Phylogenetic diversity patterns of woody species across different tree sizes and spatial scales in a tropical forest community on Con Dao Islands

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Mô hình đa dạng phát sinh loài thực vật thân gỗ theo các cấp kích thước cây và quy mô không gian trong quần xã cây rừng nhiệt đới trên đảo Côn Đảo

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ABSTRACT

Understanding the maintenance of diversity and the assembly of communities is a primary concern in community ecology. This study explored the phylogenetic structure of an evergreen broadleaved tree community in Con Dao National Park, Vietnam. The survey, conducted in December 2023, encompassed all tree individuals with a diameter at breast height (DBH) ≥ 2.5 cm within a 4-ha study plot. These individuals were identified by species name, and their DBH was measured. Subsequently, a community phylogenetic tree was constructed using the Phylomatic online platform. The 4-ha study plot was subdivided into there different subplots based on three spatial scales (25 m × 25 m, 50 m × 50 m, and 100 m × 100 m) and all trees were classified into three different DBH classes (2.5 cm ≤ DBH < 10 cm representing small trees; 10 cm ≤ DBH < 20 cm as medium trees; and DBH ≥ 20 cm as large trees). The net relatedness index (NRI) and net nearest taxon index (NTI) were utilized to evaluate the phylogenetic structure and infer ecological processes. Our findings revealed a consistent decrease in both NRI and NTI with increasing spatial scales and tree sizes. These results suggest an overdispersed phylogenetic structure within the community across different spatial scales and tree sizes. Additionally, negative density dependence was found to have a pronounced effect on the phylogenetic structure, with a more significant impact on tree individuals from small and medium DBH classes than large ones. This study underscores the significance of phylogenetic density dependence as a primary mechanism governing species diversity and shaping the community structure of evergreen broadleaved forests in Vietnam.

Keywords:
Density dependence, evergreen forest, neutral theory, phylogenetic structure, species coexistence.

***Từ khóa**:*
Cấu trúc phát sinh loài, lý thuyết trung lập, rừng thường xanh, sự chung sống của các loài, sự phụ thuộc vào mật độ.

TÓM TẮT

Cơ chế duy trì tính đa dạng và thúc đẩy sự chung sống của các loài luôn là chủ đề trọng tâm trong sinh thái học. Nghiên cứu này được thực hiện nhằm tìm hiểu cấu trúc phát sinh loài của quần xã cây rừng lá rộng thường xanh ở Vườn quốc gia Côn Đảo. Một cuộc điều tra thực địa đã được tiến hành trên ô tiêu chuẩn rộng 4 ha, trong đó tất cả các cây có đường kính ngang ngực (DBH) ≥ 2,5 cm được xác định tên loài và đo DBH. Cây phát sinh loài của quần xã được xây dựng trên công cụ hỗ trợ trực tuyến Phylomatic. Ô tiêu chuẩn được chia thành các ô thứ cấp theo ba quy mô không gian khác nhau (25 m × 25 m, 50 m × 50 m và 100 m × 100 m), trong khi các cây được nhóm vào một trong ba cấp kích thước DBH (cây nhỏ, cây nhỡ và cây lớn). Chỉ số mức độ liên quan họ hàng (NRI) và chỉ *số phân loại họ hàng gần nhất (NTI) được sử dụng để đánh giá cấu trúc phát sinh cũng như suy luận các quá trình sinh thái chi phối sự chung sống của các loài. Kết quả nghiên cứu chỉ ra rằng, các giá trị NRI và NTI liên tục giảm khi quy mô không gian và kích thước cây tăng lên. Cấu trúc phát sinh loài của quần xã biểu hiện phân tán trên các quy mô không gian và cấp kích thước cây khác nhau. Cơ chế phụ thuộc vào mật độ được chứng minh là ảnh hưởng đến cấu trúc phát sinh loài và tới các cây nhỏ và nhỡ nhiều hơn so với các cây lớn.*

1. INTRODUCTION

Global environmental changes and anthropogenic disturbances increasingly impact plant biodiversity and ecosystem functioning at regional and local scales [1]. Identifying the drivers that underlie the spatial distribution of biodiversity within local communities is a critical issue in ecology and conservation. It can also provide insights into community assembly mechanisms [2].

Over the past few decades, numerous theories have been proposed to elucidate the mechanisms behind constructing ecological communities and the underlying processes that govern species coexistence [3]. Among these theories, three fundamental mechanisms—niche-based processes (niche theory), neutral processes (neutral theory), and negative density-dependence (Janzen-Connell hypothesis)—have played pivotal roles in explaining the diversity of biological communities [4]. The niche theory postulates that various species demonstrate distinct resource utilization capabilities within a community [5]. According to this theory, species coexistence occurs when the distinctions in niches between species outweigh the differences in their fitness. Essentially, the niche theory underscores the significance of deterministic processes and resource partitioning in facilitating species co-occurrence.

In contrast, based on ecological equivalence, the neutral theory believes that all species within a community share equal levels of competitiveness, migration, birth, and death rates [6]. According to the neutral theory, species coexistence is regulated by probabilistic dispersal, ecological drift, or historical inertia [7]. The viewpoint of the neutral theory has challenged the traditional concept of niche differentiation and underscored the importance of stochastic processes in structuring the community [8]. The Janzen-Connell hypothesis is a prominent theory explaining plant species diversity in tropical forests [9, 10]. It posits that particular natural enemies decrease the survival of offspring when they are densely clustered around their parent plants, thereby providing less common species with a competitive advantage [11]. Initially, this concept suggests that mortality rates also disproportionately increase as plant density rises, leading to fewer offspring surviving beneath their parent plants [12]. Historically, early ecological theories tended to neglect the impact of evolutionary processes at the community scale [13]. However, there is a growing recognition that the regional evolutionary history and the species pool at the regional level significantly influence the structure of local communities [14]. Consequently, analyzing the evolutionary relationships among species within a community emerges as an indispensable component for comprehending the current configuration of the community.

Dobzhansky said, *"nothing in biology makes sense except in the light of evolution"* [15]. This statement is accurate as the species are not ecologically identical, and species interactions are governed by species function resulting from evolution [16]. The research methodologies used in evolutionary studies have expanded their scope into community ecology [17]. Integrating DNA sequence data to delineate evolutionary relationships among species enhances the assessment of community species composition [18]. This integration also plays a pivotal role in identifying niche conservatism, relying on the phylogenetic signal inherent in functional traits within the community [19]. This holistic approach facilitates a more comprehensive understanding of the mechanisms governing the construction of community biodiversity. Instead of relying solely on ecological similarities among species, researchers now leverage the phylogenetic relationships within a community to draw inferences about the underlying processes influencing species diversity [20]. In cases where habitat filtering predominantly influences ecological trait evolution, the result is clustering structures guided by phylogenetic conservatism [21]. Conversely, phylogenetic conservatism contributes to developing dispersion structures when competitive exclusion takes precedence [22]. In scenarios where neutral processes play a pivotal role, the distinctive outcome is the emergence of random community phylogenetic structures [23].

In community phylogenetic structure research, several measures of α-diversity, such as phylogenetic diversity, the net relatedness index (NRI), and the nearest taxon index (NTI), are commonly employed [24]. The NRI assesses phylogenetic relationships among different species within a group by quantifying the average phylogenetic distance among taxa on a phylogenetic tree. Conversely, the NTI gauges phylogenetic relationships by computing the average distance to the nearest taxon for terminal taxa on a phylogenetic tree. Both NRI and NTI serve as indicators of the degree of phylogenetic clustering. Positive values (above 0) for these indices indicate a higher degree of clustering than observed in a community randomly assembled from the available species pool, suggesting a more closely related phylogenetic structure. Conversely, negative values (below 0) for NRI and NTI imply that the species are more phylogenetically dispersed than in a randomly assembled community. When both NRI and NTI values are zero, the phylogenetic relationships within the community resemble those in a community formed randomly, indicative of a random phylogenetic structure [25].

The application of phylogenetic structural indices to investigate the mechanisms governing the coexistence of plant species holds significant importance in tropical forest research [26]. Nestled within Vietnam’s Ba Ria-Vung Tau province, Con Dao National Park is situated on the Con Dao Islands, approximately 80 km from the mainland. This region’s intricate interplay of climatic and topographic elements has fostered the convergence and amalgamation of diverse plant communities on the smaller islands scattered across the archipelago. Consequently, Con Dao National Park stands out as a distinctive area in southern Vietnam, characterized by its pristine ecological composition and species diversity, particularly compared to other locations within similar latitudes. Despite these notable distinctions, a research gap exists concerning the phylogenetic structures within the forest communities of this national park.

This study addresses specific inquiries through an analysis of the phylogenetic structure within the woody plant community, conducted across various spatial scales within a 4-ha study plot located in the evergreen broadleaved forest of Con Dao National Park. In particular, three questions were raised: (i) how does the phylogenetic structure vary across different null models and spatial scales? (ii) what specific variations can be identified in the phylogenetic structure concerning different diameter-at-breast-height classes of woody plant species at local spatial scales? (iii) what ecological mechanisms play a fundamental role in influencing the phylogenetic structure of the evergreen broadleaved forest community in Con Dao National Park?

2. RESEARCH METHODS

2.1. Study site

This study was conducted within Con Dao National Park, situated on the Con Dao Islands of Vietnam, specifically within Ba Ria-Vung Tau province [27]. Positioned between 8º36’-8º48’ North latitude and 106º31’-106º46’ East longitude, this national park spans a natural area of 19,883.15 ha, with 5,145.11 ha designated as forested areas. Situated approximately 80 km from the mainland, the national park experiences two distinct seasons: the rainy season from May to October and the dry season from November to April. The climate of the Con Dao Islands features an average annual temperature of 26.2ºC, with relative humidity often reaching 90%, and an annual rainfall of 2,200.3 mm [28]. The topography of Con Dao National Park mainly comprises low mountains ranging from 50 to 200 m *a.s.l*.

The study plot is distributed in an evergreen broadleaved forest, a typical vegetation type on the Con Dao Islands. The study area harbors a diverse array of broadleaved species. According to Quy et al.’s report, the dominant tree species in this area consist of *Knema pierrei* Warb., *Syzygium cumini* (L.) Skeels, *Garcinia celebica* L., *Arytera littoralis* Blume, *Diospyros silvatica* Roxb., *Pterospermum lanceifolium* Roxb., and *Xerospermum glabrum* Pierre [29].

2.2. Sample plot establishment and data collection

A 4-ha study plot was established within the evergreen broadleaved forest of Con Dao National Park. This primary plot was subdivided into 64 subplots, each measuring 25 m × 25 m. To enhance the granularity of the investigation, these subplots were further partitioned into 400 more minor subplots, each measuring 10 m × 10 m. Within these more minor subplots, a comprehensive survey focused on individual trees with a diameter at breast height (DBH) ≥ 2.5 cm. Systematic recording of essential details, including species identification and DBH measurements, was executed for each tree. Specimens were collected and sent to the herbarium at Con Dao National Park for tree identification and confirmation.

We utilized data from the field survey to strategically divide the 4-ha study plot into subplots characterized by three spatial scales: 25 m × 25 m, 50 m × 50 m, and 100 m × 100 m. The main objective of this study is to examine the correlation between the phylogenetic structure of the community and the various spatial scales employed. To investigate the dynamics of the phylogenetic structure across different DBH classes, all individual trees with a DBH of ≥ 2.5 cm in the 4-ha study plot were systematically sorted into three size classes: small (2.5 cm ≤ DBH < 10 cm), medium (10 cm ≤ DBH < 20 cm), and large (DBH ≥ 20 cm).

2.3. Phylogenetic tree construction

The phylogenetic tree, encompassing sixty-three tree species within a 4-ha study plot of Con Dao National Park, was constructed using the Phylomatic online platform (*http://www.phylodiversity.net*). This advanced tool, operating on the APG III system for classifying angiosperms, can automatically generate a phylogenetic tree when provided with data at the species, genus, and family levels [30]. To estimate the ages of these tree species, we consulted both fossil records and molecular data available in extensive databases. Furthermore, the ‘bladj’ algorithm, an integral component of the Phylocom software, was used to refine the lengths of the phylogenetic relationships among the studied plant species. The resultant phylogenetic tree, integrating these sixty-three species, is illustrated in Figure 1.

2.4. Phylogenetic community structure

In recent years, the net relatedness index

(NRI) and the nearest taxon index (NTI) have frequently been applied in examining the community phylogenetic structure [24]. These indices are valuable tools for investigating the intricate phylogenetic relationships within biological communities. Specifically, the NRI provides insight into the mean phylogenetic distance (MPD) among all possible pairs of species within a community. This metric (NRI) effectively characterizes the overall phylogenetic structure governing species formation within the community, excelling particularly in identifying instances of phylogenetic clustering. The NTI evaluates the mean nearest taxon distance (MNTD) between each species and its closest relatives. This index sheds light on the patterns of community phylogenetic relatedness among closely related species and demonstrates a heightened sensitivity in detecting instances of phylogenetic overdispersion. The NRI and NTI were calculated using the following formulas [17, 26]:

$$\mathrm{NRI} = -1 \times (\mathrm{MPD}_{obs} - \mathrm{mean}\ (\mathrm{MPD}_{null}))\ /\ \mathrm{sd}\ (\mathrm{MPD}_{null}) \qquad \text{(eq.1)}$$

$$\mathrm{NTI} = -1 \times (\mathrm{MNTD}_{obs} - \mathrm{mean}\ (\mathrm{MNTD}_{null}))\ /\mathrm{sd}\ (\mathrm{MNTD}_{null}) \qquad \text{(eq.2)}$$

where,

MPD_{obs} represents the observed mean phylogenetic distance;

MNTD_{obs} denotes the observed mean nearest taxon distance between all possible pairs of taxa in each subplot.

The mean (MPD_{null}) and mean (MNTD_{null}) are the average values derived from a null distribution, where species names were randomly shuffled on the tips of the community phylogeny 999 times. Subsequently, the MPD and MNTD values were calculated for each subplot at three scales: 25 m × 25 m (64 subplots), 50 m × 50 m (16 subplots), and 100 m × 100 m (4 subplots). Sd (MPD_{null}) and sd (MNTD_{null}) represent the standard deviations of MPD_{null} and MNTD_{null}, respectively. A positive NRI or NTI indicates that the community comprises closely related species with a clustered phylogenetic structure. Conversely, a negative NRI or NTI suggests that the species in the community are more distantly related than expected, indicating an overdispersed phylogenetic structure.

By comparing observed and simulated values of phylogenetic distance in each subplot at three scales: 25 m × 25 m (64 subplots), 50 m × 50 m (16 subplots), and 100 m × 100 m (4 subplots), this study aims to determine whether the community phylogenetic structure among different subplots at the same spatial scale is significantly overdispersion, clustered, or random. Each null model used in measuring phylogenetic structure corresponds to different assumptions and can be broadly categorized into unconstrained and constrained types [31]. The average phylogenetic distance and nearest taxon distance for all species pairs within a subplot are initially calculated for the unconstrained type (taxa labels). Subsequently, while keeping the total species count and individual counts constant, species names in the subplot are randomly sampled 999 times from the species pool. This process generates the distribution of average phylogenetic distance and nearest taxon distance for species within the subplot under the random null model. Finally, the observed values are standardized using the results from the random distribution. In the case of the constrained type, the independent swap algorithm is employed. This null model maintains the frequency of each species across different subplots and species richness within each subplot but alters the probability of co-occurrence between species. This is achieved by swapping grid points in a matrix representing pairs of species that co-occur or do not co-occur in plots (0, 1) and (1, 0), where 1/0 denotes the presence/absence of a species in a subplot.

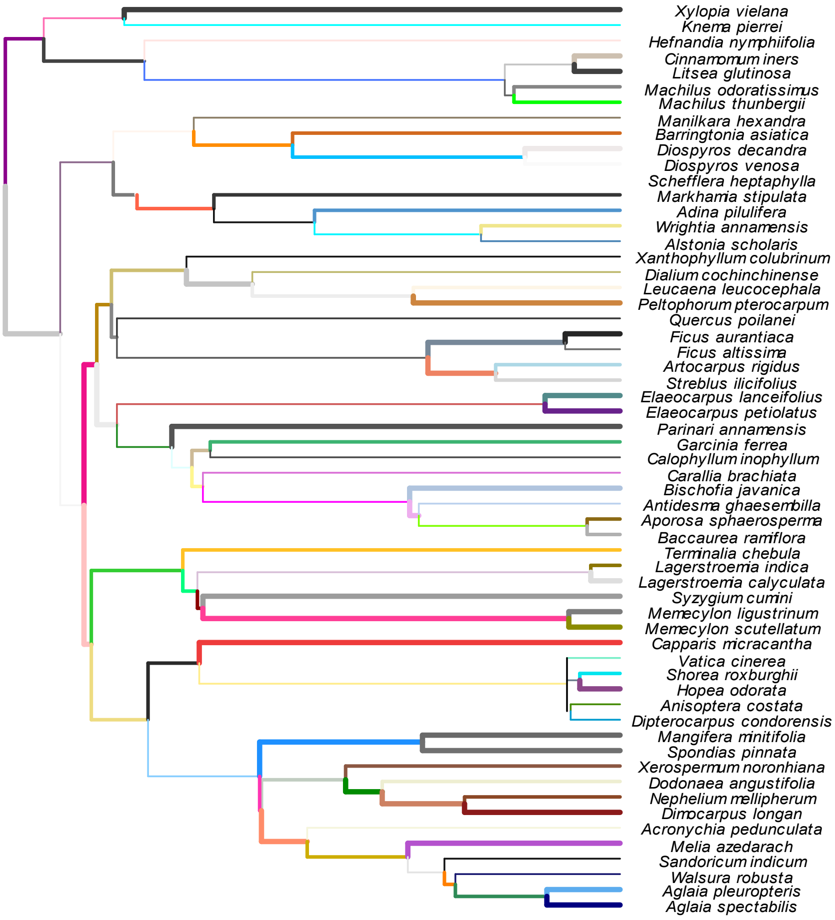

Figure 1. Phylogenetic relationship among sixty-three woody species of the evergreen broadleaved forest in Con Dao National Park

The NRI and NTI are utilized to signify the phylogenetic structure of species at the local scale, investigating the dynamic changes in phylogenetic structure as size classes increase and thereby delving into the mechanisms that influence the assembly of community species composition. The Wilcoxon rank-sum test method was used to examine whether statistically significant differences exist in paired NRI and NTI values between various spatial scales and tree size classes. The Wilcoxon rank-sum test was applied to calculate the test statistic by summing the ranks of absolute differences between observed values and the centre of the null hypothesis using different signs. This method is suitable for paired comparisons in t-tests, necessitating only a symmetric distribution of paired data differences without assuming a normal distribution. NRI and NTI indices are computed using the 'picante' package in R 4.3.3 [32].

3. RESULTS

3.1. Phylogenetic structure of tree community

A thorough analysis was conducted on 5,653 individual trees, each with a DBH of ≥2.5 cm, representing sixty-three tree species belonging to thirty-five families within a 4-ha study plot. Two null models, constrained and unconstrained, were applied across various spatial scales, as detailed in Tables 1 and 2.

The findings revealed a consistent decline in the values of NRI and NTI across different spatial scales under the constrained null model. Negative values of NRI and NTI at all three spatial scales indicated a phylogenetically overdispersed community. Furthermore, as the spatial scale increased, there was a significant reduction in both NRI and NTI values, suggesting increased phylogenetic overdispersion. The results also indicated a clustered phylogenetic structure of the community at the spatial scale of 25 m × 25 m under the unconstrained null model, while at spatial scales of 50 m × 50 m and 100 m × 100 m, the structure demonstrated overdispersion. This divergence in phylogenetic structure also became more pronounced with increased spatial scale.

Figure 2 illustrates the NRI and NTI values for subplots within the study plot under different null models and spatial scales. The results demonstrated that the community's phylogenetic structure comprised clustering and overdispersion across various null models and spatial scales. Under the constrained null model, most NRI and NTI values were negative, indicating a prevalence of subplots with a phylogenetically overdispersed structure. Moreover, the number of subplots with NRI and NTI values below zero increased with the spatial scale, signifying an intensification of phylogenetic overdispersion within the community. In contrast, NRI and NTI values were relatively evenly distributed under the unconstrained null model, yet the community's phylogenetic overdispersion escalated with increasing spatial scale under this null model.

Table 1. Mean pairwise phylogenetic distance (MPD) and net relatedness index (NRI) across various null models and spatial scales

Spatial scale	MPD.rand.mean	MPD.obs.mean	SD	NRI	Null model
25 m × 25 m	243.29	239.66	4.48	-0.81	Constrained
	239.29	239.66	6.23	0.06	Unconstrained
50 m × 50 m	239.69	236.86	3.04	-0.93	Constrained
	237.50	236.86	4	-0.16	Unconstrained
100 m × 100 m	237.98	235.45	2.04	-1.24	Constrained
	236.93	235.45	2.6	-0.57	Unconstrained

Note: MPD.rand.mean: Represents the mean Mean Pairwise Distance (MPD) in null communities, where MPD measures the average phylogenetic dissimilarity between species pairs; MPD.obs.mean: Denotes the mean observed MPD in the community, representing the average phylogenetic dissimilarity among species pairs in the actual community; SD: Stands for Standard Deviation, providing a measure of the amount of variation or dispersion in the data set, specifically applied to the MPD values in both null communities and the observed community.

Table 2. Mean nearest neighbor phylogenetic distance (MNND) and nearest taxon index (NTI) across various null models and spatial scales

Spatial scale	MNTD.rand.mean	MNTD.obs.mean	SD	NTI	Null model
25 m × 25 m	185.60	168.05	17.38	-1.01	Constrained
	166.60	168.05	20.68	0.07	Unconstrained
50 m × 50 m	151.98	137.24	12.93	-1.14	Constrained
	140.41	137.24	14.4	-0.22	Unconstrained
100 m × 100 m	127.33	115.2	8.6	-1.41	Constrained
	117.92	115.2	9.38	-0.29	Unconstrained

Note: MNTD.rand.mean: Represents the average Mean Nearest Taxon Distance (MNTD) observed in null communities; MNTD.obs.mean: Indicates the average observed MNTD within the community; SD: Stands for Standard Deviation, measuring the extent of variation in the dataset, typically applied to MNTD values in both null communities and the observed community.

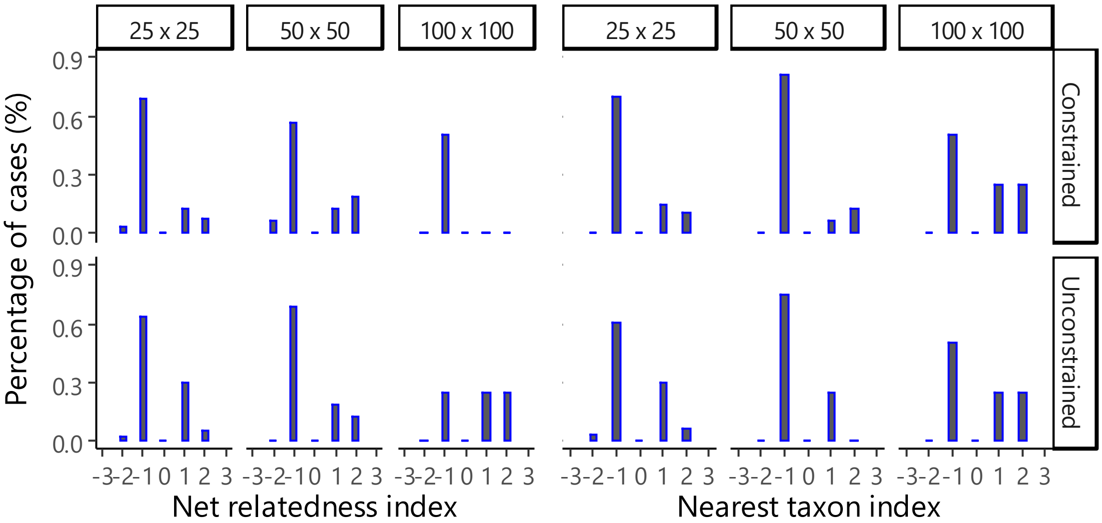

Figure 2. Distribution of NRI and NTI across various null models and spatial scales

3.2. Phylogenetic structure across different DBH classes

As the spatial scale expands, the NRI and NTI values within the evergreen broadleaved tree community gradually decline, transitioning from small to large DBH classes, as illustrated in Figure 3. Statistical analysis using the Wilcoxon rank-sum test revealed significant differences in NRI and NTI values among size classes at all three spatial scales ($p < 0.05$), with paired NRI and NTI values diminishing as tree size increases, as detailed in Table 3. This observed statistical significance persists consistently across all tree-size classes and spatial scales ($p < 0.05$). Both NRI and NTI values exhibit a continuous decrease with the expanding spatial scale, indicating a close association between the phylogenetic structure of species in the study plot and both tree size and spatial scale.

Figure 3 visually depicts that NRI and NTI values for tree individuals in small, medium, and large classes decreased as the spatial scale increased, signifying an augmentation in phylogenetic overdispersion with spatial scale. NRI and NTI values decreased within the same spatial scale as tree size increased, suggesting an intensified phylogenetic overdispersion within the community structure. Notably, the spatial scale significantly influenced the phylogenetic structure of small and medium tree-size classes. In contrast, its impact on NRI values in the large-size class was minimal, as evident from the slope of the trend lines in Figure 3.

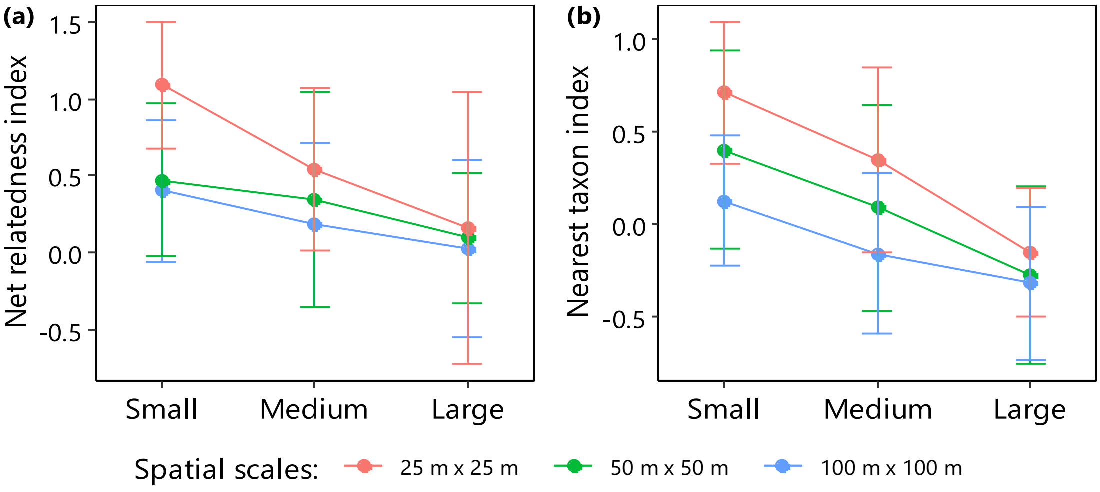

Figure 3. Dynamics of NRI (a) and NTI (b) across different DBH classes and spatial scales

Table 3. The relationship between phylogenetic structure, tree sizes, and spatial scales

Spatial scale and tree size		Model	Wilcoxon statistic	p-value
Spatial scale	25 m × 25 m	NRI vs. DBH	2624	2.20E-16
		NTI vs. DBH	2432	2.20E-16
	50 m × 50 m	NRI vs. DBH	256	3.90E-11
		NTI vs. DBH	128	4.28E-14
	100 m × 100 m	NRI vs. DBH	24	0.005772
		NTI vs. DBH	8	0.000224
Tree size	Small tree	NRI vs. scale	896	2.20E-16
		NTI vs. scale	552	2.20E-16
	Medium tree	NRI vs. scale	1284	2.38E-13
		NTI vs. scale	1108	2.78E-15
	Large tree	NRI vs. scale	1252	1.09E-13
		NTI vs. scale	788	2.20E-16

4. DISCUSSION

4.1. Phylogenetic structure of tree community

Analyzing phylogenetic diversity patterns by applying various null models offers an alternative avenue for understanding community assembly mechanisms [33]. Kembel and Hubbell's research highlights the potential pitfalls associated with null models, emphasizing the occurrence of Type I errors (overestimating significance) and Type II errors (underestimation of significance) in community phylogenetic diversity simulations [34]. Furthermore, Kembel et al. demonstrated that the constrained null model proves more effective in detecting phylogenetic structures in communities influenced by habitat filtering [35].

In our study, an unconstrained null model unveiled a clustered species assemblage within the phylogeny at the 25 m × 25 m spatial scale, employing a null model with shuffled taxa labels. This clustering aligns with niche theory, suggesting that habitat filtering fosters the coexistence of species with similar ecological traits, resulting in a phylogenetic structure characterized by clustering among closely related species [17]. Yuan et al. supplemented this notion, providing evidence that terrain and soil habitat differentiation accounted for variations in habitat among most species in their study [36]. Although habitat filtering influenced the phylogenetic structure at the 25 m × 25 m spatial scale under the unconstrained null model, its explanatory power was incomplete in our study. This was attributed to the observation that the phylogenetic structure exhibited overdispersion at the 25 m × 25 m spatial scale under the constrained null model.

The phylogenetic structure displayed overdispersion under two null models at larger spatial scales, precisely the 50 m × 50 m and 100 m × 100 m spatial scales. This aligns with previous studies, such as those by Wright and Webb et al., which underscored the role of negative density dependence among species at small spatial scales in maintaining species diversity within communities [37, 38]. Several studies have proposed that an increase in spatial scales promotes niche expansion, thereby enhancing the degree of aggregation in community phylogenetic structure [39, 40]. However, Bin et al. found that neutral processes were significant at the 50 m × 50 m spatial scales, while habitat filtering played a crucial role at the 100 m × 100 m spatial scale [41].

In our 4 ha study plot, the designated study scales were relatively small compared to the BCI forest [42]. Our findings also indicated that negative density dependence among species with similar or closely related phylogenetic relationships leads to mutual exclusion, contributing to the observed phylogenetic overdispersion structure of the community to some extent.

4.2. Phylogenetic structure across tree size classes

Through a detailed examination of the

phylogenetic structure across various tree size classes at specific spatial scales within the evergreen broadleaved forest on the Con Dao Islands, our study has revealed significant insights. The results unequivocally demonstrate a substantial reduction in the indices of community phylogenetic structure as tree sizes increase. Simultaneously, the intensity of phylogenetic overdispersion increases at large spatial scales, indicating the influence of negative density dependence on the spatial distribution patterns of plant populations within the study plot.

When examining different DBH classes, it becomes evident that smaller tree individuals in the study plot exhibit lower phylogenetic dispersion intensity than their larger counterparts. This observation suggests heightened competition among tree individuals in larger DBH classes. The DBH of trees serves as a temporal indicator of their growth. As tree DBH increases, the community's phylogenetic structure tends towards overdispersion, forming a close relationship with spatial scale [40]. This phenomenon may be attributed to limitations in seed dispersal from parent trees, where small and medium-sized individuals tend to aggregate [43]. With increasing tree DBH, competition intensifies among individuals, leading to augmented distances between them, resulting in phylogenetic overdispersion or evenness [44].

Spatial-temporal scale studies on the community's phylogenetic structure affirm that negative density dependence among species are crucial in influencing community renewal, tree spatial distribution patterns, and community structure [13, 38]. Consequently, negative density dependence is essential for maintaining species diversity within the evergreen broadleaved forest on the Con Dao Islands.

Our findings indicated that woody species' negative density dependence significantly influences species' phylogenetic structure with a DBH ≥ 2.5 cm in the Con Dao evergreen broadleaved forest at a spatial scale of 4 ha (local scale). However, our study still needs to provide conclusive evidence regarding whether negative density dependence impacts community phylogenetic structure at larger scales (regional scale). Besides, studies by Jansen et al. and Webb et al. have established that negative density dependence significantly influences the phylogenetic structure of communities from seed to seedling stages [38, 45]. Due to the absence of seedling data in the present study, the role of negative density dependence during the seedling stage in enhancing diversity and community phylogenetic structure is still conclusive. The research gap underscores the need for future studies to delve into the dynamics of evergreen broadleaved forests in Vietnam, explicitly addressing the abovementioned unresolved aspects.

5. CONCLUSION

Our study is one of the few attempts to connect ecological theory and community phylogenetics in Vietnam, which needs comprehensive, muti-scale empirical studies. We measured all trees with a DBH ≥ 2.5 cm within a 4-ha study plot in an evergreen broadleaved forest on Con Dao Islands. Subdividing the 4-ha study plot into subplots at various spatial scales and DBH classes allowed us to discern phylogenetic diversity patterns following tree size classes and spatial scales. Using the NRI and NTI indices, we uncovered a consistent decrease in both these phylogenetic diversity indices as spatial scales and tree sizes increased. This observation indicated an overdispersed phylogenetic structure across different spatial scales and tree-size classes. Furthermore, our findings showed the substantial impact of negative density dependence on phylogenetic structure, with a more pronounced influence on trees at small and medium DBH classes. This result emphasized the pivotal role of negative density dependence in driving species diversity and shaping the community structure. Our results are expected to a valuable reference on forest dynamics and contributed to conservation strategies to maintain the enduring stability of evergreen broadleaved forests in Vietnam.

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