Dominance index	0.05	0.04
Simpson's diversity index	0.94	0.95
Shannon-Wiener diversity index	3.23	3.32
Evenness index	0.40	0.46

Table 2. Characteristics of abundant tree species in both study plots

No	Tree species	P1			P2		
		N	DBH (cm)	IVI (%)	N	DBH (cm)	IVI (%)
1	*Garuga pierrei*	282	10.08 ± 10.89	8.98	232	11.30 ± 13.26	7.72
2	*Tarrietia javanica*	383	5.62 ± 6.39	7.28	330	4.52 ± 3.58	5.14
3	*Ormosia balansae*	138	17.05 ± 12.97	7.26	187	14.75 ± 10.81	6.60
4	*Bursera tonkinensis*	384	6.15 ± 4.16	6.72	253	6.67 ± 4.12	4.41
5	*Paviesia annamensis*	240	9.18 ± 7.64	6.02	239	6.94 ± 4.86	4.32
6	*Litsea glutinosa*	229	8.06 ± 6.21	4.96	264	8.26 ± 6.70	5.49
7	*Castanopsis indica*	168	10.21 ± 8.27	4.65	-	-	
8	*Polyalthia nemoralis*	303	5.02 ± 1.77	4.58	244	5.53 ± 1.88	3.78
9	*Syzygium wightianum*	179	9.36 ± 7.04	4.40	81	11.56 ± 8.17	1.54
10	*Erythrophfloeum fordii*	63	18.52 ± 15.35	3.96	36	19.33 ± 21.97	2.47
11	*Mallotus paniculatus*	265	4.01 ± 0.98	3.76	114	3.71 ± 0.73	1.63
12	*Amoora gigantea*	148	7.99 ± 6.73	3.28	96	8.89 ± 6.93	2.08
13	*Cinnamomun bejolghota*	100	10.71 ± 9.25	3.00	267	13.01 ± 10.59	8.51
14	*Vatica odorata*	48	17.67 ± 15.90	2.94	48	23.46 ± 16.73	3.24
15	*Gironniera subaequalis*	92	9.71 ± 6.65	2.27	137	11.19 ± 9.28	3.73
16	*Endosperrmun sinensis*	54	11.77 ± 13.18	2.14	83	21.67 ± 13.33	4.63
17	*Sindora cochinchinensis*	41	16.52 ± 13.44	2.12	33	15.77 ± 14.19	2.77
18	*Garcinia oblongifolia*	121	6.23 ± 4.08	2.11	67	6.22 ± 3.48	1.11
19	*Canarium album*	46	15.01 ± 8.88	1.79	155	11.03 ± 6.04	3.68
20	*Koilodepas hainanense*	104	5.83 ± 2.61	1.68	80	8.41 ± 4.52	1.54
21	*Cassine glauca*	74	8.41 ± 5.51	1.59	89	8.69 ± 7.66	1.97
22	*Vitex trifolia*	33	14.83 ± 9.63	1.30	-	-	
23	*Litsea vang*	71	6.54 ± 3.30	1.27	76	8.72 ± 4.67	1.50
24	*Symplocos laurina*	55	9.31 ± 5.61	1.25	145	11.81 ± 6.86	3.71
25	*Alangium ridleyi*	40	7.89 ± 5.19	0.81	49	9.10 ± 6.27	1.04
26	*Engelhardtia roxburghiana*	-	-		63	28.78 ± 11.91	4.84
27	*Antheroporum pierrei*	-	-		47	19.81 ± 7.39	2.00
28	*Knema pierrei*	-	-		46	10.05 ± 4.86	0.99
29	*Polyalthia cerasoides*	-	-		33	25.59 ± 20.80	1.40
30	*Madhuca pasquieri*	-	-		32	14.69 ± 9.76	1.07

N - number of individuals; IVI - Important Value Index, (relative abundance + relative basal area)/2, expressed as percentage proportion; DBH - Diameter at Breast Height (mean ± Standard deviation).

3.2. Analysis of ISAR

Twenty-five (P1) and twenty-eight (P2) tree species, respectively, were taken into ISAR analysis containing their abundances of more than 30 individuals (Table 2). The selected species shared 23 similar species in two study plots. After initial tests, the two null models of Complete Spatial Randomness (CSR) and Heterogeneous Poisson (HP) were used to analyze data in P1 and P2, respectively.

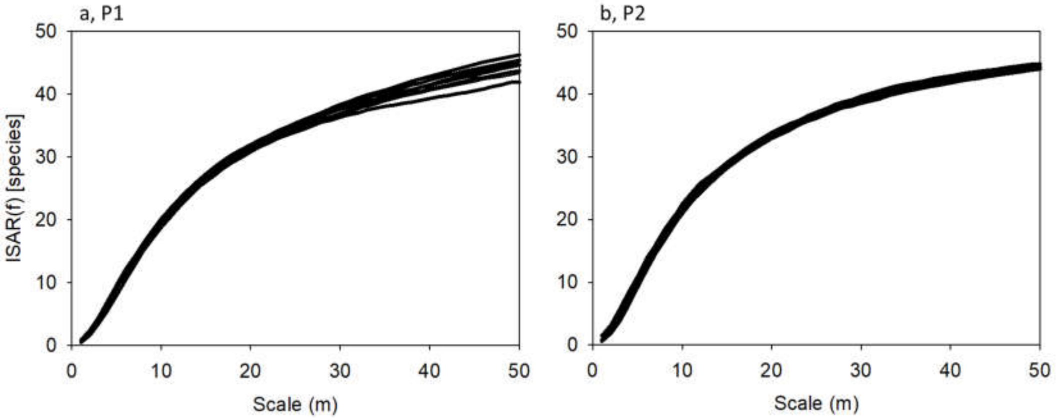

Figure 1. The ISAR function analyses for abundant species with $p \leq 0.05$ under null models of CSR in P1 (a) and HP in P2 (b)

The GoF tests with α level of 0.05 were conducted for all analyzed dominant tree species to assess the overall fit of the empirical ISAR curves with the two null models over scales $r = 1 - 50$ m. The ISAR results showed that all species had around 40 to 45 interspecific neighborhoods up to scales 50 m. A similar trend of the focal species was found that the number of inter-specific neighborhoods linearly increased with increasing of spatial scales and was more or less diverse than expected by chance (Figure 1). Because of the difference between the observed ISAR function and the simulation envelopes of the heterogeneous Poisson null model were small, therefore we shown the difference between the observed ISAR function and the expected ISAR function under the null model (Figure 2 and 3).

Ten of 25 species in P1 (Figure 2) and eleven of 28 species in P2 (Figure 3) were significant with $p < 0.05$. In P1, species abundance did not show a trend of significant departure from the null model, particularly, except high abundant species (*B. tonkinensis, T. javanica* and *M. paniculatus*), three low abundant species with 24 to 69 trees/ha (*O. balansae*, *G. oblongifolia* and *V. odorata*) were also significant from the GoF test. Similarly in P2, low abundant tree species such as *C. glauca*, *E. roxburghiana*, *P. thorelii* and *M. pasquieri* with abundance of 16 to 45 individuals/ha also showed significant departure from the null model.

Results from Figure 2 showed that five species (*B. tonkinensis, T. javanica*, *P. annamensis*, *A. gigantea* and *O. balansae*) were identified as accumulators of diversity and five others (*M. paniculatus, L. glutinosa* , *S. wightianum*, *G. oblongifolia* and *V. odorata)* were regarded as diversity repellers at different spatial scales. Some species were diversity accumulators at small scales but diversity repellers at larger scales such as *B. tonkinensis*, *T. javanica*, *G. oblongifolia* and *V. odorata.*

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.

In P2, all eleven tree species were regarded as diversity accumulators that have more number of interspecific species in their neighborhoods than expected at their significant scales under the null model of HP.

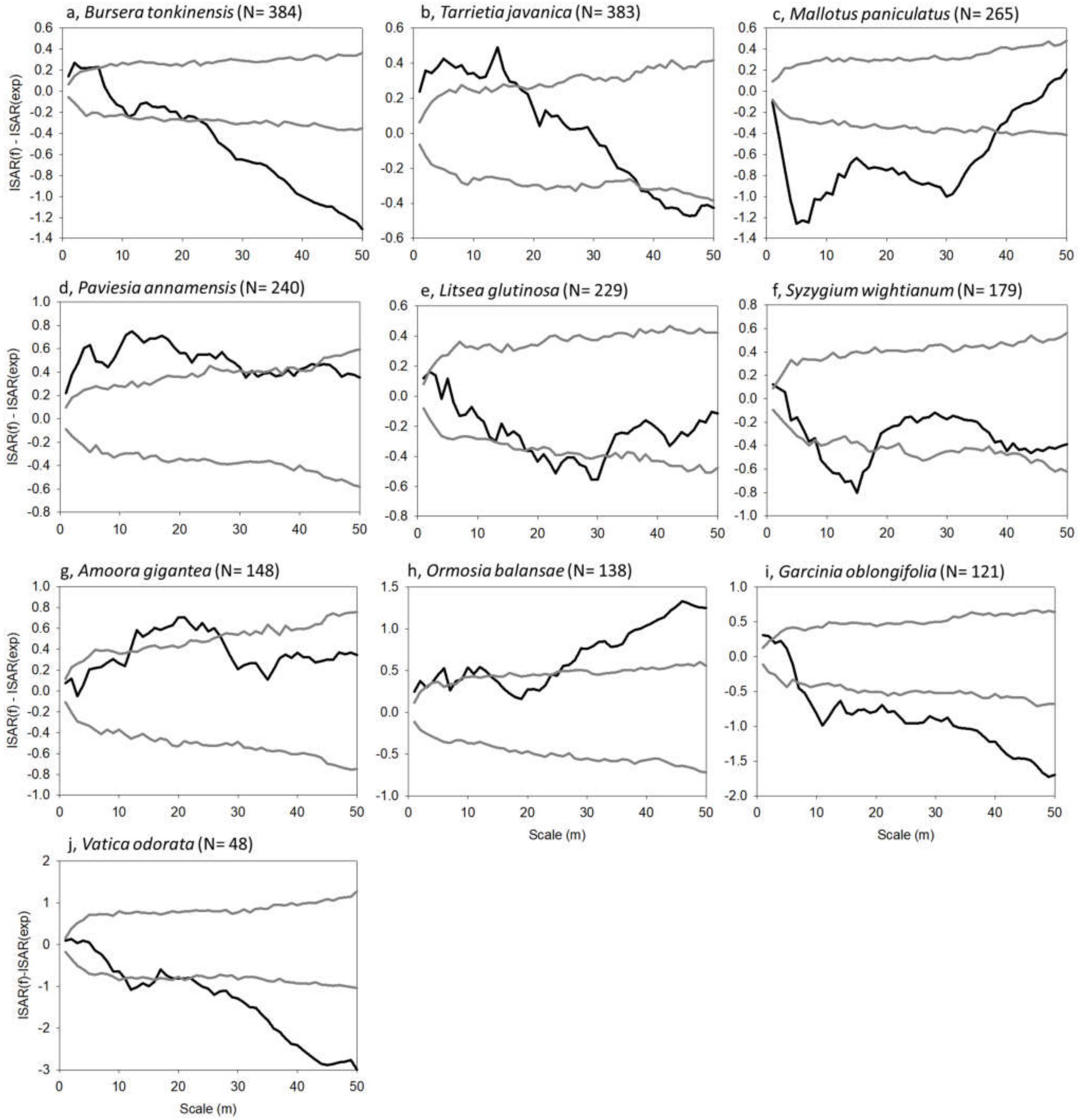

Figure 2. Results of ISAR analyses for ten dominant species in P1 with $p < 0.05$

(Black lines show $ISAR_f(r)$-$ISAR_{exp}(r)$, 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)

The ISAR results also showed considerable variation of tree sizes and abundance among focal species. For example, diversity accumulators were large trees with *O. balansae, C. bejolghota, P. cerasoides* and *E. roxburghiana*; medium tree with *G. pierrei*, *C. glauca* and *A. gigantea*; and small trees were *T. javanica* and *P. annamensis*. In addition, diversity repellers were small trees (e.g., *G. oblongifolia*, *B. tonkinensis*), medium trees (e.g., *S. wightianum*) and large trees (e.g., *V. odorata*) (Table 2). Abundance of focal species also varied from low to high (16 to 190 individuals/ha). Consequently, tree size and abundance showed no clear effect on species richness of neighborhoods.

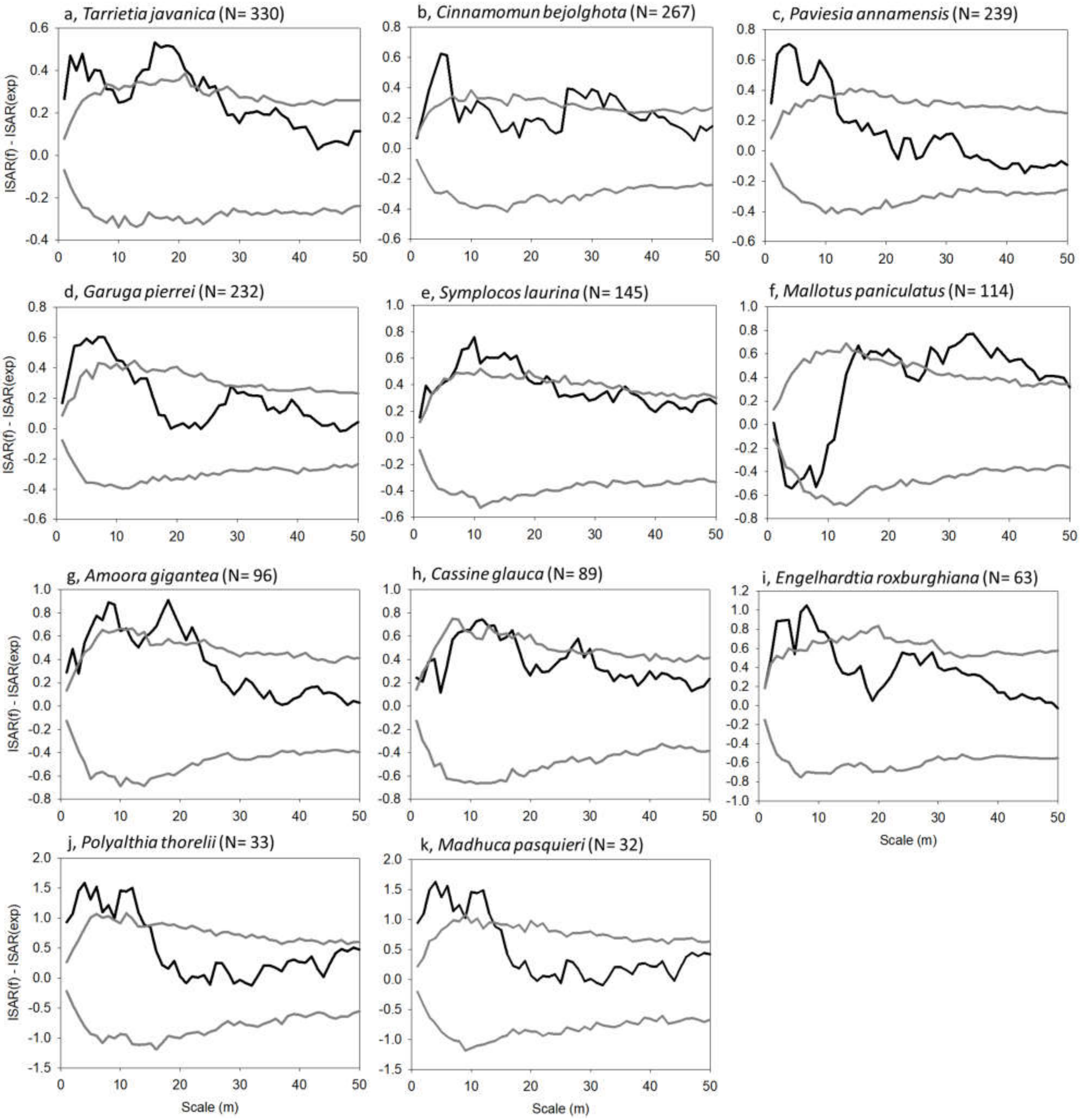

Figure 3. Results of ISAR analyses for eleven abundant species with $p < 0.05$

(Black lines show $ISAR_f(r)$-$ISAR_{exp}(r)$, the observed ISAR function minus the expectation of the heterogeneous Poisson null model; Grey lines show the simulation envelopes minus the expectation of the null model; N- number of tree individuals)

4. DISCUSSION

Recently, uni- and bivariate analyses of spatial point pattern technique are commonly used in ecology to investigate spatial patterns of plants and to make inference on ecological processes structuring plant communities (Wiegand and Moloney, 2004; Law et al., 2009). However, those spatial statistics do not effectively summarize diversity patterns at the community level (Illian and Burslem, 2007; Wiegand et al., 2007). Current technique of spatial statistics, ISAR, allows to assess spatial patterns of species specific associations with neighborhood diversity and species dynamics in diverse communities such as rich-species communities by expanding Ripley's K functions. In this study, we applied ISAR in spatial distribution analyses of tree species in tropical rain forests in order to better understand species specific associations with diversity patterns. Spatial distribution of plants strongly depends on their dispersion and habitat condition (Wiegand et al., 2007a; Tsai et al., 2015). The ISAR does not work on the population level but on the community level and the shape of its curves depends on local stem density and the dispersion of target species.

Effect of logging regimes leads to low number of accumulators and high number of repellers in P1 than P2. That can be explained by lower number of interspecific and higher number of intraspecific neighbors surrounding focal tree species under conventional logging than reduced impact logging stands. Conventional logging could facilitate regeneration of offsprings surrounding logged mother trees.

High local density of species leads to reduce the ISAR because of fewer hetero-specific neighborhoods (Wiegand et al., 2007a). The accumulators in rare species were also detected by Wiegand et al. (2007a), and were assumed that rare species were intermingled in a large area of high diversity species (Fibich et al., 2016). Wills et al. (1997) hypothesized the accumulation role of rare species as the ‘safety in diversity’, thus the presence of rare species in high diverse clumps should be advantageous for biodiversity maintenance against natural enemies (e.g. pathogens or herbivores).

Wiegand et al. (2007a) assumed that a species which managed to be local dominant for stems a competitive species due to strongly localized dispersal and high seed output would contribute to the local success. If a species with a highly aggregated distribution, it will be surrounded by more conspecific individuals and fewer hetero-specific individuals than expected on average (Wiegand et al., 2007a). Aggregated patterns are very common in tree species distributions in tropical forests, especially in species-rich tropical rain forests containing many rare and a few common species (He et al., 1997; Condit et al., 2000; Li et al., 2009). The presence of diversity accumulating species suggested that negative density dependence within species would stronger than between species (Comita and Hubbell, 2009). This process is consider as a fundamental driver to the maintenance of biodiversity in tropical forests (Wright, 2002).

A challenge is to clarify effects of plant-plant interactions and habitat association. Here, we applied the scale separation approach by using the null models of CSR for P1 and HP with bandwidth $R = 50$ m for P2 and observed significant patterns up to a distance of 50 m. The results pointed out that some species were significant from the null models up to large scales of 40 to 50 m while most species specific effect on local diversity appeared at scales < 30 m. Note that the effects of habitat heterogeneity were removed at scales > 50 m by using the heterogeneous Poisson null model. Diversity accumulators in this study are compatible to positive association of species at scales smaller than 15 m which has been found in high tree species diversity forests (Nguyen et al., 2016). The positive associations between tree species would exhibited potential effects of species herd protection (Nguyen 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, even conspecific density remains constant (Peters, 2003; Comita et al., 2007). In general, these findings supported for the presence of scale separation in the spatial structure of the studied forest. The spatial segregation hypothesis of Pacala and Levin (1997) emphasized the role of intraspecific competition which supports species coexistence and therefore maintaining species diversity during the course of succession (Murrell et al., 2001).

5. CONCLUSION

In this study, we used an individual species based approach to study spatial patterns of species diversity in two diverse forest communities. We found that it is challenged in spatial ecology to find balanced interspecific patterns of species diversity. We also anticipated that applying ISAR analysis will be increasing in order to describe complex, rich-species communities and to link spatial patterns to ecological processes structuring forest community.

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QUAN HỆ ĐA DẠNG LOÀI THEO DIỆN TÍCH CỦA CÂY RỪNG NHIỆT ĐỚI SAU KHAI THÁC CHỌN Ở LÂM TRƯỜNG TRƯỜNG SƠN, TỈNH QUẢNG BÌNH

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TÓM TẮT

Việc giải thích tính đa dạng loài cao của rừng mưa nhiệt đới là một thách thức cho các nhà sinh thái học kéo dài trong nhiều thập kỷ. Chúng tôi áp dụng một kỹ thuật phân tích của thống kê không gian là quan hệ đa dạng loài theo diện tích - Individual species area relationship (ISAR) để nghiên cứu cấu trúc đa dạng của rừng lá rộng thường xanh dựa vào từng cá thể loài. ISAR là sự kết hợp của quan hệ đa dạng loài theo diện tích và hàm thống kê Ripley's K để ước lượng chỉ số đa dạng α cho từng loài cụ thể trong cửa sổ di động hình tròn có bán kính thay đổi tính từ vị trí các cá thể của một loài cây được nghiên cứu. Dữ liệu được thu thập từ 02 ô tiêu chuẩn 2 ha của rừng lá rộng thường xanh ở tỉnh Quảng Bình. Tất cả các loài cây có ít nhất 30 cá thể/loài đều được phân tích. Kết quả cho thấy có 21 trong 53 loài cây đã đạt mức ý nghĩa thống kê 0,05 trong cả 2 ô tiêu chuẩn. Trong đó, 5 loài tích lũy đa dạng (diversity accummulators) và 5 loài giảm trừ đa dạng (diversity repellers) được nhận dạng ở ô tiêu chuẩn P1; 11 loài được cho là tích lũy đa dạng ở ô tiêu chuẩn P2 tại các phạm vi không gian khác nhau. Đa dạng không gian của loài cây xuất hiện chủ yếu ở các phạm vi dưới 30 m, trong khi tính đa dạng không gian của một số loài xuất hiện ở các phạm vi lớn hơn. Tính đa dạng không gian được cho là không bị ảnh hưởng bởi đường kính và độ phong phú của loài cây. Ảnh hưởng của cách thức khai thác chọn đến đa dạng loài được thể hiện bởi số lượng ít các loài tích lũy đa dạng và nhiều loài giảm trừ đa dạng bởi khai thác thường (P1) so với khai thác tác động thấp (P2). Bên cạnh ảnh hưởng của cách thức khai thác, các quá trình sinh thái như phát tán hạn chế, bảo vệ nhóm loài và chia tách không gian được cho là những nguyên nhân chính đã điều chỉnh mô hình đa dạng không gian của lâm phần được nghiên cứu.

Từ khóa: Đa dạng không gian, mô hình không gian, quan hệ đa dạng loài theo diện tích, rừng mưa nhiệt đới.

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