Interspecific association patterns of woody species in an evergreen broadleaved forest of Con Dao National Park, Vietnam

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Mối quan hệ của các loài cây gỗ trong rừng lá rộng thường xanh ở Vườn quốc gia Côn Đảo, Việt Nam

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ABSTRACT

The interspecific associations among tree species in natural forest stands help to reveal mechanisms for maintaining species diversity and provide theoretical foundations for vegetation restoration and regeneration. This study focused on woody species within a 4-ha study plot established in an evergreen broadleaved forest in Con Dao National Park, Vietnam. We analyzed the interspecific associations among sixty-four recorded woody species in the study plot based on their presence and absence in subplots at two sampling scales: 10 m × 10 m and 20 m × 20 m. The results indicated that most of the 3,969 pairs of the sixty-four species exhibited independent associations, confirming an individualistic hypothesis proposed by Gleason. Furthermore, species interactions of common species were stronger than those of rare ones, indicating that species abundance influenced interspecific associations, and this result acknowledges the presence of random processes in driving species coexistence. A comparison of observed communities and random communities based on null models revealed that deterministic processes play a dominant role in governing species co-occurrence within the tree communities in the study area. Our study provides insights into the complex dynamics of species interactions within forest ecosystems, contributing to our understanding of biodiversity maintenance and offering valuable guidance for conservation and restoration efforts.

TÓM TẮT

Mối quan hệ giữa các loài cây trong rừng tự nhiên giúp tiết lộ các cơ chế duy trì sự đa dạng loài và cung cấp cơ sở lý thuyết cho việc phục hồi và tái thiết thảm thực vật. Nghiên cứu này tập trung vào các loài cây gỗ trong 01 ô tiêu chuẩn có diện tích 4 ha được thiết lập trong rừng lá rộng thường xanh ở Vườn Quốc gia Côn Đảo. Phân tích mối quan hệ giữa 64 loài cây ghi nhận trong ô nghiên cứu đã được thực hiện dựa trên sự xuất hiện và vắng mặt của chúng trong các ô thứ cấp ở hai quy mô lấy mẫu khác nhau. Kết quả nghiên cứu chỉ ra rằng, hầu hết trong số 3969 cặp của 64 loài có mối quan hệ độc lập, điều này thừa nhận một phần giả thuyết do Gleason đề xuất. Mặt khác, sự tương tác giữa các loài phổ biến mạnh hơn so với các loài hiếm, cho thấy rằng độ phong phú của loài ảnh hưởng đến các mối quan hệ loài và xác nhận sự có mặt của các yếu tố ngẫu nhiên trong việc thúc đẩy sự chung sống của các loài. Kết quả so sánh quần xã quan sát và các quần xã ngẫu nhiên dựa trên mô hình lý thuyết cho thấy các quá trình xác định đóng vai trò chủ đạo trong việc chi phối sự hiện diện của các loài cây trong quần xã ở khu vực nghiên cứu. Nghiên cứu này có thể được xem như tài liệu tham khảo có giá trị về động thái rừng lá rộng thường xanh, góp phần nâng cao hiểu biết về cơ chế chung sống của các loài cây rừng nhiệt đới.

1. INTRODUCTION

The formation and evolution of ecological communities depend on interspecific associations that arise from various factors, such as species interactions, co-actions within food chains, and shared responses to environmental pressures [1]. These associations are significantly shaped by species-specific trait differences and unique ecological strategies, which impact population dynamics and the overall functioning of ecological systems [2]. Studying interspecific associations provides valuable insights into species' intricate interactions and ecological relationships, thereby contributing to an enhanced understanding of community dynamics [3].

The formation of ecological communities is central to niche theory [4], which posits that these communities emerge through species colonization and coexistence within specific habitats, representing subsets of a broader regional species pool [5]. This intricate process is governed by environmental filtering and species interactions, giving rise to positive spatial associations when species share environmental preferences and traits shaped by filters [6]. Conversely, negative spatial associations may result from niche overlaps driven by competition or resource divergence [7]. Thus, community dynamics reflect a complex interplay of environmental factors and species interactions within ecosystems [8].

In contrast, neutral theory challenges the idea that species coexistence relies on niche distinctions, proposing instead that species assemble randomly, primarily constrained by dispersal limitations, thereby influencing community structure [9]. Recent studies underscore the significant role of stochastic events in shaping species coexistence dynamics [10]. Despite ongoing debates between niche and neutral theories regarding the mechanisms governing species coexistence, the prevailing consensus in community ecology emphasizes the importance of examining evidence related to deterministic and stochastic processes in

shaping natural community structures [11]. This investigative approach often involves using appropriate null models to evaluate patterns of species association [12].

In 1926, Gleason presented a viewpoint suggesting that species colonization occurs randomly, constrained only by their dispersal abilities [13]. Notably, Gleason argued for the independence of a species' spatial distribution, irrespective of the distribution patterns of other species. This conceptual model holds implications for understanding species' spatial relationships, leading to several expected outcomes. Firstly, in regions with high species diversity, if spatial variations in distribution are random, the variability in species numbers corresponds to the predicted value determined by each species' relative frequency. Secondly, most species exhibit independent associations without significant positive or negative interactions, indicating a lack of pronounced relationships. Lastly, common species demonstrate stronger interspecific associations compared to rarer ones, implying that the extent of interspecific associations depends on species abundance.

In contrast to Gleason's perspective, in 1916, Clements introduced the notion of superorganismic plant communities. This concept portrayed communities as organic amalgamations intricately regulated by habitat conditions and interspecific associations, marking a significant departure from prevailing viewpoints [14]. Clements' theoretical framework challenged Gleason's later proposed expectations, rendering them unsustainable within this paradigm shift. The ongoing discourse surrounding these differing perspectives underscores the critical need for additional empirical investigation to unravel the complexities of species interactions and distributions [15].

Island ecosystems offer unique opportunities to unravel the complexities inherent in plant communities due to their clearly defined boundaries, which facilitate a thorough exploration of the limitations on species dispersal [16]. This study focuses on

the woodland community of Con Son Island, situated within the Con Dao archipelago. The forest ecosystem on Con Son Island is distinguished by its vegetation, shaped by a tropical monsoon climate, and characterized by high species diversity.

Our study addresses three fundamental questions: (i) what are the interspecific associations among woody species within the Con Son Island forest community? (ii) does the strength of interspecific associations correlate with species abundance, explicitly investigating whether common species exhibit more robust associations? (iii) to what extent do stochastic processes influence the patterns of interspecific association? The outcomes of this study aim to shed light on the factors steering community assembly through spatial interactions among species. Additionally, it seeks to enhance our understanding of the mechanisms controlling interspecific associations and the processes that have structured the tree communities on the Con Dao Islands.

2. RESEARCH METHODS

2.1. Study area

The study was conducted within Con Dao National Park, located on the Con Dao Islands of Vietnam, specifically within Ba Ria-Vung Tau province. Spanning between 8º36'-8º48' North latitude and 106º31'-106º46' East longitude, this national park encompasses a natural area of 19,883.15 ha, with 5,145.11 ha designated as forested regions. Positioned approximately 80 km from the mainland, the park experiences two distinct seasons: the rainy season, from May to October, and the dry season, from November to April of the subsequent year. 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 [17].

Con Dao National Park's topography mainly consists of low mountains, with elevations ranging from 50 to 200 m a.s.l. The study area is situated within an evergreen broadleaved forest, a prevalent vegetation type on the Con Dao Islands, characterized by its diverse and abundant broadleaved tree species. According to Quy et al.'s report, dominant tree species in the study area include *Knema pierrei* Warb., *Syzygium cumini* (L.) Skeels, *Garcinia celebica* L., *Arytera littoralis* Blume, *Diospyros silvatica* Roxb., *Pterospermum lanceifolium* Roxb., and *Xerospermum glabrum* Pierre [17].

2.2. Data collection

The study plot is situated within the strict protection zone of Con Dao National Park, positioned at 8º43'15.33'' North latitude and 106º36'48.62'' East longitude. This intentional choice is aimed at eradicating human-induced disturbances, notably activities like woodcutting, non-timber forest product harvesting, and tourism. Furthermore, the core zone of this national park experiences relatively lower susceptibility to natural disasters such as storms and wildfires. Quy et al. assert that the core zone of reserves or national parks serves as a natural laboratory, providing ideal conditions for studying ecological dynamics in environments with minimal human impact [18].

The study conducted from March to July 2023 involved four field surveys utilizing a square-grid sampling technique to ensure precise and comprehensive data collection. The 4-ha study plot was divided into 100 subplots, each measuring 400 m^2. Data collection encompassed all trees with a diameter at breast height (dbh) ≥ 5 cm within each subplot.

Tree species identification in the subplots utilized a comparative morphology approach, supplemented by reference materials such as "Timber resources in Vietnam" and "An illustrated flora of Vietnam" [19, 20]. Tree species identification is carried out by taxonomic experts from the Vietnam National University of Forestry - Southern Campus. When uncertainties arise, specimens are gathered for comparison and the scientific names are reevaluated based on reference specimens housed at the herbarium of Con Dao National Park. Standardization of scientific nomenclature was achieved with

guidance from resources like the Plants of the World Online (*https://powo.science.kew.org*) and the World Flora Online (*http://www.worldfloraonline.org*). Tree dbh was measured using a diameter calliper, while the total height of each tree was recorded with a Blume-Leiss meter.

To establish relative coordinates, the origin of the reference system was set at the intersection of the two edges of the study plot in the north and south directions. A laser distance meter (Leica Disto-D2) and compass were employed to determine the relative coordinates of each tree within the study plot.

2.3. Data analysis

2.3.1. Importance value index

The importance value index (IVI) serves as a comprehensive metric to assess the relative significance of species within a forest community, reflecting their dominance in a specific plot. A species' IVI magnitude is directly proportional to its dominance within the plot. The calculation of IVI followed the equation [21]:

$$IVI = (Relative\ dominance + Relative\ abundance + Relative\ frequency) \times 100/3 \quad (eq.1)$$

$$Relative\ dominance = d_i / \sum_{i=1}^{S} d_i \qquad Relative\ abundance = n_i / \sum_{i=1}^{S} n_i$$

$$Relative\ frequency = f_i / \sum_{i=1}^{S} f_i \quad (eq.2)$$

where,

S represents the total number of species;

d_i corresponds to the basal area of the ith species;

n_i signifies the number of individuals of the ith species;

and f_i denotes the number of subplots in which the ith species occurred.

Species exerting significant ecological influence were identified as those with an IVI ≥ 5% within the 4-ha study plot. The collective IVI of tree species surpassing 50% was designated as the dominant species group within the forest stand [22].

2.3.2. Assessment of species associations

In this study, Schluter's variance ratio (VR) method was utilized to assess the independence of species spatial distribution. The calculation of VR is outlined as follows [23]:

$$VR = S_T^2 / \delta_T^2 = \left[\frac{1}{N} \sum_{i=1}^{N} (T_j - t)^2 \right] / \sum_{i=1}^{S} P_i \times (1 - P_i) \quad (eq.3)$$

$$P_i = \frac{n_i}{N} \quad W = VR \times N$$

where,

n_i represents the number of subplots containing species i;

N indicates the total number of subplots;

S represents the total number of species;

T_j signifies the number of species occurring in subplot j;

and t denotes the average number of species in subplots.

A VR value greater than 1 suggests a positive association among species, while a value less than 1 indicates a negative association. A VR value of 1 implies independence among species (non-association). The significance of interspecific association is determined by a non-significant interval (p > 0.05) when $\chi_{0.95(N)}^2 < W < \chi_{0.05(N)}^2$, where W is the VR calculated for all species. A significance level of *p* < 0.05 is assigned when W is either less than $\chi_{0.95(N)}^2$ or greater than $\chi_{0.05(N)}^2$.

Acknowledging the consensus from numerous studies that species association is contingent on spatial scale [2, 17], our current analysis explores interspecific associations among tree species at two distinct spatial scales. Specifically, we utilized 20 m × 20 m subplots as our primary analytical units, further dividing 100 of these subplots into 400 subsets of 10 m × 10 m each. This comprehensive analysis encompasses all sixty-four woody plant species within the expansive 4-ha study plot. We employed the association coefficient (AC) formulated by Hurlbert to quantify the strength of interspecific associations. The computational equation for AC is articulated as follows [24]:

$$AC = \begin{cases} (ad - bc)/\left[(a+b)(b+d)\right] & (ad \geq bc) \\ (ad - bc)/\left[(a+b)(a+c)\right] & (ad < bc,\ d \geq a) \quad \textit{(eq.4)} \\ (ad - bc)/\left[(b+d)(d+c)\right] & (bc > ad,\ d < a) \end{cases}$$

In equation 4, the variables are defined as follows: a represents the subplot where both species coexist, b denotes the count of subplots exclusive to species 1, c signifies the count of subplots complete to species 2, and d corresponds to the number of subplots where neither species is present.

The association coefficient (AC) falls within the [-1, 1] range. A higher AC value, approaching 1, indicates a stronger positive interspecific association, while a lower AC value nearing -1 suggests a more pronounced negative interspecific association. An AC value of 0 signifies a state of relative independence between species.

The significance of associations between paired species was assessed using the chi-square (χ^2) statistic, employing 2×2 contingency tables. The computation of the χ^2 value utilized Yates' correction equation, as detailed in equation 5 [25]:

$$\chi^2 = \frac{n\,(|ad - bc| - 0.5n)^2}{(a+b)\,(a+c)\,(b+d)\,(c+d)} \qquad \textit{(eq.5)}$$

where,

n denotes the total number of subplots;

and the definitions of a, b, c, and d align with those outlined in equation 4 for computing the strength of interspecific association.

If $\chi^2 < 3.841$ ($p > 0.05$), it implies insignificance in the interspecific association. When χ^2 falls between 3.841 and 6.635 (0.05 > $p > 0.01$), it indicates a certain association. Should $\chi^2 > 6.635$ ($p < 0.01$), it denotes a significant association.

To provide a more comprehensive understanding of interspecific associations within the community, a statistical analysis was conducted to calculate the proportion of species pairs showing positive or negative associations across all possible combinations. These proportions were then labelled as the ratio of positive to negative associations (PNR), the proportion of positive associations (PPA), or negative associations (PNA), respectively.

Additionally, the proportion of significant associations (PSA) was determined as the ratio of species pairs exhibiting statistically significant associations.

The present study aimed to test the hypothesis that species exhibit random distribution, exploring whether deterministic processes govern interspecific associations. This methodology imposed constraints on the frequencies of individual species and the total number of species within each subplot [26]. A process involving the random permutation of species occurrences across subplots was executed to examine the impact of randomness. This procedure was iterated 1,000 times to generate diverse random communities. Subsequently, the checkerboard score (C-score) was meticulously computed for 1,000 random communities [27]. Following this computation, a comparative analysis was conducted. Interspecific association values of the natural community were juxtaposed with the corresponding values derived from the randomized communities. The overarching objective was to ascertain whether the observed interspecific association features fell within or outside the 95% threshold established by the random communities. This systematic approach was deployed to evaluate whether interspecific associations within the authentic community exhibited notable deviations from the expected outcomes under the assumption of random distribution. The C-score detects non-random structure in the species assemblage data through a presence/absence data matrix. Higher average C-scores indicate low randomness, implying a greater likelihood that the presence of other species has directly influenced the distribution of one species. Thus, the C-score should be significantly higher for a competitively structured assemblage than a randomly assembled community.

In this research, statistical analyses were carried out employing R version 4.3.3 [28]. The computation of indices such as IVI, VR, AC, and Chi-square was facilitated using R packages "*BiodiversityR*" and "*spaa*." Additionally, the C-score and the null model calculations were conducted using the 'EcoSimR' package, explicitly utilizing the Sim9 (fixed-fixed) algorithm.

3. RESULTS

3.1. Interspecific associations among woody species

Within the 4-ha study plot established in the strictly protected zone of Con Dao National Park, a comprehensive inventory recorded 5,653 woody trees encompassing sixty-four species, fifty-five genera, and thirty-five plant families. Analysis conducted at the 10 m × 10 m spatial scale highlighted the dominance of seven species (IVI ≥ 5%), collectively constituting 10.9% of the total species. However, this number reduced to six species at the 20 m × 20 m spatial scale, representing 9.4% of the overall species. *Knema pierrei*, *Garcinia ferrea*, *Syzygium cumini*, *Nephelium mellipherum*, *Diospyros decandra*, and *Calophyllum inophyllum* emerged as the dominant species across both spatial scales. Most notably, the IVI ranking of these six dominant species remained consistent, with *Knema pierrei* maintaining the highest dominance and exhibiting IVI of 13.1% and 11.3% at the 10 m × 10 m and 20 m × 20 m spatial scales, respectively.

In the analysis involving 3,969 species pairs encompassing sixty-four distinct species, the PNA was 59.41%, representing 2,358 species pairs. At the same time, the PPA was 40.59%, comprising 1,611 pairs, at the 20 m × 20 m spatial scale. However, only 11.29% (448 pairs) of these associations exhibited statistical significance, indicating that the co-occurrence of 448 species pairs within the same community surpassed expectations based on their relative abundance. Most species pairs within the community (88.71%, corresponding to 3,521 species pairs) displayed no significant association. Furthermore, the overall association among the sixty-four species within the study plot leaned towards negative association (VR = 0.79, W = 78.82), suggesting that the species richness of the community was lower than anticipated based on the relative abundance of the species (Table 1).

The overall associations among species remained negative at the 10 m × 10 m spatial scale (VR = 0.91, W = 363.43). The PNA at this spatial scale was notably higher at 69.14%, with 2,744 species pairs demonstrating negative associations, whereas positive associations comprised 30.86% (1,125 pairs). Among the 3,969 species pairs analyzed, 777 (19.58%) exhibited significant associations, including 252 species pairs with substantial positive and 525 species pairs with significant negative associations. Nonetheless, most species pairs (3,192, accounting for 80.42% of the total species pairs) did not display substantial associations. Results from statistical analysis also showed that as the spatial scale increases, the PNR also tends to increase clearly (Table 1).

Table 1. Interspecific association among woody species across varied spatial scales

Statistical calculation	Spatial scale	
	10 m × 10 m	20 m × 20 m
Variance ratio (VR)	0.91	0.79
W-statistic	363.43	78.82
Ratio of positive to negative associations (PNR) (%)	44.63	68.32
Proportion of positive associations (PPA) (%)	30.86	40.59
Proportion of negative associations (PNA) (%)	69.14	59.41
Proportion of significant associations (PSA) (%)	19.58	11.29
Proportion of insignificant associations (%)	80.42	88.71
Proportion of significant positive associations (%)	6.35	3.32
Proportion of significant negative associations (%)	13.23	7.97

3.2. Correlation between strength of interspecific associations and importance value index

A significant positive correlation was observed between the strength of interspecific associations and the species' IVI across both spatial scales examined. At the 20 m × 20 m spatial scale, the coefficient of determination for this correlation was 0.38, indicating a significant relationship with a p-value of less than 0.01. Similarly, at the 10 m × 10 m spatial scale, the coefficient of determination was 0.41, also significant at the

$p < 0.01$ level (Fig. 1). These findings suggest that the interspecific association of species pairs is notably influenced by the frequency and abundance of the species involved. A higher co-occurrence of species pairs tends to yield a correlation coefficient closer to 1, indicating a strong positive association between the pairs. In contrast, a lower co-occurrence of species pairs, which suggests the presence of rarer species within the community, results in a correlation coefficient closer to -1, signifying a strong negative association between the pairs.
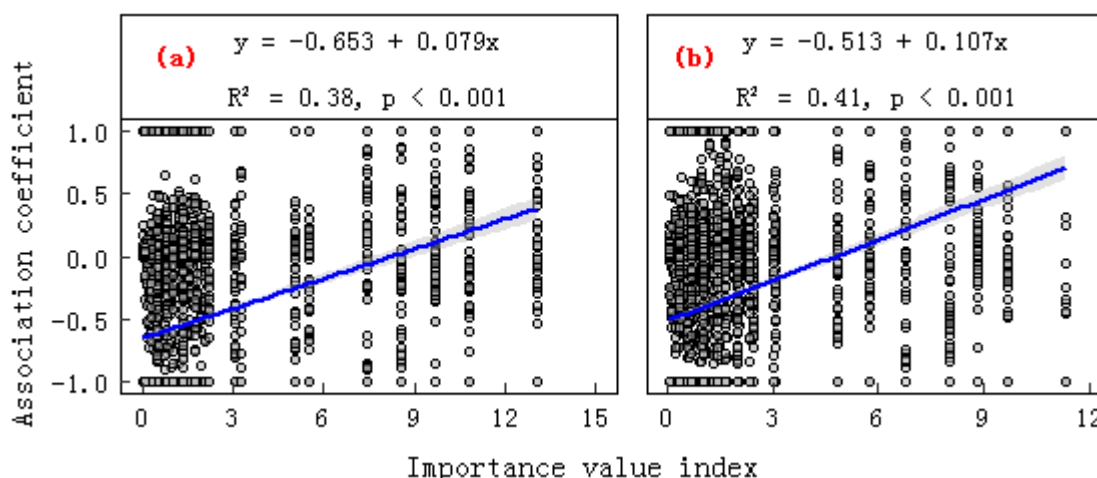

Figure 1. Relationship between IVI and species association strength (AC) across various spatial scales
(a) 10 m × 10 m and (b) 20 m × 20 m scales; grey circles represent the observed values, and the solid blue line indicates the regression function's trendline. Additionally, the 95% confidence interval is displayed as the grey area. R-squared (R^2) is a statistical measure that represents the proportion of variance in the dependent variable (association coefficient) that is explained by the independent variable (IVI) in a linear regression model; R^2 ranges from 0 to 1, with higher values indicating a better fit of the regression model to the data.

3.3. Relationship between interspecific associations and random processes

The expected C-scores were notably high in both spatial scales, indicating increased species segregation (Fig. 2). Co-occurrence analysis revealed significant deviations from a random pattern in species distribution across the two spatial scales. These findings suggested that one species's presence directly influences others' distribution. The studied community exhibited a competitive structure significantly different from a randomly assembled community.

4. DISCUSSIONS

For over a century, ecologists have engaged in a continuous discourse regarding the structural dynamics of ecological communities and the underlying mechanisms driving their

variability [12, 14]. This study delved into the intricacies of community organization within the evergreen broadleaved forest of Con Dao National Park. Analyzing 3,969 species pairs encompassing sixty-four distinct species, our findings highlighted noteworthy patterns. Specifically, at the spatial scale of 10 m × 10 m, 777 pairs, constituting 19.58% of the total pairs, exhibited significant associations, while at the 20 m × 20 m scale, 448 pairs (11.29% of the total) demonstrated significant associations. These outcomes strongly imply that a substantial portion of species within the study plot manifests independence from one another, corroborating earlier observations within the evergreen broadleaved forest of the study area [17, 18]. The implications of these results, to a certain extent, support

Gleason's individualistic hypothesis [13].

Traditionally, the prevailing notion attributed interspecies associations in ecological communities to species' ecological traits, habitat requirements, and niche differentiation at local scales [6, 18]. However, our results challenged this perspective. We uncovered a remarkably positive correlation between species' IVI and the strength of interspecific associations across various spatial scales. This observation suggested that species abundance significantly shapes interspecies associations, a trend consistent with numerous prior studies. For example, Lieberman and Lieberman, in their research on tropical forests in the Americas, observed a predictive relationship between species abundance and the likelihood of species pairs becoming nearest neighbors, with most species pairs' occurrence frequencies conforming to random expectations [29]. Similarly, He found analogous outcomes in examining the evergreen broadleaved forest in Heishiding Natural Reserve in Guangdong province, China [30]. These collective findings resonate with predictions from community random models, proposing that species coexistence partially emerges from stochastic diffusion and colonization processes [31, 32]. This insight fundamentally enriches our comprehension of species coexistence dynamics. It underscores that negative species associations aren't exclusively driven by dissimilar habitat preferences or interspecific exclusion [33]; instead, the restricted dispersal of rare species can lead to their spatial segregation, rendering them absent from most communities [34]. Conversely, positive species associations, stemming from shared habitat preferences and interspecific facilitation, reflect the net influence of niche effects on the heightened likelihood of overlap among common species [35].
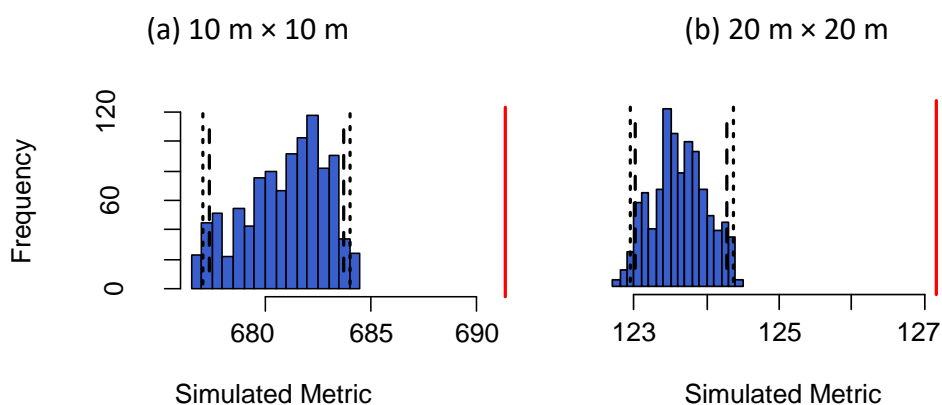

Figure 2. Comparisons of observed species associations and expected species associations

In each graph, blue bars are histograms of expected values for species co-occurrence (C-scores), the vertical red line indicates the observed value, long-dash lines indicate the one-tailed 95% limits, and the short-dash lines the two-tailed 95% limits.

In our study, a distinct pattern emerged when examining spatial scales, revealing a significant increase in the prevalence of positively associated species pairs compared to their negatively associated counterparts as spatial scales increased. This phenomenon is closely linked to the heightened presence of rare species, with a substantial proportion of the negative associations stemming from the dispersal limitations experienced by these less common species. Moreover, rare species tend to exhibit geographical confinement, resulting in spatially segregated distributions and thereby fostering a prevalence of negatively associated species pairs [36]. This finding corroborates the notion proposed by Zhou et al., suggesting that as community structure moves towards stability, the proportion of positive to negative associations tends to increase [37]. Community stability can be assessed through various methodologies, including environmental indicators, statistical

models, and mathematical simulations such as the Godron stability index [38]. By employing the method utilized in this study, which involves examining the variation of the positive-to-negative association ratio over different spatial scales to assess forest stand stability, this study introduced a novel approach to studying forests in Vietnam.

Additionally, our analysis uncovered a noticeable degree of covariance in the spatial distribution of species across both spatial scales (VR < 1). Furthermore, when considering a scenario where species form random communities amid conditions of random aggregation, the computed C-score indicates that the actual species segregation exceeds the 2.5%-97.5% threshold of 1,000 expected values of random communities. This highlights the substantial influence of niche-based processes in shaping the forest community within the study area concerning interspecies associations. Thus, the interplay among dispersal constraints, rarity-driven spatial isolation, and niche-based processes collectively shapes the observed associations and community structure within the forest stand under investigation.

5. CONCLUSIONS

This study has identified dominant species in the forest stand across various spatial scales, revealing no significant differences in their numbers. Additionally, the findings highlight a notable positive correlation between species abundance and the strength of interspecific associations. Specifically, common species are more likely to form strong pairwise associations. This suggests that robust associations are attributed to the higher abundance of the two species rather than solely arising from habitat convergence or species interactions. Furthermore, negative associations or the absence of associations between two species may be linked to the limited distribution ranges of rare species, resulting in spatial isolation rather than the commonly assumed differences in habitat adaptability or intense competition. Overall, beyond species' ecological habits, habitat requirements, and interspecific relationships,

species abundance is a crucial factor influencing interspecific associations. We argue that niche theory comprehensively elucidates the construction of forest communities and interspecific association patterns on the Con Dao Islands. Moreover, this study highlights, from the perspective of interspecific association, the significant roles of species independence and stochastic factors in shaping the coexistence patterns of species within the forest community in the study area. Finally, this study corroborates the findings of numerous previous investigations, emphasizing the critical importance of spatial scale in addressing issues related to forest ecology [39, 40].

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