SPATIAL DISTRIBUTION AND ASSOCIATION PATTERNS OF *HOPEA PIERREI* HANCE AND OTHER TREE SPECIES IN THE PHU QUOC ISLAND EVERGREEN BROADLEAVED FOREST OF VIETNAM

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Abstract. The present study was conducted to better understand the ecology, spatial patterns and associations of *Hopea pierrei* – a vulnerable plant in the Vietnam Red Book and on the IUCN's Red List – in the medium natural evergreen broadleaved forest of Phu Quoc National Park, Kien Giang Province, Vietnam. Data was collected from all woody tree individuals with a diameter at breast height (dbh) ≥ 2.5 cm in three 1-ha plots (100 m × 100 m). The spatial point-pattern analysis method was used to analyze the data with Programita Noviembre 2018 and R 4.1.1 software. Our findings suggested that *H. pierrei* was aggregated and randomly distributed at various scales in the area where it appeared. The spatial patterns of *H. pierrei* were influenced by environmental heterogeneity. The intraspecific associations of *H. pierrei* were mainly attraction associations, while its interspecific associations with sixteen dominant species were mainly independent. Processes such as seed dispersal and self-thinning are the main mechanisms underlying the spatial patterns and associations of *H. pierrei*. Based on the present findings, it is possible to regulate density and choose an appropriate planting-hole distance when restoring forests or planting new forests with *H. pierrei* and dominant species with which it grows.

Keywords: *threatened species, point-pattern, interspecific association, ecological characteristics, conservation planning*

Introduction

The spatial patterns of species and interspecies interactions at different spatial scales have been considered evidence reflecting the dynamics of stands over time (Hai and Bang, 2020). Over the past 50 years, ecologists around the world have proposed many hypotheses, such as Neutral theory, Niche theory, and the Janzen-Connell hypothesis, to explain the spatial pattern and association of forest tree species (Quy et al., 2021a). Among the proposed hypotheses, Neutral theory holds that all individuals in a community are strictly equivalent regarding their prospects of reproduction and death (Hubbell, 2001; Chave, 2004). Niche theory emphasizes that different species are best suited to different habitats in which they are completely dominant and more abundant than in less suitable habitats (Hubbell, 2005). Janzen (1970) and Connell (1971) hypothesized that host-specific pests reduce recruitment near conspecific adults, thus

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freeing up space for other plant species. Although different theories can explain the mechanism of species coexistence on a certain spatial and temporal scales, no theory can explain the coexistence of species in different communities on a global scale (Yao et al., 2018; Liza et al., 2014). Therefore, studying the mechanisms of plant species coexistence is still very challenging and requires further in-depth research.

Dien and Hai (2016) suggested that the spatial distribution pattern of a forest tree population can be determined as aggregated, random or regular based on the coordinates of tree individuals in the population. According to Tilman (2004), the spatial patterns of forest trees are explained by the influence of environmental heterogeneity and species equilibrium status depending on dispersal limitation and plant–plant interactions, such as competition or facilitation. In a tropical rainforest, intra- and interspecific interactions are more complicated than in other forest types because this forest type has a very diverse tree species composition but a low density of each species (Dien and Hai, 2016; Quy et al., 2021a). Spatial point-pattern analysis (SPPA) in ecological research uses forest tree individuals with coordinate pairs to represent points on a two-dimensional spatial plane from which we can learn the arrangement or spatial patterns and associations among them in a space bandwidth (Franklin et al., 2010; Ben-Said, 2021). However, the application of SPPA to explain the role of theoretical ecological processes that affect the spatial distribution and association patterns of forest tree species is still limited, especially in Vietnam as well as many other tropical countries in Southeast Asia (Ben-Said, 2021; Quy et al., 2021a).

The Dipterocarpaceae family has 16 genera with 515 species; there are 13 genera with 470 species in Asia (Ashton, 1982; Bawa, 1998). The tree species of the Dipterocarpaceae family play important ecological and economic roles in Southeast Asian tropical rainforests (Trung, 1999; Turner, 2001). In Vietnam, Dipterocarpaceae species are mainly distributed in the South and Central Highlands regions (Con, 1991; Linh, 1996). The studies of Trung (1985) and Them (1992) showed that a region of South Vietnam has an evergreen forest type belonging to the flora of Malaysia - Indonesia with tree species of the Dipterocarpaceae family dominating; these tree species are mainly large timber trees, often used in construction, house building, handicraft production, and household appliances as well as for export. Dipterocarpaceae species are usually distributed at altitudes below 1,000 m a.s.l (Bunyavejchevin, 1983; Loc and Hiep, 1987). Forty-two species of the Dipterocarpaceae family have been recorded in Vietnam, many of which are of high conservation value and are included in the Vietnam Red Book (2007) and the IUCN’s Red List (Nghia, 2003; Long et al., 2018).

Hopea pierrei Hance belongs to the genus *Hopea* of the Dipterocarpaceae family (Hop, 2002; Huy et al., 2012). This species is naturally distributed in Southeast Asian countries, including Cambodia, Laos, Malaysia, Indonesia, Thailand, and Vietnam. *H. pierrei* grows and develops well on red–yellow Feralit soil, but its ability to adapt to harsh environmental conditions is poor. *H. pierrei* is very sensitive to toxic chemicals (Appanah et al., 1998); therefore, *H. pierrei* forests in South Vietnam, Laos, and Cambodia were devastated during the Vietnam War (Ho, 1999; Ban et al., 2007). Adult trees of *H. pierrei* produce many fruits, the ability to regenerate by seeds is good, and juvenile trees are shade tolerant, whereas adult trees are light demanding (Ho, 1999; Hop, 2002). *H. pierrei* wood is hard, fine-grained, very durable in the air, not subject to termites, often used in construction and shipbuilding, and very valuable in the domestic consumption and export markets (Hop and Quynh, 2003). *H. pierrei* is a native species of Vietnam that is naturally distributed in some provinces, such as Thua Thien Hue, Dak Lak, Kien Giang, and Ho Chi Minh provinces (Lan et al., 2006). The number of *H. pierrei* individuals in the wild is low; the distribution area is narrow due to the influence of previous wars and illegal logging (Ban et al., 2007). *H. pierrei* is one of the twenty-eight species of plants prioritized for conservation in Vietnam and is listed in Vietnam Red Book (2007) and on the IUCN's Red List (2017) as "Vulnerable" due to many threats (Ban et al., 2007). Research on the ecological characteristics of *H. pierrei* in Vietnam and around the world is relatively limited, and most previous studies focused on its geographical distribution and description for species identification. There have been no studies using SPPA method to assess the ecological characteristics of this species in Southeast Asian tropical rainforests in general and in Vietnam in particular. Therefore, this study was carried out to provide in-depth scientific information for the conservation of the species *H. pierrei*.

We used SPPA method to explore the spatial patterns and associations of *H. pierrei* in the medium natural evergreen broadleaved forest belonging to Phu Quoc National Park, Phu Quoc Island, Kien Giang Province, Vietnam. The present study was focused on four (4) research questions: (i) In Phu Quoc Island evergreen broadleaved forests, which species often grow with *H. pierrei*, and what are their ecological roles? (ii) Are the spatial patterns of *H. pierrei* affected by environmental conditions? (iii) What is the difference between the intra- and interspecific associations of *H. pierrei*? (iv) Which underlying ecological mechanisms explain the spatial patterns and associations of *H. pierrei* and other tree species?

We will elucidate the ecological processes that help *H. pierrei* dominate in the area where it is distributed, and the findings will also provide information about the ecological characteristics of *H. pierrei* to serve as a basis for developing silvicultural measures to restore forests and expand the distribution area of this species.

Materials and methods

Study area

The study was conducted from March 2021 to July 2021 with three field surveys in Phu Quoc National Park, Phu Quoc Island, Phu Quoc District, Kien Giang Province, Vietnam (10°12'7" to 10°27'2" North latitude, 103°50'4" to 104°04'40" East longitude) (*Fig. 1)*.

The total forest land area under management by Phu Quoc National Park is 29,135.9 ha. Phu Quoc Island is located in a tropical monsoon climate zone with an equatorial nature but is strongly influenced by ocean dynamics, with two distinct seasons: the rainy season (from May to October) and the dry season (from November to April of the next year). The average temperature is 27.1 °C, while the average rainfall is 3,037 mm. The average wind speed is 3.9 m/s, with two main wind directions during the year: the prevailing East-North monsoon in the dry season (wind speed 2.8-4.0 m/s) and the West-South wind prevailing in the rainy season (wind speed 3.0-5.1 m/s). Strong winds on the island often occur in June-August, and the highest wind speed is up to 31.7 m/s. The elevation of the terrain decreases from north to south and west to east, ranging from 20-603 m a.s.l., with slopes of 5-45° (Quan et al., 2014).

The study plots are located in the restricted area of Phu Quoc National Park, which is less affected by human activities than other areas. Coordinates of the plots were as follows (*Fig. 2*): Plot 1 (Plot 1 - P1), 10°26'12.50" N latitude, 103°59'42.52" E longitude; Plot 2 (Plot 2 - P2), 10°23’2.80” N latitude, 104° 0’47.03” E longitude; and Plot 3 (Plot 3 - P3), 10°20’50.43” N latitude, 104° 3’17.40” E longitude. The dominant plant species in the study area include *Hopea pierrei, Diospyros venosa, Syzygium cuminii, Memecylon ligustrinum, Garcinia delpyana, Olea dioica, Garcinia vilersiana, Syzygium cuminii, Syzygium zeylanicum,* and *Diospyros sylvatica* (Quan et al., 2014).

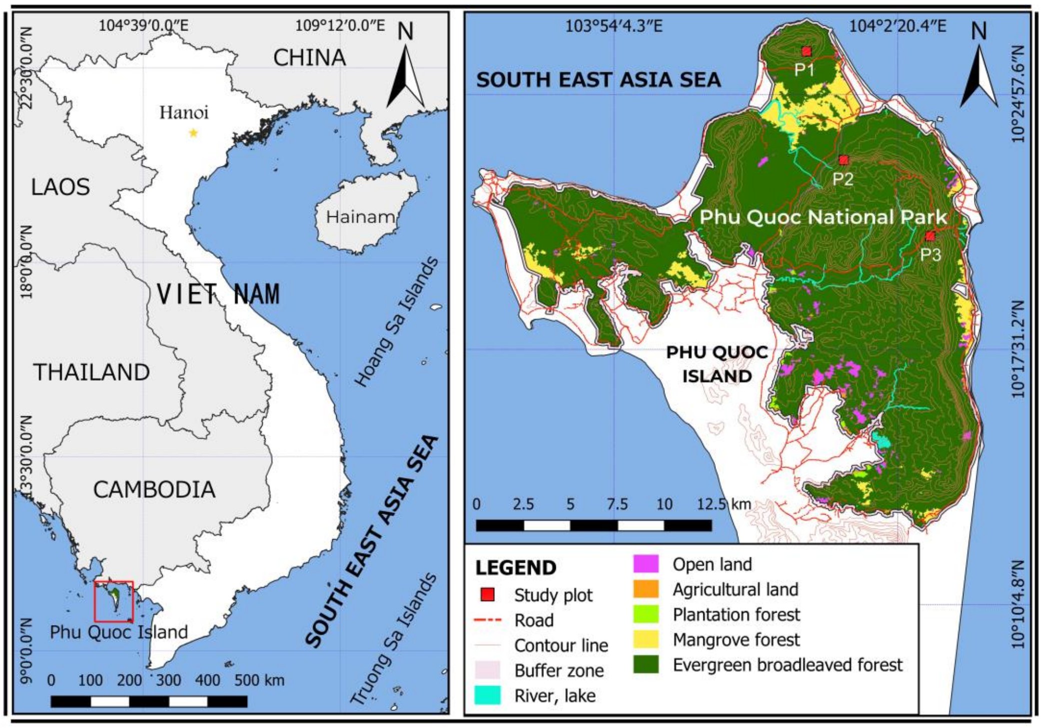

Figure 1. *Map of the study area. Maps of Vietnam (left) and Phu Quoc Island (right)*

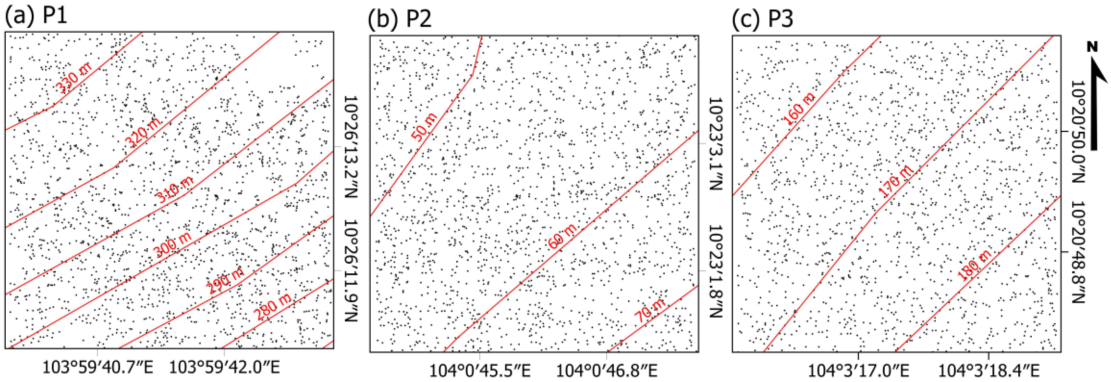

Figure 2. *Distribution maps of investigated trees in the three 1-ha study plots with 10 m contour lines of altitude (red lines)*

Data collection

In the study area, we selected stands where *H. pierrei* trees were concentrated and dominant to establish three 1-ha plots (100 m × 100 m). Using the square grid method, each plot was divided into 25 subplots; each subplot had an area of 400 m^2 (20 m ×

20 m) to facilitate the survey and data collection and avoid missing investigated trees. In the subplot, information was collected for all tree individuals with a diameter at breast height (diameter at breast height - dbh) ≥ 2.5 cm, including the name of the tree species; dbh was measured by a diameter caliper, canopy diameter was measured with a measuring tape in two directions (east-west and south-north), and the overall height of trees (overall height of trees - H) was measured by a Blume-Leiss meter. The intersection point between the two edges of the plot in the north and south directions was taken as the origin according to the reference system, and the relative coordinates of each tree in the plot were determined by a laser distance meter (Leica Disto - D2) and compass.

Identification of tree species

The tree species were identified by the comparative morphology method, and the references used included Plants of Vietnam (Ho, 1999) and Vietnam Forest Trees (Hop, 2002). The scientific names of the species were corrected according to Kew Royal Botanic Gardens (http://www.plantsoftheworldonline.org), the World Flora Online (http://104.198.148.243).

All individual trees were assigned to one of three basic life-history stages, namely, juvenile (dbh < 5 cm), subadult (5 cm ≤ dbh < 10 cm), or adult (dbh ≥ 10 cm). The identification of trees was performed in the field during the plot inventory. When a tree could not be identified to species in the field, voucher specimens were collected, prepared, and subsequently identified by taxonomic specialists after the fieldwork.

Data analysis

Different parameters were calculated as below:

$$\mathbf{d} = \frac{n_i}{S} \qquad \text{(Eq.1)}$$

where d is the stem density of species i (the number of individual trees ha^{-1}), n_i is the total number of individual trees calculated for species i (the number of individual trees) and S is the study plot area (in ha) (Brower et al., 1997).

$$\mathbf{BA} = \boldsymbol{\pi} \times \mathbf{r^2} = \frac{3.142 \times dbh^2}{200^2} \qquad \text{(Eq.2)}$$

where BA is the tree basal area (m^2), r is the radius and dbh is the diameter at breast height (cm) (Brower et al., 1997).

$$\mathbf{V = H \times BA \times F} \qquad \text{(Eq.3)}$$

where V is the tree volume (m^3), H is the overall height of the tree (m), and F is the form factor.

Dominance was calculated by the important value index (IVI%) of the species through the number of individual trees and tree basal area. IVI% was calculated for all tree species in the stand with a dbh ≥ 2.5 cm according to the following formula:

$$\mathbf{IVI\%} = \frac{RD + RBA}{2} \qquad \text{(Eq.4)}$$

where RD is the relative density and RBA is the relative basal area. The relative basal area is defined as the total basal area of species i as a percent of the total basal area of all species. The ecological value of a species in a forest stand is obtained by determining its importance value index (Curtis and Macintosh, 1951).

According to Marmillod (1982), only tree species with an IVI% > 5% are truly ecologically significant in the stand. On the other hand, according to Trung (1978), a species group with a total value of IVI% ≥ 50% for the total number of species can be considered the dominant tree species group in the stand.

The evergreen broadleaved forest types of the study area were determined based on the volumes of the stand and Circular No. 33 issued in 2018, Circular of Vietnam Ministry of Agriculture and Rural Development: Regulations on survey and inventory and monitoring forest developments (Vietnam Ministry of Agriculture and Rural Development, 2018). In this classification, the rich forest type has a volume of > 200 m^3 ha^{-1}, the medium forest type has a volume of 100-200 m^3 ha^{-1}, and the poor forest type has a volume less than 100 m^3 ha^{-1}.

Analysis of spatial pattern and association

The data was analyzed by using Programita Noviembre 2018 (http://programita.org/) and R version 4.1.1 software (R Development Core Team, 2021). SPPA was performed using Programita software (Wiegand and Moloney, 2004). The package ‘spatstat’ implemented in R software was used to analyze spatial patterns and intra- and interspecific associations (Baddeley et al., 2015). We used the spatstat package to make a distribution map of all species in the study area, the pair-correlation function, Ripley’s K functions, and the L-function, as explained by many researchers worldwide (Dixon, 2002; Sotirios and Alan, 2005; Getzin et al., 2006; Bolibok, 2008; Nguyen, 2017; Wédjangon et al., 2020; Quy et al., 2021a, c).

The environmental homogeneity of the study plots was assessed based on the spatial pattern of all individual trees with a dbh ≥ 15 cm by comparing the results of the two functions $g_{11}(r)$ and $L_{11}(r)$ (Dien and Hai, 2016). Individual trees with a dbh ≥ 15 cm were selected because they are capable of living in all possible areas and have undergone natural selection. Heterogeneous environmental conditions will be reflected in the distribution heterogeneity of adult trees (Getzin et al., 2008; Hai et al., 2014). We assumed no interaction between the points in the patterns.

Based on the coordinates of all individuals of *H. pierrei* and other dominant species in the study plots, the univariate pair-correlation function $g_{11}(r)$ was used to analyze the spatial pattern of species. The bivariate pair-correlation function $g_{12}(r)$ was used to analyze the intraspecies associations of *H. pierrei* at the different life-history stages as well as the interspecies associations between *H. pierrei* and the other dominant species in the study plots. The pair correlation function g(r) is the derivative of Ripley’s K function given by $g(r) = K'(r)/(2\pi r)$, which shows the expected density of points at a distance r from any point (Ripley, 1976). According to the tree-tree distances, the function $g_{11}(r)$ (univariate pair-correlation function) describes the spatial distribution of trees at radius r using a standardized density. Consequently, when this parameter equals 1, it indicates complete spatial randomness, > 1 indicates aggregation, and < 1 indicates regularity at distance r among trees with the pattern. The function $g_{12}(r)$ (bivariate pair-correlation function) was used to describe the spatial association between two types of points. The function $g_{12}(r)$ is the expected density of points of type 2 at a distance r beginning from a randomly chosen point of type 1. Similar to the univariate version, =1 indicates independence, <1 indicates repulsion, and > 1 indicates attraction between two tree species at distance r (Nguyen et al., 2014).

To eliminate errors in the judgment of spatial distribution, when conducting the analysis, it is necessary to pay attention to the selection of the null model (the theoretical model used to test the homogeneity of the environmental conditions) (Tuan et al., 2018). The null models used in this study included the following: (1) The null model of complete spatial randomness (complete spatial randomness - CSR) was used for the univariate pair-correlation function $g_{11}(r)$ and $L_{11}(r)$ function of all individual trees with a dbh $\geq$ 15 cm in the plots. (2) The null model of inhomogeneous Poisson process (inhomogeneous Poisson process - IPP) was used to analyze the spatial patterns of species when the environment of the plots was heterogeneous; conversely, if the environment was homogeneous, then the null model of CSR was used. (3) The null model of independence was used to test for intra- and interspecific associations of *H. pierrei* at the different life-history stages and between *H. pierrei* and the dominant species in the stand by immobilizing the position of the type 1 points (species 1) and randomly moving the positions of all type 2 points (species 2) around type 1 points. The null model of independence was used in the analysis of the bivariate pair-correlation function $g_{12}(r)$; we assumed that the two point patterns were created by two independent processes.

Epanechnikov kernel estimation was used for the intensity function with a bandwidth radius R = 30 m and a ring width (bins) of 1 m to analyze the spatial distribution and association patterns of forest tree species (Dien and Hai, 2016). All spatial models were performed in Programita 2018 software with 999 Monte Carlo simulations, using the 5th lowest and highest values of the 999 simulations to build approximately 95% confidence intervals. The distribution map of forest tree species was created with the 'spatstat' (https://cran.r-project.org/web/packages/spatstat/) and 'ggplot2' packages (https://cran.r-project.org/web/packages/ggplot2/) in R 4.1.1 software. All the R scripts used in this study can be found on GitHub (https://github.com/quyforest/hopea-pierrei).

Results

Composition of tree species growing with H. pierrei and their ecological roles

A total of seventy-six species were identified in the three 1-ha study plots of the medium natural forest type in Phu Quoc National Park. The number of tree species did not differ significantly among the study plots, but the density and volume of the stands were significantly different. The forty-eight species recorded in P1 had the highest density but the lowest volume among the three study plots (2,049 individuals ha^{-1} and 144.1 m^3 ha^{-1}); the numbers of species in P2 and P3 were forty-five (1,884 individuals ha^{-1} with 176.3 m^3 ha^{-1}) and fifty-one (1,671 individuals ha^{-1}, 185.1 m^3 ha^{-1}), respectively. The species composition according to the IVI% value is shown in *Table 1*.

According to the species composition of the study plots expressed by IVI% values, *H. pierrei* along with eleven other species, namely, *A. quocense, S. cuminii, S. roxburghii, S. cinereum, O. dioica, C. parthenoxylum, D. venosa, M. ligustrinum, S. superba, C. dryobalanoides,* and *D. sylvatica*, was an ecologically significant species (IVI% value > 5%). *H. pierrei* had the highest IVI% value in P2 (19.5%), and it combined with nine other dominant species (*S. cuminii, C. parthenoxylum, D. venosa, M. ligustrinum, S. roxburghii, O. dioica, G. delpyana, G. vilersiana,* and *D. sylvatica*) to form the dominant tree species group (total IVI% of the ten species > 50%). The IVI%

value of *H. pierrei* was lower than that of the other dominant species in P1 and P3, where it ranked 3rd (P1) and 2nd (P3); Additionally, in these two plots (P1 and P2), *H. pierrei* combined with twelve other dominant species to form another dominant species group. Based on the IVI% values of the dominant species, P3 had the fewest species in the three plots (forty-six species), but *H. pierrei* had the highest IVI% value, which indicates that its ability to assert spatial dominance was better than that of other dominant species and even better than its ability to do so in P1 and P2.

The values of N, dbh, H, BA, V, and IVI% for dominant species with ≥ 50 individual trees are shown in *Table A1* in the *Appendix*.

Table 1. *Composition of tree species in the stands*

Plot	S	**N**	**V**	**Composition of species by IVI% value**
P1	48	2,049	144.1	20.7 *Archidendron quocense* + 12.5 *Syzygium cinereum* + 8.0 *Hopea pierrei* + 6.7 *Olea dioica* + 5.2 *Shorea roxburghii* + 4.1 *Garcinia delpyana* + 4.1 *Syzygium zeylanicum* + 3.8 *Calophyllum dryobalanoides* + 3.8 *Diospyros sylvatica* + 3.6 *Memecylon ligustrinum* + 3.3 *Syzygium cuminii* + 3.2 *Gironniera cuspidata* + 3.1 *Diospyros venosa* + 34.3 Other species
P2	46	1,884	176.3	19.5 *Hopea pierrei* + 14.5 *Syzygium cuminii* + 5.7 *Cinnamomum parthenoxylum* + 5.1 *Diospyros venosa* + 5.1 *Memecylon ligustrinum* + 4.3 *Shorea roxburghii* + 3.9 *Olea dioica* + 3.6 *Garcinia delpyana* + 2.8 *Garcinia vilersiana* + 2.5 *Diospyros sylvatica* + 32.9 Other species
P3	51	1,671	185.1	13.7 *Archidendron quocense* + 11.9 *Hopea pierrei* + 10.3 *Schima superba* + 7.8 *Shorea roxburghii* + 7.6 *Calophyllum dryobalanoides* + 6.7 *Syzygium cuminii* + 5.5 *Diospyros sylvatica* + 4.7 *Olea dioica* + 3.9 *Diospyros venosa* + 3.7 *Vatica odorata* + 2.7 *Garcinia delpyana* + 2.5 *Memecylon ligustrinum* + 2.1 *Garcinia vilersiana* + 35.6 Other species

S - Number of species; N - number of individuals; IVI - importance value index expressed as a percentage; V – stand volume (m^3 ha^{-1})

Environmental heterogeneity effects

The results of testing the null model of CSR with the univariate function $L_{11}(r)$ showed that the cumulative density of all trees with a dbh ≥ 15 cm was similar in P2 and P3; these plots had no patterns of aggregation at scales of 5-30 m, and their spatial patterns were random (*Fig. 3f, i*); for P1, the opposite was true, with the adult trees showing an aggregated pattern at scales of 8-22 m (*Fig. 3c*). In addition, the univariate pair-correlation function $g_{11}(r)$ also showed that the adult trees in two plots (P2 and P3) followed a random pattern at scales of 0-30 m (*Fig. 3e, h*), but the adult trees in P1 showed all three patterns (aggregation, random, and regular) at scales of 0-30 m (*Fig. 3b*). In addition, the distribution map of the adult trees in P2 and P3 showed that the adult trees were distributed in most of the locations in these two study plots (*Fig. 3d, g*), whereas the adult trees were not distributed in many locations of P1 (*Fig. 3a*). According to the test results of the two functions $g_{11}(r)$ and $L_{11}(r)$, the hypothesis about environmental homogeneity could be rejected for P1 and accepted for P2 and P3. Therefore, the null models that were selected to perform the spatial pattern and association analysis of the species were the null model of IPP (P1) and the null model of CSR (P2 and P3).

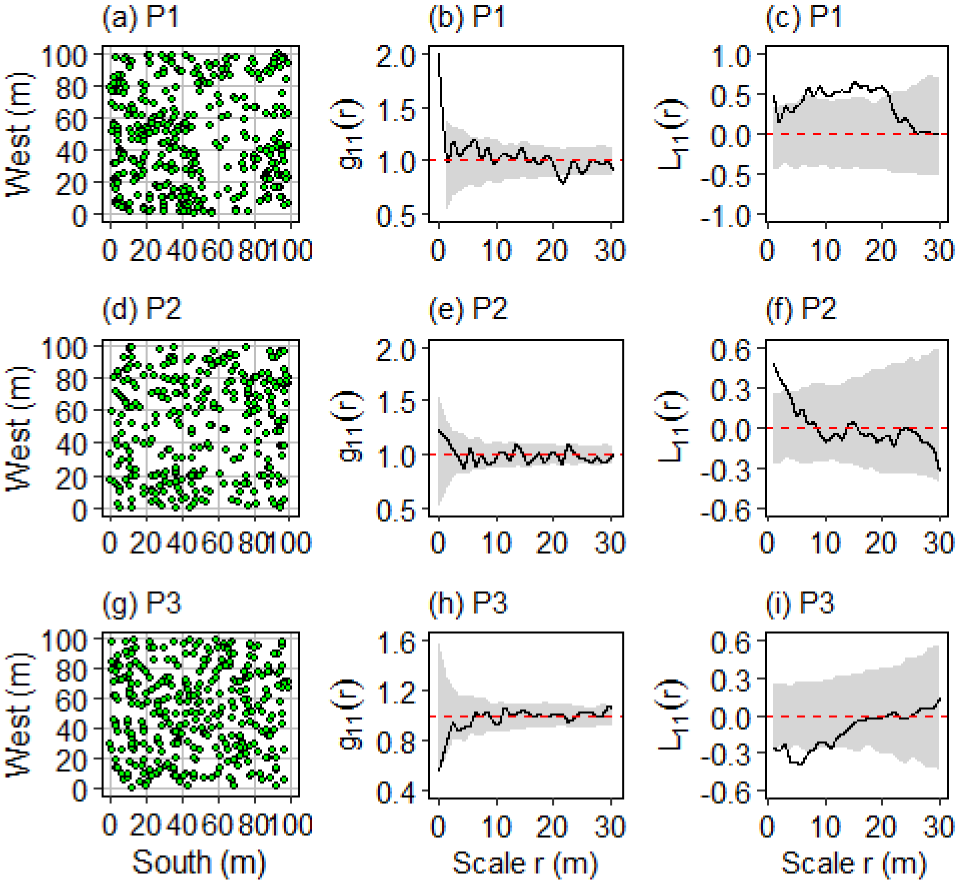

Figure 3. *Distribution map and spatial pattern of all individual trees with a dbh ≥ 15 cm in the study plots (they were analyzed by functions $g_{11}(r)$ and $L_{11}(r)$ under the null model of CSR. The dark line lying beyond the confidence envelope region (gray area) indicates a significant departure from the null model of CSR. The gray envelope region is the $p = 0.05$ confidence intervals from 999 Monte Carlo simulations (values < 1 indicate regularity; values > 1 indicate aggregation; values = 1 indicate randomness). The red dashed line is the expectation for spatial randomness between individual trees*

Spatial patterns of H. pierrei

The results of spatial pattern analysis of *H. pierrei* showed that all individual trees of this species showed only an aggregated pattern at scales of 0-30 m in a heterogeneous environment (*Fig. 4b*). However, individual trees of *H. pierrei* showed both aggregated and random patterns when the environment was homogeneous (*Fig. 4d, f*), and aggregation was found at scales of < 20 m. On the other hand, the distribution map of all individuals of *H. pierrei* showed that this species was highly concentrated in the eastern part of the study plot, where the elevation was lower than that in other locations in the plot (*Fig. 4*). This result showed that the same species, in this case *H. pierrei*, can exhibit a spatial pattern that differs among plots in a study area and it proved that heterogeneous environmental conditions significantly affected the spatial pattern of the study species.

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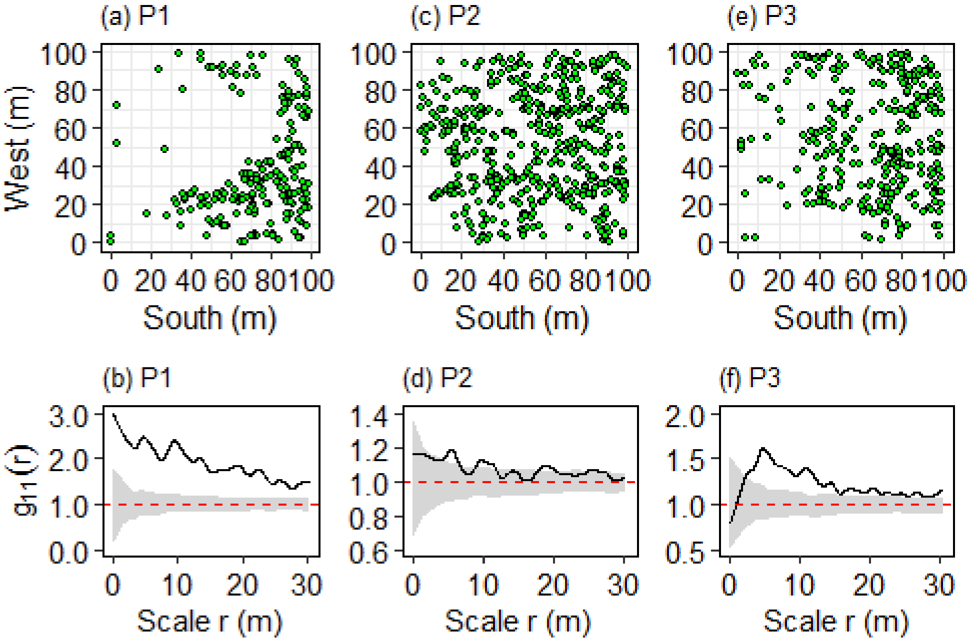

Figure 4. *Distribution map and spatial pattern of all individual trees of H. pierrei in the plots. The dark line lying beyond the confidence envelope region (gray area) indicates a significant departure from the null model. The gray envelope region is the p = 0.05 confidence intervals from 999 Monte Carlo simulations (values < 1 indicate regularity; values > 1 indicate aggregation; values = 1 indicate randomness). The red dashed line is the expectation for spatial randomness between individual trees of H. pierrei species*

The spatial patterns of *H. pierrei* at the different life-history stages are shown in *Figure 5,* in which *Figure 5a-c* show the spatial distribution patterns of the individual trees of this species in a heterogeneous environment under the null model of IPP (P1) and *Figure 5d-i* show the case of environmental homogeneity under the null model of CSR (P2 and P3). Just as the spatial pattern of all the individual trees of *H. pierrei* was considered above (*Fig. 4*), the spatial patterns of this tree species also showed a very clear difference among life history-stages when the environmental conditions in the study plot were variable. For the case of environmental homogeneity, the spatial pattern of *H. pierrei* tended to change from aggregation at the juvenile stage (*Fig. 5d, g*) to random at the subadult stage (*Fig. 5e, h*) and regular at the adult stage (*Fig. 5f, i*). In the case of environmental heterogeneity, *H. pierrei* showed only an aggregated pattern at the juvenile tree stage but an aggregated and random pattern at the subadult and adult stages, respectively (*Fig. 5a, b, c*).

Intraspecific associations of H. pierrei

The intraspecific associations of *H. pierrei* were analyzed using the bivariate pair-correlation function $g_{12}(r)$ (*Fig. 6*). The results showed that attraction associations accounted for a high proportion of 88.89% (eight of nine patterns) of the total associations. The repulsion association accounted for 11.11% (one of nine patterns) of the total associations. There was no repulsion in the intraspecific associations of *H. pierrei* with environmental homogeneity (*Fig. 6d-i*). Conversely, under environmental heterogeneity (*Fig. 6a-c*), there was repulsion in the intraspecific associations of *H.*

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pierrei, which was found between subadult and juvenile trees (*Fig. 6c*). If environmental heterogeneity was ignored, there were only attraction associations among the intraspecific associations of *H. pierrei* at all life-history stages (*Fig. 6d-i*).

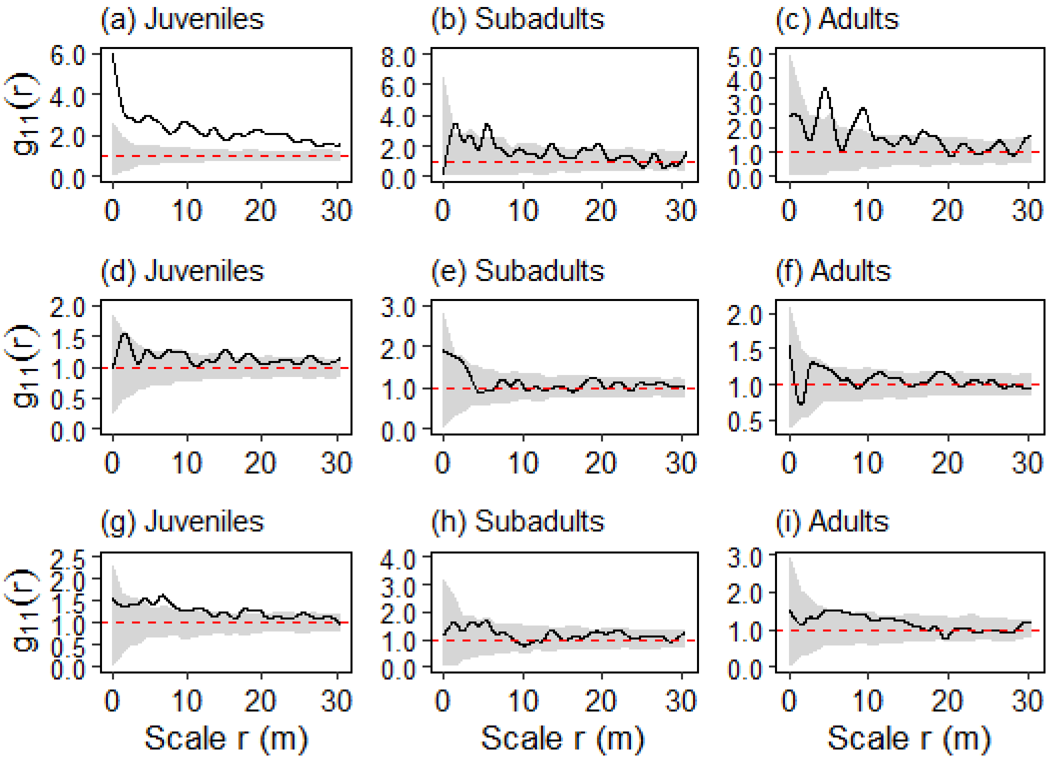

Figure 5. *Spatial distribution patterns of H. pierrei at different life-history stages in P1 (a-c), P2 (d-f), and P3 (g-i). The dark line lying beyond the confidence envelope region (gray area) indicates a significant departure from the null model. The gray envelope region is the p = 0.05 confidence intervals from 999 Monte Carlo simulations (values < 1 indicate regularity; values > 1 indicate aggregation; values = 1 indicate randomness). The red dashed line is the expectation for spatial randomness between individual trees of H. pierrei species at each life-history stage*

Interspecific associations of H. pierrei

The results of the spatial associations between *H. pierrei* and the species of the dominant species group in the three study plots (*Fig. 7*) showed that the majority of dominant species had an independent association with *H. pierrei* at scales of 0-30 m. An attraction association was found mainly at scales > 15 m. In contrast, a repulsion association was found at scales < 15 m. There was a difference in the interspecific associations of *H. pierrei* when the environmental conditions of the study plot changed. Under conditions of environmental heterogeneity, the number of species that had an independent association with *H. pierrei* tended to decrease as the scale increased; conversely, under conditions of environmental homogeneity, the number of species that had an independent association with *H. pierrei* tended to increase with increasing scale. Among the sixteen dominant species tested for associations with *H. pierrei* (*Figs. A1, A2, A3* in the *Appendix*), seven showed repulsion associations at all scales within 0-30 m, including *A. quocense, O. dioica, D. sylvatica, D. venosa, M. ligustrinum, S.*

roxburghii, and *V. odorata*. Three species showed attraction associations at scales < 20 m, including *S. cinereum*, *G. delpyana*, and *S. superba*.

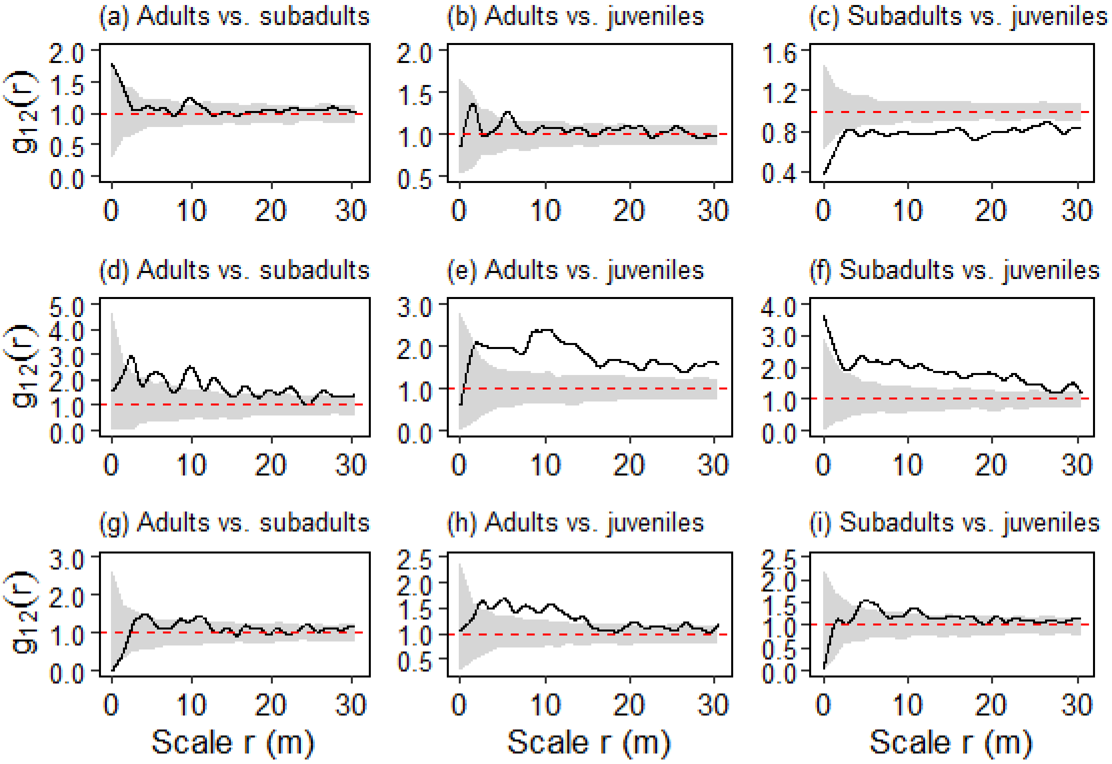

Figure 6. *Intraspecific associations of H. pierrei of P1 (a-c), P2 (d-f), and P3 (g-i) as analyzed by the bivariate pair-correlation function $g_{12}(r)$. The dark line lying beyond the confidence envelope region (gray area) indicates a significant departure from the null model of independence. The gray envelope region is the p = 0.05 confidence intervals from Monte Carlo simulations (values < 1 indicate repulsion; values > 1 indicate attraction; values = 1 indicate independence between two life-history stages). The red dashed line is the expectation for spatial independence between individual trees at two different life-history stages of H. pierrei*

Discussion

Tree species often growing with H. pierrei

In tropical forests, the tree species composition is very complex. To reflect the true status of the stand, it is necessary to identify the dominant tree species for management purposes (Quy et al., 2021b). The dominant species is the species that can significantly control forest plant community structure. The dominance of a tree species is expressed as the number of individuals of the species in the stand and the relative spatial relationship. The traditional methods of determining the predominance of tree species mainly use several ecological criteria of the tree species, such as the relative density, relative coverage, and relative total basal area of each species (Them, 2004; Hop et al., 2021). In addition, some authors believe that species composition may also reflect the dominant conditions of tree species in the stand (Quy et al., 2021b). Dominant tree species are the foundation of the entire forest plant community, and they greatly affect the stability of the community due to their high adaptability to the environment. The

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dominant species also determine the composition, morphology, and structure of the community, as well as the main features of the environment within the plant community (Thin, 2004).

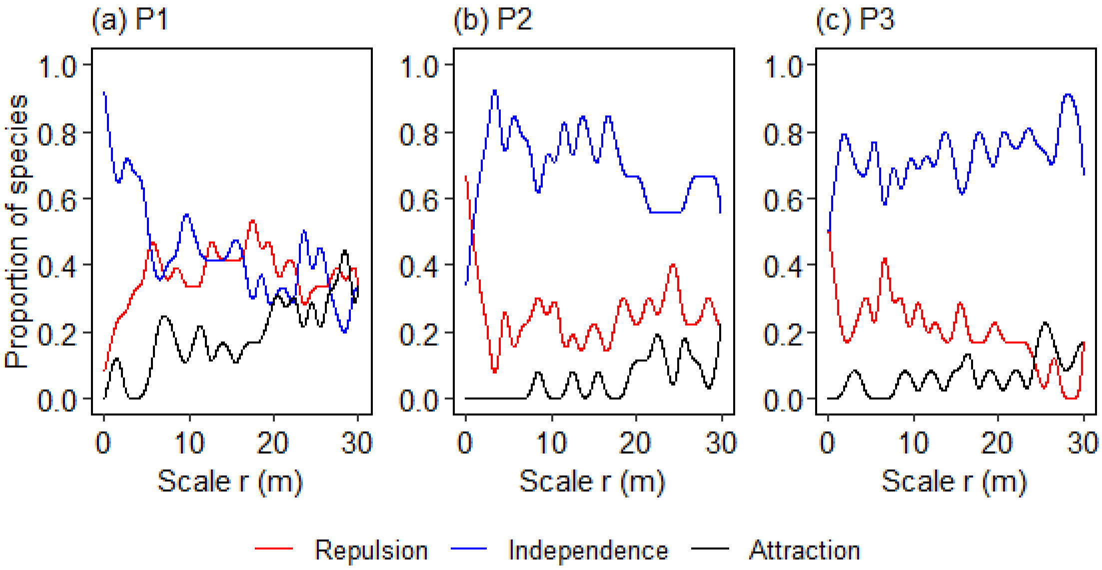

***Figure 7.** Interspecific association patterns of H. pierrei and the species of the dominant species group as analyzed by the bivariate pair-correlation function $g_{12}(r)$ under the null model of independence*

Each type of vegetation was formed in different environments, so there were different dominant tree species (Lan et al., 2006). The results of the dominance analysis of tree species in the three study plots showed that *H. pierrei* often grew with sixteen other species, namely, *A. quocense, S. cinereum, O. dioica, S. roxburghii, G. delpyana, S. zeylanicum, D. sylvatica, C. dryobalanoides, M. ligustrinum, S. cuminii, G. cuspidata, D. venosa, C. parthenoxylum, G. vilersiana, S. superba*, and *V. odorata*. *H. pierrei* combined with these sixteen species to form a typical forest ecosystem on Phu Quoc Island, Vietnam.

Environmental heterogeneity effects

The spatial pattern of plant populations can be affected by environmental heterogeneity, such as variation in exposed rocks, slope, canopy cover, and soil nutrients, and in such cases, populations will exhibit spatial patterns that are not the same in different environments, such as aggregated, random or regular patterns (Hu et al., 2019). Getzin et al. (2008) suggested that if forest trees were aggregated at scales of > 10 m, the aggregation could be explained by environmental heterogeneity. Environmental heterogeneity in the same study plot is a very common phenomenon in tropical rainforests, with the cumulative density of adult individuals tending to change from a random pattern to an aggregated pattern at scales greater than 20 m (Wiegand et al., 2007). Wu et al. (2018) also suggested that environmental heterogeneity played an important role in species spatial aggregation in a study on the spatial patterns and associations of the main tree species in the evergreen broadleaved forest of Zhejiang

Province, China. Similarly, Tuan et al. (2018) found that environmental heterogeneity in the study plots was the main reason for the large variation in the structural characteristics of the stand at different locations in the plot, thus creating spatial structural diversity of the research object. In our study, two *H. pierrei* populations (P2 and P3) showed both aggregated and random patterns when the null model of CSR was used as a theoretical model under environmental homogeneity. However, the spatial patterns of the *H. pierrei* population were only aggregation patterns at scales of 0-30 m when the null model of IPP was used as the theoretical model. In the results of environmental heterogeneity effects and the spatial patterns of *H. pierrei* in this study, we also found that environmental heterogeneity had a great influence on the spatial patterns of the studied species.

Spatial patterns of H. pierrei

The difference in spatial distribution patterns of plant species is often the result of the combined effects of many factors, such as the biological characteristics of the species, environmental factors, and especially the dispersal mechanism (Condit et al., 2000). Wu et al. (2018) found that *Cyclobalanopsis glauca* produces an acorn-like ovoid fruit, which combined with the steep slope of the study area, leads to the fruit and seeds of this species falling to the ground after a period and being driven to the foot of the mountain or places with shallower slopes and forming a clustered distribution at small scales. This phenomenon is very common in the Zhejiang evergreen broadleaved forest of China where the authors conducted the study. Hu et al. (2019) found that *Cunninghamia lanceolata* has a random distribution in all study plots at scales of 0-30 m because its seeds show low germination and the seedling survival rate is low, which causes the number of individuals of the species in the stand to be very low in the secondary forests of Hunan Province, China. Nguyen et al. (2014) also suggested that the dispersal limits of *Streblus macrophyllus* (fleshy fruit) regulated the spatial distribution patterns of this plant in the Cuc Phuong evergreen broadleaved forest of Vietnam. In our study, the spatial patterns of *H. pierrei* showed that this species was spatially aggregated at scales up to 20 m under environmental heterogeneity (*Fig. 2d, f*). On the other hand, based on the distribution map of *H. pierrei* and natural conditions in the study area, the spatial distribution patterns of *H. pierrei* were consistent with its ecological characteristics. *H. pierrei* produces a winged fruit (Ho, 1999; Ban et al., 2007); thus, *H. pierrei* has the ability to disperse seeds very well, and seedlings are often distributed far away from the mother tree and form a clumped distribution at large scales. On the other hand, the main wind direction on Phu Quoc Island is west-south, and this wind direction prevails in the rainy season (May-October); this is also the fruit ripening season of *H. pierrei*. Therefore, the number of *H. pierrei* individuals was more concentrated in the eastern area of the study plots than in the western area. The difference in the spatial distribution patterns of *H. pierrei* in the plots could be because P1 is located closer to the west coast of the island and P2 and P3 are located far inland and farther away from the west coast than P1.

The clumped distribution of *H. pierrei* at small scales is beneficial for juvenile trees at the early stage because this species is shade tolerant at this stage but will experience strong intraspecific competition for nutrients between individuals at later time points in the juvenile stage. Therefore, the opportunity for juvenile and subadult trees overtop the canopy of the mother plant is limited. For this reason, it is very important to develop appropriate silvicultural measures for increasing the number of *H. pierrei* adults in areas where juvenile and subadult trees can be placed in more suitable locations in the stand (under the canopy or near the mother tree) or in suitable parts of the ecological restoration area on Phu Quoc Island.

From the analysis results of the spatial distribution patterns of *H. pierrei*, it could be concluded that in addition to the influence of environmental heterogeneity, seed dispersal is a main determinant of the spatial distribution patterns of this species in the evergreen broadleaved forest in Phu Quoc National Park. In addition, the ecological characteristics of *H. pierrei* (a shade-tolerant plant at the juvenile stage) also showed that gap regeneration is not the mechanism explaining the spatial distribution pattern of *H. pierrei*. The spatial distribution of *H. pierrei* at different life-history stages showed a shift from a clustered distribution at the juvenile stage to a random distribution at the subadult stage and that there was strong competition between the adult individuals. The adult trees of *H. pierrei* were regularly distributed at scales of 2-3 m (*Fig. 5f*) and 18-19 m (*Fig. 5i*), which is evidence that *H. pierrei* has a self-thinning ability. Thus, self-thinning is also a mechanism underlying the spatial distribution pattern of *H. pierrei*.

Intra- and interspecific associations of H. pierrei

The spatial association patterns of forest tree species may reflect the biology of the population (Veblen et al., 1979). Hubbell (2001) suggested that direct tree-tree interactions occur at a distance of less than 30 m in the spatial association of forest tree species. The intraspecific association patterns of *H. pierrei* were mainly attraction patterns, accounting for 88.89%, while intraspecific competition accounted for 11.11% and occurred only when there was environmental heterogeneity. In our study, the association patterns between *H. pierrei* and the dominant species were mainly independent at scales of 0-30 m. Competition between *H. pierrei* and other dominant species was found at scales < 15 m. The results of our study are consistent with those of some previously published studies. Yang et al. (2014) found that the interspecies competitive relationship among plant species was mainly driven by competition for nutrients at small scales (<15 m) when studying the spatial association patterns of major tree species in the evergreen broadleaved secondary forest of Tai Bai Shan, China. Dien and Hai (2016) also found a competitive relationship between tree species in the evergreen broadleaved forest of A Luoi of Thua Thien - Hue Province, mainly at scales below 15 m. Hu et al. (2019) also suggested that competition or attraction relationships between species often appear at small scales; as the scale increases, the number of individuals in the large diameter class decreases, and the distance between them increases. Thus, most species are usually independent when considered at a large scale.

Conclusion

This study was conducted in the medium evergreen broadleaved forests of Phu Quoc National Park in Vietnam to understand the ecological mechanisms that regulate the spatial distribution and association patterns of *H. pierrei*. This Dipterocarpaceae species is a threatened species in South Asia, classified as “Vulnerable” in the Vietnam Red Book and on the IUCN’s Red List.

In the medium evergreen broadleaved forests of Phu Quoc National Park, *H. pierrei* often grows with sixteen dominant tree species, namely, *A. quocense, S. cinereum, O. dioica, S. roxburghii, G. delpyana, S. zeylanicum, D. sylvatica, C. dryobalanoides, M. ligustrinum, S. cuminii, G. cuspidata, D. venosa, C. parthenoxylum, G. vilersiana, S.*

superba, and *V. odorata*. The ability of *H. pierrei* to occupy space was better than that of other dominant tree species when it was not affected by environmental factors. *H. pierrei* had both spatial distribution patterns (clustered and random distributions) where it was distributed. The spatial distribution patterns of *H. pierrei* were strongly influenced by heterogeneous environmental conditions, and when the environment was heterogeneous, this species showed only a clustered distribution at scales of 0-30 m. The spatial distribution patterns of *H. pierrei* at different life-history stages showed a shift from a clustered distribution at the juvenile stage to a random distribution at the subadult stage and a regular distribution at the adult tree stage. Among the types of intraspecific associations, repulsion associations of *H. pierrei* at different life-history stages were very infrequent (11.11%) and only occurred when the environment in the study plot was not homogeneous; attraction associations accounted for a high proportion (88.89%). Regarding interspecific associations at a distance of 0-30 m, *H. pierrei* mainly had independent associations with dominant species. In addition, seven of the sixteen dominant species had repulsion associations with *H. pierrei* at all scales of 0-30 m, namely, *A. quocense, O. dioica, D. sylvatica, D. venosa, M. ligustrinum, S. roxburghii*, and *V. odorata*, and three of the sixteen dominant species had attraction associations with *H. pierrei* within $r < 20$ m, namely, *S. cinereum, G. delpyana*, and *S. superba*. Seed dispersal and self-thinning are the ecological mechanisms driving the spatial distribution and association patterns of *H. pierrei*, leading to the formation of a clustered distribution at scales > 20 m and individuals distributed more in the western part of the study plots.

When restoring or planting new forests, imitating the laws of the natural world is always a way to avoid risks and obtain good results early. The results of this study have great significance for adjusting the density of *H. pierrei* and its neighboring species. The adjustment should be in the direction of increasing the density of species that have an attraction association and reducing the density of the species that have a repulsion association with *H. pierrei*. In addition, the interspecific associations of *H. pierrei* should also be considered in order to build a plant list and select an appropriate planting hole-spacing when restoring a forest or planting a new forest to expand the distribution area of *H. pierrei* in areas similar to the study area.

Regarding future research on *H. pierrei*, we recommend focusing on the influence of environmental factors such as soil nutrients, soil moisture, and temperature on the spatial distribution of *H. pierrei*, which will allow data collected on the ecological characteristics of this tree species to be more systematic, complete and detailed.

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APPENDIX

Table A1. *Characteristics of dominant species in three study plots*

Plot	Tree species	N	dbh	H	BA	V	IVI
P1	*Archidendron quocense*	267	14.2 ± 7.7	13.2 ± 2.4	5.45	37.41	20.7
	Syzygium cinereum	300	10.3 ± 3.8	11.5 ± 1.7	2.84	15.8	12.5
	Hopea pierrei	199	9.9 ± 3.7	11.9 ± 1.7	1.73	9.98	8
	Olea dioica	152	10.8 ± 3.5	12.0 ± 1.7	1.53	8.84	6.7
	Shorea roxburghii	129	9.7 ± 4.2	11.4 ± 1.7	1.14	6.52	5.2
	Garcinia delpyana	125	8.9 ± 1.9	10.9 ± 1.3	0.82	4.12	4.1
	Syzygium zeylanicum	57	14.2 ± 6.9	12.4 ± 2.2	1.11	7.02	4.1
	Diospyros sylvatica	111	8.9 ± 3.0	11.0 ± 1.6	0.77	4.07	3.8
	Calophyllum dryobalanoides	85	10.2 ± 5.1	11.5 ± 2.4	0.87	5.33	3.8
	Memecylon ligustrinum	102	9.4 ± 3.4	9.8 ± 1.8	0.79	3.71	3.6
	Syzygium cuminii	65	11.6 ± 5.0	12.2 ± 2.1	0.82	4.8	3.3
	Gironniera cuspidata	79	10.0 ± 3.4	11.6 ± 2.0	0.69	3.9	3.2
	Diospyros venosa	94	8.6 ± 2.8	10.7 ± 1.6	0.6	3.07	3.1
	Thirteen dominant species	1765	10.7 ± 4.9	11.7 ± 2.1	19.15	114.57	82.2
	Thirty-five other species	284	12.4 ± 6.8	12.2 ± 2.4	4.47	29.53	17.8
	All (forty-eight species)	2049	10.9 ± 5.3	11.8 ± 2.1	23.62	144.1	100
P2	*Hopea pierrei*	464	10.3 ± 4.7	10.7 ± 2.5	4.7	27.75	19.5
	Syzygium cuminii	168	15.3 ± 9.6	12.1 ± 3.7	4.3	31.75	14.5
	Cinnamomum parthenoxylum	72	14.0 ± 9.1	12.3 ± 4.3	1.57	12.51	5.7
	Diospyros venosa	173	8.3 ± 1.9	9.2 ± 1.6	0.98	4.29	5.1
	Memecylon ligustrinum	155	9.2 ± 2.6	9.1 ± 1.9	1.11	4.85	5.1
	Shorea roxburghii	115	9.8 ± 3.6	10.0 ± 2.1	0.99	5.01	4.3
	Olea dioica	104	10.0 ± 3.1	10.2 ± 1.7	0.9	4.48	3.9
	Garcinia delpyana	107	9.4 ± 2.6	9.9 ± 1.3	0.8	3.75	3.6
	Garcinia vilersiana	84	9.2 ± 2.3	9.6 ± 1.7	0.6	2.7	2.8
	Diospyros sylvatica	69	9.3 ± 4.4	9.7 ± 2.0	0.57	2.92	2.5
	Ten dominant species	1511	10.5 ± 5.4	10.3 ± 2.6	16.51	100.02	67.1
	Thirty-six other species	373	14.1 ± 10.8	11.9 ± 4.3	9.2	76.28	32.9
	All (forty-six species)	1884	11.2 ± 7.0	10.6 ± 3.1	25.71	176.3	100
P3	Archidendron quocense	105	18.3 ± 11.1	16.6 ± 4.5	3.78	34.66	13.7
	Hopea pierrei	297	9.0 ± 4.3	12.1 ± 2.8	2.32	14.91	11.9
	Schima superba	63	21.5 ± 11.4	16.8 ± 4.9	2.92	27.43	10.3
	Shorea roxburghii	109	13.4 ± 7.4	13.9 ± 3.9	2	15.46	7.8
	Calophyllum dryobalanoides	73	15.6 ± 10.3	15.6 ± 5.3	1.98	18.45	7.6
	Syzygium cuminii	129	10.1 ± 6.6	12.5 ± 3.3	1.48	11.01	6.7
	Diospyros sylvatica	78	13.0 ± 8.3	12.9 ± 3.7	1.45	10.57	5.5
	Olea dioica	91	9.7 ± 6.6	12.6 ± 3.1	0.97	8.17	4.7
	Diospyros venosa	117	7.9 ± 2.7	11.0 ± 2.0	0.64	3.41	3.9
	Vatica odorata	63	11.6 ± 6.3	14.1 ± 3.9	0.86	6.58	3.7
	Garcinia delpyana	73	8.9 ± 3.1	11.6 ± 1.9	0.5	2.82	2.7
	Memecylon ligustrinum	62	9.4 ± 4.2	11.2 ± 2.4	0.51	2.98	2.5
	Garcinia vilersiana	71	6.9 ± 1.8	10.1 ± 1.3	0.28	1.32	2.1
	Thirteen dominant species	1331	11.4 ± 7.7	12.9 ± 3.8	19.68	157.76	64.4
	Thirty-eight other species	340	10.1 ± 6.3	12.1 ± 3.2	3.79	27.34	35.6
	All (fifty-one species)	1671	11.1 ± 7.5	12.8 ± 3.7	23.47	185.1	100

N - number of individuals; dbh - diameter at breast height (mean ± Standard deviation) (cm); H - overall height of tree (mean ± Standard deviation) (m); BA - Tree basal area (m^2); V – stand volume (m^3 ha-^{1}); IVI - importance value index expressed as a percentage

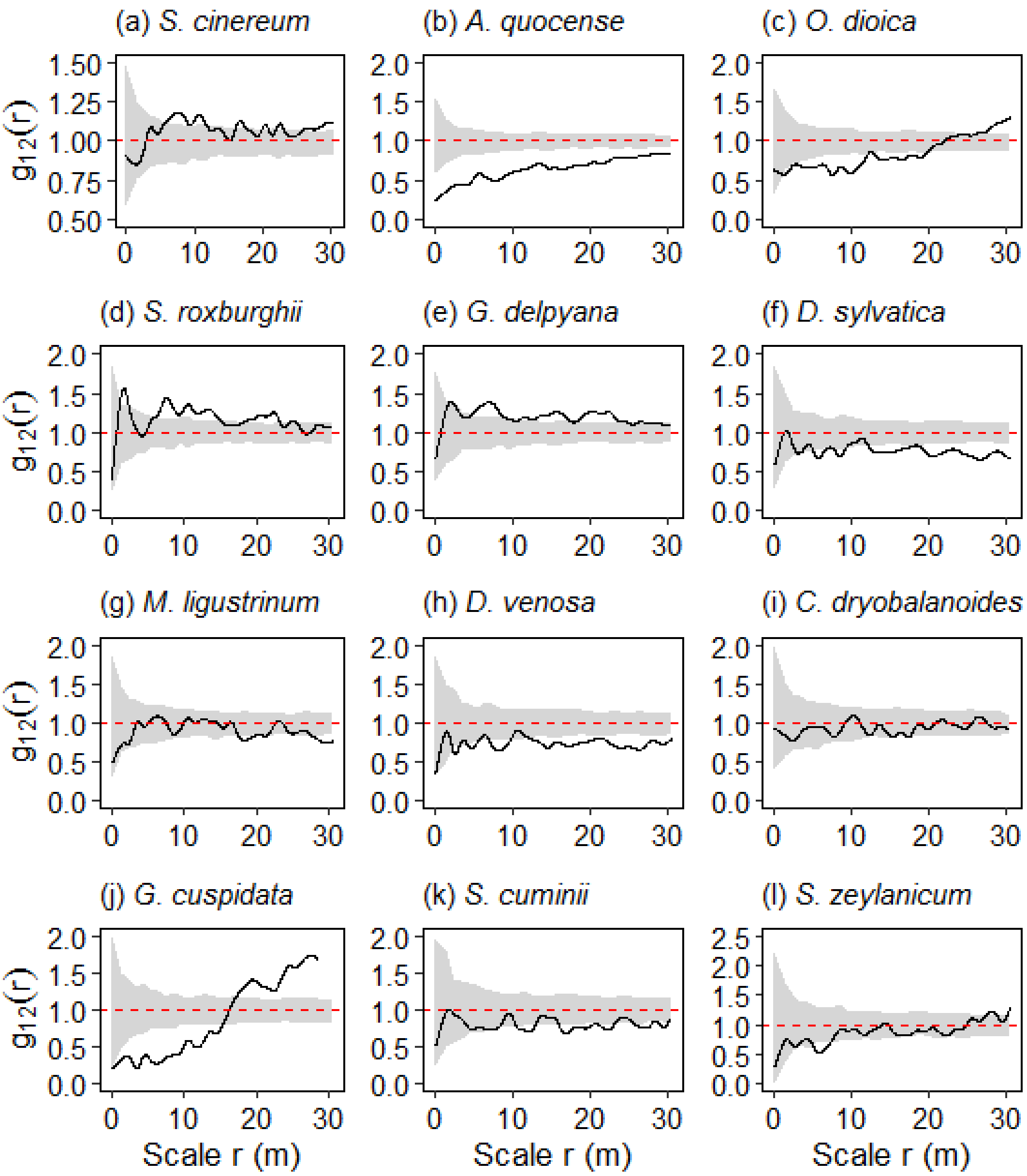

Figure A1. *Interspecific association patterns of H. pierrei and the species of the dominant species group as analyzed by the bivariate pair-correlation function* $g_{12}(r)$ *in P1. The dark line lying beyond the confidence envelope region (gray area) indicates a significant departure from the null model of independence. The gray envelope region is the* $p = 0.05$ *confidence intervals from 999 Monte Carlo simulations (values* < 1 *indicate repulsion; values* > 1 *indicate attraction; values* $= 1$ *indicate independence between two tree species). The red dashed line is the expectation for spatial independence between individuals of H. pierrei and the dominant species*

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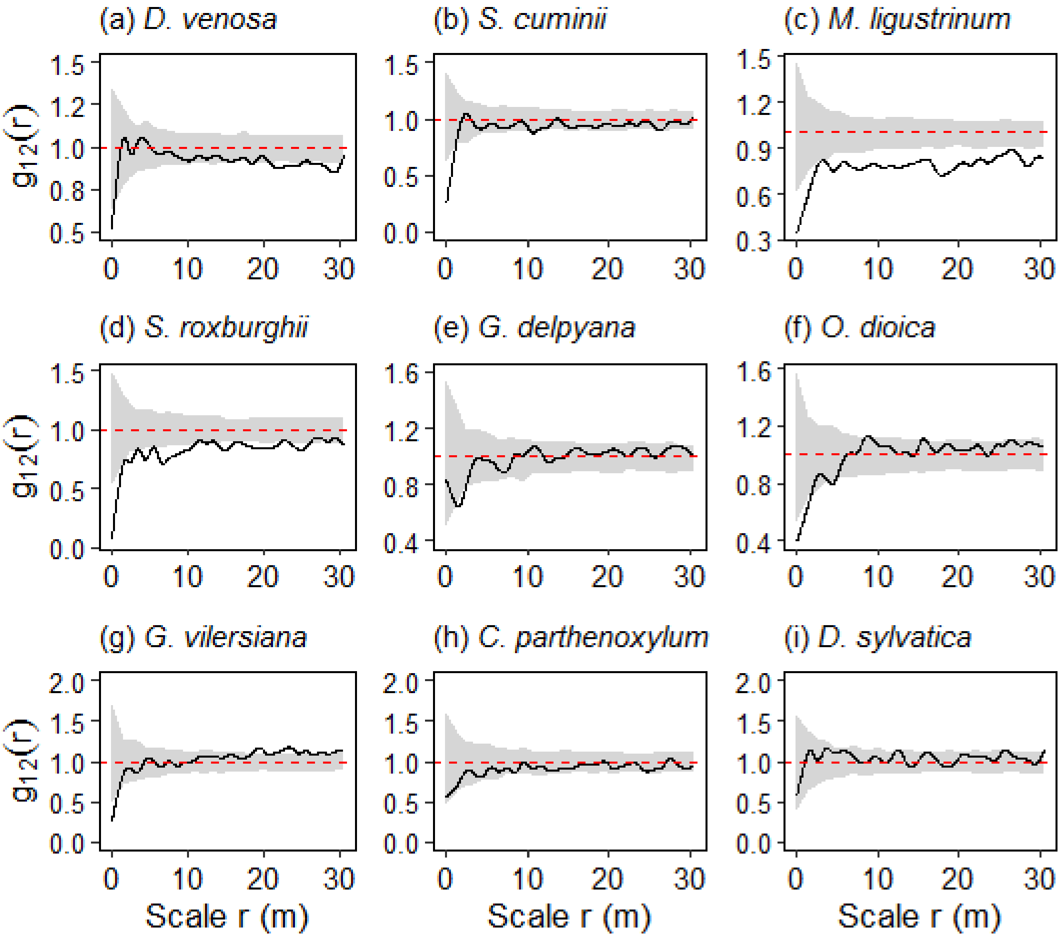

Figure A2. *Interspecific association patterns of H. pierrei and the species of the dominant species group as analyzed by the bivariate pair-correlation function* $g_{12}(r)$ *in P2. The dark line lying beyond the confidence envelope region (gray area) indicates a significant departure from the null model of independence. The gray envelope region is the* $p = 0.05$ *confidence intervals from 999 Monte Carlo simulations (values* < 1 *indicate repulsion; values* > 1 *indicate attraction; values* $= 1$ *indicate independence between two tree species). The red dashed line is the expectation for spatial independence between individuals of H. pierrei and the dominant species*

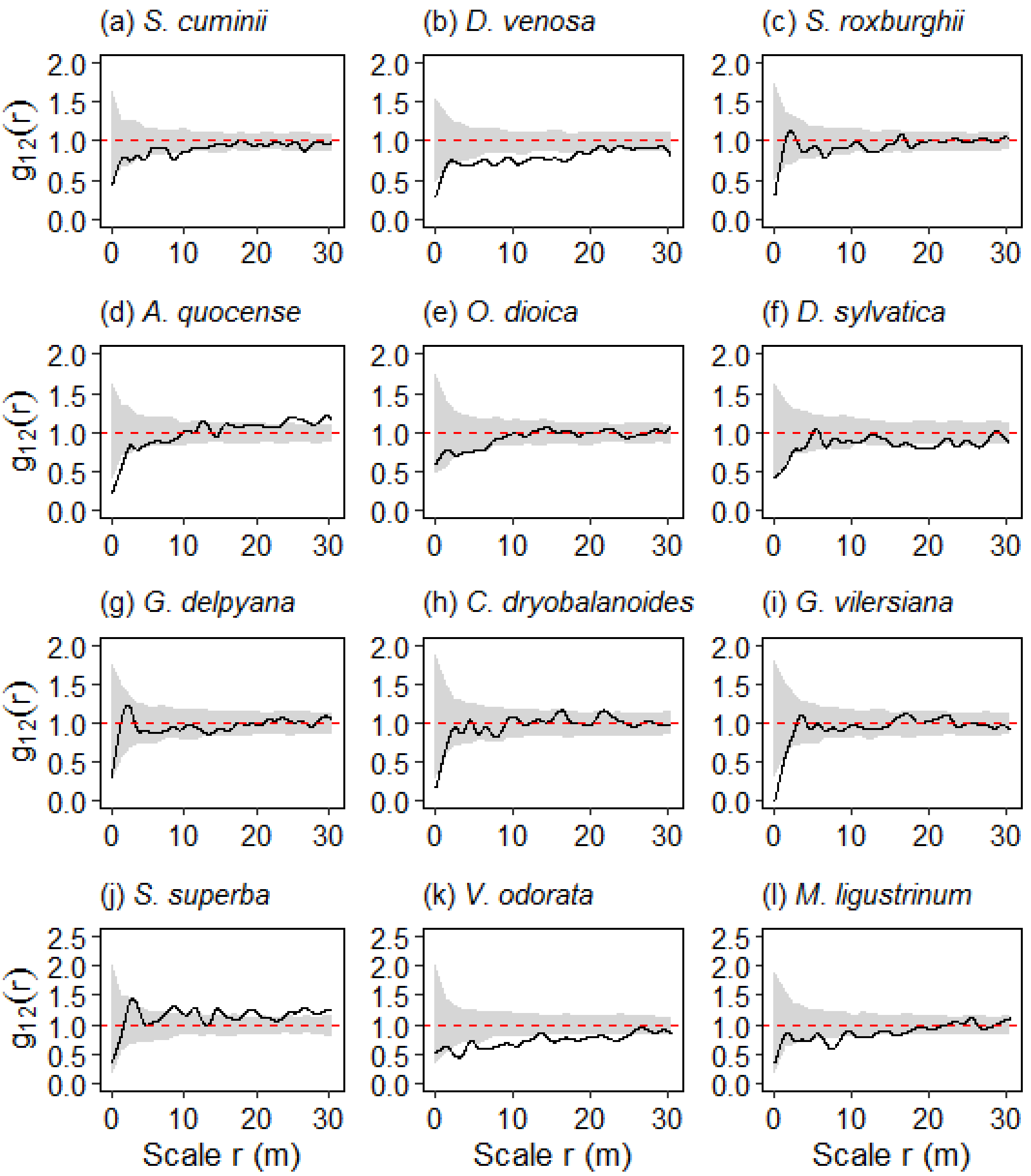

Figure A3. *Interspecific association patterns of H. pierrei and the species of the dominant species group as analyzed by the bivariate pair-correlation function $g_{12}(r)$ in P3. The dark line lying beyond the confidence envelope region (gray area) indicates a significant departure from the null model of independence. The gray envelope region is the $p = 0.05$ confidence intervals from 999 Monte Carlo simulations (values < 1 indicate repulsion; values > 1 indicate attraction; values $= 1$ indicate independence between two tree species). The red dashed line is the expectation for spatial independence between individuals of H. pierrei and the dominant species*