

## SPATIAL ASSOCIATION AND DIVERSITY PATTERNS OF DOMINANT TREE SPECIES IN THE BROADLEAVED EVERGREEN FOREST, SOUTHERN VIETNAM

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**Abstract.** The present study aimed to clarify underlying processes driving the coexistence of woody species in the evergreen broadleaved forest of Southern Vietnam. In 2022, we established two 2-ha study plots in Dong Nai Culture and Nature Reserve, Dong Nai province, Vietnam, and fully mapped all trees with a diameter at breast height (dbh)  $\geq 2.5$  cm, their species name and dbh were recorded. Spatial analyses and models of individual species-area relationships were used to measure species interactions, scale dependence, and species diversity at different scales. Our findings showed that dominant species exhibited mainly aggregated spatial patterns at small scales of  $r < 30$  m and independent association patterns accounted for a high proportion at scales of 1-50 m (89.9%-94%). Intra- and interspecific interactions were mainly observed at small scales of  $r < 30$  m. The spatial patterns of species diversity were influenced by asymmetric interactions of tree individuals at different life-history stages. Dispersal limitation and interspecific interactions controlled the spatial distribution, association patterns, and diversity of species. Our study suggests that the unified neutral theory and asymmetric competition theory are appropriate explanations for tree species diversity in the evergreen broadleaved forest.

**Keywords:** *aggregation, individual species-area relationships, interspecific associations, spatial analysis, spatial patterns, species coexistence, tropical rainforest*

### Introduction

Forest management that follows a natural approach has become an inevitable trend in modern forest management (Christensen and Emborg, 1996). At the same time, the goals of traditional forest management have primarily focused on timber production, while modern forest management aims to achieve a more diverse range of goals, such as maintaining and enhancing native biodiversity (Mitchell et al., 2002; Nuske et al., 2009), improving the stability of forest structure (Emborg et al., 2000), and providing ecological value (Nielsen et al., 2007). The success of modern forest management in achieving these goals depends on an understanding of forest ecosystems of forestry policy-makers (Quy et al., 2021a).

Low-impact natural forests with human activities are the ideal model to imitate in the restoration or reforestation of areas where the forest has been destroyed; however, without understanding the laws of the natural world, humans can go astray when trying to create models by themselves (Burslem et al., 2005). Studying the spatial pattern, association, and diverse structure of forest tree species can enhance the understanding of forest ecosystems (Lan et al., 2012; Guo et al., 2014; Rockwell et al., 2017; Cysneiros et

al., 2018). Spatial patterns and associations of species are related to the development stages of forest (Silva et al., 2014; Gu et al., 2019), seed dispersal of plants, the interaction between species, and changes in environmental conditions (Couteron and Kokou, 1997; Larson et al., 2016). For example, the heterogeneous spatial pattern of forest trees can indicate heterogeneous environmental conditions (Getzin et al., 2008), and the clumped distribution pattern of the forest tree (aggregation) at a small scale is evidence of limited dispersal (Piao et al., 2013; Wu et al., 2018), and the regular distribution pattern of the adult trees indicate natural self-thinning and competition among them (Cheng et al., 2014; Quy et al., 2021b). Previous studies suggested that the spatial distribution of species and species composition have a close relationship, in which species composition and density control the spatial distribution pattern of forest tree species (Quy et al., 2021a). Consequently, combining spatial distribution research with plant diversity research is considered one of the better research ideas than independent studies (Chesson, 2000; Yousef and Krzysztof, 2017). This direction of research can provide a direct and comprehensive understanding of the ecological processes that occurred at both the population and plant community levels (Wiegand et al., 2007a), supporting biodiversity conservation and serving as a practical reference for forest dynamics (Powell, 1990), helping to understand better the underlying processes that maintain and drive the coexistence of species in communities (Chesson et al., 2004; Sproull et al., 2015; Rico-Gray, 2018).

The ISAR (individual species-area relationship) model is used to study plant diversity in the spatial pattern of forest trees. It is a combination of the SAR (species-area relationship) method and the SPPA (spatial point pattern analysis) method (Yan et al., 2015) and utilizes Ripley's K, a spatial statistical function, to estimate the expected alpha diversity index for a focal species in a circular moving window with the center of the circle being one individual of the focal species (Yao et al., 2014). The ISAR model presents a novel approach to exploring the laws and mechanisms of species coexistence in forest plant communities. It considers not only the spatial distribution of species but also the number of species and the influence of each species on neighborhood species richness at various scales (Yang et al., 2013). The influence of a focal species on neighborhood species diversity can be classified as promoting (diversity accumulator), inhibiting (diversity repellent), or neutral (not affecting other species) for neighboring species abundance (Wiegand et al., 2007a). Diversity-promoting species increase the abundance of neighboring trees, while diversity-inhibiting species decrease the abundance of neighboring trees. Neutral species do not affect the species diversity around them (Gong et al., 2011; Wei et al., 2014). In the forest stand, the target species significantly affects spatial distribution, growth, and development of neighboring species (Burslem et al., 2005). According to the law of interactions of species, the effect of one species on neighboring species determines the number of species living around it. If the effect is positive, many species will coexist around it; if the effect is negative, the number of neighboring species will be less (Lieberman and Lieberman, 2007; Fan et al., 2014). Therefore, determining whether the influence of one species is negative or positive on the diversity of neighboring species in the forest stand is essential in modern forest management and business. This knowledge can be a basis for adjusting species density to maintain biodiversity (Ma et al., 2014).

The ISAR model, proposed by Wiegand et al. (2007a), has been widely used in studies related to plant diversity. Over the past decade, the ISAR model has helped to understand the spatial structure of species-rich communities and uncover the underlying

ecological processes in forest plant communities (Rayburn and Wiegand, 2012; Zhang et al., 2014). Despite this, the study of spatial distribution patterns of forest tree species in general, and the application of the ISAR model in plant diversity research, in particular, have not been of interest in Vietnam or many other tropical countries in Southeast Asia (Quy et al., 2021a; Ben-Said, 2021).

Previous studies have verified that competition between plant species shapes the structure of the community at diverse scales (Fischer and Miles, 1973; Craine and Dybzinski, 2013). A remarkable characteristic of natural forests is that they exhibit high levels of diversity, especially in tropical forests, where various species coexist within a limited space (Leigh et al., 2004) — explaining competition, particularly the asymmetry competition between individuals in the same habitat, challenges ecologists (Getzin et al., 2006). Passarge and Huisman (2002) classified plant competition into two categories: competition for resources such as nutrients and water and competition for space, including light competition. Plant species compete fiercely for resources in resource-limited such as high mountains and deserts (Gioria and Osborne, 2014; Zhang et al., 2018). In tropical forests, competition for resources between species is undeniable. However, several studies have demonstrated that spatial competition is typically more prevalent than resource competition (Schwinning and Weiner, 1998; Freckleton and Watkinson, 2001; Jia et al., 2016). As such, in this study, we focus predominantly on clarifying spatial competition between tree species in evergreen broadleaved forests.

The research subjects of this study are woody tree species in the evergreen broadleaf forest type in Dong Nai Culture and Nature Reserve, Dong Nai province, Southern Vietnam. The univariate and bivariate pair correlation functions were used in spatial analysis, and the ISAR models of the target species (species with 30 or more individual trees in each study plot) were built to learn about spatial distribution, association patterns, and their influence on the diversity of neighboring species. The study aims to answer four (4) research questions: (i) What are the spatial distribution characteristics and association patterns of target species? (ii) Are spatial patterns and associations of species affected by spatial scale? (iii) How does the individual size of the target species affect the diversity of neighboring species in the community? (iv) What ecological process maintains tree species diversity in evergreen broadleaved forests?

## Materials and methods

### Study area

The study was carried out over six months, from 1st May 2022 to 24th October 2022, with eight field surveys conducted in the Dong Nai Culture and Nature Reserve located in Dong Nai province in southern Vietnam. The reserve covers a total natural area of 100,571 ha, of which the forest and forestry land area is 68,051 ha, and the wetland area is 32,520 ha. The geographical coordinates of this reserve are 11°08'55"-11°51'30" North latitude and 106°90'73"-107°23'74" East longitude (*Fig. 1*). The climate in Dong Nai province is characterized by two distinct seasons - the rainy season from May to October and the dry season from November to April of the following year. The average temperature in the area is 26.4°C, and the relative air humidity is 81%, while the average annual rainfall ranges from 2,000-2,800 mm (Tuan, 2017; Tuan and Bao, 2020).

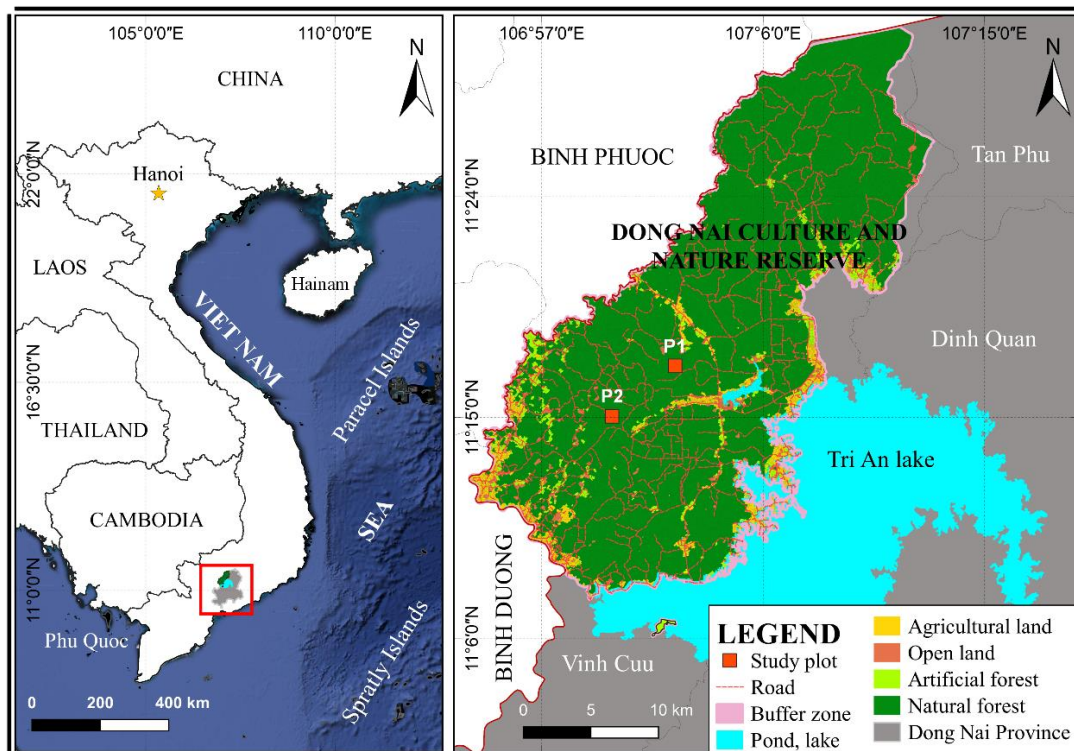
The topography of the study area is characterized by lowland hills, with an average height of 110 m above sea level and slopes ranging from 5°-25°. The plant community in the area is a tropical moist evergreen broad-leaved forest, which includes typical species such as *Shorea guiso*, *Nephelium cuspidatum*, *Syzygium zeylanicum*, *Diospyros venosa*, and *Vatica odorata* (Hung and Potokin, 2019).

### Data collection

In spatial point pattern analysis, disentangling the effects of human activities, environmental filtering, and dispersal limitation on the spatial distribution of trees is challenging (Yang et al., 2016). Hence, the present study has established plots in a strictly protected nature reserve subdivision with less human impact. This approach allows us to replicate the structures and processes of natural forests. Many previous studies also selected this approach because they believed that such forest stands are considered ideal models for investigating the spatial structure of trees (Ding et al., 2015; Qiu, 2017).

We established two study plots, each with an area of 2 ha (100 m × 200 m), within the evergreen broadleaved natural forest type of Dong Nai Culture and Nature Reserve. The study plot was divided into 50 subplots, each with an area of 400 m<sup>2</sup> (20 m × 20 m) to facilitate investigation and data collection and avoid missing survey trees. In each subplot, we collected information on all trees with a diameter at breast height (dbh) ≥ 2.5 cm, including the species name and dbh.

The individual trees in each study plot were mapped and then divided into one of three life-history stages based on tree size: juvenile (dbh < 5 cm), subadult (5 cm ≤ dbh < 10 cm), or adult (dbh ≥ 10 cm) (Nguyen et al. 2014; Quy et al. 2021b).



**Figure 1.** Map of the study area. Maps of Vietnam (left) and Dong Nai Culture and Nature Reserve (right)

## Data analysis

### *Uni- and bivariate pair correlation functions*

The homogeneous environmental conditions of study plots were evaluated by analyzing the spatial distribution pattern of adult trees ( $\text{dbh} \geq 10$  cm) using two functions,  $g_{11}(r)$  and  $L_{11}(r)$  (Besag, 1977; Getzin et al., 2008). Trees with  $\text{dbh} \geq 10$  cm were selected as they can survive in all possible areas and have undergone natural selection (Getzin et al., 2008). The distribution heterogeneity of these trees reflects the presence of heterogeneous environmental conditions. We assumed no interaction between points in the patterns. The distribution heterogeneity of these trees reflects the presence of heterogeneous environmental conditions. We assumed no interaction between points in the patterns.

The univariate pair-correlation function,  $g_{11}(r)$ , was used to analyze the spatial pattern of trees. The bivariate pair-correlation function,  $g_{12}(r)$ , was used to examine the interspecies association. The pair correlation function,  $g(r)$ , which is the derivative of Ripley's K function, is given by  $g(r) = K'(r) / (2\pi r)$ . It shows the expected density of points at a distance  $r$  from any point (Ripley, 1976). Based on the tree-tree distances, the function  $g_{11}(r)$  describes the spatial distribution of trees at radius  $r$  using a standardized density. When  $g_{11}(r) = 1$ , it indicates complete spatial randomness (CSR),  $< 1$  indicates regularity, and  $> 1$  indicates aggregation among trees at distance  $r$ .

The spatial association between two types of points, two tree species, was described by the function  $g_{12}(r)$ . The function  $g_{12}(r)$  is the expected density of points of Type 2 at a distance  $r$  from a randomly chosen point of Type 1. Like the function  $g_{11}(r)$ , when  $g_{12}(r) = 1$ , it indicates independence,  $> 1$  indicates attraction, and  $< 1$  indicates repulsion between two tree species at distance  $r$  (Quy et al., 2021b).

Ecological processes such as plant-plant interactions and dispersal limitations affect the spatial patterns of trees (Qiu, 2017). These processes have a more pronounced spatial signal than other processes, such as negative density dependence (Terborgh, 2012; Fibich et al., 2021). Although spatial point model analysis effectively detects ecological processes, spatial patterns can also result from first-order effects, such as habitat heterogeneity (Wiegand et al., 2007b; Mehlreter and Garcia-Franco, 2008; Yang et al., 2016), which can cause higher tree densities in favorable locations due to differences in microhabitats and plant preferences or lower densities in less favorable locations (Murrell, 2009). Recently, the importance of habitat heterogeneity in determining plant spatial patterns has been recognized (Getzin et al., 2008). Several methods have been developed to test for its existence (Bagchi et al., 2011). In this study, we used the null model of CSR (homogenous Poisson process) on adult trees with a  $\text{dbh} \geq 10$  cm in study plots (Wiegand and Moloney, 2004). By comparing the observed spatial pattern of adult trees with a null model, we could evaluate whether the observed pattern was significantly different from that expected by chance (Getzin et al., 2006). We will look for significant positive deviations from the homogenous Poisson process at scales larger than the average interspecies interaction distance to confirm the presence of environmental heterogeneity (Uriarte et al., 2004). At distances beyond 10 m, previous studies have shown that species interactions in humid rainforests are often reduced (Wiegand et al., 2007b). To detect positive deviations, we compared the functions  $g_{11}(r)$  and  $L_{11}(r)$  of adult trees in each plot with the fifth lowest and highest values out of 199 simulations of the homogeneous Poisson process. We assumed that the habitat of the study plots was homogeneous. The inhomogeneous Poisson process

(IPP) null model will be used to analyze spatial patterns of species if significant deviations of the  $g_{11}(r)$  and  $L_{11}(r)$  functions are found at the scale beyond 10 m. This result also means that the habitat on the study plot is inhomogeneous.

Conversely, if the habitat is homogeneous, the null model of CSR will be used to perform further spatial analysis. The null model of independence was used to test for interspecific associations of pair species by immobilizing the position of the Type 1 points (Species 1) and randomly moving the positions of all Type 2 points (Species 2) around Type 1 points. We used the functions  $g_{12}(r)$  and  $g_{21}(r)$  simultaneously to analyze the spatial association of each species pair because they may have asymmetric interactions (Perry et al., 2006; Quy et al., 2021b).

The spatial analysis utilized the Epanechnikov kernel to estimate the intensity function with a bandwidth radius of  $R = 50$  m and a bin (ring width) of 1 m to examine the spatial distribution and association patterns of forest tree species (Quy et al., 2021b). The analysis was conducted using Programita November 2018 software and included 199 Monte Carlo simulations, following the approach of Wiegand and Moloney (2004). To construct approximately 95% confidence intervals, we utilized the 5th lowest and 5th highest values of the 199 simulations. Finally, the tree distribution map was generated using QGIS Version 3.1.6 software (<https://qgis.org/>).

#### *Individual species-area relationship*

The ISAR model was used to estimate the number of species in the circle of radius  $r$ , with each tree of the target species as the center of a circle. The ISAR model can quantify the neighboring tree species richness around the target species based on the species-species interactions. The value of the ISAR model is calculated according to the formula of Wiegand et al. (2007a):

$$\text{ISAR}_i(r) = \sum_{j=1}^N [1 - P_{ij}(0, r)] \quad (i \neq j) \quad (\text{Eq.1})$$

The ISAR model was utilized to estimate the number of species in a circle with a radius of  $r$  around each tree of the target species. This model is based on species-species interactions and can quantify the richness of neighboring tree species around the target species. The ISAR value is calculated using the formula of Wiegand et al. (2007a), where  $i$  represents the target species,  $j$  is the neighboring species,  $N$  is the total number of species, and  $P_{ij}(0, r)$  is the probability of species  $j$  not appearing in the circle of radius  $r$  with the center of the circle being each tree of species  $i$ . If  $\alpha = \pi r^2$ , the function  $\text{ISAR}(\alpha)$  is the classical function of SAR (Wiegand et al., 2007a).

The null model is used in the ISAR model analysis to test the influence of the target species on neighboring species. This model helps determine if the target species promotes or inhibits diversity or if the target species is neutral at neighboring scales (Wiegand et al., 2007a; Yan et al., 2015). The appropriate null model is selected based on the homogeneity of environmental conditions in the study plot. If the plot is heterogeneous, the null model of the IPP is used, and if the plot is homogeneous, the null model of CSR is used. The 95% confidence interval from 199 Monte Carlo simulations tests the significant difference between the target species and the composition of neighboring species. Suppose the  $\text{ISAR}(r)$  value of target species is greater than the simulated value in the 95% confidence interval. In that case, the

neighboring species of the target species has a high diversity within the  $r$  radius at significance level  $\alpha = 0.05$ , and the target species is considered a diversity accumulator. Suppose the ISAR( $r$ ) value is smaller than the simulated value. In that case, the diversity of the neighboring species of the target species is low, and the target species is considered a diversity repeller. Conversely, if the ISAR( $r$ ) value is within the 95% confidence interval of the simulation model, the target species is considered a neutral species (Wiegand et al., 2007a; Yang et al., 2013). The Goodness-of-Fit test of the simulation model is also used to remove the spatial statistical error (Type I) and the minimal deviation of the ISAR( $r$ ) estimate from the results analysis of the study model (Loosmore and Ford, 2006).

The ISAR model analysis involved varying the radius of a circular moving window from 1-50 m around the location of individual trees of a target species. Programita version November 2018 software was used to perform the ISAR model analysis and the GoF test. The 5th lowest and highest values of the 199 Monte Carlo simulations were used to build the confidence interval, resulting in a confidence interval of approximately 95% (Wiegand and Moloney, 2004).

To examine the influence of the individual size of the target species on neighboring species diversity in the plant community, we constructed ISAR models based on the size and number of individual trees of the target species. The different types of ISAR models used are shown in *Table 1*.

**Table 1.** ISAR model types are built to study the structure of species diversity

ISAR model type	Classification criteria	
	Target species	Neighboring species
Overall model	All individual trees	All individual trees
Type 1	All juvenile trees	All individual trees
Type 2	All subadult trees	All individual trees
Type 3	All adult trees	All individual trees

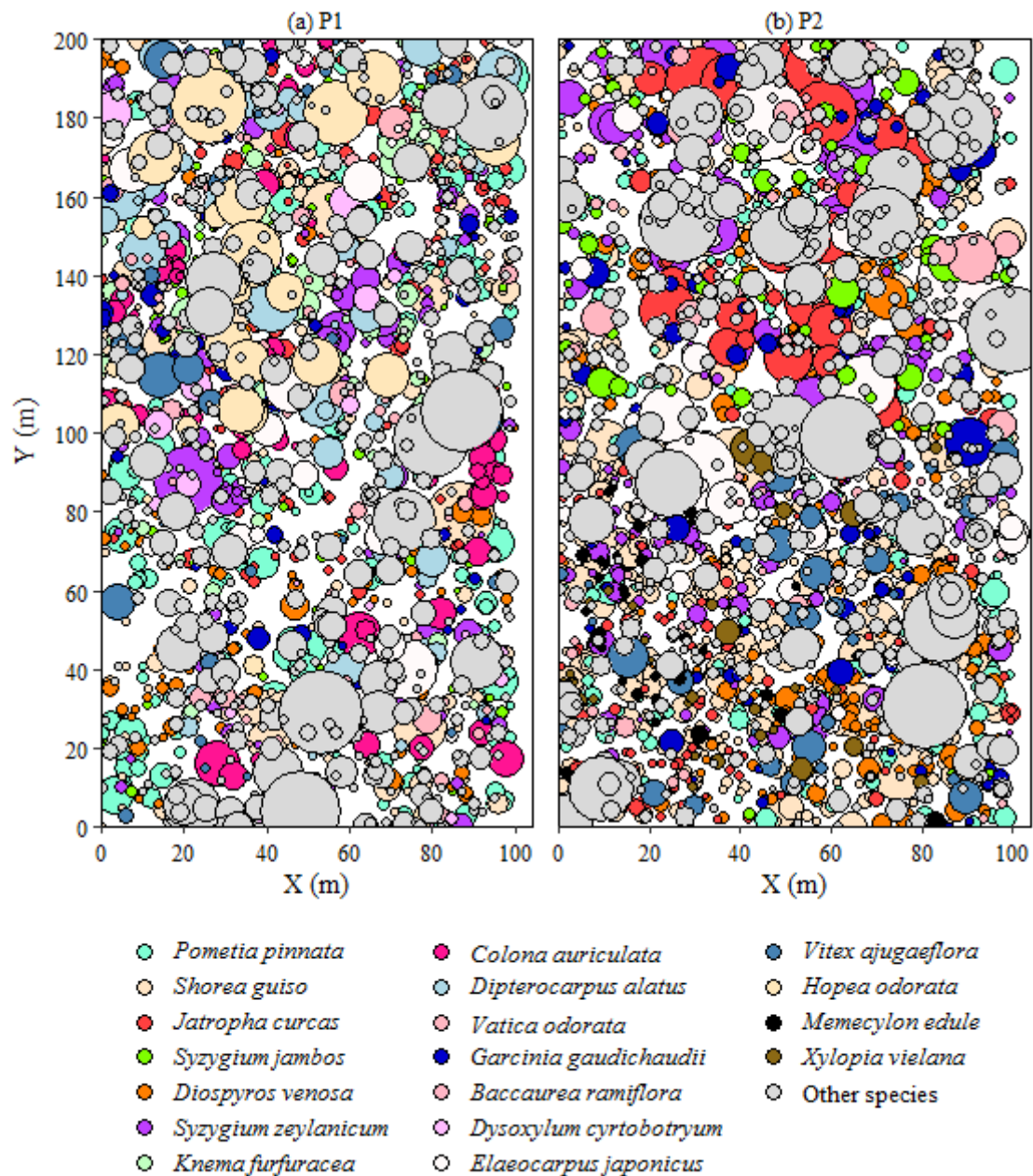
## Results

We recorded eighty tree species in Plot 1 (P1) and seventy-seven in Plot 2 (P2). Of these, fifty-one were common to both plots. Despite having fewer tree individuals and a lower basal area, P1 had higher species diversity than P2. We determined the dominant species in each plot based on their total importance value index, with sixteen species and 77.2% of tree individuals in P1 and twelve species and 79.3% of individuals in P2 being dominant. *Figure 2* shows the distribution map of all individuals in the two study plots, while *Table A1* in the Appendix provides information on the characteristics of the dominant species.

### *Homogeneity of habitat in the study plots*

To test the homogeneity of habitat in the study plots, we conducted a spatial pattern analysis of all adult trees using the null model of CSR. Our results showed that the spatial pattern of adult trees in P1 tended to shift from regularity to randomness at distances above 7 m (*Fig. 3a*), whereas, in P2, the spatial pattern tended to change from randomness to aggregation at distances above 8 m (*Fig. 3b*). The results for the function  $g_{11}(r)$  were consistent with those of the function  $L_{11}(r)$ , indicating that the adult trees in

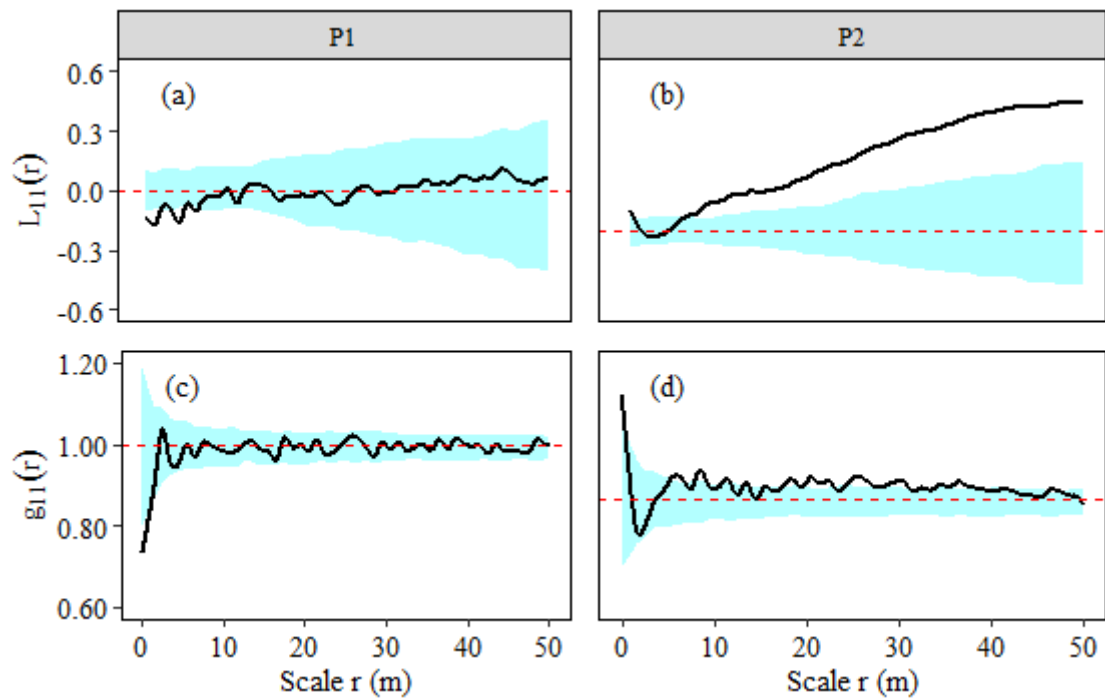
P1 were mainly randomly distributed across scales of 3-50 m (Fig. 3c), whereas in P2, they were mostly aggregated at scales of 7-35 m (Fig. 3d).



**Figure 2.** Distribution maps of trees in the two study plots. The size of the circle is related to the dbh of the tree

Comparing the two functions  $g_{11}(r)$  and  $L_{11}(r)$ , we concluded that the adult trees in P1 were relatively homogeneously distributed, while those in P2 were inhomogeneously distributed. This result suggests that the environmental conditions in P1 were relatively homogeneous, whereas those in P2 were heterogeneous. Therefore, we selected the null model of CSR for P1 and the null model of IPP for P2 to perform the spatial distribution analysis of the target species.



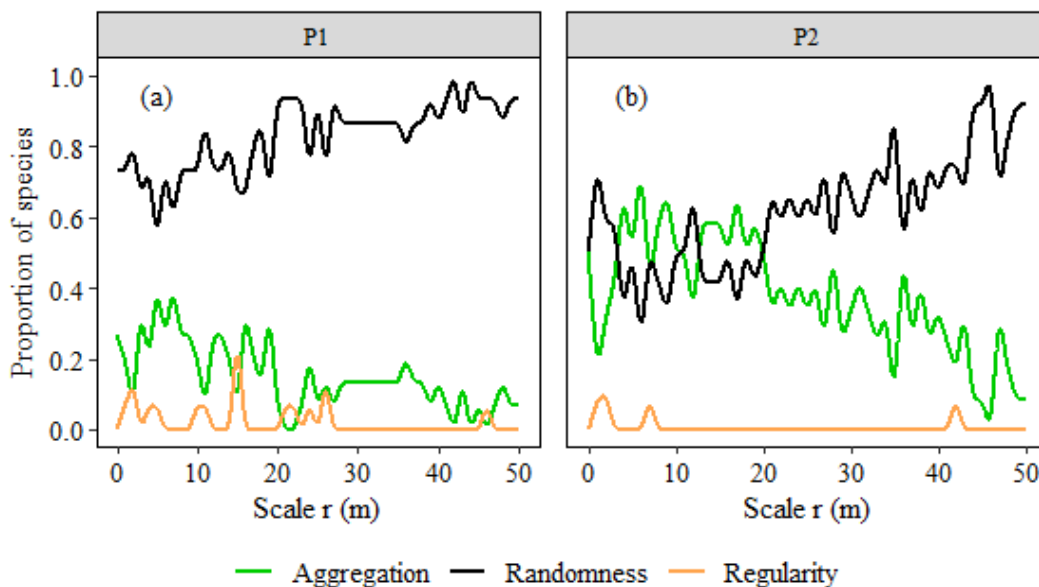


**Figure 3.** Spatial patterns of all adult trees in the study plots were analyzed by the function  $g_{11}(r)$  and  $L_{11}(r)$  function under the null model of CSR. The dark line is an observed pattern, and lying beyond the cyan area (confidence envelope region) indicates a significant departure from the null model of CSR. The cyan envelope region is the  $p = 0.05$  confidence intervals from 199 Monte Carlo simulations (values  $< 1$  indicate regularity; values  $> 1$  indicate aggregation; values  $= 1$  indicate randomness). The red dashed line is the expectation for spatial randomness between trees

### Spatial pattern of tree species

The spatial patterns of the sixteen target species in P1 were analyzed using the function  $g_{11}(r)$  at spatial scales ranging from 1-50 m (Fig. A1). The results showed that 83.7% of the species had a random distribution pattern at all scales ranging from 1-50 m (Fig. 4a). At scales smaller than 30 m, the proportion of species with an aggregated pattern was higher than at larger scales  $> 30$  m, and as the scale increased, the intensity of aggregation tended to decrease. Similarly, regularity was more common at scales smaller than 30 m, accounting for 3.6% of the spatial patterns, and disappeared at larger scales of 30 m. Of the sixteen target species, two species (*Shorea guiso* and *Jatropha curcas*) were found to be aggregated at all distances ranging from 1-50 m, while eleven species were aggregated at small scales  $r < 30$  m. Five species were randomly distributed at scales ranging from 1-50 m.

Analyzing the spatial patterns of twelve target species in P2 revealed a clear difference between scales smaller than 30 m and those larger than 30 m (Fig. A2). At scales smaller than 30 m, approximately 50% of the species showed aggregation or randomness. In contrast, at larger scales, the spatial patterns were primarily random, accounting for roughly 70% of the species (Fig. 4b). As with P1, the intensity of aggregation and regularity of the species tended to decrease as the scale increased in P2. These two spatial distribution patterns (aggregation and regularity) mainly appeared at scales smaller than 30 m.



**Figure 4.** The spatial distribution patterns of species analyzed by the function  $g_{11}(r)$  under the null model of CSR (P1) and the null model of the IPP (P2)

### ***Spatial associations of species***

The study analyzed 210 spatial association patterns of sixteen target species in P1 and 132 spatial association patterns of twelve target species in P2 using the functions  $g_{12}(r)$  and  $g_{21}(r)$  under the null independence model. Results showed that the number of independence accounted for a high proportion (approximately 93%) at scales of 0-50 m in both study plots, while the number of attractions and repulsions accounted for a low proportion (4.5 and 2.5%, respectively). The independent spatial association tended to increase as the spatial scale increased, whereas the positive and negative associations tended to decrease, disappearing at scales above 30 m (Fig. 5).

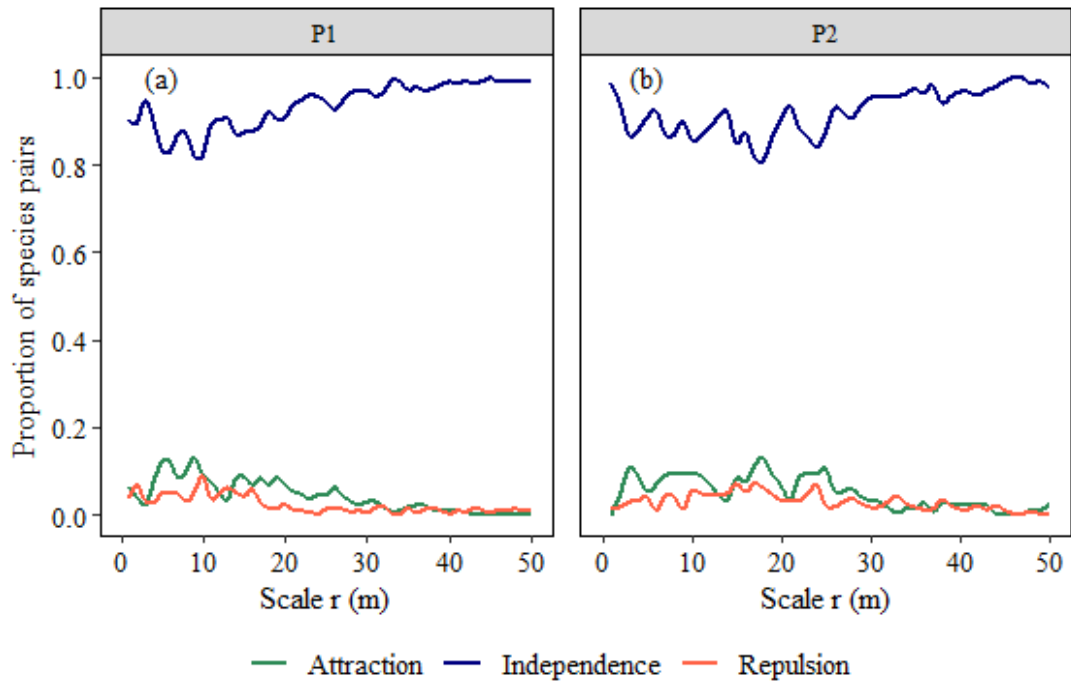
### ***Individual species-area relationship***

The overall ISAR model of the sixteen target species in P1 is presented in Figure 6a and c, with the ISAR models of five target species showing significant differences compared to the null model of CSR. The number of neighboring species of the five target species was 40-55 at scales above 30 m, with the accumulators and repellers mainly appearing at small scales of 1-30 m. Among these five species, neutrals predominated at all scales of 1-50 m (94%).

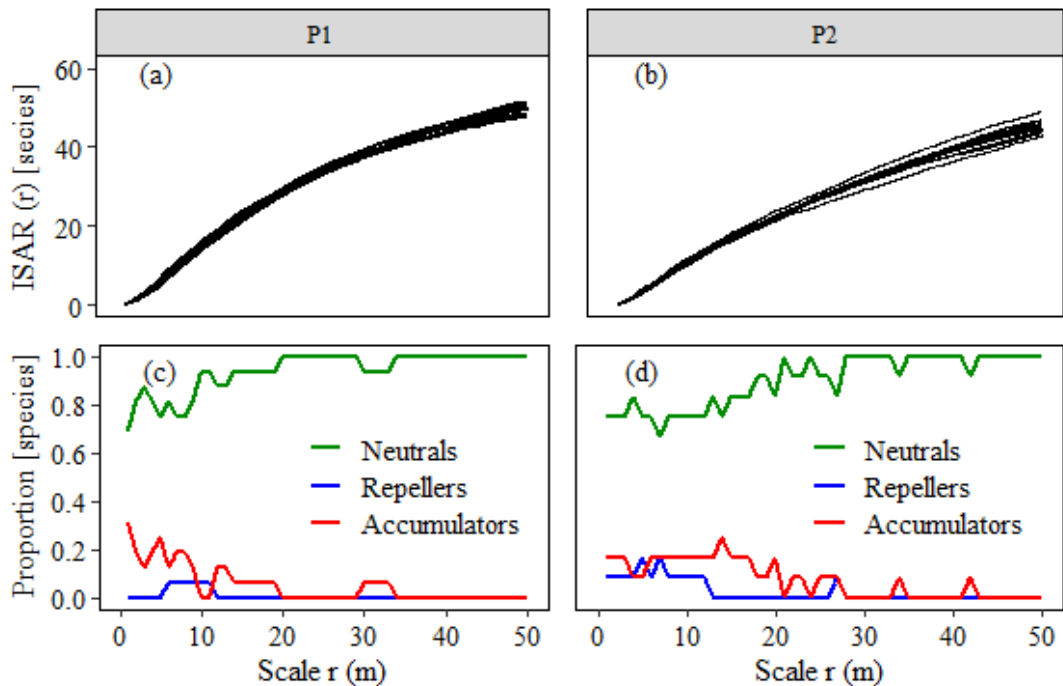
Similarly, among the twelve species in P2 analyzed by the null model of the IPP (Fig. 6b, d), the ISAR models of five species were significantly different, with approximately 45 other neighboring species at scales up to 50 m. The accumulators and repellers appeared mainly at spatial scales below 30 m, while the number of neutral species accounted for a high proportion (89.9%) at all study scales of 1-50 m.

Regarding the life-history stages, the study found that the number of accumulators at the juvenile stage was greater than that of the subadult and adult stages (Fig. 7). This result indicated that juvenile trees promote the diversity of neighboring species more than subadult and adult trees, with diversity accumulator species becoming diversity repeller or neutral species as tree size increases. The three types of ISAR models of

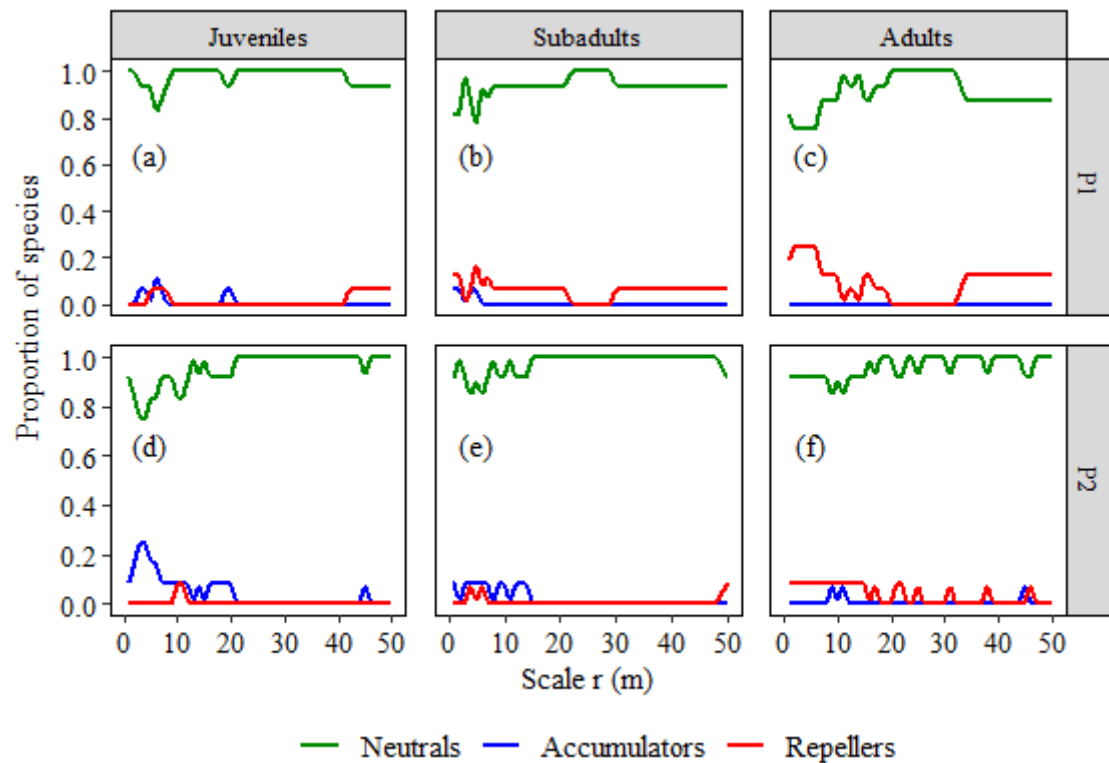
target species at different life-history stages (*Types 1, 2, and 3 in Fig. A3*) also showed that the number of neutral species accounted for a higher proportion than the number of accumulators and repellers at scales of 1-50 m (*Fig. 7a-f*).



**Figure 5.** The association patterns of species in the study plots were analyzed by the function  $g_{12}(r)$  under the independent null model



**Figure 6.** Results of overall ISAR model analyses from 199 Monte Carlo simulations under the null model of CSR in P1 (a, c) and the IPP in P2 (b, d); significant at  $\alpha < 0.05$



**Figure 7.** Analytical results of ISAR models of target species according to life-history stages from 199 Monte Carlo simulations under the null model of CSR in P1 (a- c) and the IPP in P2 (d- e); significant at  $\alpha < 0.05$

## Discussion

### *The heterogeneity of environmental conditions in the study plot*

Our study found a difference between the two study plots regarding habitat conditions, which was demonstrated by the dissimilar spatial distribution pattern of adult trees in these two plots. Specifically, the adult trees in P1 were relatively homogeneously distributed at 0-50 m, whereas those in P2 were inhomogeneously distributed at scales above 10 m.

The spatial distribution pattern of forest trees is closely related to the spatial scale and environmental conditions, such as exposed rock, slope, canopy cover, and nutrients in the soil (Hu et al., 2019). Different species exhibit dissimilar spatial distribution patterns under different environmental conditions, such as randomness, aggregation, and regularity (Condit et al., 2000; Getzin et al., 2006; Stoll and Bergius, 2005). In the same study plot, the heterogeneity of environmental conditions may only affect the spatial distribution of some species at a small scale, but it is the primary factor that affects the spatial distribution of all species at a large scale (Yuan et al., 2011; Wu et al., 2018). If the spatial pattern of adult trees is aggregated at scales of  $r > 10$  m, this could be explained by environmental heterogeneity (Getzin et al., 2008). Environmental inhomogeneity is a widespread phenomenon in the tropical rainforest. One manifestation of environmental inhomogeneity is that the cumulative density of adult tree individuals tends to shift from randomness to aggregation at distances greater than 20 m (Wiegand et al., 2007b). The inhomogeneity of environmental conditions plays a

critical role in forming the plant community, which is one of the main reasons leading to significant variation between the characteristics of forest stands in different locations and creating the spatial diversity pattern of species (Tuan et al., 2018).

### *Spatial distribution patterns of species*

The spatial distribution pattern of species visually reflects the spatial structure, dynamics of populations, and ecological processes that control the functional stability of the forest tree community (Liu et al., 2021). Many previous studies have used the spatial point pattern analysis method to study the spatial distribution and associations of species in the same plant community, helping to understand the ecological characteristics of species and forest dynamics (Murrell et al., 2001; Szmyt and Tarasiuk, 2018).

Our results showed that the spatial distribution pattern of species depends on the spatial scale. The spatial distribution patterns of species differed in aggregate intensity between two scales of  $r < 30$  m and  $r > 30$  m. When the tree-tree distance increased, the number of species had an aggregation that decreased, and their spatial patterns tended to shift from aggregation at a small scale ( $r < 30$  m) to randomness at a large scale ( $r > 30$  m).

The results of the spatial pattern analysis of species in our study are consistent with the growth law of forest trees proven in many studies on tropical forests. The spatial pattern of species is related to their self-adaptation mechanisms during plant-plant interaction (Cysneiros et al., 2018). At small scales, tree species are mainly affected by limited dispersal and species competition or combinations of these factors, but at a large scale, they are limited by biological characteristics and environmental heterogeneity (Zhang et al., 2010; Inman-Narahari et al., 2014; Lara-Romero et al., 2016).

In our study plots, the number of species that had a clumped distribution pattern (aggregation) accounted for a higher proportion than the random and regular distribution patterns at a small scale of  $r < 30$  m (P2) when the environmental conditions were inhomogeneous. Conversely, in inhomogeneous environmental conditions, the number of species with a clumped distribution pattern accounted for a lower proportion than random distribution patterns (P1). The spatial pattern of one plant population reflects the population's adaptation strategies to the environmental conditions and intraspecific interactions of individuals (Quy et al., 2021c). In the spatial distribution patterns of one forest tree species, the clumped distribution pattern shows that the intraspecific interaction of individuals is positive (attraction) (Akhavan et al., 2012). The random distribution (randomness) reflects intraspecific interaction as non-interaction (independence), and the regular distribution (regularity) indicates that there is negative interaction (repulsion) among individuals of the same species (Yuan et al., 2011). At different developmental stages, forest trees exhibit distinct spatial patterns. For instance, trees tend to have a clumped distribution pattern at the juvenile tree stage, which protects the species group from harsh environmental conditions and harmful organisms. However, as individual trees grow, the demand for nutritional space increases, resulting in intraspecific competition (Dien and Hai, 2016). This competition leads to natural self-thinning (Quy et al., 2021c) and an increase in the distance between trees, causing the spatial pattern of forest trees to become random or regular at larger scales. Previous studies have shown that intraspecific competition affects tropical tree species less (Burslem et al., 2005). Therefore, our analysis revealed many species with a random distribution pattern, indicating that aggregation intensity decreased as the spatial scale increased.

### *Spatial associations of species*

The spatial distribution patterns and species associations result from long-term interactions between plants and the environment (Nathan, 2006). The interaction between individuals influences the growth, reproduction, and survival of individual trees. Therefore, tree-tree interactions are crucial in maintaining community structure and forest ecosystem function (Burslem et al., 2005).

In our study, species pairs with independent associations were very high at all scales  $r$  of 1-50 m. This result is consistent with the unified neutral theory (Hubbell, 2001), which hypothesizes species may be functionally identical and drift randomly in abundance. Many ecologists have suggested that tree species rarely compete with neighboring species in tropical forests where species diversity is very high (Caswell, 1976; Bell, 2001). Therefore, the proportion of independently related species pairs is often remarkably high. Our study results on spatial associations of species are also wholly similar to those in studies by Wiegand et al. (2007b) and Nguyen et al. (2018). The number of attractions and repulsions between the study plots was similar regardless of the differences in the environmental conditions of the study plots.

On the other hand, we found that the number of attractions and repulsions almost disappeared at scales above 30 m. This finding is consistent with some previous studies. For example, Uriarte et al. (2004) and Hubbell (2001) indicated that tree-tree interactions mainly appear at distances smaller than 30 m.

The analytical results of the spatial associations of species in our study exhibit many similarities with the study results in the Xishuangbanna National Nature Reserve, China. Lan et al. (2012) discovered that the number of species pairs with attracted patterns accounted for a higher proportion than repulsions at  $r < 30$  m scales. This phenomenon could be due to the aggregation intensity decreasing as the scale increased. In tropical forests, the composition of tree species is diverse. However, the density of each species is low, leading to a decrease in species interaction as their abundance drops at large scales.

In our study, the proportion of repulsion is negligible at small scales, but it provides evidence of the existence of local environmental factors. These factors create intra- and interspecific competition between individuals regarding growth rate, light requirements, nutrients, and water sources (Volkov et al., 2009). Adult and subadult trees with large canopies can cover the juveniles in the early life-history stage (Burslem et al., 2005). When juvenile trees grow, the light needs to increase during their growth, creating competition for light (Cysneiros et al., 2018). After the juvenile tree stage, competition for light between individuals eliminates the less competitive neighboring individuals. This process reduces aggregate intensity at the subadult and adult stages, increasing the tree-tree distance and forming a random or regular distribution (Du et al., 2017).

### *Individual species-area relationship*

The high diversity of tropical forests can be attributed to various environmental factors such as niche partitioning, competition, and mutualism among species (Wright, 2002; Kraft et al., 2008). However, the coexistence of multiple species in tropical forests is still an enigma for ecologists, and many hypotheses have been proposed to explain it. These hypotheses are not mutually exclusive, and their importance depends on the spatial and temporal scales at which they are applied (Quy et al., 2021c).

The results of the ISAR model analysis in our study showed that the diversity of neighbors of the target species was dependent on the spatial scale and individual size.

Diversity accumulator and repeller species were found mainly at scales below 30 m. Besides, the influence of individual size on the spatial pattern of neighboring species diversity varied among different life-history stages of the target species. Specifically, at the juvenile stage, the diversity of neighbors was higher than that of subadult and adult trees. This finding indicated that juvenile trees play a crucial role in maintaining the species diversity of the plant community. These findings supported the asymmetric competition theory proposed by Weiner (1990), which states that larger individuals take up a disproportionate share of resources and are detrimental to the growth of smaller individuals.

The results of our study add to the understanding of the mechanisms driving species diversity in tropical forests. However, further research is needed to explore the interactions among different environmental factors that shape the community structure and diversity of these forests.

Our analytical results of the ISAR model for the target species across life-history stages (Type 1, 2, and 3) bear many similarities with those of previous studies. For instance, Gong et al. (2011) used the ISAR model to investigate the formation of evergreen broadleaf forest tree communities in the Dinghu Mountain range, Guangdong province, China. They observed a decrease in diversity accumulators as tree size increased. Our study found that the number of neutral species always exceeded the number of accumulators and repellers species across all analyzed ISAR model types. This finding suggests that the diversity of plant species in tropical forests is not dependent on a few species. We share the same view as Wiegand et al. (2007a) and Yan et al. (2015), who also concluded that the coexistence of species relies on the overall interaction of all species in the plant community.

## Conclusion

The present study was conducted in the Dong Nai Culture and Nature Reserve in Dong Nai province, Southern Vietnam, to enhance our understanding of the spatial patterns, associations, and species diversity structure of dominant tree species in the evergreen broadleaf forest type.

With four research questions posed initially, the main results of the study are as follows: (i) The dominant species in the study area exhibited a mainly aggregated spatial pattern at small scales of  $r < 30$  m; the spatial association of species was found to be independent, with a high proportion at all scales of 0-50 m. (ii) Spatial patterns and species associations depended on spatial scale, with tree-tree interactions mainly occurring at scales below 30 m. (iii) The species diversity structure of the community was influenced by asymmetric interactions between individuals at different life-history stages, with the richness of neighboring species around small-sized individuals being higher than that around large-sized individuals; the number of neutrals exceeded that of accumulators and repellers, highlighting that specific species did not dominate the maintenance of tree species diversity but depended on the overall interaction of all species in the plant community. (iv) The spatial distribution and association patterns of woody species were controlled by environmental conditions heterogeneity, limited dispersal, and species-species interactions.

Our findings suggest that it is crucial to protect the current status of forest resources and avoid adverse human impacts to maintain the diversity of woody species in the study area. Silvicultural measures aimed at increasing the density of diversity

accumulations and reducing the density of diversity repellers may not be necessary. In future forest restoration or planting projects involving dominant tree species in areas with similar climatic and site conditions to the study area, selecting tree species that promote diversity (accumulations) while limiting the selection of species that inhibit diversity (repellers) should be prioritized.

Finally, to systematize the rules and mechanisms for maintaining species diversity in tropical rainforests in Vietnam, we recommend performing ISAR model analysis in different forest types in future studies.

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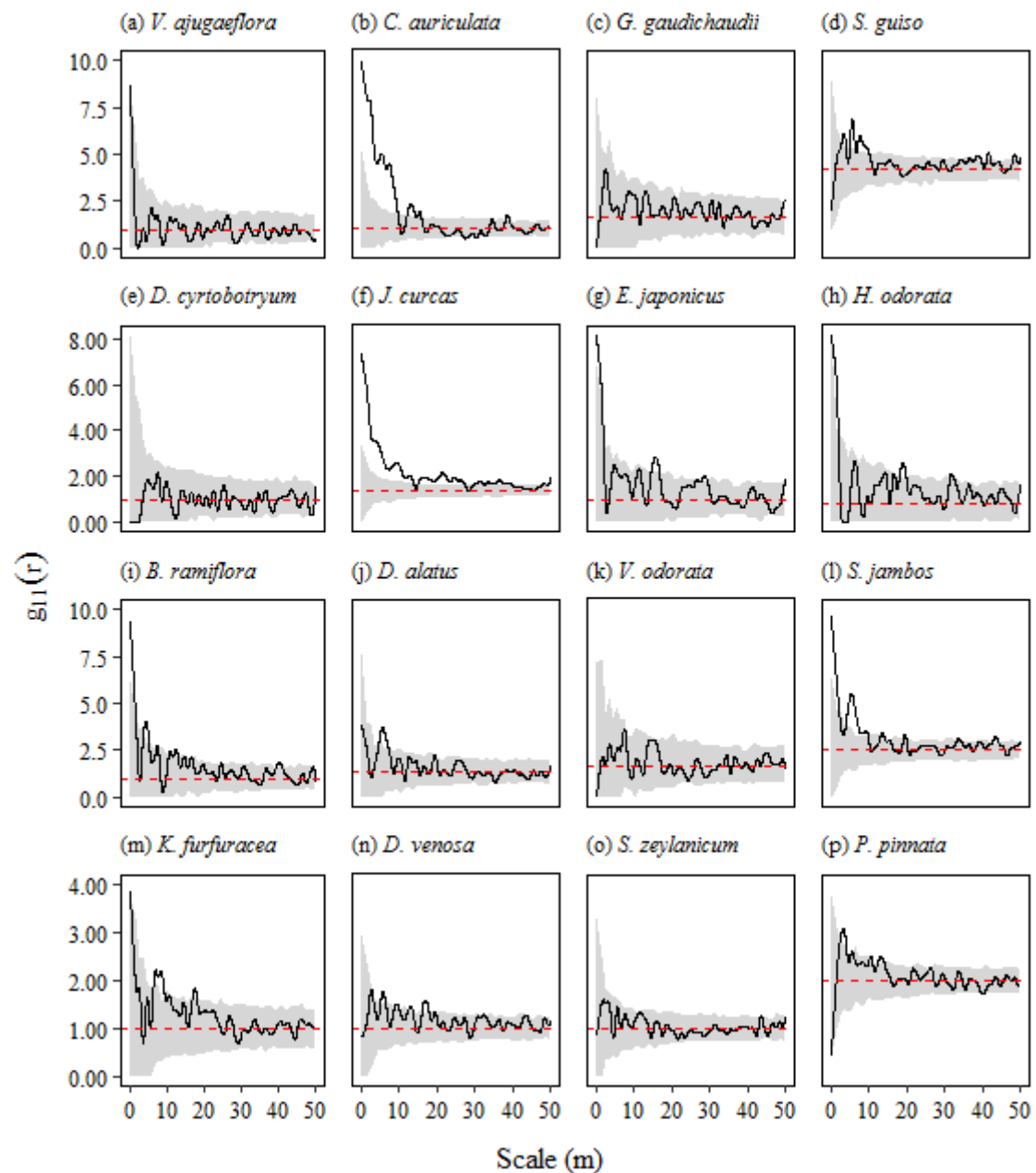
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## APPENDIX

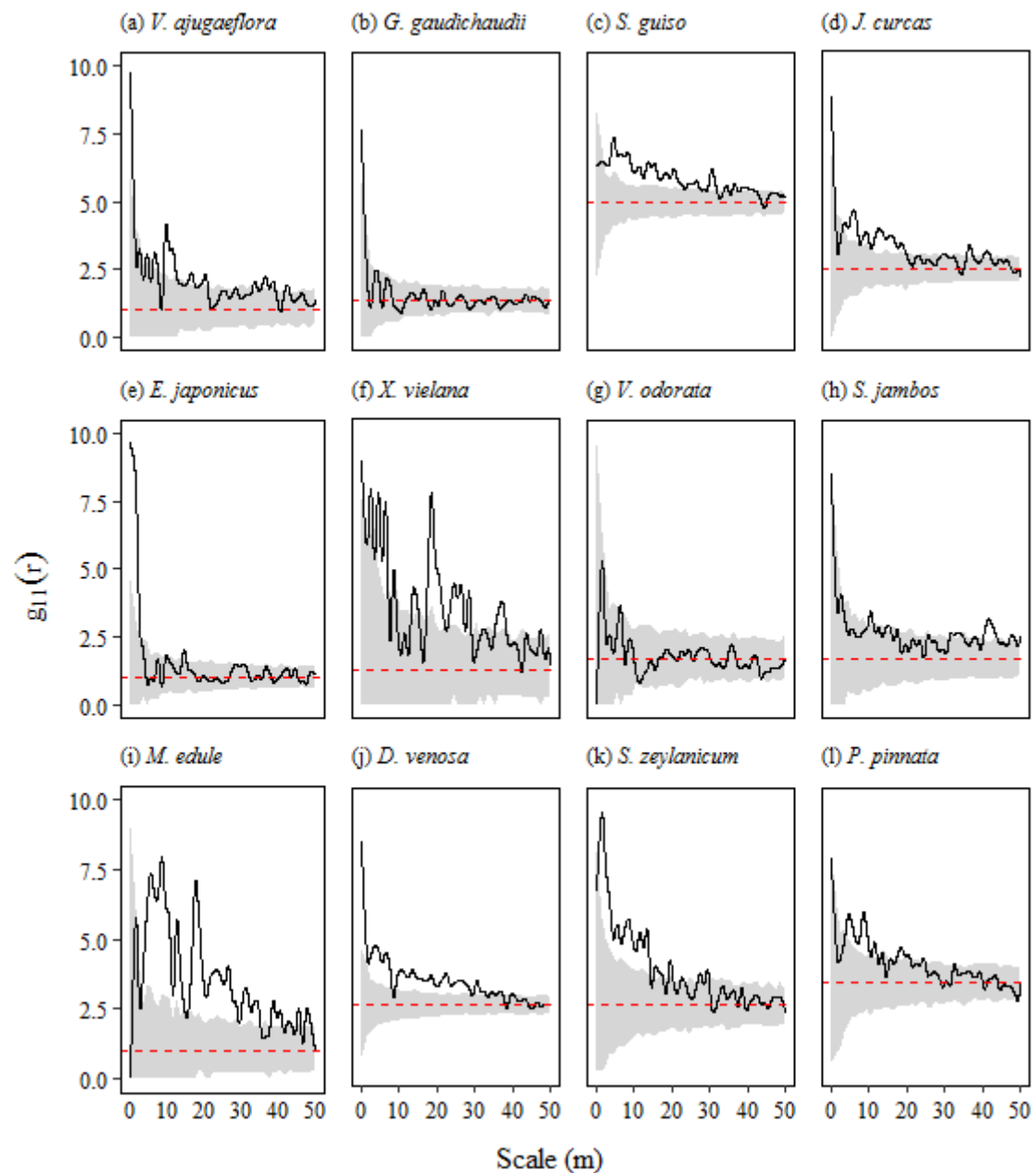
**Table A1.** Characteristics of common species in both study plots

No	Tree species	P1				P2			
		N	DBH	BA	IVI	N	DBH	BA	IVI
1	<i>Pometia pinnata</i>	247	16.3 ± 8	6.42	13.1	326	11.4 ± 4.2	3.79	9.9
2	<i>Shorea guiso</i>	232	12.8 ± 9.5	4.64	10.8	648	13.5 ± 7.5	12.29	23.9
3	<i>Jatropha curcas</i>	177	10.2 ± 3.9	1.67	6.2	169	15.1 ± 12.9	5.28	8.1
4	<i>Syzygium jambos</i>	159	8.1 ± 1.8	0.86	4.8	71	13.6 ± 6.2	1.26	2.5
5	<i>Diospyros venosa</i>	128	10.3 ± 3.9	1.23	4.5	237	11.8 ± 4.9	3.06	7.4
6	<i>Syzygium zeylanicum</i>	125	14.4 ± 9.3	2.90	6.2	205	15.7 ± 10.4	5.75	9.2
7	<i>Vatica odorata</i>	55	12.7 ± 6.2	0.86	2.3	67	12.8 ± 7.7	1.18	2.4
8	<i>Garcinia gaudichaudii</i>	52	13 ± 5.1	0.80	2.1	95	13.3 ± 6.1	1.61	3.3
9	<i>Elaeocarpus japonicus</i>	40	18.5 ± 13.5	1.64	2.8	75	21.1 ± 16	4.12	5.2
10	<i>Vitex ajugaeflora</i>	39	16.1 ± 9.3	1.05	2.1	47	17 ± 9.3	1.39	2.2
11	<i>Hopea odorata</i>	30	33.5 ± 17.1	3.32	4.4	-	-	-	-
12	<i>Baccaurea ramiflora</i>	46	9.8 ± 3.6	0.40	1.6	-	-	-	-
13	<i>Dipterocarpus alatus</i>	67	20.7 ± 12.3	3.06	5.0	-	-	-	-
14	<i>Knema furfuracea</i>	73	16.3 ± 6.9	1.81	3.8	-	-	-	-
15	<i>Dysoxylum cyrtobotryum</i>	40	13.4 ± 8.3	0.78	1.8	-	-	-	-
16	<i>Colona auriculata</i>	71	18.5 ± 7.5	2.23	4.2	-	-	-	-
17	<i>Xylopia vielana</i>	-	-	-	-	33	12.3 ± 6.7	0.51	1.1
18	<i>Memecylon edule</i>	-	-	-	-	38	9.6 ± 2.8	0.30	1.0
19	Dominant tree species	1581	13.8 ± 8.9	33.68	75.5	2011	13.6 ± 8.4	40.54	76.3
20	Other species	467	14.5 ± 10.5	11.89	24.5	524	15.1 ± 11.4	14.86	23.7
21	All species	2048	14 ± 9.3	45.57	100	2535	13.9 ± 9.1	55.41	100

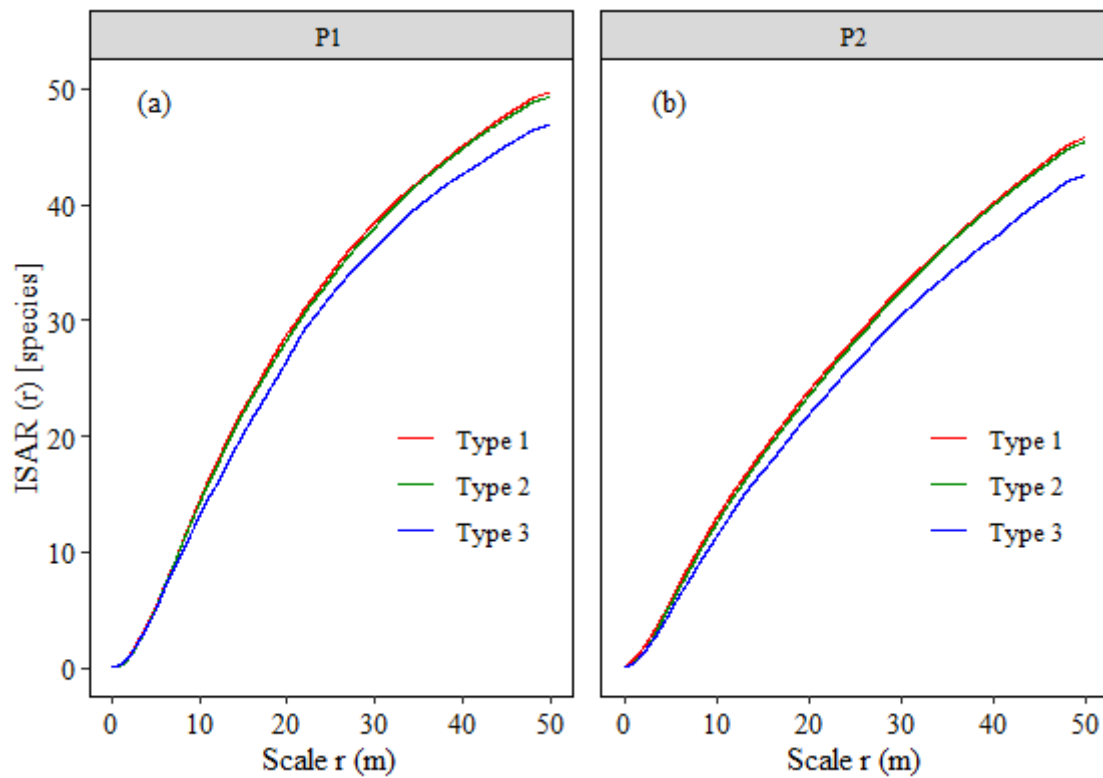
N - number of individuals; DBH - diameter at breast height (mean ± Standard deviation) (cm); BA - Tree basal area (m<sup>2</sup>); IVI - importance value index expressed as a percentage, (relative abundance + relative basal area)/2



**Figure A1.** Spatial distribution patterns of 16 target species analyzed using the function  $g_{11}(r)$  under the null model of Complete Spatial Randomness (CSR) in P1. The observed pattern is represented by the dark line, and values lying beyond the gray area (confidence envelope region) indicate a significant deviation from the null model of CSR. The gray envelope region represents the  $p = 0.05$  confidence intervals derived from 199 Monte Carlo simulations, where values  $< 1$  indicate regularity, values  $> 1$  indicate aggregation, and values  $= 1$  indicate randomness. The red dashed line represents the expectation for spatial randomness between individual trees



**Figure A2.** Spatial distribution patterns of 12 target species analyzed using the function  $g_{11}(r)$  under the null model of Inhomogeneous Poisson Process (IPP) in P2. The observed pattern is represented by the dark line, and values lying beyond the gray area (confidence envelope region) indicate a significant deviation from the null model of IPP. The gray envelope region represents the  $p = 0.05$  confidence intervals derived from 199 Monte Carlo simulations, where values  $< 1$  indicate regularity, values  $> 1$  indicate aggregation, and values  $= 1$  indicate randomness. The red dashed line represents the expectation for spatial randomness between individual trees



**Figure A3.** Analytical results of three Individual Species-Area Relationship (ISAR) models of target species obtained from 199 Monte Carlo simulations under the null model of Complete Spatial Randomness (CSR) in P1 (a) and the Inhomogeneous Poisson Process (IPP) in P2 (b). The significance level is  $\alpha < 0.05$ ; Type 1, Type 2, Type 3 see Table 1