

Structuring mechanism of tree species diversity pattern in an evergreen broadleaved forest in Con Dao National Park, Vietnam

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Cơ chế hình thành mô hình đa dạng của các loài cây trong rừng lá rộng thường xanh ở Vườn quốc gia Côn Đảo, Việt Nam

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ABSTRACT

The spatial structure of a community and the ecological mechanisms that control it are central themes in community ecology. This study aimed to investigate the ecological mechanisms driving the coexistence of tree species in the evergreen broadleaved forests in Con Dao National Park, Vietnam. We employed two null models: complete spatial randomness and inhomogeneous Poisson process within the framework of the individual species-area relationship model. The analyses focused on the effects of habitat filtering and species interactions. We discovered habitat heterogeneity in a 4-ha study plot that contained 5,653 tree individuals belonging to sixty-four plant families. The results demonstrated the critical role of habitat filtering and species interactions in maintaining species diversity within the plant community. The study also indicated that the local diversity structure of tree species depended on the spatial scale. This study went beyond niche and neutral theories by emphasizing the significance of ecological field theory and the principle of asymmetric competition in explaining the coexistence of tree species in evergreen broadleaved forests. Our findings may provide valuable insights into biodiversity conservation and the management of evergreen broadleaved forests, helping to improve further plant diversity conservation activities in the study area.

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TÓM TẮT

Cấu trúc không gian của quần xã và các cơ chế sinh thái điều chỉnh nó là chủ đề trọng tâm trong sinh thái học. Nghiên cứu này được thực hiện nhằm khám phá các cơ chế sinh thái thúc đẩy sự chung sống của các loài cây trong rừng lá rộng thường xanh ở Vườn quốc gia Côn Đảo của Việt Nam. Hai mô hình lý thuyết là ngẫu nhiên hoàn toàn trong không gian và Poisson không đồng nhất đã được sử dụng trong nghiên cứu dựa trên khuôn khổ của mô hình mối quan hệ loài theo diện tích. Các phân tích không gian tập trung vào sự ảnh hưởng của quá trình lọc môi trường sống và sự tương tác giữa các loài cây. Kết quả nghiên cứu cho thấy, điều kiện môi trường trong ô nghiên cứu rộng 4 ha chứa 5.653 cá thể cây thuộc 64 họ thực vật là không đồng nhất. Bên cạnh đó, nghiên cứu đã chứng minh vai trò quan trọng của quá trình lọc môi trường sống và sự tương tác giữa các loài trong việc duy trì tính đa dạng loài của quần xã thực vật. Kết quả nghiên cứu cũng chỉ ra rằng, cấu trúc đa dạng cục bộ của các loài cây phụ thuộc vào quy mô không gian. Nghiên cứu này đã vượt ra ngoài tầm bao phủ của các lý thuyết về sinh thái và trung lập khi xác nhận tầm quan trọng của lý thuyết trường sinh thái và nguyên tắc cạnh tranh bất đối xứng trong việc giải thích sự chung sống của các loài cây trong rừng lá rộng thường xanh. Những phát hiện trong nghiên cứu có thể cung cấp thông tin có giá trị về mặt bảo tồn đa dạng sinh học cũng như quản lý rừng lá rộng thường xanh, giúp cải thiện hơn nữa các hoạt động nhằm bảo tồn đa dạng thực vật ở Vườn quốc gia Côn Đảo.

Từ khóa:

các quá trình sinh thái, chọn lọc môi trường sống, đa dạng loài, lý thuyết ổ sinh thái, quy mô không gian, sinh thái quần xã.

1. INTRODUCTION

The genesis and preservation of species diversity constitute a focal subject in ecology [1]. Over the decades, ecologists have proposed many theories and hypotheses, including the succession theory, the metapopulation theory, the theory of natural selection, the theory of island biogeography, and more than 100 other theories [2]. Among these, the niche and neutral theories are the most widely recognized [3]. Niche theory emphasizes the impact of deterministic processes, such as competition and habitat filtering, on the organization and diversity of biological communities [4, 5]. In contrast, neutral theory operates on the premise that species are ecologically equivalent [6]. Therefore, under neutral theory, the perpetuation of diversity relies on stochastic fluctuations in birth, death, immigration, and migration of individuals rather than on niche differentiation of species. An apparent dichotomy characterizes the relationship between niche and neutral theories. However, recent studies have suggested an intriguing complementarity between them [7-9]. Analyzing community spatial structure can illuminate the relative importance of deterministic and stochastic processes corresponding to these two theories in maintaining species diversity [9]. Understanding these underlying processes holds significant theoretical value, enabling accurate forecasting and effective management of the impacts of environmental shifts on biomes.

The spatial arrangement of trees significantly impacts the coexistence of plant species within a forest community [8]. Therefore, understanding the spatial distribution of tree populations is crucial for illuminating the underlying processes that shape observed patterns. Thanks to advancements in spatial statistics, spatial species data serve as the foundation for constructing biological models that can reveal past ecological processes [10]. We can trace these ecological processes by integrating biological models with spatial statistical techniques. One such integrated tool is the Individual Species-Area Relationship (ISAR)

model [11]. ISAR investigates the local diversity structures surrounding individual species, focusing on the interactions among interspecific neighbouring trees. This model evaluates species diversity patterns by estimating the number of interspecific species found near a focal species and comparing it to the expected species richness [12]. Classifying a species as a neutral, diversity accumulator or diversity repeller depends on the richness of its neighbouring species [7]. If the richness of the surrounding species falls within the anticipated diversity range, the focal species is considered neutral [11]. However, the richness of other species surrounding the focal trees is significantly higher or lower than expected. In that case, the focal species is categorized as a diversity accumulator or a diversity repeller [12]. The ISAR model has been utilized as a framework for various studies. For instance, Wiegand *et al.* [13] examined a 50-ha plot on Panama's Barro Colorado Island and a 25-ha plot in Sri Lanka. Their findings revealed that most tropical tree species exhibit neutral effects on large spatial scales. In the needle-leaf temperate forests of Jilin, China, Xu *et al.* [14] suggested that neutral and accumulator species contribute to shaping species diversity. Another study conducted by Nguyen Van Quy *et al.* [15] in the evergreen broadleaved forest of southern Vietnam advocated the findings above and highlighted the role of diversity accumulator species in facilitating species coexistence at small spatial scales.

Previous studies on species diversity in Vietnam have primarily focused on community non-spatial structure [16]. Otherwise, based on phenomenological and ecological systems theories, these studies have yet to identify the mechanisms that form and maintain species diversity from a population perspective. It is crucial to quantify the relative contribution of species to community diversity through ISAR analyses, as it has significant practical implications [14]. For example, the selection of diversity repeller species should be limited in new afforestation or forest enrichment initiatives. Moreover, adjusting the spatial distribution of diversity accumulator species within a forest stand can promote community diversity [16]. Based on this reality, the current

study established a 4-ha (200 m × 200 m) study plot within the evergreen broadleaved forest on Con Dao Islands. This study addresses the following questions: (i) Are the environmental conditions in the study plot homogeneous? (ii) How does the heterogeneity of environmental conditions in the study plot (if any) influence the ISAR model of focal species? (iii) Which of the analyzed species are diversity accumulators, repellers, and neutral species? (iv) Which theory, niche or neutral, provides a better explanation for the coexistence of tree species in the evergreen broadleaved forest in the study area?

2. RESEARCH METHODOLOGY

2.1. Study area

The study was conducted at Con Dao National Park on Con Dao Islands of Vietnam, specifically within Ba Ria - Vung Tau province. This national park is between 8°36'-8°48' North latitude and 106°31'-106°46' East longitude. Located approximately 80 km from the mainland, the park spans a natural expanse of 19,883.15 ha, with forested areas accounting for 5,145.11 ha of this area. The climate on Con Dao Islands is characterized by two distinct seasons: the rainy season, which begins in May and ends in October, and the dry season, which runs from November until April of the following year. The average annual temperature is 26.2°C. The relative humidity often reaches 90%, with the average annual rainfall totalling 2,200.3 mm. The topography of Con Dao National Park is mainly composed of low mountains, with elevations varying from 50 to 200 m a.s.l. [17].

The study plot is within an evergreen broadleaved forest, a typical vegetation type found on Con Dao Islands. The natural stand encompasses an area characterized by a rich and diverse composition of broadleaved tree species. According to Nguyen's report [18], the dominant tree species in the study area are *Knema pierrei* Warb., *Syzygium cumini* (L.) Skeels, *Garcinia celebica* L., *Arytera littoralis* Blume, *Diospyros silvatica* Roxb., *Pterospermum lanceifolium* Roxb., and *Xerospermum glabrum* Pierre.

2.2. Data collection

In 2023, a study plot spanning 4 ha (200 m

× 200 m) was established within a naturally occurring evergreen broadleaved forest on Con Son Island, part of Con Dao Islands. The coordinates of the study plot stand at 8°43'15.33" North latitude and 106°36'48.62" East longitude. A square grid was utilized to ensure comprehensive data collection and minimize the omission of surveyed trees. The study plot was further segmented into 400 subplots, each measuring 100 m² (10 m × 10 m). All trees displaying a diameter at breast height (dbh) ≥ 2.5 cm in the study plot were mapped. Additionally, their species name was identified, and their dbh was measured. A "spatial instead of time" method was applied to categorize the trees within the study plot according to their respective life stages [3]. This method is centred around categorizing trees based on their dbh. Consequently, trees were classified into three stages: saplings (2.5 cm ≤ dbh < 10 cm), intermediate trees (10 cm ≤ dbh ≤ 20 cm), and adult trees (dbh > 20 cm).

2.3. Data analysis

2.3.1. Identification of dominant species

The important value index (IV) was used to ascertain the dominant species in the forest stand. This index evaluates each species' abundance and dominance within the study plot. We utilized the following formula to calculate the IV for each species [16]:

$$IV_i = (N_i\% + G_i\%)/2 \quad (\text{eq. 1})$$

where,

IV_i is the important value index of species i ;

$N_i\%$ is the relative density of species i ;

$G_i\%$ is the relative basal area of species i .

2.3.2. Individual species-area relationship (ISAR)

The ISAR model was utilized in this study to assess the impact of focal species on species coexistence within a forest stand. This model enables the estimation of the number of other species located within a circular window, having a radius of r , centred on an individual tree of a particular focal species. The ISAR value was calculated using Wiegand et al.'s formula [13].

$$ISAR(r) = \sum_{j=1}^N [1 - P_{ij}(0, r)] \quad (i \neq j) \quad (\text{eq.2})$$

where,

i and j represent focal and neighbouring species, respectively;

N denotes the total number of species;

$P_{ij}(0, r)$ represents the probability of species j not occurring in a circular window centred around an individual of the species i .

Two null models were used to assume the neutrality of focal species in this study, including complete spatial randomness (CSR) and inhomogeneous Poisson process (IPP). The implicit impact of tree-tree interactions, resulting from their spatial distributions, can be effectively modelled using the null model of CSR [12]. However, this approach fails to yield satisfactory results due to the high heterogeneity of habitats [19]. Plant species are sensitive to local variations in their habitat, including soil composition, topography, and solar radiation [12]. Therefore, considering habitat heterogeneity is essential to avoid misinterpretations of interspecies interactions [11]. Associations between species and their habitats can increase or decrease the likelihood of a specific species being found in a particular location [12]. If habitat heterogeneity exists within our study plot, it could be attributed to topographical and soil factors. The human disturbance was not considered here because the study plot is in a strictly protected zone in Con Dao National Park. The null model of IPP was implemented to view the local tree density [11]. This approach aids in eliminating the confounding impact of habitat heterogeneity on the diversity patterns of focal species.

Both null models were used to determine if a focal species is a diversity accumulator species, diversity repeller species, or neutral species. In the case of the CSR null model, the locations of the focal species were randomized, while the positions of all other trees remained unchanged. This randomization process was repeated in 999 Monte Carlo simulations [11]. For the IPP null model [12], the density of individuals was simulated based on the intensity of the focal species. Firstly, a Gaussian kernel estimated the pixel image of the focal species' tree density. Subsequently, random points uniformly distributed within the pixel sequence were generated. The maximum

bandwidth was set to one-quarter of the side length of the study plot to ensure that spatial patterns of focal species were unaffected by the edge effect. Then, 999 Monte Carlo simulations were conducted using the ISAR Enero 2019 software for ISAR analysis. From the results of these simulations, the fifth-highest and fifth-lowest values were selected to establish an approximate 95% confidence interval. Lastly, Miser's method was employed to conduct a goodness-of-fit test of the simulation patterns via the GoF test software reserved for ISAR analysis. This step is to ensure the accuracy of the analytical results and avoided inflation of type-I error [20].

Several methods can be employed to evaluate habitat heterogeneity within a study plot, for example, fractal analysis, physical and chemical analysis, and species diversity measure [21]. This study used the chi-square test to scrutinize the habitat inhomogeneity. The chi-square test is based on the density of intermediate and adult trees (with a dbh ≥ 10 cm) in the subplots. The obtained p-value > 0.05 suggested a uniform distribution of intermediate and adult trees; this implies a homogenous habitat in the study plot. Conversely, if the p-value < 0.05 , it signified a heterogeneous habitat.

3. RESULTS

3.1. Forest stand characteristics

A total of 5,653 individual trees belonging to sixty-four tree species were recorded in the study plot (Table 1). Among these sixty-four species, twenty-six were classified as "abundant species," with each species having thirty or more individuals. These abundant species were selected as the focal species for the ISAR analysis. Seven of the twenty-six focal species had ecological significance, with an IV $> 5\%$. These species were *K. pierrei*, *G. ferrea*, *S. cumini*, *D. silvatica*, *A. littoralis*, *P. pierrei*, and *S. luzonensis*. Despite constituting fewer than half of the total species within the study plot, focal species accounted for 92.3% of the individuals. Conversely, the thirty-eight other species comprised only 7.7% of the total individuals within the study plot but significantly contributed to the species diversity of the community.

Table 1. Basic characteristics of tree species in the 4-ha plot

No.	Scientific name	N	dbh (cm)	IV (%)
1	<i>Knema pierrei</i> Warb.	943	12.3 ± 6.3	13.3
2	<i>Garcinia ferrea</i> Pierre.	865	10.5 ± 4.4	10.7
3	<i>Sandoricum koetjape</i> (Burm.f.) Merr.	652	13.6 ± 7.2	10.0
4	<i>Arytera littoralis</i> Bl.	480	16.9 ± 9.8	9.3
5	<i>Diospyros silvatica</i> Roxb.	552	10.5 ± 6.7	7.2
6	<i>Smilax luzonensis</i> Presl	181	24.3 ± 17.9	6.1
7	<i>Pterospermum pierrei</i> Hance.	263	19 ± 8.6	5.4
8	<i>Machilus thunbergii</i> var. <i>condorensis</i> Lec.	125	25.5 ± 8.5	3.6
9	<i>Clausena excavata</i> Burn. f.	182	13.2 ± 5.9	2.6
10	<i>Bischofia javanica</i> Bl.	41	36.2 ± 20.2	2.3
11	<i>Dipterocarpus condorensis</i> Pierre	72	23.9 ± 14.8	2.2
12	<i>Aglaiia poulocondorensis</i> Pell	85	17.3 ± 14	1.9
13	<i>Syzygium cumini</i> (L.) Druce.	55	25.6 ± 15	1.8
14	<i>Ficus altissima</i> Bl.	32	31.8 ± 21.5	1.6
15	<i>Schefflera octophylla</i> (Lour.) Harms.	79	17.2 ± 10	1.5
16	<i>Xanthophyllum colubrinum</i> Gagn.	43	24.6 ± 15.4	1.4
17	<i>Memecylon scutellatum</i> (Lour.) Naud.	103	11.1 ± 4.7	1.3
18	<i>Litsea pierrei</i> Lec.	78	14.6 ± 8.7	1.3
19	<i>Gluta megalocarpa</i> (Evt.) Tard.	52	19.7 ± 11.6	1.2
20	<i>Adenanthera pavonica</i> var. <i>microsperma</i> Niels.	86	10.2 ± 4.3	1.0
21	<i>Streblus asper</i> Lour.	43	21.4 ± 9.7	1.0
22	<i>Alstonia scholaris</i> (L.) R. Br.	50	16.4 ± 8.6	0.9
23	<i>Antidesma cochinchinensis</i> Gagn.	37	15.7 ± 12.1	0.7
24	<i>Terminalia calamansanai</i> (Bl.) Rolfe.	45	12.5 ± 6.9	0.7
25	<i>Aglaiia euphoroides</i> Pierre.	39	12.6 ± 5.7	0.5
26	<i>Garcinia oliveri</i> Pierre.	35	10.2 ± 4.1	0.4
27	Twenty-six focal species	5218	14.9 ± 10.2	90.1
28	Thirty-eight others	435	18.0 ± 13.9	9.9
29	All (sixty-four species)	5653	14.8 ± 10.2	100

Note: N - number of individuals; IV - importance value index (%); dbh - diameter at breast height (mean ± standard deviation) (cm).

3.2. The habitat heterogeneity in the study plot

Figure 1 illustrates the density map of intermediate and adult trees in the study plot. Upon observing the Figure 1, it becomes evident that the tree density across various locations in the study plot was uneven. The validity of this observation was supported by the results of the chi-square test conducted based on tree density. The p-value < 0.05 indicated a significant difference in tree density among the subplots. Consequently, it could be inferred that the habitat in the study plot was inhomogeneous.

3.3. Spatial diversity patterns of species

The analysis focused on exploring the spatial diversity patterns of focal species using different null models, specifically CSR and IPP. The results showed a rapid increase in species around the focal species at small

spatial scales (0-10 m). However, as the spatial scale expanded to 10-50 m, the rate of species increase gradually decreased and eventually levelled off (Fig. 2a-b). This indicated the impact of spatial scale on species' spatial diversity patterns. Null models used in this study showed unique trends in the distribution of neutral species and diversity repeller species across different spatial scales. With the null model of CSR, there was a notable decrease in the proportion of neutral species as the spatial scale increased. On the other hand, the null model of IPP showed the opposite trend. A similarity was observed despite the contrasting trends of species significance across different spatial scales under CSR and IPP null models. Specifically, diversity accumulator species were more dominant at small spatial scales (0-10 m) than large scales (10-50 m).

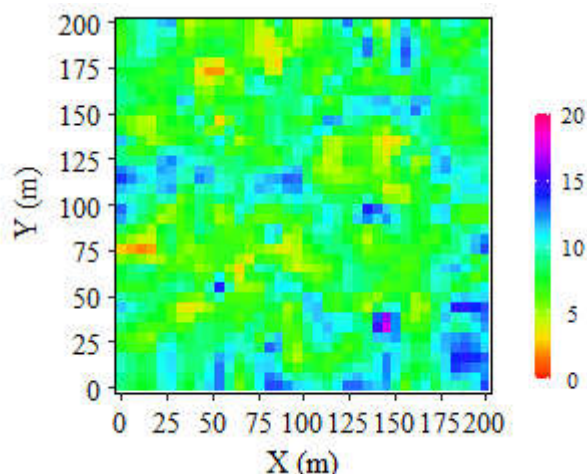


Figure 1. The density map of intermediate and adult trees in the study plot

The map utilizes a range of gradient colours to represent the fluctuations in tree density per square meter within the study plot. Darker hues indicate higher tree densities, while lighter shades correspond to lower densities. A conditional Monte Carlo test of CSR was conducted using quadrat counts to assess the spatial distribution pattern. The test statistic employed the Pearson chi-square statistic, yielding a chi-square value of 443.33 with a corresponding p-value of 0.01

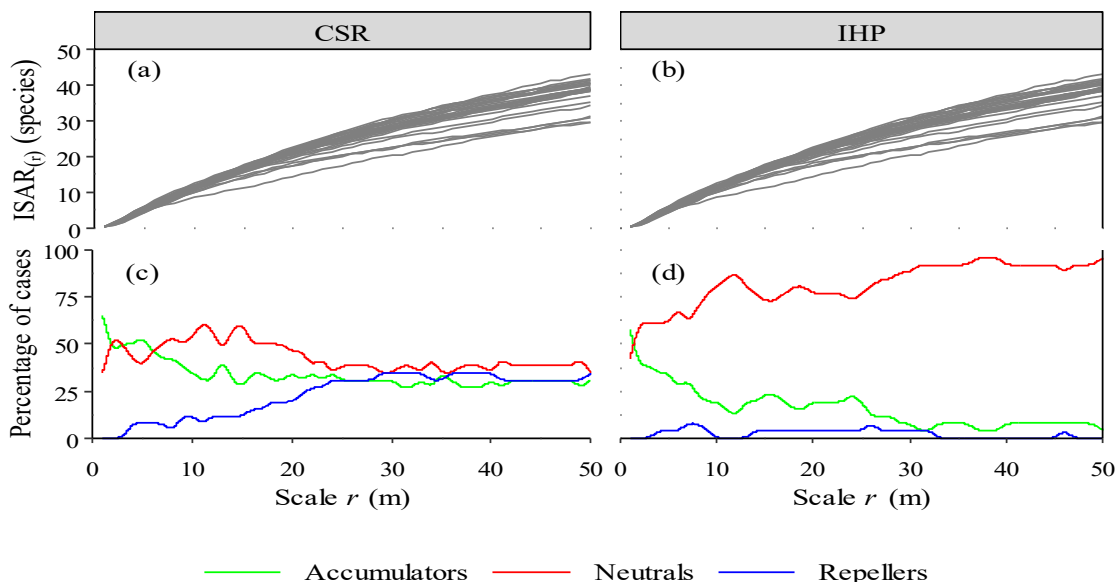


Figure 2. Spatial diversity patterns of focal species under null models of CSR (a, c) and IPP (b, d)

The figures labelled a-b present data regarding neighbouring species at various distance intervals (0-50 m) around the focal species. This information offers valuable insights into the spatial extent of interactions between the focal species and others in its local habitat. In cases where the number of neighbouring species is significantly high or low within a specific distance interval, this suggests the presence of robust interspecific interactions, such as competition or facilitation. Moving on to figures c-d illustrate the proportions of diversity accumulator, repeller, and neutral species at different spatial scales

A paired sample t-test was employed to analyze the difference in spatial diversity patterns of focal species under various null models. The result indicated a significant difference in diversity accumulator, repeller, and neutrals proportions between the null model of CSR and the null model of IPP. This result underscored the habitat filtering process's substantial impact on the

community's species diversity structure.

The null model of IPP was used to evaluate the impact of interactions between trees on the structure of species diversity across spatial scales ranging from 0 to 50 m (Fig. 4). The findings showed a neighbouring diversity of 23 among 26 focal species that differed significantly from the expected diversity. Upon examining the 26 focal species, we found that

except for seven species - *A. cochinchinensis*, *A. poulocondorensis*, *B. javanica*, *D. condorensis*, *G. megalocarpa*, *S. koetjape*, and *S. octophylla*, the remaining species were diversity accumulators at small spatial scales (0-10 m). Barring *A. littoralis*, *D. condorensis*, *M. thunbergii*, *P. pierrei*, and *S. asper*, most focal species demonstrated neutral effects at larger spatial scales over 30 m. The ISAR analyses also indicated that the focal species

could either be a diversity accumulator or a diversity repeller species at small spatial scales (0-10 m) and exhibit neutral effects at large spatial scales (10-50 m). This result was evident in the case of the species *S. asper*. Another significant finding was that diversity repeller species consistently possess a larger dbh than most neutral species or diversity accumulation species.

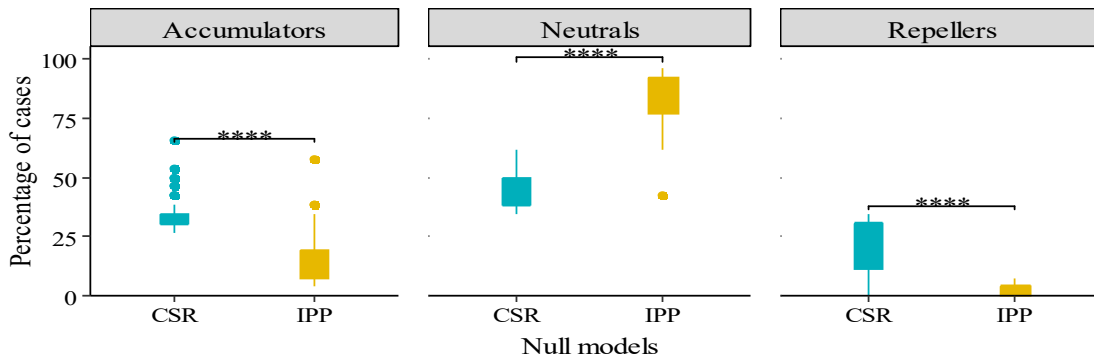


Figure 3. The differences in spatial diversity patterns of focal species between null models of IPP and CSR were assessed using a paired sample t-test

The significance level of the t-test: **** p -value < 0.0001

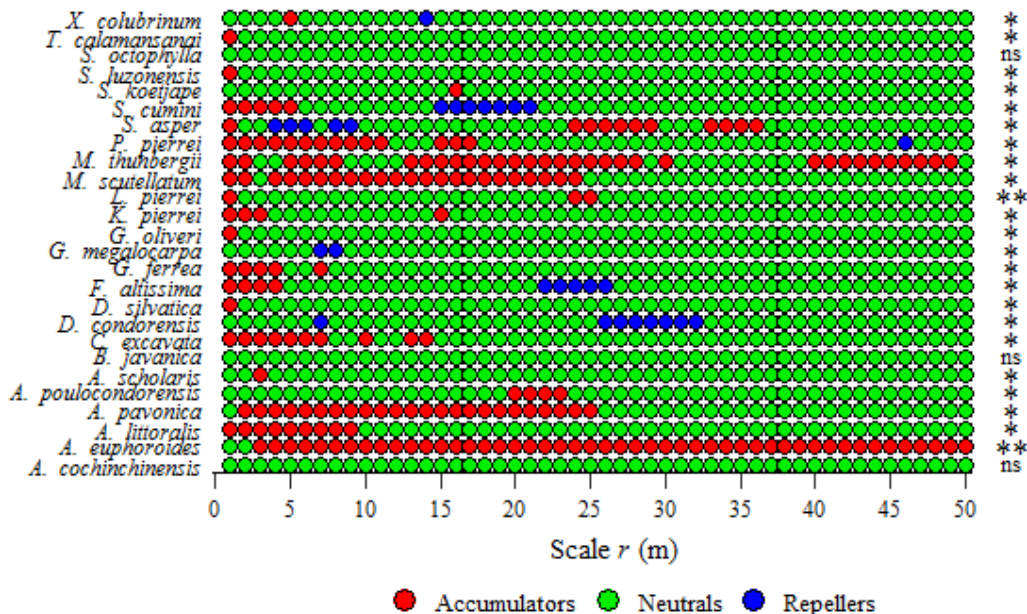


Figure 4. Results of ISAR analyses for focal species in the study plot

The significance levels of the GoF test are denoted as follows: * for $p < 0.05$, ** for $p < 0.01$, and "ns" indicates non-significance

4. DISCUSSION

4.1. The heterogeneity of environmental conditions in the study plot

In this study, the tree density map clearly illustrated the irregular distribution of intermediate and adult trees across the study plot. This irregularity is depicted through variations in colour and intensity observed in

different locations on the tree density map (Fig. 1). Many authors have suggested that it is necessary to perform a statistical analysis using a chi-square test to validate this observed inhomogeneity [21, 22]. This test aims to determine whether there are significant differences in tree density among the subplots [21]. Our results from the chi-square test

indicated a statistically significant difference in tree density among the subplots. This implied that the variations in tree density across the study plot were not random. Fletcher and Fortin [23] have utilized methods such as the chi-square test and tree density mapping to suggest that underlying factors or conditions influence the spatial distribution of trees [23]. These factors could include variations in soil characteristics or microclimatic conditions [12]. The tree density map and the statistical analysis result support the conclusion that the habitat in our study plot is inhomogeneous. In other words, the study plot provides a variety of environmental conditions for the growth and development of tree species. Habitat filtering can be metaphorically viewed as a "filter" that precludes species from inhabiting mismatched environments, thus leading to the congregation of species sharing similar ecological characteristics [24]. Habitat filtering on the study plot has important ecological significance, as it can influence the composition and diversity of plant species and the interactions between plants and their habitat [25]. The spatial distribution of trees was closely linked to environmental conditions, including exposed rock, slope, canopy cover, and nutrients in the soil [26]. Different species exhibited distinct spatial distribution patterns in response to varying environmental conditions, which could include random, aggregated, and regular distribution patterns [19]. Within the same study plot, environmental heterogeneity only influenced the spatial distribution of certain species at a small scale [27]. However, it was the primary driver affecting the spatial distribution of all species at a large scale [28]. Habitat inhomogeneity in the study plot was a universal phenomenon in the tropical rainforest and was crucial in shaping the plant community [13]. Habitat filtering or habitat inhomogeneity contributes significantly to the differences observed in the forest stand across different locations, creating a spatial diversity pattern among species [24].

4.2. Spatial diversity patterns of species

Ecologists have devoted significant efforts to comprehending community assembly rules, vital in shaping nonrandom patterns within

multispecies assemblages. However, these assembly rules pose challenges due to limited experimental testing and ongoing controversies [29]. This issue stems from the fact that diverse mechanisms, both deterministic and stochastic, can produce similar patterns of species diversity [14]. Recent studies have utilized null models to address the issue above [30]. These statistical tools (null models) provide a means to test whether observed patterns are likely to occur without specific mechanisms, thereby contributing significantly to the community ecology.

In the current study, a combination of the ISAR model with null models of CSR and IPP was performed to assess the effect of tree species in the evergreen broadleaved forests on species richness at neighbourhood scales 0-50 m. The null model of IPP eradicates the habitat filtering effect, enabling a more robust investigation into how focal tree species help sustain the diversity of neighbouring species [12]. The analysis corresponding to the null model of IPP suggested that diversity accumulator and neutral species function in scales of 0-30 m. Most species still demonstrated a neutral effect on spatial scales exceeding 30 m, suggesting a neutral effect appears across both small and large scales. Our findings diverge from those of Ma et al. [31], as these authors postulated that species only exhibit neutral effects at spatial scales beyond 30 m. The presence of neutral species at small scales (0-30 m) in our study could be related to the ecological field theory [32]. This theory suggests that the distance between individuals determines the intensity of species interactions. The closer the individuals, the stronger the species interactions. Their interaction weakens as the distance between the tree and the tree increases. The ecological field is often paired with resource interference among plants. Hence, the neutral effect at small spatial scales could result from resource interference, subducting the overall interaction of species.

Our study findings also reiterated that species interaction mainly transpires at small scales < 30 m [33]. At the same time, the neutral effect dominates at large spatial scales, aligning with the neutral theory [7]. In contrast to the null model of IPP, the null model of

CSR considers the influence of environmental factors on the local diversity structure surrounding the focal species. The difference in the number of neutral species, diversity accumulator species, and diversity repeller species between the two null models, CSR and IPP, indicated a statistically significant distinction between these two null models. This difference underscored the significance of the local environmental conditions and species interactions in shaping the species diversity of the community. The difference between the two null models, as the paired sample t-test examined, indicated that habitat filtration significantly impacts species coexistence and aligns individuals with their suitable habitats. This study further corroborates that the niche theory is suitable for explaining tree species coexistence in the evergreen broadleaved forest. Since Hubbell introduced the neutral theory [34], debates have ensued over whether the niche or neutral theory provides a more compelling explanation for species coexistence. Our results accepted that both the niche theory and the neutral theory could elucidate the process of plant communities' diversity maintenance, and the relative contributions of both theories are related to the spatial diversity pattern of species. Furthermore, this study's findings underscore ecological field theory's role in illuminating tree species diversity within the evergreen broadleaved forest.

The present study found that diversity repeller species have a larger dbh than most neutral species or diversity accumulator species. This finding significantly reflected the principle of asymmetric competition and its essential role in explaining species coexistence in the study area. According to this principle [35], larger tree individuals often dominate resource allocation, which can negatively impact the growth and development of nearby trees. Consequently, species richness in the proximity of larger trees is usually low, and these larger trees are often diversity repellers.

5. CONCLUSIONS

In the present study, CSR and IPP null models, grounded in the ISAR framework, were utilized to delve into the hypothesized ecological mechanisms that underpin tree species coexistence in the evergreen

broadleaved forests of Con Dao Islands. These models incorporate the effects of habitat filtering (represented by the null model of CSR) and species interactions (represented by the null model of IPP). By analyzing data collected from 5,653 trees belonging to 64 plant families within a 4-hectare plot, our study elucidated several key findings: (1) There was a pronounced environmental heterogeneity in the investigated plot; (2) Both habitat filtering and species interactions played crucial roles in maintaining species diversity within the plant communities of the study area; (3) The local diversity structure of tree species was dependent on the spatial scale under consideration; and (4) Beyond just the niche and neutral theories, the ecological field theory and the principle of asymmetric competition also provided valuable insights into understanding tree species coexistence in the evergreen broadleaved forest.

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